

## Research Article

# Reconciling natural history and species ecology: *Myristica beddomei* (Myristicaceae) in the Western Ghats, India.

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### Abstract

Natural history is an important component of any ecological or conservation research. Very often this is not given adequate attention, and observations on the genera or species are often generalized to other, supposedly similar, congeneric species. In this study, we document the natural history of fruit-frugivore interactions of *Myristica beddomei* (Myristicaceae) found in the mid-elevation evergreen forests of the Western Ghats, India, and determine how different these interactions are compared to other Myristicaceae species. *M. beddomei* has a single hard seed covered by an orange-yellow aril. Species of Myristicaceae are usually dispersed by large frugivorous birds, and also by primates in the Neotropics. In South Asia, Myristicaceae dispersal is usually by large birds such as hornbills, but our observations over several years indicate that *M. beddomei* is not bird-dispersed, even though some fruit traits suggest bird dispersal. Our observations suggest that obligate seed predators like macaques and squirrels can facilitate dispersal of the species. We discuss these observations and explore why such outliers might have evolved in the region

**Keywords:** Frugivore, seed predation, KMTR, *Myristica beddomei*, dormouse.

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## Introduction

Understanding an organism's natural history is fundamental to its conservation [1-3]. However, many factors contribute to incomplete natural history details for the majority of known species, including rarity, newly discovered species, and poor documentation, as is the case with many common species, especially insects. In such cases congeneric or sympatric species observations are often used as surrogates for the natural history of the focal species [4]. Though this approach can be helpful, at times it may not be reliable because the species may differ in ways that are not obvious, yet can have a strong ecological or evolutionary significance. Even though molecular tools are available to detect morphologically similar species, the ecological variance of such closely associated species has always been a challenge for ecologists [5].

The tree family nutmeg, with over 20 genera and ca. 500 species spread across tropical Asia, Africa, America and the Pacific islands, has several common features [6-7]. Species are generally evergreen trees, with tawny or red sap in the bark or around the heartwood. The fruits are dehiscent, have brightly coloured arils, and are adapted for bird dispersal [8-12]. Three major genera are found within the Western Ghats of India, namely *Gymnacranthera* (1 species), *Myristica* (4 species) and *Knema* (1 species) [13].

In many places, birds such as hornbills, pigeons and starlings are the seed dispersers of *Myristica* species in South- East Asia [14] and Sri Lanka [11]. This information led to the generalization that all Myristicaceae species are bird-dispersed, without the species-specific ecological studies required, particularly in the Old World tropics. In the Neotropics, birds such as toucans and trogons as well as primates are also well-documented dispersers of Myristicaceae seeds [8,15-17]. In the Western Ghats of India, the *Myristica* genus is particularly poorly studied, and no detailed observations on fruit-frugivore interactions are currently available. The genus is recorded in the diet of some frugivores like hornbills [18, Ravikanth personal communication] and primates [19,20], but no extensive observations exist on the processing of fruits and seeds by any frugivore.

In this study, we investigated the fruit-frugivore interactions in *M. beddomei*, a species that has not been studied at all, and compare our observations with existing information for two other species of Myristicaceae found in the Western Ghats. More specifically, we ask: 1. How different are the fruits of *M. beddomei* from other species of *Myristica*? 2. What are the potential fruit visitors of *M. beddomei*? 3. What are the functional roles of these visitors: are they seed predators or seed dispersers? Finally, we further emphasize the need for species-specific studies of frugivore interactions of congeneric species that may appear morphologically similar.

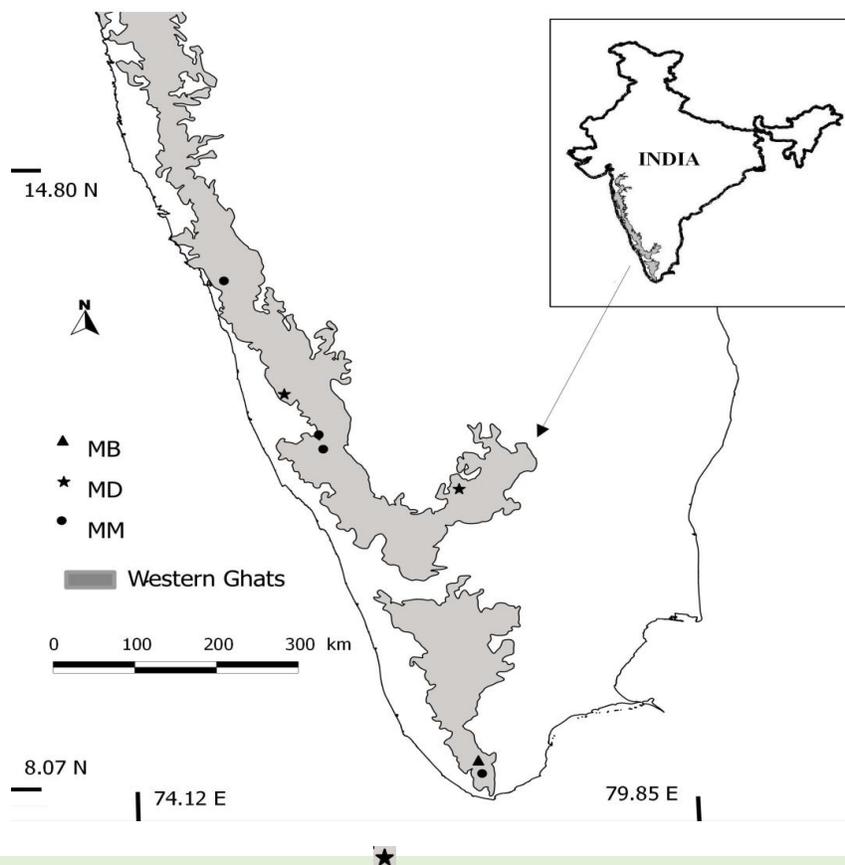
## Methods

The study was conducted during mid-March to end of May 2006 in Kakachi, a mid-elevation wet evergreen forest (8.552 to 8.53' N and 77'38 to 77.40' E) within the Kalakad Mundanthurai Tiger Reserve (KMTR), southern India. The study was carried out in a 300 ha primary evergreen forest within the elevation range of 1,250 to 1,550 m asl. These evergreen forests receive >3500 mm annual rainfall from both the southwest and northeast monsoons. January to May and the month of September are the dry seasons, and other months experience at least 100 mm rainfall. Mean annual temperature is 24<sup>o</sup> C, with mean minimum temperature ranging from 14<sup>o</sup> to 19<sup>o</sup> C and maximum temperature ranging from 17<sup>o</sup> to 28<sup>o</sup> C [21].

The species *Myristica beddomei* King Ann. Calc. is distributed from 1,000 to 1,500 m asl in the Western and Eastern Ghats [13]. It is a dominant, sub-canopy dioecious species [22] that flowers in early April-mid May in Kakachi. The fruits mature during April and May the following year, with most individuals fruiting in alternate years (T. Ganesh personal observation). There is only one species of *Myristica* in Kakachi, which was earlier

referred to as *M. dactyloides* [19,22], but has recently been correctly identified as *M. beddomei* (R. Ganesan personal communication). The fruits are a schizocarp, and each seed is coated by orange-yellow aromatic protein-rich aril, thought to be an adaptation to attract large frugivorous birds (Fig.3 a,b). The aril is collected as a Non-Timber Forest Product in many parts of the Western Ghats and used for spice and medicines [23,24, Chetana personal observation].

Information from other *Myristica* species was collated from the literature (Gamble and Fischer 1915-35). In addition, fruit/seed specimens were collected in many parts of Western Ghats given in the map (Fig. 1).



**Fig. 1. Map showing the *Myristica* species collected from different parts of the Western Ghats of India (Note: MB: *Myristica beddomei*; MD: *Myristica dactyloides*; MM: *Myristica malabarica*).**

#### *Fruit characteristics of Myristica species*

We collected 10 fresh fruits from beneath 10 randomly selected trees in the study area over the fruiting period. A total of 100 fruits and seeds were collected, and their length, width, and fresh mass were recorded. Mean values were calculated. The diameter at breast height (dbh) and height of the sampled fruiting trees were also measured.

### *Fruit-frugivore interactions*

Arboreal animal activity was observed at selected fruiting *Myristica* trees in 2006 (n = 6) and 2007 (n = 4). Each tree was monitored from 06:00 to 18:00 hrs for one day, for a total of 120 hours of observations (19 hrs were lost to rain). During bouts of animal activity, we scanned the whole tree and recorded the species and number of individuals in the tree. Scans of 1-5 minutes on random individual animals recorded handling behaviour of the fruit/seed and where possible, the number of seeds eaten or discarded. Trees were a minimum distance of 2 km from each other. In addition, we opportunistically scanned 132 trees for eight years (2001-2008) during the fruiting season for potential visitors, to record total diversity of fruit visitors to *M. beddomei*.

### *Post dispersal seed predators- camera traps*

Four infra-red camera-traps (CEDT, Indian Institute for Science, Bangalore) were used to monitor a post-dispersal seed removal experiment [25]. The camera-traps were installed beneath fruiting *Myristica* trees facing a cluster of 10 fresh *Myristica* fruits. Four trees were sampled and a total of 40 fruits were under observation each day/night. Fruits were placed 3 to 4 feet from the trap. Each fruit was engraved with an 'X' on the outer rind prior to putting it in the cluster so that experimental fruits were not confused with naturally fallen fruit. The camera-trap was set up on 24 hour mode at 30-second interval between pictures to minimize missing any individuals. Each camera was checked every other day for battery power, number of pictures taken, and the number of seeds removed from the marked fruits. A camera trap was set for 14 consecutive days under each tree, and 56 (14 x 4) days of day-night sampling was done using the four camera traps in one location. Five locations were sampled within the study area within the broad fruiting period of *M. beddomii* from mid-March to end July. A total of 280 (56 x 5) days were sampled. Fruits in the cluster were changed every 7 days after the initial setup to maintain the freshness of fruits. The photographed species were identified and categorised as seed dispersers or seed predators [26]. Capture rate (captures/hours) was calculated on the basis of 12 hour periods for nocturnal species and diurnal species.

Post-dispersal seed predation on the ground was observed by fixing a 2 m thin nylon thread on the seed with non-toxic glue to record seed movements by nocturnal frugivores. The threads were traced the next morning. Twenty seeds were sampled. This was to ascertain the fate of the seeds once they are removed from under the tree. We also scanned hollows in the mid storey and subcanopy for dormouse and wood rat presence and possible hoarding of seeds by them. The fate of the seeds in these hollows was ascertained.

We also set up a few camera traps on the tree canopy and did extended watches (about 30 hours) on the fallen fruits and on the trees at night to document the nocturnal frugivores including bats.

## **Results**

### *Natural history comparison*

The three species of *Myristica* differed in their size and dispersal ability (Table 1). *Myristica beddomei* had globose fruits and seeds and the fruits do not dehisce on the tree. Once ripe, the fruits fall to the ground and after a day split open to reveal the seed and aril. The mean fresh fruit length of *M. beddomei* was 56.6 mm (range 31 - 67 mm, n = 100), width 51 mm (range: 30 - 68 mm), mean fruit fresh mass was 74 g (range 40 - 150 g). Mean length of fresh seeds was 34 mm (range 25 – 57 mm), mean width was 30 mm (range 21- 50 mm), and mean fresh mass was 18 g (range 10 - 40 g, n = 100). The average tree height was  $12 \pm 2.5$  m (mean  $\pm$  SE, n = 60) and average diameter at breast height was  $39 \pm 10$  cm (n = 60).

Table 1. Comparison of fresh fruit and seed characteristics of three species of *Myristica* from the hills of the Western Ghats, India [\*13, 27] (Note: NA – not available, NB- not by birds, L - length, W - width).

Fruit characters	<i>M. dactyloides</i> (MD)		<i>M. malabarica</i> (MM)		<i>M. beddomei</i> (MB)	
	Literature *	Observation	Literature*	Observation	Literature*	Observation
Fruit length (L) mm	60	50 - 72	50 - 75	40 - 56	60	31 - 67
Fruit width (W) mm	30	40 - 55	18 - 35	40 - 55	40	30 - 68
Fruit (dehiscent on tree)	Yes	Yes	Yes	Yes	Yes	No
Fruit weight (range) gm	-	44 (10 - 40)		35 (30 - 41)		74 (40 - 150)
Seed length (L) mm	-	33 - 47		26 - 50		23 - 57
Seed width (W) mm	-	23 - 30		16 - 29		20 - 50
Seed (L/W) mm	-	1.49		1.85		1.15
Seed weight (range) gm	-	10 (8 - 13)		10 (5 - 18)		18 (10 - 40)
Aril	Yes	Yes	Yes	Yes	Yes	Yes
Dispersal modes	Birds	NA	Birds	Birds	Birds	NB

Higher seed size ratio (length(L)/width(W)) was recorded in *M. malabarica* ( $1.85 \pm 0.03$  mm), followed by *M. dactyloides* ( $1.49 \pm 0.03$  mm), and the least for *M. beddomei* ( $1.15 \pm 0.02$  mm), whose seeds are spherical compared to the other two species. These differences among the species showed significance (KW :  $\chi^2 = 107.80$ ,  $df = 2$ ,  $P = 0.0001$ , Fig.2).

The width of the seed was also higher in *M. beddomei* ( $29.29 \pm 0.45$  mm), followed by *M. dactyloides* ( $24.84 \pm 0.56$ ) and *M. malabarica* ( $21.01 \pm 0.19$ ). In general *M. beddomei* was heavier and more spherical than the other two species. These differences in the species were significant ( $\chi^2 = 61.07$ ,  $df = 2$ ,  $P = 0.00001$ , Fig. 2).

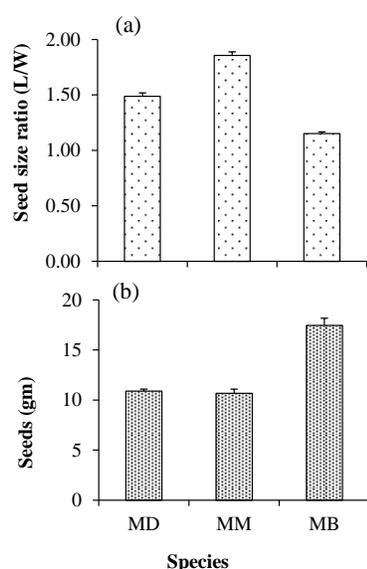


Fig. 2. Mean ( $\pm$  SE) seed size ratio(L/W) (a), and average seed weight in g (b) in three species of *Myristica dactyloides* (MD), *Myristica malabarica* (MM), and *Myristica beddomei* (MB) in the Western Ghats.

### Seed dispersal and seed predations

A total of three species of diurnal arboreal mammals were recorded, two primates – *Trachypithecus johnii* (Nilgiri langur) and *Macaca silenus* (Lion-Tailed Macaque) – and one tree squirrel, the *Ratufa indica* (Indian Giant squirrel). The Lion-tailed macaque and Indian giant squirrel removed the fruits, ate the aril and discarded the seeds (100%), while the Nilgiri langur was a major pre-dispersal seed predator, destroying 97% (33/34) of the seeds and young fruits that it consumed (Table 2). The macaque occasionally removed the fruit and moved away from the tree, but the giant squirrel usually ate the aril within the tree; thus, the possibility of seed dispersal away from the tree exists for the macaque but not for the squirrel. During the 101 hours of observations, a total of 102 seeds were removed by the frugivores and 32 % (33/102) of these seeds were preyed upon by the langur.

Table 2. Pre dispersal seed predation of *M. beddomei* (Total 101 hrs of observations).

Species	Fruits handled	Parts eaten	No. seed eaten (%)
<i>Trachypithecus johnii</i> (langur)	34	Seed+aril	33 (97)
<i>Macaca silenus</i> (macaque)	15	aril	0 (0)
<i>Ratufa indica</i> (squirrel)	53	aril	0 (0)

During the post-dispersal seed predation and dispersal experiment, we photographed 227 individual animals over 253 camera trap days. We identified a total of six vertebrate species, four of which were seed predators. *Platacanthomys lasiurus* (Malabar spiny dormouse) was the most common visitor, followed by *Rattus rattus wroughtoni* (White-bellied wood rat) and arboreal Nilgiri langur and *Funambulus sublineatus* (dusky striped squirrel) (Table 3). The latter two were diurnal visitors. In our observations of *P. lasiurus* at night, seeds were removed from the fallen fruit and taken to a branch (Fig.3c) and eaten after often discarding the aril. The tree hollows of the *P. lasiurus* had only fragments of the seed and all our tagged seeds were eaten. Species-level seed predation rates could be close to 100% for *P. lasiuru* and *T. johnii*. In the case of the wood rat and the squirrel, removal was low and we are not sure how many of the seeds are eaten or hoarded, as *Funambulus* is known to hoard seeds on ground.

Table 3. Post-dispersal seed predator capture rate/hrs (Total = 280\* trap days) of *M. beddomei*.

Species names	Total individuals	Capture/hrs *	% of seed predation.
<i>Platacanthomys lasiurus</i>	221	0.0329	
<i>Rattus rattus wroughtoni</i>	3	0.0004	100
<i>Funambulus sublineatus</i>	2	0.0003	
<i>Trachypithecus johnii</i>	1	0.0001	

\*Only 253 days were used for the analysis because of failure and spurious triggers

## Discussion

### *Why is there no bird dispersal?*

Though the genus *Myristica* is widely accepted as dispersed by birds [28,29], our observational study of *M. beddomei* at Kakachi failed to document a single bird eating the fruits or seeds of this species. Several earlier years of observation on various different trees in the site from 1991 onwards also did not show any bird activity on the tree (T. Ganesh, unpublished data). This is not because the birds known to disperse other *Myristica* species are absent, since the study site lies within the range of *Ocyrceros griseus* (Malabar Grey Hornbill), *Buceros bicornis* (Great hornbill) and *Ducula badia* (Mountain Imperial Pigeon) [30]. However, these birds, especially the hornbills, are rare and the pigeon is seasonal, although it does occur during *M. beddomei* fruiting season.

The lack of any dehiscence of fruits on the tree may preclude any bird frugivory at all in *M. beddomei*. The fruits do not dehisce on the tree but do so after falling on the ground (Fig. 3b). In addition the seeds ratio was lowest while seed diameter and weight was highest in *M. beddomei* (Table 1). This indicates a spherical and heavy seed. One of the major determinants of fruit choice is the width of fruit or seed [31, 32]. Except for hornbills, such large diameter seeds exceed the weight of bird-dispersed *Myristica* seeds that large birds like *Ducula* can handle [33], whereas hornbills are known to take the large-seeded fruits of *Myristica elliptica* and *M.iners* in southern Thailand [34]. But as mentioned earlier, hornbills are uncommon and were not seen during eight years of observations at our site.

Species that are known to be seed predators of other tree species, such as the *Ratufa indica* and the *Macaca silenus*, turned out to be seed dispersers of *Myristica beddomei* (Table 2). However, the question remains why this species has evolved some characteristics that appear to facilitate bird dispersal? Has the site lost avian frugivores? There appears to have been no extinction at the site in the recent past that would have deprived the seed dispersal services for the species. Elsewhere in the Western and Eastern Ghats also there seems to be no major loss of large avian frugivores where *M. beddomei* is found. The other characteristics of *M. beddomei*, such as the non-dehiscent nature of the fruit on the tree and large spherical seed, however, point toward a non-avian dispersal strategy (we did not see bats coming to the fruit, which is not surprising as the fruits have no adaptation to attract bats, such as smell or fibrous fruits [35]). Whether this dispersal mechanism has evolved more recently due to a depauperate avian frugivore fauna in the Western Ghats mediated by conspecific competition is unknown and is an area of potential research.

### *Unique function of aril*

The aril is considered a reward for avian frugivores [36,37,8]. However, species that are known to be seed predators such as *Ratufa indica* and *Macaca silenus* turned out to be seed dispersers of *M. beddomei* by consuming the aril and discarding the seed (Table 2). Earlier studies from other parts of Western Ghats also recorded the macaque foraging on *M. beddomei* fruits [20,38], but it was not clear which part of the fruit was being eaten and what was discarded. Indian giant squirrels are known to hoard seeds in their nest elsewhere in the Western Ghats [39], but we did not see any hoarding of *M. beddomei* seeds at our study site. We have no information about the predation of the other two species of *Myristica*, and anecdotal observations exist only of dispersal by birds.

### Seed escape

Once the seeds escape, either being discarded by the macaque or Giant squirrels or dropped accidentally by the Nilgiri langur, dormouse or others, the seeds get buried under the leaf litter of the forest. There, several invertebrate seed predators, especially weevils and members of family Scarabaeidae, prey upon the seeds. Once the seeds germinate, the radicles are eaten by the larvae of earwigs, and fungus further reduces the chances of successful establishment of the seeds (Chetana, unpublished data). In spite of lack of primary dispersers (birds), high post-dispersal mortality, and attack by invertebrates and fungal pathogens, the species is doing well, as indicated in tree sample plots established in the site. The adult density of *M. beddomei* was 27 trees/ha, sapling density (1-10 cm dbh) 73/ha [22], and seedling density 2,634/ha (R. Ganesan, unpublished data).

Frugivores that function as both predators and dispersers are considered to switch function depending on food abundance [36,40]. In the case of *M. beddomei*, certain individuals fruit asynchronously with the remainder of the population and suffer 100% predation by langurs, which suggests the possibility of predator satiation in peak fruiting (unpublished data). However, during peak fruiting of *Myristica* (May-June), the forest is devoid of large seeds and fruit, and this is actually a period of community-level fruit shortage [21], yet the “seed predators” did not behave as seed predators, instead feeding on the aril of *M. beddomei*. These animals also fed on substantial amounts of fruits; for instance, the giant squirrel was observed to consume 16 fruits out of 300-350 in the tree on a single visit, while the macaque also consumed quite a few fruits but kept moving (T. Ganesh personal observation). Feeding on arils and not on seeds may have some relationship with the nutrient requirements of the squirrel and macaque. Both species are omnivores, with nutrient demands very different from the leaf monkey, which is an folivore and seed predator [41,19]. The site is known for high levels of seed predation in many large-seeded species [22,41], and therefore one would expect most fruits to be eaten before the fruits dehisce and attract bird dispersers. We observed this in an adjacent fragmented forest devoid of seed predators, where large numbers of fruits on trees were left without dehiscing and many fell to the ground.

Such natural history observations are essential for each species before detailed ecological studies and conservation issues are addressed. *M. beddomei*, as seen from our observations, is very different from what has been assumed for the *Myristica* genus. The complete lack of bird dispersal in *M. beddomei* is probably unique to Myristicaceae, as far as we know from the published literature. The evolutionary reasons for this are not obvious, which only reinforces the need to understand the ecology of the species. We also call for detailed natural history observations of other *Myristica* in the Western Ghats to obtain a better understanding of the fruit-frugivore interactions in the genus.



a. (Photo by R. Ganesan).



b. (Photo by R. Ganesan).



c. (Photo by H.C.Chetana)

**Fig.3. *Myristica beddomei* undeheised fruits of on a. tree, b. dehisced fruits on ground and c. Malabar spiny dormouse the major seed predator of *Myristica beddomei*.**

## Implication for conservation

The mid-elevation forests of the Western Ghats where *M. beddomei* occurs are heavily fragmented and degraded, but the site in KMTR is unique because large stretches of evergreen forest have not seen any major changes in the recent past. There are also no records of any major hunting or poaching in the region. Few tree species have been extracted for timber and paper, although fruits of *M. beddomei* have been removed (prior to 40 years ago) [42]. *M. beddomei* also occurs along the Western Ghats in fragmented and degraded forests where densities of seed predators/dispersers are likely to be low and seed dispersal by macaques, which are severely affected by fragmentation [43], may be an extremely rare event. In such cases there is a chance for alternate dispersers to compensate for the service, but in the case of *M. beddomei* it's unlikely because there are no alternate dispersers. Moreover, when species like the giant squirrels, which are normally seed predators, discard the seed intact, the seeds are generally dropped under the tree, which further limits dispersal [44]. The loss of dispersers in such dispersal-limited species therefore could have larger consequences on species recruitment than in species where there is some compensation. This further necessitates conservation action in the Western Ghats, particularly addressing fragment connectivity, to prevent genetic bottlenecks in *M. beddomei*.

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## Reference

- [1] Bartholomew, G. A. 1986. The role of natural history in contemporary biology. *BioScience* 36:324-329.
- [2] Cotterill, F. P. D. 1995. Systematics, biological knowledge and environmental conservation. *Biodiversity Conservation* 4: 183-205.
- [3] Beehler, B. M. 2010. The forgotten science: a role for natural history in the twenty-first century?. *Journal of Field Ornithology* 81:1-4.
- [4] Ganesan, R. 2003. Identification, distribution and conservation of *Phyllanthus indofischeri*, another source of Indian gooseberry. *Current Science* 84: 1515-1518.
- [5] Avise, J. C. 1994. Molecular markers: natural history and evolution. Springer.
- [6] de Wilde Wjjo. 1991. The genera of Myristicaceae as distinguished by their inflorescences, and the description of a new genus, *Bicuiba*. *Beiträge zur Biologie der Pflanzen* 66: 95–125.
- [7] de Wilde Wjjo. 1994. Taxonomic review of *Myristica* (Myristicaceae) in the Pacific. *Blumea* 38: 349–40.
- [8] Howe, H. F. and Kerckhove, G. A. V. 1981. Removal of Wild Nutmeg (*Virola Surinamensis*) Crops by Birds. *Ecology* 62:1093-1106.
- [9] Knight, R. S. and Siegfried, W. R. 1983. Inter-relationships between types, size and colour of fruits and dispersal in southern African trees. *Oecologia* 56:405-412.
- [10] Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L. H., Erard, C., Hecketsweiler, P., Mounqazi, A., Roussillon, C. and Thiollay, J.M. 1985. Fruit characters as a basis of fruit choice and seed dispersal by a tropical vertebrate community. *Oecologia*, 65: 324-337.

- [11] Jayasekara, P., Takatsuki, S., Weerasinghe, U. R. and Wijesundara, S. 2003. Arboreal fruit visitors in a tropical forest in Sri Lanka. *Mammal Study* 28:161-165.
- [12] Russo, S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136:80-87.
- [13] Gamble, J. S. and Fischer, C. E. C. 1915–1935. Flora of the Presidency of Madras. Parts I to XI, Secretary of State for India, London.
- [14] Corlett, R. T. 2002. Frugivory and seed dispersal in degraded tropical East Asian landscapes. In: *Seed dispersal and frugivory: Ecology, evolution and conservation*. Levey, D. J., Silva, W. R., and Galetti, M. (Eds.), pp. 451-465. CABI Publishing, Wallingford, UK.
- [15] Howe, H. F. 1981. Dispersal of a Neotropical Nutmeg (*Virola sebifera*) by Birds. *The Auk* 98:88-98.
- [16] Russo, S. E. 2005. Linking seed fate to natural dispersal patterns: Factors affecting predation and scatter-hoarding of *Virola calophylla* Seeds in Peru. *Journal of Tropical Ecology* 21, 243-253.
- [17] Holbrook, K. M., Loiselle, B. A., 2009. Dispersal in a Neotropical tree, *Virola flexuosa* (Myristicaceae): Does hunting of large vertebrates limit seed removal?. *Ecology* 90, 1449-1455.
- [18] Kannan, R. and James, D. A. 1999. Fruiting phenology and the conservation of the great pied hornbill (*Buceros bicornis*) in the Western Ghats of southern India. *Biotropica* 31:167-177.
- [19] Oates, J. F., Waterman, P. G. and Choo, G. M. 1980. Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45:45-56.
- [20] Singh, M. R., Singh, M. E., Kumar, M. A., Kumara, H. N., Sharma, A. K. and Sushma, H. S. 2000. Niche separation in sympatric Lion tailed macaque (*Macaca silenus*) and Nilgiri langur (*Presbytis johnii*) in an Indian tropical rain forest. *Primate Report* 83-95. ( ).
- [21] Ganesh, T. and Davidar, P. 1999. Fruit biomass and relative abundance of frugivores in a rain forest of southern Western Ghats, India. *Journal of Tropical Ecology* 15:399-413.
- [22] Ganesh, T., Ganesan, R., Devy, M. S., Davidar, P. and Bawa, K. S. 1996. Assessment of plant biodiversity at a mid-elevation evergreen forest of Kalakad- Mundanthurai Tiger Reserve, Western Ghats, India. *Current Science* 71:379-392.
- [23] Murthy, I. K., Bhat, P. R., Ravindranath, N. H. and Sukumar, R. 2005. Financial valuation of non-timber forest product flows in Uttara Kannada district, Western Ghats, Karnataka. *Current Science* 88:1573-1579.
- [24] Asher, S. K., Shinde, V. S., Ghogare, R. B., Thube, A. R., Date, Y. P., Paimode, S. R. and Kale, A. R. 2007. Study of important Medicinal plants from parner Tahasil, dist. Ahmednagra, India. In: *Environmental protection*. Aravind K and Nehar, S. ( Eds.), pp 71-77. Daya publishing house, India.
- [25] Prasad, S., Pittet, A. and Sukumar, R. 2010. Who really ate the fruit? A novel approach to camera trapping for quantifying frugivory by ruminants. *Ecological Research* 25:225-231.
- [26] Menon, V. 2003. A Field Guide to Indian Mammals, Dorling Kindersley, New Delhi.
- [27] Ramesh, B. R., Ayyappan, N., Grard, P., Prosperi, J., Aravajy, S., Pascal, J. P., 2010. BIOTIK : Biodiversity Informatics and co-Operation in Taxonomy for Interactive Shared Knowledge Base. Western Ghats v.1.0.A multimedia identification system of evergreen tree species of the Western Ghats, India. Collection Ecologie no. 46, French Institute of Pondicherry, Pondicherry. [DVD] [Online Application].
- [28] Kannan, R. and James, D. A. 1997. Hornbills seem to time their breeding to the peak availability of fruits (i.e., the dry season; for a description of their breeding biology. *Journal Bombay natural. History Society* 94: 451-465.
- [29] Kitamura, S. 2011. Frugivory and seed dispersal by hornbills (*Bucerotidae*) in tropical forests. *Acta Oecologica* 37: 531-541.
- [30] Raman, T. R.S. and Sukumar, R. 2002. Responses of tropical rainforest birds to abandoned plantations, edges and logged forest in the Western Ghats, India. *Animal Conservation* 5: 201-216.

- [31] Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- [32] Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129: 471-485.
- [33] Meehan, H. J., McConkey, K. R. and Drake, D. R. 2005. Early fate of *Myristica hypargyrea* seeds dispersed by *Ducula pacifica* in Tonga, Western Polynesia. *Austral Ecology* 30:374-382.
- [34] Kitamura, S., Thong-Aree, S., Madsri, S. and Poonswad, P. 2011. Characteristics of hornbill-dispersed fruits in lowland dipterocarp forests of southern Thailand. *The Raffles Bulletin of Zoology* 24: 137–147.
- [35] van der Pijl, L. 1982. Principles of dispersal in higher plants. 3<sup>rd</sup>. Springer, Berlin, Germany.
- [36] Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465-492.
- [37] Endress, P. K. 1973. Arils and aril-like structures in woody ranales. *New Phytology* 72:1159-1171.
- [38] Sushma, H. S., and M. Singh. 2006. Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India. *Behavioral Ecology* 17: 479-490.
- [39] Somanathan, H., Mali, S. and Borges, R. M. 2007. Arboreal larder-hoarding in the tropical Indian giant squirrel *Ratufa indica*. *Ecoscience* 14:165-169.
- [40] Forget, P.-M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12:751-761.
- [41] Ganesh, T. and Davidar, P. 2005. Fruiting phenology and pre-dispersal seed predation in a rainforest in southern Western Ghats, India. In: *Tropical fruits and frugivores: The search for strong interactors*. Dew, J.L. and Boubli, J.P. (Eds.), pp. 93-118. Springer, Dordrecht.
- [42] Ganesan, R. and Davidar, P. 2003. Effect of logging on the structure and regeneration of important fruit bearing trees in a wet evergreen forest, southern Western Ghats, India. *Journal of Tropical Forest Science* 15: 6-11.
- [43] Kumara, N. H. and Sinha, A. 2009. Decline of the endangered lion-tailed macaque *Macaca silenus* in the Western Ghats, India. *Oryx* 43: 292-298.
- [44] Nathan, R. A. N. and Casagrandi, R. 2004. A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *Journal of Ecology* 92: 733-746.