The Tree Travelogues*
Seed Dispersal by Frugivores

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Seed dispersal is crucial for forest regeneration. Different tree species have different seed dispersal mechanisms. In this article, we explore how fruit-eating animals or frugivores, assist trees in seed dispersal.

1. The Moving Trees

Seeds are the offspring of adult parent trees. In a world without any seed dispersal (Box 1) mechanism in place, these seeds would fall right under the adult tree. In such a situation, the parent and the offspring would compete over the same resources such as soil nutrients and water; the parent would also intercept most of the sunlight, making germination difficult for the offspring. Additionally, these offspring would be susceptible to damage by the herbivores that target the parent or by the pathogens infecting the parent. Therefore, theoretically, greater the distance between the parent tree and the point of deposition of its seeds, the higher would be the chances of seed survival. While some tree species may not need any external vector for the dispersal of their propagules (autochory; eg. Delonix regia or gulmohar which has fruits that burst and release the seeds), others have developed different mechanisms for effecting their seed dispersal (see Box 2). For example, species may have their seeds dispersed by wind (anemochory; eg. Shorea robusta or sal which has light, winged seeds), or water (hydrochory; eg. Dalbergia sissoo or shisham). In tropical forests, however, the vast majority of tree species are assisted in seed dispersal by animals (zoochory; Figure 1). Seeds may get stuck to the animal pelage or plumage, and

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Box 1. Glossary of Terms

Seed dispersal: Movement of seeds away from parent plants, usually mediated by abiotic or biotic agents or intrinsic explosive mechanisms.

Seed dispersal effectiveness: Number of new adult trees produced by the dispersal activities of a disperser.

Germination percent: Percentage of seeds monitored, which show germination i.e. emergence of radicle.

Latency period: Duration between sowing of seeds and the emergence of radicle.

Seedling establishment: The stage when the emerged seedling is no longer attached to the seed and its root is firmly in the soil.

Provisioning: Offering of food beyond the natural supply and/or quality of the animals’ environment. This may be direct when humans provide hand-outs to animals at tourist locations or temples or indirect when animals obtain foods from crops, kitchen, gardens, garbage dumps.

Gut retention time: Time required for frugivore-consumed seeds to pass through the digestive tract.

Vagility: Degree to which an organism can move/spread within an environment.

Anthropocene: the current geological age during which anthropogenic interventions have had a dominant impact on climate and other environmental variables.

Axil: Upper angle between two parts of a plant eg. stem and petiole.

Box 2. Modes of Seed Dispersal


Hydrochory (Ancient Greek: húdōr – ‘water’): Dispersal of seeds by water.

Zoochory (Ancient Greek: zōion – ‘animal’): Dispersal of seeds by animals.

thereby get transported (epi/ectozoochory). Fruit-eating animals or frugivores may disperse the seeds by swallowing the entire fruit and passing the intact seeds into their faeces, away from the parent tree (endozoochory). Certain frugivores may also effectively act as seed dispersers by expectoration or spitting the seeds after cleaning the fruit pulp at a distance from the parent tree.
Different frugivores vary with respect to seed dispersal effectiveness (Box 1). These variations arise because of differences in the morphology, physiology, behaviour, and ecology of different species. The effectiveness of frugivore-mediated seed dispersal has two aspects – quantitative and qualitative. The quantitative component refers to the number of seeds carried by the frugivore from the parent plant. The quality of seed dispersal is a function of seed handling and the spatial pattern of seed deposition. A disperser is considered ‘effective’ if it (a) carries seeds away from the parent plant, thereby decreasing the risk of seed or seedling mortality due to pathogens, seed predators and herbivores (escape hypothesis), (b) deposits them at a site conducive for seed germination and seedling development (directed dispersal hypothesis), and (c) thereby ensures that the offspring establish (Box 1) themselves in suitable and uncompetitive environments, which increases the probability of seedling survival (colonization hypothesis).
2. Dispersers Come in Many Forms and Sizes

Compared to avian/mammalian frugivores, fishes are undervalued with respect to their role as seed dispersers. However, many studies have reported the presence of intact seeds in the digestive tracts of fishes across Asia, Africa and South America, making them potentially important seed dispersers. Seeds discovered from the fish gut are also found to have higher germination success than intact seeds collected from the fruits. Fishes may also carry seeds across very large distances. For example, in Peru, the tambaqui fish (*Colossoma macropomum*), is known to carry seeds to a mean distance of 337–552 m and a maximum distance of 5495 m; comparable to African hornbills and Asian elephants [1].

Very little is known about the seed dispersal effectiveness of amphibians. Frogs are usually known to be carnivorous and primarily feed on arthropods. However, non-carnivorous feeding behaviour has been reported in *Bufo marinus*, *B. regularis*, and *Rana esculenta* [2]. The only study till date that has assessed the role of an amphibian as seed disperser suggests that the tree frog, *Hyla trunctata*, regularly feeds on the fruits of *Anthurium harrissii*, *Erythroxylum ovalifolium*, and two unidentified species in Brazil. *A. harrissii* seeds found in their gut were viable. The researchers further suggested that being handled by frogs increased the probability of seed survival as the frogs defecated the seeds on the axils (*Box 1*) of conspecific plants rather than on the dry, sandy soil. Seed dispersal by amphibians definitely requires further assessment.

Reptiles, like fishes, have also not been acknowledged as important seed dispersers. Existing studies, however, show that they can indeed be important seed dispersers across a range of habitats. In the xeric habitats of the Canary Islands, the endemic lizard *Gallotia galloti* acts as a seed disperser for seven plant species over short distances [3]. In Brazil, 19 faecal samples from the red-footed tortoise (*Geochelone carbonaria*) and the yellow-
footed tortoise (*G. denticulata*) contained 646 seeds of 11 plant species. Based on this diversity, the gut retention times (*Box 1*), and the movement patterns of the tortoises, it was suggested that these species may be effective dispersal agents [4].

Ecologists have recognized the importance of birds as seed dispersers since the 1970s. Long gut retention times, as well as large flight distances, allow birds to carry seeds far away from the parent trees. Some species of pigeons (genus *Columba*) can disperse large seeds across long distances over land or sea. Particularly important for smaller trees and shrubs, bulbul (*Pycnonotus* spp.) swallow and defecate smaller seeds while seeds >10 mm in diameter are regurgitated; the gut retention time of seeds is around 5 mins to 1 hour. Asian hornbills (*Buceros* spp.) represent the most significant single family of seed dispersers for large-fruited species in the canopy. Reported to disperse seeds of 748 plant species from 252 genera and 79 families, they are particularly important as dispersal agents of fruits of the following families: Moraceae, Lauraceae, Meliaceae, Myristicaceae and Annonaceae [5]. Although many seeds are deposited at the roosting and nesting sites, many seeds are also carried by hornbills over large distances due to their long gut retention times. The impact of being ingested by birds on germination may be plant species-specific. For example, upon experimenting with captive individuals of the thrush *Turdus merula* and the warbler *Sylvia melanocephala*, it was found that while gut passage enhanced the germination percent (*Box 1*) and/or reduced the latency period (*Box 1*) of seeds of two out of five plant species, the reverse was true for the remaining three [6]. It has also been observed that certain birds provide directed dispersal service i.e., transport seeds to areas more conducive for germination. For example, in the lower montane rainforest of Costa Rica, the three-wattled bellbird, *Procnias tricarunculata*, consistently deposited seeds of *Ocotea endresiana*, a neotropical shade-tolerant tree, at song perches within canopy gaps. As seedling mortality due to pathogens was lower in these gaps than in the surrounding forest, seedling survival of bellbird-dispersed seeds was higher than the survival of seeds deposited by other

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birds close to the parent tree [7].

Mammals, whose vagility (Box 1) is comparable to that of birds, include important seed dispersers. Bats are known to disperse more seeds than birds, especially those of pioneer plant species, and primarily so in disturbed habitats, across active and abandoned agricultural fields, plantations and forests [8]. Many other mammals have also been studied for their seed dispersal effectiveness. Primates comprise 25–40% of the frugivore biomass of most tropical forests and are considered important agents of seed dispersal for a broad range of tree species. The role of primates in seed dispersal has been studied in many sites in Asia, Africa, and Central and South America. The primate taxonomic groups that have been investigated in this context include prosimians, New World and Old World monkeys, and apes. Primates possess an array of dental, oral, digestive, locomotor, and sensory adaptations that enable them to be effective dispersers. For example, some species have enlarged, laterally splayed canines which enable them to use hard-husked fruits. Their long daily path lengths combined with their higher gut retention times ensure that the seeds are dispersed far away from the parent trees. Their relatively larger gape sizes also allow them to consume fruits (and disperse seeds thereof) of a wide variety of plant species.

For example, a single group of gibbons (Hylobates muelleri) disperse about 16400 seeds/sq.km/year from 160 species in Borneo. Germination percentage has been reported to increase after passage through the guts of strictly frugivorous primates; gut-passed larger seeds also usually germinate faster than the control seeds. Larger primates such as the chimpanzee (Pan troglodytes) are also known to carry seeds to a distance of 3 km [9]. Similarly, elephants – African (Loxodonta Africana and Loxodonta cyclotis) and Asian (Elephas maximus) – can deposit seeds at points far away from the parent trees. In fact, owing to their large body sizes, ranging patterns and long gut retention times, elephants can swallow larger numbers of fruits than any other frugivore, and deposit intact seeds at sites conducive for germination. Up to 30 species were reported to be dispersed by the African forest ele-
phant (*Loxodonta cyclotis*) in Tai National Park, Ivory Coast. As much as 75% of tamarind seeds swallowed by Asian elephants were found to be intact. For these seeds, the mean and maximum gut retention times were 40 hours and 5 days, respectively. Some seeds also germinate faster due to scarification in elephant guts, although the effect on germination may vary from species to species [10].

3. The Road Ahead

Effective seed dispersal is critical for forest regeneration, and many animal species fulfil this important ecological role. So far, I have discussed the importance of fruit-eating animals as important seed dispersers. However, species that are not classified as frugivores per se may also act as seed dispersers. For example, macaques are usually known to be omnivorous. Nevertheless, the Japanese, northern pig-tailed, and rhesus macaques have been found to be important seed dispersers. Similarly, animals that are predominantly carnivorous may also act as seed dispersers. For example, in an undisturbed area of south-eastern Spain, seeds of 27 plant species, accounting for 40% of all the fleshy-fruited plants of the region, were found in carnivore faeces [11]. Animals that are labelled seed predators may also be effective seed dispersal agents. While rodents are generally considered to be seed predators, many species such as the Korean field mouse (*Apodemus peninsulae*), agouti (*Dasyprocta punctata*), and red acouchi (*Myoprocta exilis*) are important dispersal agents of *Prunus armeniaca, Virola nobilis*, and *Vouacapoua americana* seeds, respectively [12]. It is thus important to identify such species to gain a better understanding of their ecological function and thereby facilitate protection measures for their future survival.

Globally, rising anthropogenic pressures have led to habitat loss and forest fragmentation. Under such situations, the significance of various seed-dispersing agents increases manifolds in the context of forest regeneration and recruitment. This holds true especially for fruits with large seeds.
bodied animals as seed dispersers is well-understood. For example, larger fish seem to be particularly important as seed dispersers; the probability of seed dispersal increases up to 28% with every centimetre increase in fish length [13]. Similarly, elephants are considered ‘mega-gardeners’ of the forests [10]. However, larger species are also the most vulnerable to habitat loss and poaching. And herein lies the importance of understanding the seed dispersal effectiveness of smaller, common species which are characterized by dietary flexibility and the ability to adapt to a vast range of habitats (ecologically-resilient species).

For instance, in the forests of tropical and subtropical Asia where forests are degraded or native mammal fauna is overtly poached, the widespread and disturbance-tolerant macaques may be the only seed dispersers, especially for the large fruit/seed-bearing species. Indeed, at the Buxa Tiger Reserve, West Bengal, rhesus macaques disperse through spitting or defecation 84% of the 49 plant species they feed on. Ninety-six percent of the handled seeds were found undamaged, and 61% of the species for which germination tests were performed had enhanced germination. Fifty percent of monitored seeds germinated in situ and 22% established seedlings [14]. It has been further suggested that the typically elephant-dispersed fruits may survive even after the extirpation of the megaherbivore due to the dispersal activities of smaller, common frugivores like macaques, rodents, and bovids. The extirpation or even a decline in the number of such common animals may curb tropical forest regeneration and recruitment. Hence, the roles of these species as seed dispersers clearly require further investigation.

An effective disperser should disperse the seeds of many plant species, but the number of species which qualifies as ‘many’ is a function of plant community composition and fruit availability. Thus, further research is required to investigate how dietary diversity and, consequently, seed dispersal effectiveness of frugivores may vary with resource availability across different spatiotemporal scales. As fruits of a certain species may be dispersed by
many frugivores and a single frugivore may disperse the seeds of many plant species, seed dispersal networks are established within communities (*Figure* 2). Certain plant-frugivore interactions may be more specialised and stronger than others within such assemblages. Thus, a complete understanding of the importance of any frugivore as a seed disperser would require examining the different dispersal interactions that it is a part of. Such studies would also help us determine how vulnerable different plant species are to changes in frugivore abundance.

Research on rhesus macaques shows that irrespective of fruit availability, macaque frugivory (and, therefore, seed dispersal) declines when humans feed them (*Figure* 3). The daily ranges of macaques also decrease during provisioning (*Box* 1), resulting in shorter dispersal distances. Additionally, during provisioning periods, macaque-handled seeds are usually deposited on tarmac.
Figure 3. Humans may influence the role of primates as seed dispersers by provisioning them. Provisioning may be indirect (left) or direct (right). Photo: Asmita Sengupta

roads, thereby precluding seed germination [15]. Thus, to ensure the conservation of species and their ecological functions, anthropogenic pressures need to be curbed. If in the future, most of the forests are lost and there is a scarcity of natural resources, it is likely that some ecologically-resilient animals would still survive. But whether these animals will have any seeds to disperse depends on whether we choose to keep our forests pristine and stop interfering with their diets by providing food subsidies. While this is easier said than done in the Anthropocene (Box 1), spreading awareness about the ill-effects of anthropogenic activities, and being more responsible about our own actions may be the only way ahead.

Suggested Reading


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