Dispersal modes of tree species in the wet forests of southern Western Ghats

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Dispersal modes of tree species in a wet evergreen forest at Kakachi in the Kalakad–Mundanthurai Tiger Reserve, southern India are described here. Frugivore visitors to 82 tree species were observed. Biotic agents involved in seed dispersal and seed predation were six species of birds and five species of mammals. Bird-dispersed species were the most common species (59%), followed by mammal-dispersed species (26%). Primates were less important than bats and civets in seed dispersal. Fifteen per cent of the species had no apparent adaptation for abiotic dispersal (mechanically dispersed) except one wind-dispersed species. Many bird-dispersed species occurred at low density but the total density of bird-dispersed species compares with that of mammal and mechanically dispersed species. Edge or gap habitat species were less abundant than the closed forest ones in all three types of dispersal modes. Species level comparison with other wet forest sites indicates a high degree of similarity between Kakachi and La Selva in central America.

TROPICAL forests represent an arena for many biotic interactions among a wide array of plants, vertebrates and invertebrate species[1]. This is evident from observations at a community level on plant–pollinator and plant–disperser interactions[2]. However, tropical forests differ in their pollinator/disperser assemblages. For instance, community level seed dispersal has shown that sites in Neotropics and Australia were dominated by bird dispersal while those in southeast Asia exhibited no such adaptation for biotic dispersal agents[2,3]. Pan-tropical comparisons help in understanding the underlying factors contributing to such differences[1,4].

A comparison of seed dispersers in different wet forest sites in the tropics will provide insights into the broad co-evolutionary patterns between plants and their animal vectors, and the dominance and diversity of different groups in different parts of the tropics. In the wet forests, these aspects have been studied at La Selva in Central America[5], Africa[6] and to some extent in southeast Asia[7,8]. The above forests differ in terms of the number and type of frugivores and the availability of fruit resources. However, one common trend in the wet forests has been the dominance of biotic dispersal. Such trends are noticed at the species level but no attempt has been made to understand the similarities and differences at the community level. These can give insights into conservation of forest frugivores in terms of available fruit resource base for them and can be of significant use in the management of parks and reserves.

Here we give information on the various dispersal modes associated with 82 tree species and their frequency of occurrence in terms of species and density in a wet evergreen forest of Kakachi in Kalakad–Mundanthurai Tiger Reserve (KMTR). As wet forests of Western Ghats, southern India have never been subjected to such study in the past, we compare it with other wet forest sites and put the results obtained in perspective with tropical seed dispersal syndromes.

Study site

This study was conducted from 1991 to 1996 at Kakachi; an undisturbed wet evergreen forest of KMTR in the southern Western Ghats (77°30′ E and 8°40′ N), India. This reserve covers an area of 900 km^2 with an elevational range of 100 m to 1800 m. Kakachi is located at an elevation of 1250 m. It receives an annual rainfall of over 3500 mm from both the monsoons, which are active between June to August and October to December.

The vegetation is broadly classified as mid-elevation tropical wet evergreen forest[9] and has been described in detail by Ganesh *et al.*[10]. They list about 173 plants species in 3.82 ha, which comprises 42 canopy trees, 48 understorey trees, 50 shrubs, 18 ground herbs, and 15 woody lianas. The dominant plant species are *Cullenia exarillata* (Bombacaeae), *Palaquium ellipticum* (Sapotaceae) and *Aglaia elaeagnoidea* (Meliaceae)[10].

Methods

Field observations on frugivores of 82 common and uncommon tree species were carried out within a 20 km^2 area. This included 67 of the 90 (74%) tree species

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encountered by Ganesh *et al.*[10] and 15 additional species. The observations were done over a period of four years from 1991 to 1994.

Information on the frugivores visiting 82 tree species was obtained from Ganesh[11] and a few from Green and Minkowski[12]. For other species not recorded in the earlier studies, such information was obtained from direct observations on fruiting trees, evidence from fecal remains, and by examining fruit debris left behind by frugivores. Observations on frugivores were carried out along four phenology trails of 1–5 km each, maintained for long-term monitoring of tree phenology in the area. Direct observations were made along these trails for 4–5 h per species in the mornings starting from 0700 h. A minimum of 5–8 individuals were observed per species over its fruiting period. For species suspected to be visited by frugivores only in the night, nocturnal watches were kept from 1830 h till 2300 h. Extensive observation made earlier at all times of the day and all night suggested that there was no turnover of species later in the day or night.

During the observation period a record of the species – their numbers, and the way (seed swallowed, seed dropped, and seed predated) the fruits and seeds were handled – was made. Observations at night were done using night vision equipment. Frugivorous bats were caught using mist nets laid on flight paths of fruiting trees for identification while all other taxa were identified using binoculars. Some species that were very rare (1 sighting in 3–4 years) in the wet forest at Kakachi such as Hill Myna (*Gracula religiosa*), Vernal Hanging Parrot (*Loriculus vernalis*), and green pigeons (*Treron* spp.) were excluded. Similarly, understorey frugivores such as the thrushes were also excluded, as dispersal of canopy species by them is limited.

Bird-dispersed fruits were usually small and fleshy with colour ranging from purple to orange, while mammal fruits were large, fleshy and mostly green to brown in colour[11]. Fruits that had no particular adaptation for biotic dispersal agents were classified as mechanically dispersed, and most of these released their seeds once the fruits dehisced. A seed disperser here is referred to as a species that does not damage the seed while feeding on the fruit and helps in transporting the seed away from the tree.

The forest habitat was divided into closed canopy forest (= undisturbed wet forest) and gap or edge habitats which refer to gaps within undisturbed forests and edges of undisturbed forests. As species composition differs in these two habitats, they were also separately analysed for dispersal modes.

Plant species were identified using Gamble[13] and were compared with specimens at the Botanical Survey of India, MH (Madras herbarium), Coimbatore, by experienced taxonomists. Fruit samples not identified in the field were collected and preserved in 70% alcohol for later identification.

Results

Frugivory

A total of six species of birds, five species of arboreal mammals, and one species of bat regularly ate fruits or seeds. The six species of commonly occurring birds included the Black Bulbul (*Hypsipetes leucocephalus*), Yellow-browed Bulbul (*Iole indica*), Red-whiskered Bulbul (*Pycnonotus jocosus*), White-cheeked Barbet (*Megalaima viridis*), Mountain Imperial Pigeon (*Ducula badia*) and Nilgiri Wood Pigeon (*Columba elphinstonii*). The two species of pigeons are referred to as large birds while others are small birds. All canopy mammals found in Kakachi ate fruits. These include the lion-tailed macaque (*Macaca silenus*), Nilgiri langur (*Trachypithecus johnii*), Malabar giant squirrel (*Ratufa indica*), flying squirrel (*Petaurista philippensis*), brown palm civet (*Paradoxurus jerdoni*), and the bat *Cynopterus sphinx*.

All birds swallowed fruits and defecated intact seeds. There was no evidence of seed predation from the birds including the pigeons. On the other hand, four (2 primates, 2 squirrels) out of the five mammals were seed predators except for the palm civet. The single bat species was a seed disperser.

Frequency of dispersal modes

Of the 82 tree species sampled in this study, 65 (79%) produced fleshy fruits while the remaining had a hard pulp, which was not eaten by the animals. The most common seed-dispersers were birds, which accounted for 49 (59%) of the plant species (Table 1). Eighty-six per cent of these were dispersed by small birds and the remaining seven species (14%) exclusively by large birds such as the pigeons. Large bird-dispersed species that include *Litsea insignis*, *L. glabrata* and *Dysoxylum malabaricum* among others, are dispersed by imperial pigeons and occasionally by the wood pigeons. Many of the bird-dispersed species were also eaten by mammals but exclusive mammal dis-

Table 1. Number of species under the three dispersal categories and their total density/ha at Kakachi. Species under closed canopy and edge/gap habitats are also shown. Percentages in parenthesis

	Closed	Edge	Total
Species level analysis			
Birds	30 (61)	19 (39)	49 (59)
Mammals	12 (57)	9 (43)	21 (26)
Mechanical	9 (75)	3 (25)	12 (15)
Density level analysis	Closed	Edge	Total
Birds	205.54	26.08	231.62
Mammals	219.60	17.64	237.24
Mechanical	214.54	2.64	217.18

persal accounted for 21 (26%) plant species (Appendix 1). Civets and bats together dispersed 10 (67%) of the species and the rest (33%) by all mammals. Though primates and squirrels eat fruits of many other species, they function as seed predators and not as seed dispersers for them. Mechanically dispersed fruits that had no apparent adaptation for biotic dispersal, such as an aril, accounted for 12 (15%) species, including one wind-dispersed species, *Vernonia travancorica*.

The 82 tree species belonged to 32 families. Bird-dispersed species alone accounted for 22 families while mammal species belonged to 13 families and mechanically dispersed species to seven (Appendix 1). Nearly 16 (33%) bird-dispersed species were from a single family (Lauraceae), which also included three out of the five large bird-dispersed species such as *Litsea* spp. and *Beilschmiedia wightii*. Under mammal-dispersed species Elaeocarpaceae and Guttiferae were the most common whereas mechanically dispersed fruits largely belonged to Euphorbiaceae.

Density, habitat and dispersal modes

The total density of bird, mammal, and mechanically dispersed species did not vary between the dispersal modes (Table 1). The individual densities of the species in the three modes also did not vary significantly (Kruskal Wallis, $H = 2.491$, $n = 82$, p = ns). However, almost 39% of the species dispersed by birds were relatively rare and occurred only once in the 3.82 ha sampled, while comparable figures for mammals and mechanically dispersed are 23.8% and 16.7% respectively (Appendix 1). In fact, the dominant species in the forests such as *Cullenia exarillata*, *Palaquium ellipticum* and *Aglaia elaeagnoidea* were dispersed mechanically or by mammals.

The plant species sampled in this study belonged to both closed canopy forest and edge or gap habitats. The frequency of the three dispersal modes in the two habitats varied. Greater proportion of mechanically dispersed fruits and almost all large-bird dispersed species were closed forest species (Table 1). Proportion of bird and mammal-dispersed species corresponded with the availability of the species pool in the two habitats. The density of species in the edge and gap habitats was lower in all the three syndromes. The differences being more pronounced in the mammal and mechanically-dispersed fruit species, which were 50 times more abundant in the closed forest (Table 1).

Intercontinental comparisons

Dispersal modes from four sites, two in Africa and one each in Southeast Asia and Neotropics were compared with those obtained here. In four out of five sites, bird-dispersal was the most common mode (Table 2) except in Gabon where mammal dispersal is more common than the rest. Proportion of bird-dispersed species in Kakachi forest seems closer to La Selva than to the mountain forests of Malawi and Gabon in Africa. In terms of mammal-dispersed species also the resemblance exists between La Selva and Kakachi.

Discussion

The frugivore assemblage at Kakachi comprised equal proportion of bird and mammalian frugivores. Despite this, a high number of plant species depends on birds for seed dispersal, a situation similar to that in Chile[14]. There could be many reasons for this. Unlike in Chile where abundances of avian frugivores are high and aseasonal, at Kakachi most of the birds have low abundances and are seasonal[15]. Coincidentally, only few bird-dispersed species fruit each year, as there is high inter-year variation in their fruiting phenology[11]. Further, many species producing fleshy fruits for bird dispersal are low in density inside the forest although they are more diverse, and therefore can possibly sustain only few individuals of dispersers. Some or all of these reasons could be responsible for the observed patterns.

Table 2. Comparison of fruit dispersal modes across similar wet forest types. All except Malawi and Kakachi are lowland wet forests. Values are numbers of species (percentages)

	S.E. Asia Hong Kong[+]	Africa Malawi[20]	Africa Gabon*	Neotropics La Selva[#]	India Kakachi
Forest type	Lowland wet forests	Mountain wet forests	Lowland wet forests	Lowland wet forests	Mid-elevation wet forests
Birds	115 (75)	49 (94)	32 (26)	83 (50)	49 (60)
Mammals	15 (10)	3 (6)	59 (48)	62 (37)	21 (26)
Others	23 (15)	0	46 (38)	22 (13)	12 (14)
Total	153	52	122	167	82

[+]Recalculated from Corlett[8]. Mammals refer to species dispersed by monkeys, bats, and civets. Others include both mammals and birds.
*Mammals here refer to monkeys. Others include large and small rodents.
[#]Recalculated from Levey *et al.*[5]. Others here include only bats.

In most tropical sites, primates disperse many species and form important dispersal agents in the community[2,6,16,17]. However, in Kakachi, only two species of primates are found and they are primarily seed predators. Their dispersal role is limited, except for the lion-tailed macaque that proportionately disperses more species than the Nilgiri langur[11,15]. Such high levels of seed predation have been associated with lack of fleshy fruit availability[18]. In Kakachi, seeds are a more predictable resource, while fleshy fruit availability is seasonal and low in terms of its density[11]. This could have resulted in higher seed predation by the primates, as they require a higher resource base than solitary animals such as civets. Since primates are seed predators at Kakachi, the dispersal by mammals is accounted largely by civets and bats. Even in La Selva, mammal seed dispersal is high but only three species of primates help in seed dispersal and a greater proportion are dispersed by bats[5].

Inter-site comparison has shown a high degree of similarity between La Selva and Kakachi in terms of dispersal modes at the species level. These patterns when analysed at a population level for each dispersal mode can be different as shown in this study. Although there are a large number of bird-dispersed species at Kakachi, their overall availability is not different from the other modes. This gives an insight into the resource availability for the frugivores and how frugivore diversity can possibly be explained at each site. Such information when analysed across sites can help in understanding the issues of frugivore conservation such as habitat fragmentation, local extinctions, and its consequences on forest recruitment.

Though bird dispersal is the most common means of seed dispersal in Kakachi, the dominant species in Kakachi are not bird-dispersed. These either are dispersed by mammals or have no specific dispersal agent. Most of these dominant species were also closed-canopy species, which require shade for successful establishment. Bird-dispersed species were mostly edge or gap species, which thrive in the openings inside the forest. Their lower density could be attributed to fewer gaps and edge habitats available which also suggests the overall undisturbed nature of the Kakachi forest. Preliminary analysis of density across disturbance gradients indicates higher density of bird-dispersed species in disturbed forests (T. Ganesh, unpublished observations). Plant species in Kakachi, though not highly specialized, are dependent on very few vectors for seed dispersal. This is particularly important for species dispersed by large birds as elimination of these frugivores could affect the dispersal and regeneration of the dependent tree species that are in most cases also rare in the forest[11]. This needs to be kept in mind before altering the evergreen forests of Kalakad.

Appendix 1. List of species sampled, their dispersers, habitat, and density

Family	Species	Dispersers	Habitat	Density/ha
Annonaceae	*Goniothalamus wightii*	Birds	Closed	0.26
Annonaceae	*Meiogyne panosa*	Birds	Closed	0.26
Annonaceae	*Miliusa wightiana*	Birds	Closed	1.31
Caprifoliaceae	*Viburnum punctatum*	Birds	Closed	2.09
Daphniphyllaceae	*Daphniphyllum* sp.	Birds	Gap/edge	0.26
Euphorbiaceae	*Antidesma menasu*	Birds	Closed	10.99
Euphorbiaceae	*Macaranga peltata*	Birds	Gap/edge	2.62
Euphorbiaceae	*Mallotus tetracoccus*	Birds	Gap/edge	0.26
Flacourtiaceae	*Casearia ovata*	Birds	Closed	6.02
Icacinaceae	*Gomphandra coriacea*	Birds	Closed	38.48
Icacinaceae	*Nothopodytes nimmoniana*	Birds	Gap/edge	0.26
Lauraceae	*Actinodaphne bourdillonii*	Birds	Gap/edge	1.57
Lauraceae	*Actinodaphne* sp.	Birds	Gap/edge	0.79
Lauraceae	*Alseodaphne semicarpifolia*	Birds	Closed	10.73
Lauraceae	*Cinnamomum sulphuratum*	Birds	Closed	4.19
Lauraceae	*Cinnamomum filipedicellatum*	Birds	Closed	37.17
Lauraceae	*Cinnamomum travancoricum*	Birds	Closed	4.97
Lauraceae	*Cryptocarya lawsonii*	Birds	Closed	6.54
Lauraceae	*Litsea wightiana*	Birds	Gap/edge	1.05
Lauraceae	*Litsea mysorensis*	Birds	Closed	1.05
Lauraceae	*Neolitsea cassia*	Birds	Gap/edge	0.26
Lauraceae	*Neolitsea fisheri*	Birds	Closed	3.66
Lauraceae	*Persea macrantha*	Birds	Gap/edge	1.57
Lauraceae	*Phoebe lanceolatum*	Birds	Closed	0.26
Magnoliaceae	*Michelia nilagirica*	Birds	Gap/edge	0.26
Melastomataceae	*Memecylon malabaricum*	Birds	Closed	5.76
Meliaceae	*Trichilia connaroides*	Birds	Gap/edge	1.05
Moraceae	*Ficus micrococa*	Birds	Gap/edge	1.31
Myrsinaceae	*Rapanea wightiana*	Birds	Gap/edge	2.09
Myrsinaceae	*Maesa indica*	Birds	Gap/edge	0.52

Family	Species	Dispersers	Habitat	Density/ha
Myrtaceae	*Eugenia thwaitesii*	Birds	Closed	1.57
Myrtaceae	*Syzygium gardneri*	Birds	Closed	16.23
Myrtaceae	*Syzygium travancoricum*	Birds	Closed	0.52
Ochnaceae	*Gomphia serrata*	Birds	Closed	2.88
Proteaceae	*Helicia nilagirica*	Birds	Gap/edge	0.26
Rubiaceae	*Ixora nigricans*	Birds	Closed	17.02
Rubiaceae	*Octotropis travancorica*	Birds	Closed	1.05
Rubiaceae	*Pavetta thomsonii*	Birds	Closed	0.26
Rubiaceae	*Tricalysia apiocarpa*	Birds	Closed	18.06
Sapotaceae	*Isonandra lanceolata*	Birds	Gap/edge	0.52
Theaceae	*Ternstroemia japonica*	Birds	Gap/edge	0.26
Verbenaceae	*Clerodendrum viscosum*	Birds	Gap/edge	6.28
Burseraceae	*Canarium strictum*	Birds large	Closed	0.52
Cornaceae	*Mastixia arborea*	Birds large	Closed	7.85
Flacourtiaceae	*Scolopia crenata*	Birds large	Gap/edge	4.71
Lauraceae	*Beilschmiedia wightii*	Birds large	Closed	3.66
Lauraceae	*Litsea glabrata*	Birds large	Closed	0.26
Lauraceae	*Litsea insignis*	Birds large	Closed	0.26
Meliaceae	*Dysoxylum malabaricum*	Birds large	Closed	0.26
Anacardiaceae	*Holigarna nigra*	Mammals	Closed	11.52
Ebenaceae	*Diospyros malabarica*	Mammals	Closed	9.16
Ebenaceae	*Diospyros sylvatica*	Mammals	Closed	0.26
Elaeocarpaceae	*Elaeocarpus venustus*	Mammals	Gap/edge	0.26
Elaeocarpaceae	*Elaeocarpus munronii*	Mammals	Gap/edge	4.71
Elaeocarpaceae	*Elaeocarpus serratus*	Mammals	Gap/edge	0.26
Elaeocarpaceae	*Elaeocarpus tuberculatus*	Mammals	Closed	2.36
Guttiferae	*Calophyllum austroindicum*	Mammals	Closed	8.38
Guttiferae	*Garcinia travancoricum*	Mammals	Gap/edge	0.26
Meliaceae	*Aglaia elaeagnoidea*	Mammals	Closed	109.69
Meliaceae	*Aglaia tamilnadensis*	Mammals	Closed	0.26
Moraceae	*Ficus virens*	Mammals	Gap/edge	0.52
Moraceae	*Artocarpus heterophyllus*	Mammals	Closed	13.35
Myristicaceae	*Myristica dactyloides*	Mammals	Closed	25.92
Myrtaceae	*Eugenia floccosa*	Mammals	Gap/edge	0.52
Myrtaceae	*Syzygium mundagam*	Mammals	Closed	8.38
Rosaceae	*Prunus ceylanica*	Mammals	Gap/edge	0.26
Rubiaceae	*Canthium travancoricum*	Mammals	Gap/edge	0.26
Rutaceae	*Acronychia penduculata*	Mammals	Gap/edge	10.47
Rutaceae	*Vepris bilocularis*	Mammals	Closed	1.83
Sapotaceae	*Palaquium ellipticum*	Mammals	Closed	27.00
Bombacaceae	*Cullenia exarillata*	Mechanical	Closed	63.61
Compositae	*Vernonia travancorica*	Mechanical	Gap/edge	1.83
Euphorbiaceae	*Agrostistachys borneensis*	Mechanical	Closed	61.78
Euphorbiaceae	*Drypetes longifolia*	Mechanical	Closed	30.89
Euphorbiaceae	*Euphorbia antiquorum*	Mechanical	Gap/edge	0.26
Euphorbiaceae	*Mallotus resinosus*	Mechanical	Closed	3.40
Euphorbiaceae	*Epiprinus mallotiformis*	Mechanical	Closed	17.28
Fabaceae	*Heritiera papilio*	Mechanical	Closed	0.26
Fabaceae	*Ormosia travancorica*	Mechanical	Closed	5.76
Flacourtiaceae	*Hydnocarpus alpina*	Mechanical	Closed	29.84
Sapindaceae	*Dimocarpus longon*	Mechanical	Closed	0.26
Theaceae	*Gordonia obtusa*	Mechanical	Gap/edge	0.79

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