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Research Article

# Dispersal modes and spatial patterns of tree species in a tropical forest in Arunachal Pradesh, northeast India

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**Abstract**
We characterized the dispersal modes and spatial patterns of 128 tree species in a tropical semi-evergreen forest of Arunachal Pradesh, northeastern India. A high percentage of species are animal-dispersed (78%), while about 22% (28) are dispersed abiotically (wind or gravity-dispersed). Of the animal-dispersed species, 54 species were primarily bird-dispersed, 25 were mammal-dispersed, and 21 were dispersed by both groups. We hypothesized that adult tree distribution patterns were related to dispersal mode and fruit size. We predicted that tree species with mechanisms for long-distance seed dispersal are likely to show more uniform or random spatial patterns than those with limited seed dispersal. Tree species with large fruits were also predicted to have greater levels of clumping than those that have small fruits. However, all tree species had a clumped distribution pattern. At the community level, we found no differences in spatial patterns based on dispersal mode for a subset of 50 tree species. Fruit size was, however, positively correlated with higher levels of spatial aggregation suggesting that tree species distributions are to an extent limited by dispersal. The importance of dispersal mode in determining adult tree distribution patterns at the community level may be obscured by interacting effects of other factors such as patchy habitat conditions and density-dependent mortality factors at different life-history stages that ultimately determine adult tree distributions.

**Keywords:** animal-dispersed, Eastern Himalaya, fruit types, seed dispersal, vertebrate frugivores, mechanically dispersed

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## Introduction

Tropical forests harbor high tree species diversity and the mechanisms that promote such diversity have been debated extensively [1-4]. The Janzen & Connell hypothesis suggested that maintenance of tree species diversity is due to escape from seed predation near parent fruiting trees that results in recruitment away from parent trees thus preventing aggregations. However, a well-documented trait of tropical forests is the high degree of aggregation of conspecific trees at various scales, which has been attributed to patchy habitat conditions or limitations in seed dispersal [5-8]. Others have suggested that aggregation is a means of reducing competitive exclusion and promoting diversity [9, 10]. Although studies have shown that seeds and seedlings show spatial aggregation [11-15], determining whether aggregations persist up to the adult stage has been limited [16, 17] to anecdotal evidence or to a few species [3, 6, 18]. The ability of tree species to disperse seeds varies and is determined by their dispersal mode. Limited seed dispersal often results in aggregated patterns of recruitment for seeds and seedlings; however, whether these patterns persist up to the adult stage has not been well-established. Several other factors may ultimately determine the spatial patterns of adults of tree species, such as patchy habitat conditions [8] or density-dependent mortality factors at the seed and seedling stage [1,2]. While patchy habitats may result in reinforcing the spatial patterns generated by dispersal, post-dispersal seed predation may result in thinning out and modifying the spatial patterns of adult trees. While theories have emphasized the importance of dispersal mode in determining the long-term recruitment and spatial patterns of tree species, few studies have examined this at the community level [19]. Tree species with limited seed dispersal would be expected to have more aggregated spatial patterns than those that have mechanisms for long-distance seed dispersal. Earlier studies in Malaysia and the Neotropics have found that the spatial patterns of tree species were related to their dispersal modes, with mechanically dispersed species showing more aggregated patterns than vertebrate dispersed species. Bird-dispersed species had the most diffuse spatial patterns and this has been presumed to be due to greater levels of long-distance seed dispersal [3, 19]. Within animal-dispersed species, tree species with larger fruits also showed more aggregated patterns than those with small fruits [19].

In this paper, we first established the dispersal modes of tree species in a tropical semi-evergreen forest in northeastern India. We grouped these tree species based on their primary dispersal mode and established their spatial distribution using an index of clumping. We examined the hypotheses that 1) tree species with limited seed dispersal will have aggregated patterns, while those that have mechanisms for long-distance dispersal will show less aggregated patterns or random distributions, 2) tree species with large fruits and seeds will have more aggregated patterns than those with small fruits and seeds.

## Methods

*Study site*

The study was conducted in Pakke Wildlife Sanctuary (862 $km^2$, 92°36' - 93°09'E and 26°54 - 27°16'N; Fig. 1) in the foothill forests of western Arunachal Pradesh, in the Eastern Himalaya in a global biodiversity hotspot [20]. The park is surrounded by contiguous forests on most sides and bounded by rivers in the east, west, and north. The terrain is undulating and hilly, with altitude ranging from 150 m to about 2000 m above sea level. The area has a tropical and subtropical climate, with cold weather from November to February. It receives rainfall from the southwest monsoon (May-September) and the northeast monsoon (December-April). October and November are relatively dry. May and June are the hottest months. The monsoon lasts till September, but occasional rains occur throughout the year. The southwest monsoon is responsible for more than three-quarters of the annual rainfall. Thunderstorms occasionally occur in March-April. The average annual rainfall is 2500 mm. The mean (± SD) maximum temperature was 29.3°C ± 4.2 and the mean minimum temperature was

18.3° ± 4.7, based on data from 1983 to 1995 recorded by the Tipi Orchid Research Centre. The vegetation of the reserve is classified as Assam Valley tropical semi-evergreen forest 2B/C1 [21]. The forests are multi-storied and rich in epiphytic flora, woody lianas and climbers. Major emergent species include *Tetrameles nudiflora, Ailanthus grandis* and *Altingia excelsa*. The lower elevation forests are dominated by *Polyalthia simiarum, Pterospermum acerifolium, Sterculia alata, Stereospermum chelonioides*, *Ailanthus grandis* and *Duabanga grandiflora*. Evergreen species include several middle-story trees in the Lauraceae and Myrtaceae. Subtropical broadleaved forests occur at higher elevations, while bamboo, cane and palms are common near perennial streams. Along larger streams and rivers, there are patches of tall grassland. The intensive study site (ca. 12 $km^2$) was located in the southeastern part of the park in the lower elevation moist deciduous and semi-evergreen forests (150 - 600 m).

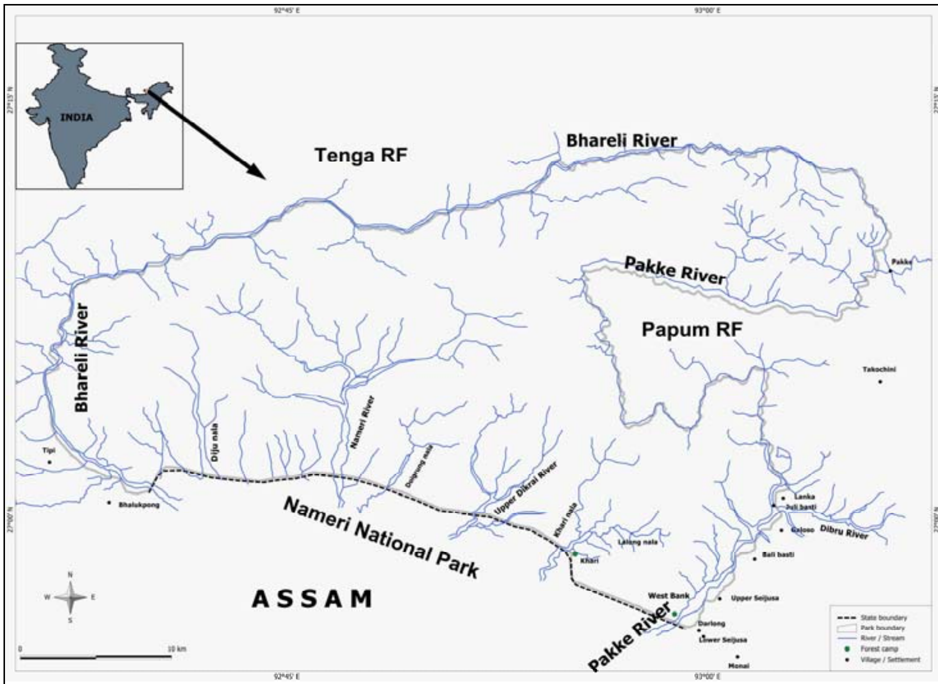



Fig. 1. Map of Pakke Wildlife Sanctuary, western Arunachal Pradesh, northeast India. The intensive study site (ca. 12 $km^2$) was located in the southeastern part of the park.

### *Fruit consumers and dispersal modes of tree species*

This work was carried out as part of a four-year (1997-2000) study on hornbill ecology [21]. Detailed quantitative information on diet (observations at nests and fruiting trees, seed counts at middens (nest and roost trees), feeding records from trail walks) was available for three hornbill species [22, 23]. Opportunistic records on diets of other avian frugivores (*ad libitum* sightings > 100 records) and mammals were made on trail walks during a prior study in 1995-96 [24] and from 1997-2000 during the study on hornbill ecology. Of the 295 bird species recorded in the sanctuary [25, 26], there are about 35-40 fruit and seed-eating bird species in the study area. These include three species of hornbills (*Buceros*, *Aceros* and *Anthracoceros*), eight species of bulbuls (*Pycnonotus*), five species of mynas (*Acridotheres*), six species of green pigeons (*Treron*), two species of Imperial pigeons (*Ducula* sp.), four species of doves (*Streptopelia*, *Macropygia* and *Chalcophaps*), four barbet species (*Megalaima*), three parakeet species (*Psittacula* and *Loriculus*), two leaf bird (*Chloropsis*) species, fairy bluebird (*Irena puella*), and two oriole species (*Oriolus*). Several other forest birds that are nectarivores/insectivores (e.g., white-eyes, flowerpeckers, cuckoos and cuckoo-shrikes, babblers, laughing thrushes, drongos, red-headed trogon [*Harpactes erythrocephalus*]) also occasionally include fruit in their diet [27, 28]. Green pigeons are known to specialise on fig fruits but are seed predators [29, 30]; parakeets are also seed predators [31]. Feeding records were available for the more frugivorous birds such as three species of hornbills, four barbets, hill myna, fairy bluebird, green pigeons and imperial pigeons, and some bulbul species. The important avian frugivores are hornbills, Mountain Imperial pigeon, barbets, hill myna, and the fairy bluebird.

Mammal species that include fruits in their diet in the area are three species of primates, seven species of viverrids and mustelids, Asiatic black bear (*Ursus thibetanus*), sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), wild pig (*Sus scrofa*), and Asian elephant (*Elephas maximus*). There is no information on the number of bat species; however, six frugivorous bat species are known from Arunachal Pradesh [32]. Four species of diurnal arboreal squirrels and several species of terrestrial rodents (primarily seed predators) also occur in the study area. Information on the species and fruit types eaten by mammals were obtained from direct sighting records of mammals at fruiting trees and indirect evidence from seeds of tree species found in scats and droppings (small carnivores), seed caches (rodents), and regurgitated seed piles (ungulates). Small carnivore and bear droppings can be easily identified; seed caches were found on the ground or in tree hollows and clearly had been made by rodents based on incisor teeth marks (we did not assign these to species). Seed piles of tree species regurgitated by ungulates are found on the forest floor and it was possible to assign to species (sambar, common muntjac, and wild pig) because these piles are associated with tracks, bedding, and resting sites of the species. The dispersal modes of 28 tree species were established from published records on the diets of birds/mammals from several studies in other Asian forests [27, 33-36] and fruit characteristics [37-39], and from literature on plant seed dispersal [40-41]. The rest were assigned based on direct observations. Figure 2 depicts fruits of some animal-dispersed tree species, some major frugivores/dispersers, seeds and seedlings of animal-dispersed tree species, and the forests of the study area.

Fruits that had no edible fruit pulp/flesh and had fruit characteristics that were obviously adapted for abiotic dispersal were categorized as mechanically dispersed. This categorization was validated by examining taxonomic literature. The important abiotic dispersal modes include wind, gravity, gyration, and ballistic. All species could not be assigned to specific categories and as sample sizes were small for each individual category, we considered them together as mechanically dispersed species. We considered only the primary phase of dispersal, although seeds of several species may be secondarily dispersed by terrestrial rodents.

*Tree species density and spatial patterns*

Tree species were identified and enumerated in 21 vegetation plots of 0.25 ha each (5.25 ha) in the intensive study site. Plants with girth at breast height (GBH) ≥ 30cm were taken in the sample (considered as adult trees in tropical forests). Every tree was marked with aluminum tags indicating the tree species and number in the plot. Many common tree species were identified with the help of tribal field assistants. Herbarium specimens were also collected for further verification with field botanists at the State Forest Research Institute, Itanagar, and Wildlife Institute of India, Dehradun. All plants not identified in the field were collected and assigned a temporary code.

Density of tree species was calculated from the 21 vegetation plots. We used the variance/mean ratio (VMR) to examine spatial distribution patterns of tree species. VMR is often used to characterize the distribution of objects in space. If the distribution is random, then the VMR is 1.0. Larger values (VMR > 1.0) correspond to existence of "clumps" or spatial clusters. Smaller values (VMR < 1.0) correspond to an "even" or "uniform" distribution in space. These properties of VMR are based on the fundamental property of the Poisson distribution that the variance and the mean are equal [42]. Variance to mean ratios was calculated for all tree species enumerated in the vegetation plots. However, we examined whether dispersal mode and fruit size was related to spatial pattern of a tree species for a subset of 50 tree species that had an adequate sample. We first examined whether there were differences in spatial patterns between species based on dispersal modes. We then tested whether fruit size was correlated with VMR for all 50 species and also examined the relationship separately for five dispersal categories: bird, mammal, wind, gravity and both (birds and mammals). Fruit diameter (mm) was used as a measure of fruit size. Data on fruit diameter were available for 12 tree species [28], while they were sourced from existing literature and floras for the remaining 38 species.

## Results

A total of 1,899 trees belonging to 165 species were enumerated in 21 vegetation plots. Of these, a total of 128 species were identified belonging to 51 families. An additional 37 species could not be identified. The total number of species ranged from 17 to 42 per plot. The most common families were Lauraceae (16 species), Euphorbiaceae (11), Moraceae (10), and Meliaceae (9).

### *Dispersal Modes*

Of the 128 species, 100 species (78%) were confirmed to be animal-dispersed. Twenty-eight species (22%) were mechanically dispersed (mainly wind- or gravity-dispersed). Plant families such as Lauraceae, Meliaceae, Myristicaceae, Anacardiaceae, Clusiaceae, Burseraceae, Moraceae, and Euphorbiaceae appear to have fruits adapted for animal dispersal and are species-rich in these forests, while most dominant wind-dispersed species belonged to families that were represented by a single genus. The list of plant species, tree density, fruit type, dispersal mode, and major consumers are given in Appendix 1.

Ornithochory (dispersal by birds) was the most prevalent among the tree species. Bird-dispersed species such as *Phoebe* sp. (Lauraceae), *Chisocheton paniculatus* (Meliaceae), and *Syzygium syzygioides* (Myrtaceae) were among the top five species in terms of tree density. The density of bird-dispersed tree species was highest (157 trees/ha), followed by mechanically dispersed species (Table 1). Mammal-dispersed species were relatively few both in terms of number of tree species and in terms of overall tree density.

Table 1. Number of species dispersed by various dispersal modes and their abundance. An additional 37 species could not be identified and were represented by 153 individuals (29 trees/ha)

| Dispersal mode | Number (%) | Tree density (/ha) |
|---|---|---|
| Birds | 54 (42.19) | 157.14 |
| Mammals | 25 (19.53) | 38.09 |
| Both | 21 (16.41) | 53.52 |
| Mechanical | 28 (21.87) | 83.81 |
| Total | 128 | 332.56 |

*Mechanically dispersed species*

The 28 mechanically dispersed species belonged to 16 families (Apocynaceae, Theaceae, Fagaceae, Juglandaceae, Simaroubaceae, Bignoniaceae, Datiscaceae, Caesalpiniaceae, Mimosaceae, Lythraceae, Malvaceae, Papilionaceae, Sapindaceae, Sterculiaceae, Hamamelidaceae). Most of these families were represented by only 1-3 species in the area and several (*Altingia excelsa, Tetrameles nudiflora, Ailanthus grandis, Alstonia scholaris, Sterculia alata*) were emergents. Seventeen species were classified as wind-dispersed, four as gravity-dispersed, three as either wind- or gravity-dispersed, three as wind- or ballistic dispersed, and one as gravity- or water dispersed. The most common fruit type was a dry indehiscent capsule with winged seeds inside (18 species); other types were follicle, pod, acorn, and samara (Table 2). Apart from the species with fruits and seeds that are obviously adapted for wind dispersal, a few species have dry indehiscent fruits with no discernible edible fleshy part and were therefore considered to be gravity-dispersed. Seeds of some of these species (Juglandaceae, Fagaceae) are edible and consumed by pre-dispersal seed predators such as arboreal squirrels and macaques, and post-dispersal seed predators such as terrestrial rodents. Though there were 28 mechanically dispersed species (440 individuals), ten species were represented by only 1-2 individuals and fruiting was not recorded in these.

Table 2. Fruit types and their dispersal modes.

| Fruit type | Bird | Mammal | Both | Mechanical | Total |
|---|---|---|---|---|---|
| Dry indehiscent/dehiscent capsule | - | - | 3 | 18 | 21 |
| Arillate dehiscent capsule | 16 | 3 | - | - | 19 |
| Berry | 5 | 5 | 2 | - | 12 |
| Drupe | 27 | 13 | 8 | - | 48 |
| Drupaceous carpel | - | - | 2 | - | 2 |
| Follicle | 2 | - | 1 | 2 | 5 |
| Aggregate of follicles | - | 2 | - | - | 2 |
| Pod | - | - | - | 3 | 3 |
| Samara | - | - | - | 1 | 1 |
| Acorn | - | - | - | 3 | 3 |
| Nutlet | - | - | - | 1 | 1 |
| Sorosis/compound berry | 1 | - | - | - | 1 |
| Syconium (fig) | 2 | 2 | 4 | - | 8 |
| Syncarp (aggregate or multiple fruit) | - | - | 1 | - | 1 |
| Achene | 1 | - | - | - | 1 |
| **Total** | 54 | 25 | 21 | 28 | 128 |

*Mammal-dispersed species*
Of the 100 animal-dispersed species, mammals consumed the fruits of 44 species, while 25 species appear to be exclusively consumed by mammals (primates, ungulates, small carnivores, bats, bear, and elephant). Tree squirrels and terrestrial rodents are usually seed predators, although they may act as seed dispersers rarely. Of the 25 species categorized as mammal-dispersed, 17 were classified based on direct observations, while the rest were established from other studies. The tree species known to be consumed primarily by mammals and their specific consumers (where known) are listed in Appendix I.

The important plant families that had mammal-dispersed species were Anacardiaceae (4), Euphorbiaceae (3), Clusiaceae (2), Elaeocarpaceae (2), and Verbenaceae (2). The most common mammal-dispersed species were *Turpinia pomifera*, *Dillenia indica*, and *Terminalia bellerica*. A total of 200 individuals belonging to 25 species were enumerated. Eighteen species were represented by fewer than 10 individuals. The fruit types consumed by mammals were mainly drupes (13) (Table 2).

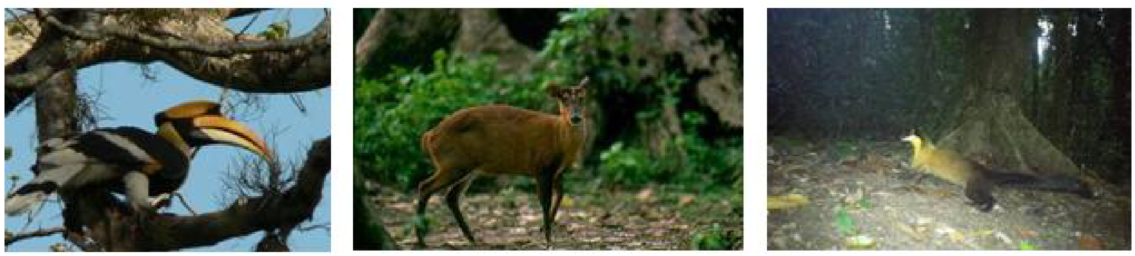
*Bird-dispersed species*
Of the 100 animal-dispersed species, 54 (42% of all species in the sample) were dispersed only by birds. The important families with fruits dispersed by birds were Lauraceae (16), Meliaceae (6), Euphorbiaceae (5), Rutaceae (3), Myrtaceae (2) and Myristicaceae (2). The most common bird-dispersed species were *Phoebe* sp. *Chisocheton paniculatus*, *Syzygium syzygioides*, *Amoora wallichi*, *Knema angustifolia* and *Livistona jenkinsiana*. A total of 825 individuals belonging to 54 species were enumerated. Thirteen species were represented by 1-2 individuals. The Lauraceae was the most species-rich family in the area; all species, except one had densities less than 5 trees/ha. The important genera of Lauraceae found in the area were *Phoebe* (4), *Litsea* (4), *Cryptocarya* (2), *Beilshmedia* (3), *Cinnamomum* (2), *Actinodaphne* (2), *Alseodaphne* (1), *Neolitsea* (1), *Persea* (1), and *Dodecadenia* (1). Fruit types consumed commonly by birds were single-seeded fleshy drupes, multi-seeded arillate capsules, single or multi-seeded berries, and figs (Table 2).

*Bird- and mammal-dispersed species*
Of the animal-dispersed species, 21 species were consumed by both birds and mammals. It is however likely that more detailed observations of fruit consumption will show that the species that are currently categorized as primarily bird-dispersed or mammal-dispersed could be dispersed by both groups. The important families were Moraceae (5), Annonaceae (2), Verbenaceae (2), Boraginaceae (2), and Burseraceae (2). A total of 281 individuals belonging to 21 species were enumerated. Six species were represented by 1-2 individuals.

*Spatial patterns of tree species*
All 128 species irrespective of dispersal mode showed a clumped distribution pattern. Most recent studies that examine spatial patterns use nearest neighbor distances obtained from mapping individual trees in very large plots (50 ha) [19]. We used multiple non-contiguous plots and calculated the variance/mean ratio for all tree species in the 21 plots of 0.25 ha. The problem with this method is that many species were not present in all plots, as plots may not be located in suitable habitat patches for particular species. Therefore, there were many “zeros” for some species, which leads to a high variance estimate. Consequently, further analysis of spatial patterns was carried out only for 50 tree species that were represented by 10 or more individuals. These were 13 mechanically dispersed species (395 individuals), 7 mammal-dispersed (136 individuals), 23 bird dispersed (717 individuals), and 7 (239 individuals) bird- and mammal-dispersed species.

Fig. 2. Fruits of animal-dispersed tree species, some frugivores/dispersers, seeds and seedlings of animal-dispersed species and the forests of the study area. Photo credits: SU Saravana Kumar (for barking deer, forest canopy and buttressed tree) and Aparajita Datta for all the rest.

Animal-dispersed fruits and seeds. Left to right: *Alseodaphne peduncularis* (Lauraceae), *Dysoxylum binectariferum* (Meliaceae), *Horsfieldia kingii* (Myristicaceae)



Some frugivores/dispersers found in these forests. Left to right: Great Hornbill *Buceros bicornis*, Indian muntjac or barking deer *Muntiacus muntjac*, Yellow-throated marten *Martes flavigula*


Left to right: seedlings of *Cinnamommum cecidodaphne* germinating in dense clumps in bear droppings, seeds of various bird-dispersed tree species belonging to Lauraceae, Rosaceae, Annonaceae, germinating seeds of *Dysoxylum binectariferum*, (an important species in hornbill diet) below a hornbill nest tree

Left to right: forest canopy in Pakke Wildlife Sanctuary, buttressed tree of *Tetrameles nudiflora*, an emergent wind-dispersed species, ripe arillate capsular fruits of *Chisocheton paniculates*, a bird-dispersed tree species

The average VMR was highest (19.68, range: 3.90 to 61.28) for **bird-dispersed** species followed by **mechanically dispersed** species (16.39, range: 2.13 to 38), **bird- and mammal-dispersed** species (14.83, range: 3.94 to 38.68) and **mammal-dispersed** species (14.48, range: 6.76 to 34.21). A Kruskal-Wallis One-way ANOVA test between all four dispersal modes did not show any difference in VMR based on dispersal mode (H = 1.130, df = 3, p = 0.77, N = 50). We then categorized the species into broad types (mechanically dispersed and animal-dispersed) and a Mann-Whitney test ($U$ = 235, p = 0.90) between 13 mechanically dispersed species and 37 animal-dispersed species also did not show any differences in VMR. We restricted the analysis to species represented by 20 or more individuals and again found no differences in VMR between 8 mechanically dispersed species and 17 animal-dispersed species (Mann-Whitney test, $U$ = 58, p = 0.56).

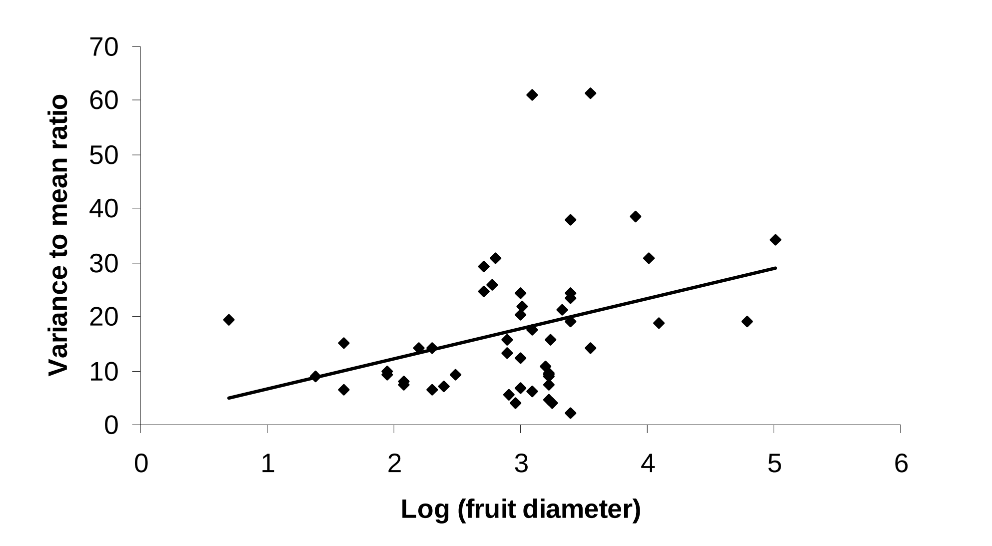



Fig. 3. Scatterplot of log fruit size (fruit diameter, mm) with variance to mean ratio (a measure of clumping) for 50 tree species (Pearson's r = 0.34, p < 0.05), in Pakke Wildlife Sanctuary, a tropical semi-evergreen forest in western Arunachal Pradesh, northeast India. Fruit size was log-transformed (natural log, Ln) as distribution of fruit sizes was skewed.

Fruit size was positively correlated with VMR when all 50 species were examined together (Pearson's r = 0.31, p < 0.05). However, fruit size was not correlated with VMR when the relationship was examined separately for bird-dispersed species (n = 23), wind-dispersed (n = 9), gravity-dispersed (n = 4), or for both bird- and mammal-dispersed species (n = 7). Fruit size showed a positive correlation with VMR only for mammal-dispersed species (Pearson's r = 0.88, n = 7, p < 0.05); however, this was mainly due to the effect of one species, *Dillenia indica*, that was an outlier with the largest fruit size and highest clumping. There was no correlation for mammal-dispersed species if this species was removed. As the distribution of fruit sizes was skewed towards smaller and medium-sized fruits, we log-transformed (LN) fruit size to re-examine the relationship. Log fruit size was positively correlated with VMR (Pearson's r = 0.34, p < 0.05, n = 50; Fig. 3). We removed two species (*Knema angustifolia* and *Livistona jenkinsiana*) from the analysis as they occur patchily in moist habitats. These two species were thus not represented in all plots and had very high values of clumping. There was greater correlation of log fruit size with VMR (Pearson's r = 0.38, p < 0.05, n = 48), after removal of these two species. Two other species, which had very large fruit sizes (*Dillenia indica* (150 mm) and *Pterygota alata* (120 mm) and may have affected the patterns, were also removed from the analysis. When all four species were removed, the relationship remained significant with fruit size (Pearson's r = 0.39, p < 0.05, n = 46) and with log fruit size (Pearson's r = 0.30, p < 0.05, n = 46).

Animal-dispersed species with medium and large fruits (> 2 cm) had a higher mean VMR (21.35, range: 6.2 to 61.28, n = 18) than those with small (≤ 2 cm) fruits (14.40, range: 3.9 to 30.94, n = 19), although the difference was not significant (Mann-Whitney test, $U$ = 131.5, p = 0.23). Mechanically dispersed species with medium and large fruits had a higher mean VMR (19.76, range: 2.13 to 30.96, n = 7) than those with small fruits (12.47, range: 6.4 to 24.3, n = 6), although the difference was not significant (Mann-Whitney test, $U$ = 15, p = 0.44) (Fig. 4).

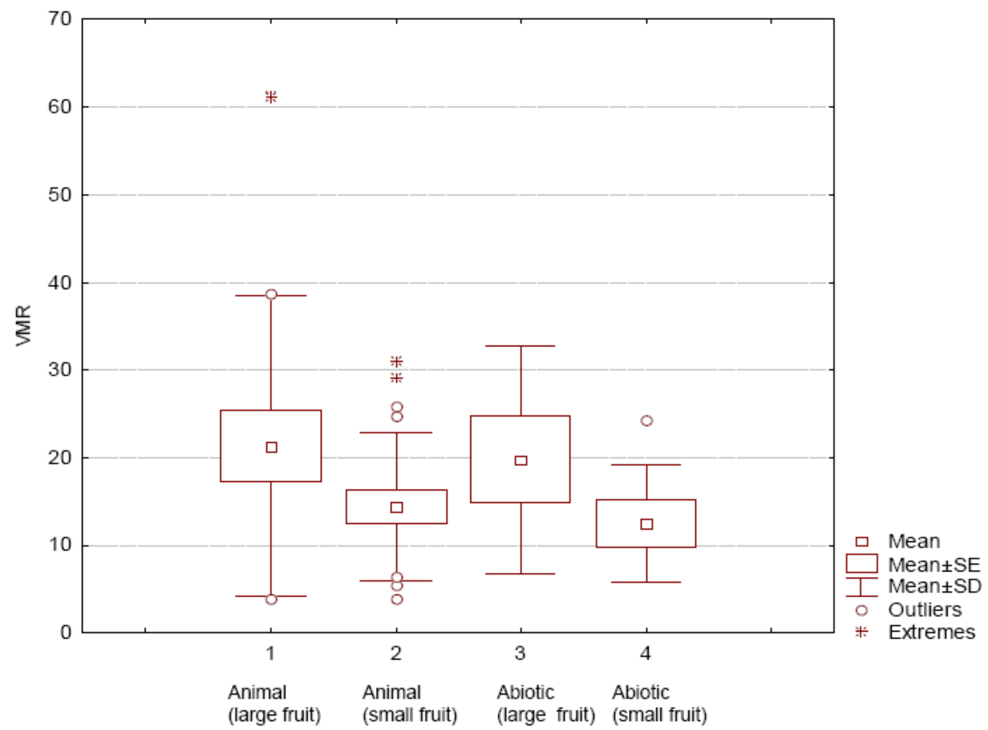



Fig. 4. Boxplot showing the mean VMR (with SD, SE) values of tree species categorized based on their dispersal mode and fruit size. On the X-axis, the categories are 1 = Animal-dispersed large fruits (> 2 cm), 2 = Animal-dispersed small fruits (≤ 2 cm), 3 = Mechanically-dispersed small fruits (≤ 2 cm) and 4 = Mechanically dispersed large fruits (> 2 cm).

We also examined whether seed size had an effect on levels of clumping. Log fruit and seed diameters were positively correlated (Pearson's r = 0.655, p < 0.05, n = 50). Seed size was not correlated with VMR (Pearson's r = 0.26, n.s.) for all species, while log seed size was weakly correlated with VMR for all species (Pearson's r = 0.29, p < 0.05). However, there was no correlation of VMR with seed size for each dispersal category examined separately. Seed size may not be a good predictor as many large fruits are multi-seeded with small seeds. Seed size was positively correlated strongly with VMR, for single-seeded species (Pearson's r = 0.52, p < 0.05, n = 25). VMR was not correlated with seed size (Pearson's r = 0.15, ns, n = 24) for multi-seeded species. However, log seed size was not correlated with VMR for either single-seeded (Pearson's r = 0.35, ns, n = 25) or multi-seeded species (Pearson's r = 0.28, ns, n = 24).

## Discussion

*Dispersal modes of tree species*

Most tree species in the study area were animal-dispersed and this was similar to estimates from other tropical forest regions [43,44] that range from 72-76% in Barro Colorado Island, Panama [45], and Hong Kong [46] to 85-90% in Thailand, Costa Rica, and Western Ghats, south India [28, 47, 48]. Dispersal by birds appears overwhelmingly important at this site, and this is evident both in terms of number and percentage of tree species dispersed by birds as well the higher density of bird-dispersed tree species. The number of avian frugivores is also high in comparison to mammalian frugivores, including several large obligate avian frugivores such as hornbills that are abundant in the study area [49].

*Spatial patterns, dispersal mode and fruit size*

Our analysis did not discern any relationship between spatial pattern and dispersal mode of tree species. All species showed clumping (VMR > 1), and there were no differences based on dispersal mode. While there were no significant differences in spatial pattern based on dispersal mode, we found that bird-dispersed species showed slightly higher aggregation levels, contrary to results from other studies [3, 19]. It has often been assumed that the greater diffused spatial pattern seen for bird-dispersed fruits is because of long-distance movements; however, large avian frugivores also often deposit seeds in a clumped manner. The higher aggregation seen for bird-dispersed species may be because a high proportion of these (17 of 23 species) are consumed/dispersed mainly by hornbills, which deposit seeds in a spatially contagious manner at nest and roost sites [29, 49]. Mammal-dispersed species in the area may show lower clumping because the main dispersers are large-bodied ungulates that carry and regurgitate seeds far away from parent fruit trees. However, even these ungulates and other mammalian frugivores such as civets often deposit seeds in small aggregated piles. Most primates are usually known to generate aggregated seed dispersal patterns; however, of the three species found here, the capped langur (*Tracypithecus pileatus*) is primarily a folivore and is known to break and digest seeds [50, 51]. Although macaques are more frugivorous and often swallow seeds whole and disperse them by spitting out after carrying them in cheek pouches [52, 53], their efficacy as important dispersers is debatable as they eat seeds and consume ripe fruits [51]. In addition, encounter rates of the three species of primates are low [24, Datta, unpubl. data].

The methods and measures used in this study are different and spatial patterns are highly scale-dependent. Our sampling was in multiple non-contiguous plots covering a total area of 5.25 ha, while other studies have been in large 50 ha plots where all individuals are mapped. A further problem could be the categorization of dispersal modes for tree species where detailed quantitative observations of fruit consumers were not made. Several species may be dispersed by a wider array of frugivores.

Fruit size appeared to show a positive relationship with spatial pattern of tree species, with large-sized fruit species showing greater aggregation. This was also noted by [19] with a larger sample of tree species. However, the relationship was not very strong, since when analyzed separately based on each dispersal category, spatial patterns of bird-dispersed species were not related to fruit size, while for mammal-dispersed species larger fruits showed greater clumping. But this was largely due to the effect of a single large-fruited species with high clumping. Wind- and gravity-dispersed species also did not show any significant relationship with fruit size, although we had limited sample sizes for these groups. Within animal-dispersed and mechanically dispersed species, although clumping was greater for tree species with large fruits, the difference was not significant. Animal-dispersed tree species with large fruits in fact showed wide variation in clumping values, indicating that other factors are influencing spatial patterns. The diverse avian and mammalian frugivores handle fruits and deposit seeds in various ways; therefore clear relationships based on broad dispersal modes may be difficult to find.

Factors affecting recruitment, such as soil, light, moisture and topographic features leading to niche differentiation may be more important in determining ultimate spacing patterns of adult trees (8, 54). For example, tree species were found to show demographic responses to variation in soil types which appeared to influence adult tree distributions [55]. Although, we did not measure habitat characteristics, there were habitat differences between plots, with some species represented patchily in a few plots with suitable habitat. For example, two species, *Knema angustifolia* and *Livistona jenkinsiana* (a palm), appear to have specialized habitat niches with more moisture with certain topographic features and where bamboo and cane were abundant. Another species, *Dillenia indica*, was mainly restricted to lower areas near perennial streams and larger rivers. The lack of a relationship between dispersal mode and adult tree spatial patterns may be due to the fact that tree distributions are a result of a combination of abiotic interactions and intra and inter-specific interactions such as competition and pathogens [1,2], as well as dispersal limitation [19, 56]. Therefore, patterns at the community level may be obscured.

This study highlights the importance of vertebrate frugivores, especially birds, in dispersal of a majority of tree species in a tropical semi-evergreen forest. There was a high representation of families such as Lauraceae, Euphorbiaceae, Moraceae, and Meliaceae, most of which are dispersed by birds. Mammals dispersed relatively fewer species. All tree species showed high clumping. Dispersal mode did not seem important in determining adult tree spacing patterns; however, tree species with larger fruits generally had higher levels of clumping, suggesting that tree species distributions may be partly dispersal limited as fruit size can constrain dispersal ability. Larger fruits therefore show greater levels of clumping than smaller fruits. An analysis that takes into account habitat requirements and recruitment needs of individual plant species, and also uses a refined classification of dispersal modes based on detailed observations of fruit consumers/dispersers, may be needed to conclusively understand the importance of dispersal mode in determining spatial patterns of tree species at the community level.

## Implications for conservation

Arunachal Pradesh, in northeast India is arguably the most biodiversity-rich region in the country [57]. Large forest areas still remain, in part due to its low human populations; official estimates report 81% of the area as being under forest cover [58]. However, recent studies have documented high rates of deforestation in the entire northeastern region, and in Arunachal Pradesh-Assam in recent years [59-61]. The state is populated by a diversity of indigenous tribes, who are largely agriculturalists dependent on shifting cultivation and hunting. Although population density is the lowest in India, the growth rate is high at almost 3% per year, increasing from 10 per $km^2$ in 1991 to 13 per $km^2$ in 2001. Fifty-six percent of forests are community-owned with an estimated area of 173,000 $km^2$ under shifting cultivation, which is a widespread practice. Poorly regulated logging has also resulted in loss of forest cover especially in the foothill forests. Other causes of forest loss have been expanding agriculture and settlements, tea estates, other development activities along with population increase, and rapid changes in lifestyle and the rural economy.

Though 12% of the geographical area has been brought under the Protected Area network, implementation of India's strong conservation laws is a challenge, especially because local tribes have a strong tradition of hunting, which has ritual significance and recreational value and remains an important means of subsistence, catering to household consumption and providing supplementary cash incomes [62-64]. In many parts of Arunachal, large vertebrates are extremely rare or have become locally extinct due to both hunting and habitat loss. Although most hunting is for domestic consumption and sale, the extent of such hunting has resulted in population declines and empty forests [62, 65, 66]. However, despite the imperfections of law enforcement and the prevalence of hunting even in Protected Areas, these areas still afford a greater level of protection to wildlife than community and reserved forests. The primary targets of subsistence hunting are large vertebrate frugivores such as hornbills, ungulates, bears, and primates [62-64, 66]. Given the importance of these faunal groups as seed dispersers of almost 80% of tree species in the area, their decline is likely to have consequences for the dispersal and recruitment of many tree species in these forests, especially several rare large-seeded tree species. Three species of hornbills also play an important role as seed dispersers of over 80 rainforest tree species in the area, nearly one-fourth of the tree species recorded from the area [22].

Pakke Wildlife Sanctuary and its adjoining forests in western Arunachal Pradesh are located within a global biodiversity hotspot [67]. This is one of the few large remaining areas of reasonably intact foothill forest. However, between 1995 and 2000 there was large-scale deforestation (an estimated 232 $km^2$) due to logging, encroachments, and agricultural expansion and settlements in adjoining forests in Assam near the Assam-Arunachal border. These foothill forests are crucial habitat for hornbills and many large terrestrial vertebrates. Prior studies have shown reduced abundance of diurnal squirrels, primates, pheasants, and hornbills in logged forests [24, 68-70].

Although the area is thinly populated and pressures on the sanctuary are low, local communities (mostly belonging to the *Nishi* tribe), are dependent on the forests for hunting, fishing, and collection of non-timber forest products, mainly in the southeastern part. The *Nishi* are mainly dependent on subsistence agriculture; there are few employment opportunities and there are conflicts with the Forest Department over crop-raiding by elephants. The local community has mostly viewed the Forest Department and the presence of a sanctuary with resentment. From 2002 onwards, the Forest Department and national conservation organizations have attempted to address the problem faced by local communities, and this has generated greater support for the park. Hunting of wildlife such as hornbills, primates and ungulates in the park appears to have declined since 2002 due to better protection by park authorities and greater awareness and enforcement of hunting bans by the *Nishi* community [65]. Our preliminary results from long-term monitoring of faunal groups suggest increased abundance of large vertebrate groups such as primates and ungulates (Datta, unpubl. data).

Our results stress the ecological and social value of preserving ecological processes that are sustained by plant-animal interactions. The study has also generated information on the natural history and ecology of several important vertebrate species and improved our understanding of the forests in the area. This knowledge can be used to enhance conservation awareness among local communities in the area.

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Appendix 1. List of identified tree species, fruit type and color, dispersal mode, major consumers and tree density (trees per ha). A total of 158 tree species are listed, of which 128 were represented in 21 vegetation plots and classified based on dispersal mode, 30 additional species were not recorded in sample plots, but observed to be consumed by animals.

| No. | Family | Tree species | Fruit type | Fruit color | Dispersal mode | Known consumers and/or dispersers | Tree density |
|---|---|---|---|---|---|---|---|
| 1 | *Actinidiaceae | *Saurauia nepalensis* | Berry | Greenish-yellow | Both | Birds & mammals | 0.57 |
| 2 | Anacardiaceae | *Choerospondias axillaris* | Drupe | Yellow | Mammals | Ungulates, elephant, Malayan giant squirrel | 0.76 |
| 3 | *Anacardiaceae | *Drimycarpus racemosus* | Drupe | Red | Mammals | Mammals | 0.95 |
| 4 | Anacardiaceae | *Lannea grandis* | Drupe | Red | Both | Primates, barbets | NR |
| 5 | Anacardiaceae | *Mangifera sylvatica* | Drupe | Green-yellow | Mammals | Primates, tree squirrels | 0.76 |
| 6 | Anacardiaceae | *Spondias pinnata* | Drupe | Orange-yellow | Mammals | Deer, wild pigs, primates (once by hornbills) | 0.19 |
| 7 | Annonaceae | *Miliusa roxburghiana* | Drupaceous carpel | Black | Birds | Birds | 0.38 |
| 8 | Annonaceae | *Polyalthia simiarum* | Drupaceous carpel | Black | Both | Hornbills, also bats | 20.95 |
| 9 | Annonaceae | *Polyalthia* sp. 2 | Drupaceous carpel | Black | Both | Hornbills, bats | 0.19 |
| 10 | Apocynaceae | *Alstonia scholaris* | Follicle | | Wind | | 0.38 |
| 11 | Apocynaceae | *Wrightia tomentosa* | Follicle | | Wind | | 0.38 |
| 12 | Bignoniaceae | *Oroxylum indicum* | Capsule | Brown | Wind | | 0.19 |
| 13 | Bignoniaceae | *Radermachera sinica* | Capsule | Greyish-yellow | Birds | Bar-tailed cuckoo dove | 1.14 |
| 14 | Bignoniaceae | *Stereospermum chelonoides* | Capsule | Brown | Wind | | 4.57 |
| 15 | *Boraginaceae | *Ehretia acuminata* | Drupe | Red-orange | Both | Birds, mammals | 0.38 |
| 16 | *Boraginaceae | *Ehretia laevis* | Drupe | Yellow-orange | Birds | Birds | 2.10 |
| 17 | Burseraceae | *Canarium resiniferum* | Drupe | Greenish-yellow | Both | Deer, wild pig, birds | 3.62 |
| 18 | Burseraceae | *Canarium strictum* | Drupe | Black | Birds | Hornbills, other birds | 0.57 |
| 19 | Burseraceae | *Garuga pinnata* | Drupe | Black | Both | Macaques, parakeets | 2.67 |
| 20 | Caesalpiniaceae | *Bauhinia purpurea* | Pod | Brown | Wind | | 9.71 |
| 21 | *Capparidaceae | *Crataeva religiosa* | Berry | Red | Birds | Parakeets, mynas | 2.10 |
| 22 | Celastraceae | *Bhesa robusta* | Capsule | Yellow | Birds | Hornbills, other birds | NR |
| 23 | *Clusiaceae | *Calophyllum polyanthum* | Capsule | Yellow | Mammals | Bats | 0.19 |

Appendix 1 continued

| No. | Family | Tree species | Fruit type | Fruit color | Dispersal mode | Known consumers and/or dispersers | Tree density |
|---|---|---|---|---|---|---|---|
| 24 | Clusiaceae | *Garcinia xanthochymus* | Berry | Yellow-brown | Mammals | Primates | 0.76 |
| 25 | Clusiaceae | *Kayea assamica* | Drupe | | Gravity/water | | 0.19 |
| 26 | Clusiaceae | *Mesua ferrea* | Drupe | Brown | Birds? | | NR |
| 27 | Combretaceae | *Terminalia bellerica* | Drupe | Grey | Mammals | Deer, primates, tree squirrels | 4.57 |
| 28 | Combretaceae | *Terminalia chebula* | Drupe | Greenish-yellow | Mammals | Deer | NR |
| 29 | Datiscaceae | *Tetrameles nudiflora* | Capsule | | Wind | | 1.90 |
| 30 | Dilleniaceae | *Dillenia indica* | Pseudocarp | Yellow-green | Mammals/water | Elephants, water | 4.95 |
| 31 | Dilleniaceae | *Dillenia pentagyna* | Pseudocarp | Yellow | Birds, mammals | Civets | NR |
| 32 | *Ebenaceae | *Diospyros toposia* | Berry | Pale yellow | Mammals | Deer, primates | 1.71 |
| 33 | *Elaeocarpaceae | *Elaeocarpus aristatus* | Drupe | Brown | Mammals | Mammals | 1.52 |
| 34 | Elaeocarpaceae | *Elaeocarpus ganitrus* | Drupe | Dull blue | Mammals | Civets, (birds occasionally ) | 1.90 |
| 35 | *Euphorbiaceae | *Aporusa octandra* | Capsule | Yellow | Both | Birds, primates | 0.38 |
| 36 | Euphorbiaceae | *Baccaurea ramiflora* | Capsule | Yellow | Mammals | Deer, wild pigs, primates | 2.48 |
| 37 | Euphorbiaceae | *Bischofia javanica* | Drupe | Yellow-green | Mammals, Birds | Barbets | NR |
| 38 | Euphorbiaceae | *Bridelia retusa* | Drupe | Yellow | Birds | Mynas, barbets | NR |
| 39 | Euphorbiaceae | *Croton roxburghii* | Capsule | | Wind or ballistic | | 11.43 |
| 40 | Euphorbiaceae | *Croton* sp.1 | Capsule | | Wind or ballistic | | 2.29 |
| 41 | Euphorbiaceae | *Croton* sp.2 | Capsule | | Wind or ballistic | | 0.19 |
| 42 | *Euphorbiaceae | *Endospermum chinense* | Capsule | Green-yellow | Mammals | Primates | 0.95 |
| 43 | *Euphorbiaceae | *Glochidion assamicum* | Capsule | Red | Birds | Birds | 0.76 |
| 44 | Euphorbiaceae | *Macaranga denticulata* | Capsule | Blackish-brown | Birds | Bulbuls | 0.19 |
| 45 | *Euphorbiaceae | *Mallotus philippensis* | Capsule | Red | Both | Birds, gravity-dispersed | 2.10 |
| 46 | Euphorbiaceae | *Ostodes paniculata* | Capsule | Grey | Wind | | NR |
| 47 | *Euphorbiaceae | *Sapium baccatum* | Capsule | Purple-black | Birds | Birds | 0.19 |
| 48 | *Euphorbiaceae | *Sapium eugeniaefolium* | Capsule | Grey | Birds? | Birds? | 3.81 |
| 49 | Fagaceae | *Castanopsis hystrix* | Acorn | Brown | Gravity | | 3.24 |
| 50 | Fagaceae | *Castanopsis indica* | Acorn | Brown | Gravity | | 4.38 |
| 51 | Fagaceae | *Lithocarpus macrophylla* | Acorn | | Gravity/wind | | 6.67 |
| 52 | *Flacourtiaceae | *Flacourtia indica* | Berry | Dull red | Birds | Birds | 0.38 |

Appendix 1 continued

| No. | Family | Tree species | Fruit type | Fruit color | Dispersal mode | Known consumers and/or dispersers | Tree density |
|---|---|---|---|---|---|---|---|
| 53 | Flacourtiaceae | *Gynocardia odorata* | Berry | Yellow-brown | Mammals | Civets | 1.52 |
| 54 | Hamamelidaceae | *Altingia excelsa* | Capsule | Dark brown | Gravity | | 2.29 |
| 55 | Hippocastanaceae | *Aesculus assamicus* | Capsule | | Gravity | | 0.38 |
| 56 | Icacinaceae | *Platea latifolia* | Drupe | Black | Birds | Hornbills, other birds | NR |
| 57 | Juglandaceae | *Engelhardtia spicata* | Samara | | Wind | | 2.48 |
| 58 | Lauraceae | *Actinodaphne angustifolia* | Drupe | Black | Birds | Hornbills, other birds | NR |
| 59 | Lauraceae | *Actinodaphne obovata* | Drupe | Black | Birds | Hornbills, other birds | 3.24 |
| 60 | Lauraceae | *Alseodaphne peduncularis* | Drupe | Black | Birds | Hornbills, other birds | NR |
| 61 | Lauraceae | *Beilshmedia roxburghiana* | Drupe | Black | Birds | Hornbills | 1.71 |
| 62 | Lauraceae | *Beilshmedia* sp. 2 | Drupe | Black | Birds | Hornbills, other birds | NR |
| 63 | Lauraceae | *Beilshmedia* sp. 3 | Drupe | Black | Birds | Hornbills, other birds | NR |
| 64 | Lauraceae | *Cinnamommum tamala* | Drupe | Black | Birds | | NR |
| 65 | Lauraceae | *Cinnamomum cecicodaphne* | Drupe | Greenish-black | Both | Hornbills, other birds, (also bears) | 0.76 |
| 66 | Lauraceae | *Cinnamomum obtusifolium* | Drupe | Black | Birds | Birds | 0.57 |
| 67 | Lauraceae | *Cryptocarya amygdalina* | Drupe | Black | Birds | Hornbills | 2.29 |
| 68 | Lauraceae | *Cryptocarya* sp. 2 | Drupe | Black | Birds | Hornbills, hill myna, pigeons | 0.76 |
| 69 | Lauraceae | *Dodecadenia grandiflora* | Drupe | Reddish | Birds | Birds | 1.90 |
| 70 | Lauraceae | *Litsea chinensis* | Drupe | Black | Birds | Hornbills, other birds | 1.33 |
| 71 | Lauraceae | *Litsea monopetala* | Drupe | Black | Birds | Hornbills, other birds | 0.19 |
| 72 | Lauraceae | *Litsea panamonja* | Drupe | Yellow | Birds | Hornbills, other birds | 0.19 |
| 73 | Lauraceae | *Litsea* sp. | Drupe | Black | Birds | Hornbills, other birds | NR |
| 74 | Lauraceae | *Neolitsea umbrosa* | Drupe | Black | Birds | Hornbills, other birds | 1.90 |
| 75 | Lauraceae | *Persea/Phoebe* sp. | Drupe | Black | Birds | Hornbills, other birds | 4.38 |
| 76 | Lauraceae | *Phoebe attenuata* | Drupe | Black | Birds | Hornbills, other birds | 2.10 |
| 77 | Lauraceae | *Phoebe cooperiana* | Drupe | Greenish-black | Birds | Hornbills, other birds | 1.33 |
| 78 | Lauraceae | *Phoebe lanceolata* | Drupe | Black | Birds | Hornbills, other birds | 0.38 |
| 79 | Lauraceae | *Phoebe* sp. | Drupe | Black | Birds | Hornbills, other birds | 26.29 |
| 80 | *Leeaceae | *Leea indica* | Drupe | Black | Birds | Birds | 3.05 |
| 81 | Lythraceae | *Duabanga grandiflora* | Capsule | Brown | Both | Birds, tree squirrels | 0.76 |

Appendix 1 continued

| No. | Family | Tree species | Fruit type | Fruit color | Dispersal mode | Known consumers/dispersers | Tree density |
|---|---|---|---|---|---|---|---|
| 82 | Lythraceae | *Lagerstroemia parviflora* | Capsule | | Wind/gravity | | 0.76 |
| 83 | Lythraceae | *Lagerstroemia speciosa* | Capsule | | Wind/gravity | | 0.19 |
| 84 | Magnoliaceae | *Michelia champaca* | Capsule | Grey | Birds? | Birds? | 0.57 |
| 85 | Magnoliaceae | *Talauma hodgsonii* | Aggregate Follicle | Grey (red seed) | Mammals | Tree squirrels | 0.57 |
| 86 | Magnoliaceae | *Talauma* sp. 2 | Aggregate Follicle | Grey | Mammals | Tree squirrels | 0.19 |
| 87 | Malvaceae | *Kydia calycina* | Samara | | Wind | | 0.19 |
| 88 | Meliaceae | *Aglaia* sp. 1 | Arillate capsule | Bi-colored (edible aril: maroon-red) | Birds | Hornbills | 5.14 |
| 89 | Meliaceae | *Aglaia* sp. 2 | Arillate capsule | Orange-yellow | Mammals | Primates | 2.48 |
| 90 | Meliaceae | *Aglaia spectabilis* | Arillate capsule | Bi-colored (edible aril: maroon) | Birds | Hornbills | 7.43 |
| 91 | Meliaceae | *Aphanamixis polystachya* | Arillate capsule | Bi-colored | Birds | Hornbills | 2.48 |
| 92 | Meliaceae | *Chisocheton paniculatus* | Arillate capsule | Bi-colored (edible aril: white-orange) | Birds | Hornbills, Mountain Imperial Pigeon | 21.52 |
| 93 | Meliaceae | *Chukrasia tabularis* | Capsule | Brown | Wind | | 1.33 |
| 94 | Meliaceae | *Dysoxylum binectariferum* | Arillate capsule | Bi-colored (edible aril: black) | Birds | Hornbills, Mountain Imperial Pigeon | 4.19 |
| 95 | *Meliaceae | *Dysoxylum hamiltonii* | Capsule | Orange | Birds | Birds | 0.19 |
| 96 | Meliaceae | *Toona ciliata* | Capsule | | Wind | | NR |
| 97 | Meliaceae | *Toona febrifuga* | Capsule | | Wind | | 0.19 |
| 98 | Mimosaceae | *Albizzia lucida* | Pod | Brown | Wind | | 0.76 |
| 99 | Mimosaceae | *Albizzia procera* | Pod | Brown | Wind | | NR |
| 100 | Moraceae | *Artocarpus chaplasha* | Syncarp | Green | Both | Hornbills, squirrels | 0.95 |
| 101 | Moraceae | *Ficus macclellandi* | Fig | Bright yellow | Both | Hornbills, other birds, civets, marten, tree squirrels | NR |
| 102 | Moraceae | *Ficus altissima* | Fig | Red | Both | Hornbills, other birds, mammals | NR |
| 103 | Moraceae | *Ficus cyrtophylla/clavata* | Fig | Orange | Both | Hornbills, other birds, mammals | NR |
| 104 | Moraceae | *Ficus elastica* | Fig | Red | Both | Birds, mammals | 0.38 |
| 105 | Moraceae | *Ficus hookeri* | Fig | Reddish-black | Both | Birds, mammals | 0.57 |
| 106 | Moraceae | *Ficus lamponga* | Fig | Reddish | Mammals | Civets, bats | 0.19 |

Appendix 1 continued

| No. | Family | Tree species | Fruit type | Fruit color | Dispersal mode | Known consumers/dispersers | Tree density |
|---|---|---|---|---|---|---|---|
| 107 | Moraceae | *Ficus mysorensis* | Fig | Reddish-black | Both | Birds, mammals | 0.19 |
| 108 | Moraceae | *Ficus nervosa* | Fig | Orange | Both | Birds, mammals | 1.33 |
| 109 | Moraceae | *Ficus pomifera (oligodon)* | Fig | Reddish | Mammals | Civets, bats | 0.19 |
| 110 | Moraceae | *Ficus scandens* | Fig | Red | Birds | Birds | 0.19 |
| 111 | Moraceae | *Ficus* sp. 1 | Fig | Red | Birds | Birds | 0.19 |
| 112 | Moraceae | *Ficus* sp. 2 | Fig | Red | Birds | Hornbills, other birds | NR |
| 113 | Moraceae | *Morus laevigata* | Compound berry/sorosis | Purple-black | Birds | Birds | 0.76 |
| 114 | Myristicaceae | *Horsfieldia kingii* | Arillate capsule | Bi-colored (edible aril: bright yellow) | Birds | Hornbills, Mountain Imperial pigeon | 1.14 |
| 115 | Myristicaceae | *Knema angustifolia* | Arillate capsule | Bi-colored (edible aril: red-orange) | Birds | Hornbills, pigeons | 6.67 |
| 116 | Myrtaceae | *Syzygium formosum* | Berry | White? | Birds | | NR |
| 117 | Myrtaceae | *Syzygium megacarpum* | Berry | Pale yellow | Both | Birds, primates | 11.62 |
| 118 | Myrtaceae | *Syzygium* sp. | Berry | Purple-black | Birds | Hornbills, other birds | 0.95 |
| 119 | Myrtaceae | *Syzygium syzygioides* | Berry | Purple | Birds | Hornbills, other birds | 16.57 |
| 120 | *Oleaceae | *Linoceira macrophylla* | Drupe | Purple-black | Both | Civets, birds | 0.76 |
| 121 | Palmae | *Livistona jenkinsiana* | Drupe | Blue-black | Mainly birds | Hornbills, hill mynas (also wild pigs, bears?) | 6.10 |
| 122 | Papilionaceae | *Dalbergia paniculata* | Pod | | Wind | | 0.19 |
| 123 | Papilionaceae | *Erythrina stricta* | Pod | | Birds? | | NR |
| 124 | *Proteaceae | *Helicia nilagirica* | Drupe | Purple | Mammals? | Tree squirrels? | 2.10 |
| 125 | Rhamnaceae | *Hovenia acerba* | Drupe | Black | Birds | Barbets | NR |
| 126 | Rhamnaceae | *Zizyphus* sp. | Berry | Yellow | Both | Hornbills, other birds | NR |
| 127 | Rhizophoraceae | *Carallia brachiata* | Drupe | Red | Birds | Birds | 1.90 |
| 128 | Rosaceae | *Pygeum acuminatum* | Drupe | Black | Birds | Hornbills, hill myna, barbets | 1.90 |
| 129 | Rosaceae | *Pygeum* sp. 2 | Drupe | Black | Birds | Hornbills | NR |
| 130 | Rubiaceae | *Anthocephalus cadamba* | Compound Fruit | Reddish-brown | Mammals | Civets, tree squirrels | NR |
| 131 | Rubiaceae | *Hyptianthera stricta* | Drupe | White | Birds | Hornbills | 0.95 |
| 132 | Rubiaceae | *Tricalysia* sp. | Drupe | ? | Both | Birds, civets | NR |
| 133 | *Rutaceae | *Evodia roxburghiana* | Berry | Red | Birds | Birds | 0.38 |
| 134 | Rutaceae | *Micromelum integerrimum* | Berry | Orange | Birds | Bulbuls | NR |
| 135 | Rutaceae | *Zanthoxylum oxyphyllum* | Capsule | Red | Birds | Birds | 1.33 |

Appendix 1 continued

| No. | Family | Tree species | Fruit type | Fruit color | Dispersal mode | Known consumers/dispersers | Tree density |
|---|---|---|---|---|---|---|---|
| 136 | Rutaceae | *Zanthoxylum rhetsa* | Capsule | Red | Birds | Hornbills, other birds | 2.67 |
| 137 | *Sabiaceae | *Meliosma dilleniaefolia* | Drupe | Yellow | Birds? | Birds? | 0.57 |
| 138 | *Sabiaceae | *Meliosma simplicifolia* | Drupe | Red | Birds? | Birds? | 0.95 |
| 139 | *Samydaceae | *Casearia graveolens* | Capsule | Orange-yellow | Birds | Birds? | 1.14 |
| 140 | Sapindaceae | *Xerospermum glabratum* | Drupe | Yellow-orange | Mammals | Tree squirrels | 0.76 |
| 141 | Simaroubaceae | *Ailanthus grandis* | Samara | | Wind | | 1.52 |
| 142 | Staphylaceae | *Turpinia pomifera* | Berry | Green-yellow | Mammals | Deer, wild pig | 7.43 |
| 143 | Sterculiaceae | *Echinocarpus assamicus* | Spiny Capsule | Brown | Gravity, rodents | | NR |
| 144 | Sterculiaceae | *Pterospermum acerifolium* | Capsule | Brown | Wind | | 8.95 |
| 145 | Sterculiaceae | *Pterospermum lanceifolium* | Capsule | Brown | Wind | | 5.71 |
| 146 | Sterculiaceae | *Pterygota alata* | Capsule | Brown | Wind | | 11.62 |
| 147 | *Sterculiaceae | *Sterculia hamiltonii* | Follicle | Red, pink | Birds | Birds | 0.57 |
| 148 | Sterculiaceae | *Sterculia villosa* | Follicle | Bi-colored (edible aril: black) | Both | Hornbills, mynas, macaques | 0.19 |
| 149 | Styracaceae | *Stryrax serrulatum* | Drupe | Black | Birds | Hornbills | 4.57 |
| 150 | Theaceae | *Schima wallichi* | Capsule | Brown | Wind | | 1.71 |
| 151 | *Tiliaceae | *Grewia microcos* | Drupe | Blackish purple | Mammals | Primates, bats, ungulates | 0.19 |
| 152 | *Ulmaceae | *Trema orientalis* | Drupe | Black | Birds | Birds | 0.38 |
| 153 | Urticaceae | *Laportea crenulata* | Achenes | White | Birds | Hornbills (once), other birds | 0.19 |
| 154 | Verbenaceae | *Callicarpa macrophylla* | Berry | Black | Birds | Birds | 4.38 |
| 155 | Verbenaceae | *Gmelina arborea* | Drupe | Green-yellow | Mammals | Deer, wild pig, primates | 0.57 |
| 156 | *Verbenaceae | *Premna benghalensis* | Drupe | Black | Mammals | Ruminants | 0.19 |
| 157 | Verbenaceae | *Vitex peduncularis* | Drupe | Black | Both | Civets, birds | 0.57 |
| 158 | Verbenaceae | *Vitex pentaphylla* | Drupe | Black | Both | Civets, hornbills | 2.48 |

* Tree species in which dispersal modes were assigned based on available literature.
NR: Tree species not recorded in sample plots, but observed to be consumed by animals.
Tree squirrels are mainly pre-dispersal seed predators, but occasionally may act as seed dispersers when seeds fall uneaten during foraging.