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Review Article

Nutmeg-vertebrate interactions in the Asia-Pacific region: importance of frugivores for seed dispersal in Myristicaceae

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Abstract

In tropical forests, large frugivores are assumed to be important seed dispersers for many large-seeded trees such as the Myristicaceae, a widespread and common family. However, not all frugivores are effective seed dispersers, and understanding which frugivores are effective is vital for conservation biology. Here, we summarize the available data on fruit characteristics and frugivores for a large number of Myristicaceae species in the Asia-Pacific region and suggest future directions for evaluating the effects of disperser loss for these trees. Studies of fruit characteristics of Myristicaceae were highly biased toward morphological information, and few studies examined reproductive phenology or fruit chemistry. We identified 338 instances of nutmeg-frugivore interactions that included 129 species of Myristicaceae and 109 species of frugivores, including 40 bird, 68 mammal, and one reptile species. Large birds were major seed dispersers for this tree family. These bird species, such as hornbills and pigeons, consumed a variety of nutmeg species, remained briefly at fruiting trees, and dispersed intact seeds far from the parent trees in the forest. Although most seeds dispersed by birds subsequently suffered high seed predation by rodents, some germinated and established as seedlings, indicating the qualitative effectiveness of large birds as seed dispersers for Myristicaceae. Mammals were also major consumers of Myristicaceae. Gibbons, macaques, and civets potentially acted as long-distance dispersers for some nutmeg species. Orangutans, leaf monkeys, squirrels, and rodents consumed a variety of nutmeg species, but their roles as seed dispersers for Myristicaceae remain unclear. Studies of nutmeg-vertebrate interactions have typically focused on frugivory, whereas few studies have specifically quantified the effectiveness of frugivores as seed dispersers; thus, it remains difficult to evaluate the effect of frugivore loss on the populations of most nutmeg species in this region. Further studies of nutmeg-frugivore interactions are of great ecological importance, and the results of such studies will contribute to a general understanding of which evolutionary forces may have shaped current nutmeg-frugivore interactions in tropical forests worldwide.

Key words: *Endocomia*, *Gymnacranthera*, *Horsfieldia*, *Knema*, *Myristica*, seed predation

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Introduction

Seed dispersal plays a critical role in the maintenance and recovery of plant diversity [1, 2]. This is especially true for the dispersal of seeds in highly diverse tropical rain forests, which usually support a wide range of potential dispersers. Most tropical woody plants have fleshy fruits [3, 4], and most tropical vertebrates eat fruits [5, 6]. In general, fruit (or seed) size usually limits the number of frugivores that can disperse the seeds [7-9]. Small fruits and large, soft fruits with many small seeds are consumed by a wide spectrum of frugivores, whereas larger fruits with a single large seed are consumed by relatively few potential dispersers [10, 11]. The seed dispersal of large-seeded plant species is therefore primarily dependent on large-bodied frugivores that are susceptible to extinction as a result of deleterious direct and indirect anthropogenic activities [9, 11-13].

The tropical rain forest tree family Myristicaceae consists of 500 species in 20 genera with a pantropical distribution centered in Malesia [14, 15]. In ecological studies of tropical rain forest tree communities, the Myristicaceae, or nutmeg, frequently ranks among one of the most important tree families, based on species frequency as well as species diversity [16]. In lowland rain forests of Malaysia, 30-40 nutmeg species have been recorded at a given study site, e.g., Lambir Hills National Park, Sarawak [17] and Pasoh Forest Reserve, Peninsular Malaysia [18]. Based on tree inventory data from 28 lowland dipterocarp rain forest locations throughout Borneo, Myristicaceae was the sixth most abundant tree family, accounting for 4.3% of all trees, and *Knema* was the eighth most common tree genus, accounting for 2.2% of trees in lowland dipterocarp forests [19]. The Myristicaceae is therefore an ideal family for studying general patterns of tropical forest diversity, and additional data for the nutmeg family will contribute valuable information to the general understanding of tropical forests.

Myristicaceae has a relatively conserved fruit and seed morphology (Fig. 1); therefore, one might expect that similar suites of frugivores consume and disperse the seeds. In the Neotropics, numerous studies related to the seed dispersal of Myristicaceae have been conducted since the 1970s, and large frugivorous birds and primates have been documented as the primary seed dispersers for this family [20]. In the Asia-Pacific region where the six genera *Endocomia*, *Gymnacranthera*, *Horsfieldia*, *Knema*, *Myristica*, and *Paramyristica* are distributed (Fig. 2), the primary seed-dispersal agents of these fruits are large birds such as fruit pigeons, hornbills, and birds of paradise [21-23]; however, the available data on seed dispersal in Myristicaceae are still limited, especially in terms of the effectiveness of dispersers [24]. Several criteria have been used to determine the efficiency and effectiveness of vertebrate frugivores as dispersers [24]; these include the size and diversity of fruits ingested, high fruit consumption, short visitation times, long gut retention times with seeds undamaged after gut passage, fruits swallowed whole with few dropped below parent trees,

behavior and movements during and after feeding, and seed deposition at suitable sites for germination.

Fig. 1. Ripe fruits of Myristicaceae in Budo-Sungai Padi National Park, southern Thailand. a: *Knema globularia*, b: *Horsfieldia tomentosa*, c: *Myristica iners*.

Although human impacts on frugivores specifically affect trees with large seeds in this region [11, 25], information on nutmeg-vertebrate interactions remains limited. Making existing data accessible to a wider audience is the first step toward applying what is known about the effectiveness of nutmeg-eating frugivores as seed dispersers for Myristicaceae and filling in gaps in knowledge. Our objectives in this study were to summarize the available data for Myristicaceae in the Asia-Pacific region in terms of (i) fruit traits and (ii) each frugivore in terms of the quantity and quality of dispersal, as well as to provide future directions for studies evaluating the effects of disperser loss for this family of trees.

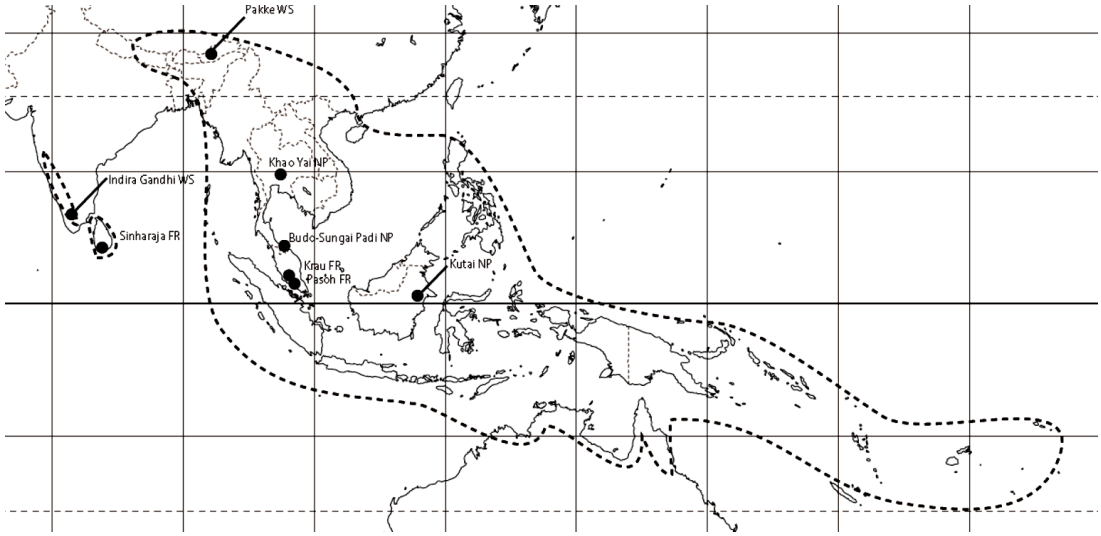

Fig. 2. Distribution of Myristicaceae in the Asia-Pacific region and the major study sites cited in this review. NP: National Park, WS: Wildlife Sanctuary.

Literature survey

We first searched for data on characteristics of nutmeg fruits using Flora Malesiana [15], which covers 335 nutmeg species distributed in Indonesia, Malaysia, Burnei Darussalam, Singapore, the Philippines, and Papua New Guinea. We supplemented this search with regional floras, including Flora of Thailand [26], Flora of China [27], Flora of the Darwin Region [28], Myristicaceae of Papua [29], and other relevant studies in India and Tonga, to cover the distribution limit of Myristicaceae in this region (Fig. 2). To obtain the mean fruit/seed sizes of each nutmeg species, we averaged the minimum and maximum sizes reported in these studies. In most cases, these values were measured from herbarium specimens; therefore, the sizes calculated from these studies were likely smaller than those for fresh fruits/seeds in the field.

We then compiled a database on nutmeg species known to be consumed and dispersed by frugivores from the Asia-Pacific region. On 20 May 2011, we searched the Web of Science to obtain publications including the keywords “nutmeg”, “Myristicaceae” and several frugivores that occur in this region, such as “hornbill,” “pigeon,” “civet,” “gibbon,” “leaf monkey,” “macaque,” and “rodent.” We also examined recent reviews on frugivory by elephants [30], hornbills [31], gibbons [32], bears [33], and orangutans [34]. We supplemented these searches with literature cited by relevant studies and searches of regional journals as well as books on primates [35, 36] and pigeons [37]. Whenever possible, we recorded body mass data for each frugivore species from various sources [36-43] and the individual sources obtained in the literature survey. Values for body mass were the average for males and females [44].

We attempted to survey all major references, but the compiled lists were not exhaustive. The literature varies in clarity and quality; we excluded general accounts that list diets without giving the original source of information found in field guides and newsletters, but we included data found in books, journals, conference proceedings, and theses. These combined approaches resulted in data from a total of 84 publications, including 13 from books/book sections, 62 from peer-reviewed journals, one from conference proceedings, and eight from theses. A high proportion of studies included data on frugivory by hornbills (23 publications), followed by leaf monkeys (22), gibbons (15), macaques (14), and pigeons (11). Several publications included frugivory data on different frugivore groups; thus, the total number of studies that focused on frugivory was over 84. Plant nomenclature was revised according to the International Plant Name Index.

Characteristics of fruits in Myristicaceae

Fruit and seed size

In total, 352 nutmeg species were compiled by literature survey, and data were obtained for fruit length and diameter (N = 322 spp.), seed length (134 spp.), and seed diameter (18 spp.). Fruit sizes of Myristicaceae strongly varied among genera and species. Mean fruit size (length × diameter) at the genus level occurred in the following order: *Gymnacranthera* (2.3 × 1.5 mm, 6 spp.), *Knema* (2.9 × 2.0 mm, 79 spp.), *Horsfieldia* (3.0 × 2.2 mm, 88 spp.), *Myristica* (4.5 × 2.9 mm, 142 spp.), *Paramyristica* (4.8 × 2.8 mm, 1 sp.), and *Endocomia* (5.2 × 2.5 mm, 4 spp.). Seed length of Myristicaceae also varied among genera and species (Fig. 3): *Endocomia* (2.4-4.5 mm, 4 spp.), *Horsfieldia* (0.9-5.5 mm, 4 spp.), *Knema* (2.1-2.5 mm, 4 spp.), *Paramyristica* (3.0 mm, 1 sp.), and *Myristica* (1.4-5.5 mm, 121 spp.).

The sizes of nutmeg fruits/seeds also varied among species within a study site. The mean diameters of flesh arillate seeds were 21 mm (14-29 mm, N = 24 spp.) in Kutai National Park, Borneo [45], and 20 mm (10-30 mm, N = 14 spp.) in Budo-Sungai Padi National Park, Thailand (S. Kitamura, unpublished data). In both study sites, the mean diameters of flesh arillate seeds of Myristicaceae

were significantly larger than those of non-Myristicaceae (Welch's t-test, t = 5.70, P < 0.001, nutmeg = 9 spp., non-nutmeg = 180 spp. in Kutai; t = 2.97, P < 0.009, nutmeg = 9 spp., non-nutmeg = 423 spp. in Budo-Sungai Padi). We did not find any study that focused on individual variation in fruit/seed sizes of Myristicaceae in this region.

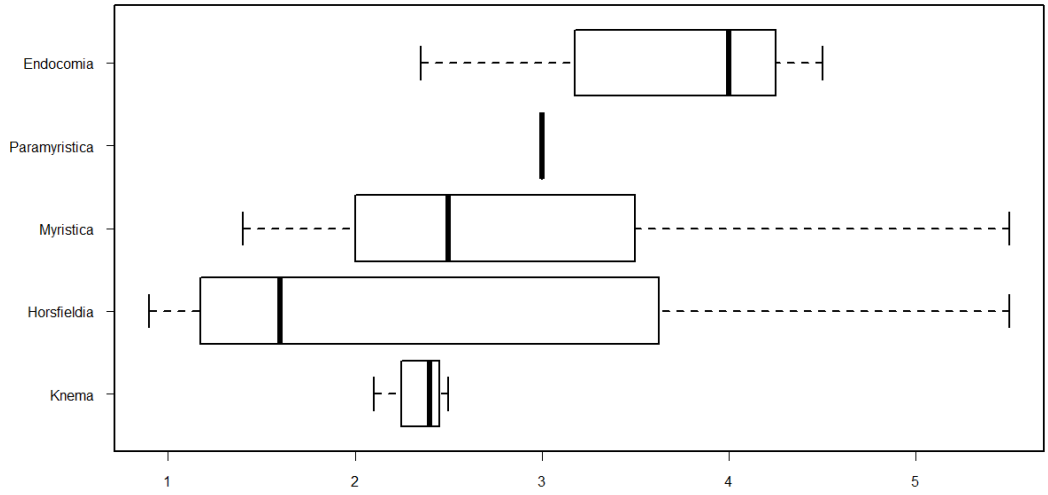

Fig. 3. Seed size variation among genera in Myristicaceae.

Phenology

At the species level, most nutmeg species fruited every year in India [46-49], Thailand [50-52], the Philippines [53], and Australia [54]. In Khao Yai National Park, Thailand, *Knema elegans* fruited at the intraspecies level in all 6 years but varied among individuals [50]. At the same site, a different nutmeg species, *Horsfieldia amygdalina* (formerly reported as *Horsfieldia glabra* in [10]), fruited every year from 1996 to 2003, except for 2000 [52]. Similarly, some nutmeg species exhibited annual fruiting patterns in lowland dipterocarp forests of Borneo, but others had supra-annual fruiting patterns [55, 56]. However, most studies on the reproductive phenology of Myristicaceae from Bornean forests did not collect large enough sample sizes to measure individual variation within a species; thus, determining differences among fruiting behaviors of Myristicaceae in this region is still difficult.

Aril color

In the literature survey, aril color was reported for 61 nutmeg species (*Endocomia*: 3 spp., *Gymnacranthera*: 3 spp., *Horsfieldia*: 19 spp. *Knema*: 19 spp., and *Myristica*: 18 spp.). Of these, red was the most common color of nutmeg arils (45 spp.), followed by orange (26 spp.), yellow (9 spp.), and pink (2 spp.). Similarly, within a study site, red arils were the most common in Myristicaceae (N = 7 spp.), followed by orange (3 spp.) in Budo-Sungai Padi National Park, southern Thailand [57].

Fruit chemistry

Little research has been conducted on fruit chemistry of Myristicaceae in this region, but available data suggest that the seeds/arils of nutmegs contain high lipid content both in the seeds [58]: *Myristica elliptica* (55.0%), *Knema hookeriana* (28.4%), and *Myristica cinnamomea* (8.5%), and in the arils [21, 58, 59]: *M. elliptica* (15.8%), *Myristica* sp. (57%), *H. amygdalina* (41.6%), and *K. elegans* (18.2%). These high lipid contents were preferred by porcupines in one Malaysian forest [58].

Diversity of nutmeg species eaten by frugivores

Regarding the taxonomic representation of nutmeg species eaten by different frugivore groups, the numbers vary widely (Table 1). We identified 338 instances of nutmeg-frugivore interactions that included 129 species of Myristicaceae, including *Endocomia* (1 sp.), *Gymnacranthera* (5 spp.), *Horsfieldia* (15 spp.), *Knema* (31 spp.), *Myristica* (43 spp.), and unidentified Myristicaceae genera (33 spp.), as well as 109 species of frugivores, including 40 bird, 68 mammal, and 1 reptile species (Fig. 4, Appendix 1).

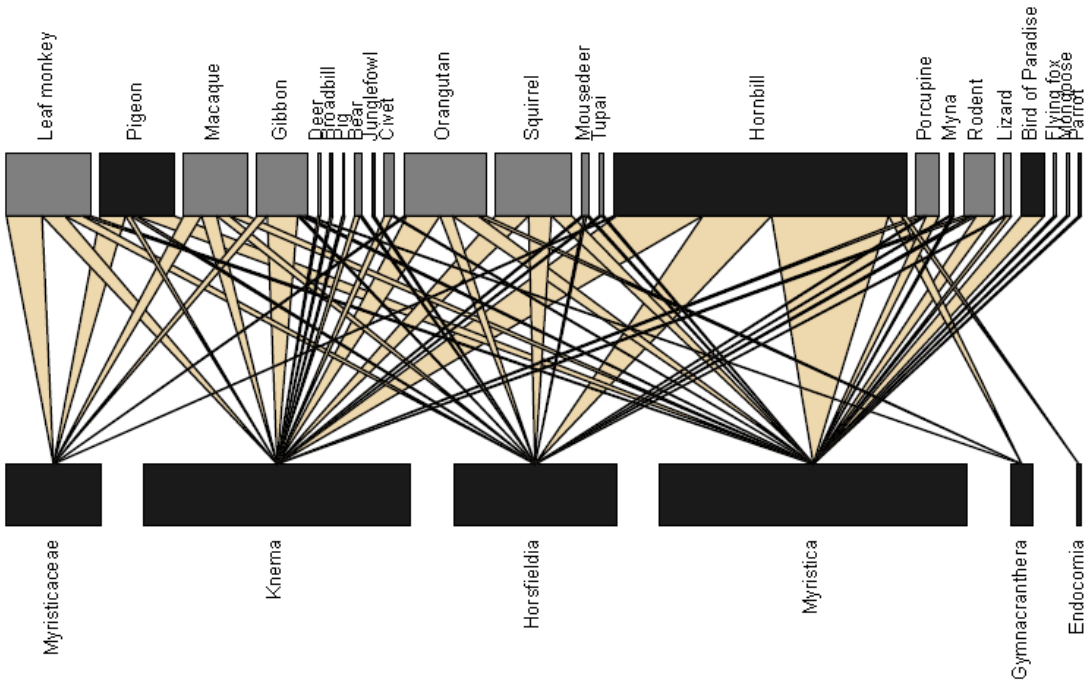

Fig. 4. The interactions between genera of Myristicaceae and frugivores in the Asia-Pacific region. Five genera and 'unknown' Myristicaceae sp. are eaten by 23 different frugivore groups (mammals and reptiles in grey, and birds in black). Width of triangles indicates the number of documented interactions.

In terms of the number of nutmeg species eaten by each frugivore group, we identified hornbills and pigeons as major consumers of Myristicaceae among birds, and primates and squirrels among mammals (Table 1). More complete diet information is available for more thoroughly studied frugivores. Furthermore, frugivores from less diverse ecosystems, such as dry forests of India, show lower nutmeg diversity in their diet. Only 27% of frugivores consumed three or more nutmeg species as part of their diets (Fig. 5a). The maximum number of nutmeg species eaten by one type of frugivore was achieved by the orangutan *Pongo pygmaeus* (27 species), followed by bushy-crested hornbills *Anorrhinus galeritus* (20), wreathed hornbills *Rhyticeros undulatus* (19), and great hornbills *Buceros bicornis* (15). We found no relationship between mean body mass and the number of nutmeg species eaten by any frugivore group (Spearman's rank correlation, $P > 0.05$).

The maximum number of frugivores that consumed specific nutmeg species was recorded for *K. elegans* (12 spp.), followed by *Horsfieldia irya* (11) and *M. elliptica* (11). Most nutmeg species (68.2%) were eaten by only one or two frugivore species (Fig. 5b). As expected, frugivores in forests with high nutmeg diversity or inhabiting long-term study sites consumed the largest numbers of nutmeg species (e.g., Borneo and southern Thailand; Fig. 2). However, the number of frugivore species recorded for a given nutmeg species was likely underestimated, as most data on nutmeg-frugivore interactions reported from this region are based on studies of frugivores and not on observations of fruiting nutmeg trees.

Table 1. Summary of nutmeg-frugivore interactions in Asia-Pacific region. Frugivore groups are listed in decreasing order of the number of nutmeg species eaten by each group.

	Body	No. of	Genus						No. of nutmeg
Frugivore group	weight (kg)	species	*Endocomia*	*Gymnacranthera*	*Horsfieldia*	*Knema*	*Myristica*	Unknown	species
Hornbill (Bucerotidae)	0.24-2.9	19	X	X	X	X	X	X	50
Pigeon (Columbidae)	0.07-0.6	11			X	X	X	X	21
Bird of Paradise (Paradisaeidae)	0.09-0.22	6					X		3
Myna (Sturnidae)	0.16	1			X		X		2
Broadbill (Eurylaimidae)	0.06	1				X			1
Junglefowl (Phasianidae)	0.58	1			X				1
Parrot (Psittacidae)	0.23	1					X		1
Bird Total		40	X	X	X	X	X	X	67
Leaf monkey (Cercopithecidae)	5.8-15.6	21			X	X	X	X	31
Orangutan (Hominidae)	57.5	1		X	X	X	X	X	24
Macaque (Cercopithecidae)	4.5-15	11			X	X	X	X	23
Squirrel (Sciuridae)	0.1-2	6			X	X	X		23
Gibbon (Hylobatidae)	5.7-12.4	9		X	X	X	X	X	15
Rodent (Muridae)	0.17-0.8	5			X	X	X		8
Porcupine (Hystricidae)	2.5-8	3			X	X	X		7
Bear (Ursidae)	46	1			X	X			3
Civet (Viverridae)	3-6.3	4				X	X		3
Mousedeer (Tragulidae)	2.3-7.5	2			X	X	X		3
Tupai (Tupaiidae)	0.17	1				X	X		2
Flying fox (Pteropodidae)	0.6	1					X		1
Deer (Cervidae)	24	1				X			1
Mongoose (Herpestidae)	2.7	1					X		1
Wild pig (Suidae)	70	1				X			1
Mammal Total		68		X	X	X	X	X	85
Lizard (Varanidae)	7	1			X		X		3
Reptile Total		1			X		X		3
Frugivore Total		109							129

Fruit tree visitation, seed retention time, and dispersal distance

Several studies observed fruit consumed from large-seeded trees in this region [13, 60, 61], but most did not include Myristicaceae; thus, the data available on the visit frequency of frugivores to nutmeg trees are limited. One of the best-observed nutmeg species was *Myristica hypargyraea* in Tonga [62]. These authors found that the Pacific pigeon *Ducula pacifica* (118 visits) visited most frequently, followed by the red shining musk parrot *Prosopeia tabuensis* (17 visits) and the insular flying fox *Pteropus tonganus* (5 visits). Most seeds of *M. hypargyraea* were estimated to be dispersed by *D. pacifica*; ca. 80% of those ingested were expelled directly beneath conspecific fruiting crowns, 20% were dispersed locally, and <0.3% were dispersed more than 300 m into a different forest type [62].

In a Bornean forest with diverse nutmeg species (12 species over 205 observation hours), Leighton found that the mean visitation rate of hornbills ranged from 0.02 to 0.72 visits per hour per crop, which was one of the most frequently visited fruiting trees by hornbills [45]. However, the author presented no data on visit lengths of hornbills or the number of arillate seeds eaten by hornbills per visit at nutmeg trees [45]; thus, we could not quantitatively estimate the effectiveness of hornbills from these data. Hornbills usually remained in fruiting trees for a median of 20 min [45, 47, 60, 61, 63], and the median seed retention time of *H. amygdalina* by captive hornbills (*B. bicornis* and *R. undulatus*) was 40-50 min; 22% of the seeds were retained longer than 1 h (S. Kitamura, unpublished data). As hourly movements of hornbills sometimes exceed 6 km in the wild (S. Kitamura, unpublished data), they are able to transport nutmeg seeds far from parent trees.

Other frugivores such as gibbons, macaques, and civets are also likely to disperse seeds 100 m beyond parent plants [64-68]; thus, they potentially act as long-distance dispersers for some nutmeg species. Squirrels sometimes carry a whole fruit in their mouth away from the Myristicaceae tree for consumption in the canopy of neighboring trees or for later consumption (M. Yasuda, personal communication), but they appear to be poor distance-dispersers, with seeds deposited no more than 10 m from the fruiting crown [69].

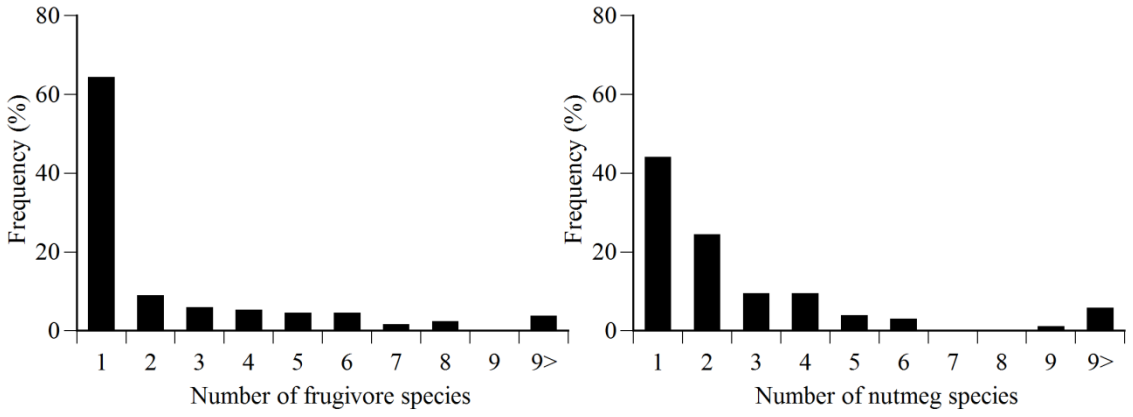

Fig. 5a Left. Frequency histogram of cumulative number of frugivores per nutmeg species in the Asia-Pacific region. Fig. 5b Right. Frequency histogram of cumulative number of nutmeg species per frugivore species in the Asia-Pacific region.

Extent of damage to seeds during consumption

We found that hornbills and pigeons as well as gibbons, macaques, and civets were reported to disperse intact seeds of Myristicaceae [10, 46, 70-72]. Hornbills and pigeons (*Ducula* spp. and *Ptilinopus* spp.) mostly swallowed arillate seeds of Myristicaceae and regurgitated the seeds intact [10, 21, 62, 70]. Of the mammals, gibbons (*Hylobates lar*) and civets (*Viverra zibetha*) in Thailand swallow both the seed and aril of *K. elegans* and then disperse the seeds through defecation [71]. Long-tailed macaques (*Macaca fascicularis*) in Singapore spit out seeds of *Knema latericia* and *Knema laurina* [72]. Other primates, such as orangutans and leaf monkeys, squirrels, and rodents consume many Myristicaceae fruits (Table 1), but the literature often does not make a clear distinction between consumption of the pulp and seeds; thus, their roles as seed dispersers for Myristicaceae remain unclear.

Despite the long list of frugivory records (Appendix 1), most studies did not investigate the potential viability of the nutmeg seeds defecated, regurgitated, spat, or dropped away from the parent trees by frugivores. The available data do not suggest any negative effects on the germination success of nutmeg seeds regurgitated by hornbills. The germination success of *Horsfieldia kingii* was similar between hornbill-regurgitated seeds (41%) and fallen seeds (33%) in India [47]. Over 90% germination success was recorded for hornbill-regurgitated nutmeg seeds, including *Horsfieldia tomentosa*, *Knema globularia*, and *Myristica iners*, but less than 10% success for *H. amygdalina* in Thailand (S. Kitamura, unpublished data). Under laboratory conditions, the germination success of nutmeg seeds was relatively high [73]: *Gymnacranthera eugeniifolia* (88%, N = 100), *Knema curtisii* (90%, N = 20), *K. laurina* (98%, N = 150), *Myristica crassa* (44%, N = 16), *Myristica malaccensis* (40%, N = 5), and *Myristica malaccensis* (73%, N = 55), except for *Knema scortechinii* (8%, N = 50). Removal of the aril before planting was advantageous for *K. laurina* (98% germination success without arils vs. 20% with arils), but not for *Knema furfuracae* (100% germination success, N = 50 seeds with arils); thus, the effects of aril removal by frugivores before seed deposition may vary among nutmeg species.

Fate of dispersed seeds

Frugivore activity is difficult to follow in the field, especially for canopy-dwelling animals. One method is to compare the survival and germination of experimentally placed seeds to mimic seed dispersal by frugivores, and another is to follow the fates of seeds dispersed by frugivores in a particular area, such as nest trees of hornbills. In a seed-removal experiment for *M. hypargyraea* on the ground in Tonga [62], the authors found that most seeds had been removed or killed by rats. Most *Myristica* seeds predicted to establish (6.5%) were dispersed by *D. pacifica*, which is more than twice the percentage of undispersed seeds that established (2.9%) around fruiting trees [62].

Hornbill-dispersed seeds around hornbill nests and roost trees were not particularly suitable for seed establishment and recruitment in general [47, 74-76]. In India, for example, hornbill-dispersed seeds of *H. kingii* around nest trees mostly died due to high seed predation by porcupines [77]. At the same site, *H. kingii* did not recruit near parent trees and showed increased seed mortality by seed-eating mammals with increasing seed density [78]. Hornbill-dispersed seeds of *H. amygdalina* were often consumed before germination at hornbill nest and roost trees in Thailand [74, 75], but some seedlings survived over 32 months (S. Kitamura, unpublished data). In Sulawesi, seedlings of *Horsfieldia brachiata* were one of the five most common seedling species around the nesting trees of the red-knobbed hornbill *Rhyticeros cassidix* [76]. Most nutmeg seeds with high seed density are likely to be eaten and consequently die before germination, but some seeds scattered by birds are likely to germinate and survive at their deposited sites, indicating their qualitative effectiveness as seed dispersers for Myristicaceae.

Summary and future directions

Many studies have reported nutmeg consumption by various kinds of frugivores in the Asia-Pacific region. Currently available data suggest that large, canopy-dwelling birds, including hornbills and pigeons, may function as major seed-dispersal agents for the Myristicaceae. Of these, the potential of hornbills as seed dispersers for large-seeded plants is well documented [31, 79]. Moreover, these birds originated in the mid-Eocene and might have assisted in the rapid colonization of large-seeded plants, including the Myristicaceae [80]. Some nutmeg seeds dispersed by hornbills germinated and survived as seedlings for several years. Based on the results summarized here, hornbills provide excellent seed-dispersal services to the Myristicaceae in this region.

Hornbills are extensively hunted by humans for their beaks, feathers, casque, and meat, and the densities and species richness of many hornbill species have now been reduced at many sites in this region [79, 81-85]. We expect that in areas in which the diversity of frugivores, particularly large avian frugivores like hornbills, has been reduced, macaques, civets, and squirrels may be the only remaining seed-dispersal agents for nutmeg trees. Indeed, some large-seeded *Myristica* trees are showing evidence of the lack of dispersal agents in Singapore [12, 86] and Lambir Hills National Park, Sarawak, Malaysia (K. Kimura, personal communication); hornbills have vanished or are nearly extinct at these sites, and other large frugivores, such as imperial pigeons (*Ducula* spp.), are very rare. In a Malaysian forest in Pasoh where at least six species of hornbills were originally distributed [87], only pig-tailed macaques (*Macaca nemestrina*) and several species of *Callosciurus* squirrels visited nutmeg trees in the canopy (M. Yasuda, personal communication). Can nutmeg trees still be dispersed by these remaining frugivores? We could not find detailed data on fruit removal for most nutmeg species in this region; thus, this question is still difficult to answer. Recent studies of other tree species in this region have revealed that frugivores that service the same plant may differ greatly in seed-dispersal effectiveness [88, 89]; therefore, similar results are expected in Myristicaceae.

Current studies on nutmeg-frugivore interactions typically focus on frugivory by certain groups of frugivores, whereas few studies quantify their effectiveness as seed dispersers for Myristicaceae. Thus, evaluating the effect of dispersal loss for this tree family in this region remains challenging. We suggest the following recommendations for future research on seed dispersal of these trees in this region. First, more information must be collected on the natural history of the dispersal ecology of the Myristicaceae. The most obvious natural history gap concerns fruit removal by each frugivore group at fruiting trees. Without such data, the effectiveness of nutmeg consumers as seed dispersers cannot be quantified. Second, many frugivores consume fallen fruits on the ground [6, 58, 90], and some potentially act as secondary dispersers for large-seeded plants [61, 91-93]. Although available data suggest that nutmeg seeds are often eaten by rodents on the ground [62, 77, 78], understanding the roles of these secondary dispersers that are tolerant of anthropogenic changes is becoming increasingly important. Third, comparative studies are needed of the dispersal ecology of sympatric nutmeg species with different seed sizes at a range of sites representing major forest types and a variety of human impacts. Nutmeg species with small seeds are expected to be dispersed by a broad assemblage of frugivores, and declines in seed removal by large frugivores might be compensated for by increases in seed removal by small frugivores. In addition, genetic tools can also be used to determine the origin/sources (maternal trees) for established recruitment and trees to determine the seed shadows generated by past and current frugivores.

Nutmeg trees are relatively abundant and well described in the literature, and most species are easily recognized in the field [16]. As elucidated by this review, further studies of nutmeg-frugivore interactions will be of great ecological importance in this region, and the results of future studies will contribute to a general understanding of which evolutionary forces might have shaped current nutmeg-frugivore interactions in tropical forests worldwide.

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Appendix 1. Nutmeg-frugivore interactions in the Asia-Pacific region.

Plant species	Frugivore species	Frugivore group	Weight (kg)	Study site	Source
Endocomia macrocoma	*Buceros bicornis*	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	Rhyticeros undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
Gymnacranthera farquhariana	*R. undulatus*	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
	Pongo pygmaeus	Orangutan	57.5	Tuanan, Indonesia	[94]
	Hylobates klossii	Gibbon	5.8	Siberut, Indonesia	[95]
	P. pygmaeus	Orangutan	57.5	Suaq Balimbing, Indonesia	[94]
	Aceros cassidix	Hornbill	2.4	Tangkoko DuaSudara, Indonesia	[63, 96]
Gymnacranthera sp.GP	*P. pygmaeus*	Orangutan	57.5	Gunung Palu, Indonesia	[94]
Gymnacranthera sp.LM001	*Anorrhinus galeritus*	Hornbill	1.1	Kutai, Indonesia	[45]
	Anthracoceros malayanus	Hornbill	1	Kutai, Indonesia	[45]
Gymnacranthera sp.MKF001	*A. cassidix*	Hornbill	2.4	Tangkoko DuaSudara, Indonesia	[63, 96]
Horsfieldia amygdalina	*Aceros nipalensis*	Hornbill	2.4	Huai Kha Khaeng, Thailand	[97]
	Anorrhinus austeni	Hornbill	0.9	Khao Yai, Thailand	[10, 59, 98]
	Anthracoceros albirostris	Hornbill	0.8	Khao Yai, Thailand	[10, 59, 98]
	B. bicornis	Hornbill	2.5	Khao Yai, Thailand	[10, 59, 98]
	R. undulatus	Hornbill	2.7	Khao Yai, Thailand	[10, 59, 98]
	Ducula badia	Pigeon	0.6	Khao Yai, Thailand	[10]
	Callosciurus finlaysonii	Squirrel	0.3	Khao Yai, Thailand	[10]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
H. brachiata	*Buceros rhinoceros*	Hornbill	2.8	Bukit Barisan Selatan, Indonesia	[99]
H. crassifolia	*P. pygmaeus*	Orangutan	57.5	Sebangau, Indonesia	[100]
	Presbytis rubicunda	Leaf monkey	6	Tanjung, Indonesia	[101]
	P. pygmaeus	Orangutan	57.5	Sebangau, Indonesia	[94]
	P. pygmaeus	Orangutan	57.5	Tuanan, Indonesia	[94]
H. glabra	*P. pygmaeus*	Orangutan	57.5	Suaq Balimbing, Indonesia	[94]
H. grandis	*P. pygmaeus*	Orangutan	57.5	Kubah, Malaysia	[94]
H. irya	*Macaca fascicularis*	Macaque	4.5	Angaur, Micronesia	[102]
	Presbytis melalophos	Leaf monkey	5.8	Krau, Malaysia	[103]
	M. fascicularis	Macaque	4.5	Krau, Malaysia	[103]
	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
	Hylobates agilis	Gibbon	6	Krau, Malaysia	[104]
	Ocyceros gingalensis	Hornbill	0.2	Sinharaja, India	[105]
	Gallus lafayetti	Junglefowl	0.6	Sinharaja, India	[105]
	Gracula ptilogenys	Myna	0.2	Sinharaja, India	[105]
	Moschiola meminna	Mousedeer	7.5	Sinharaja, India	[105]
	Funambulus layardi	Squirrel	0.1	Sinharaja, India	[105]

	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	Rhyticeros plicatus	Hornbill	1.6	Wide Bay, New Britain, PNG	[106]
H. kingii	*A. albirostris*	Hornbill	0.8	Pakke, India	[107]
	B. bicornis	Hornbill	2.5	Pakke, India	[107]
	R. undulatus	Hornbill	2.7	Pakke, India	[107]
	D. badia	Pigeon	0.6	Pakke, India	[108]
	Trachypithecus shortridgei	Leaf monkey	11.8	Pakke, India	[109]
H. motleyi	*Aceros comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	B. rhinoceros	Hornbill	2.8	Kutai, Indonesia	[45]
H. pachyrachis	*Macaca tonkeana*	Macaque	12	Lore Lindu, Indonesia	[110]
H. reticulata	*A. galeritus*	Hornbill	1.1	Kutai, Indonesia	[45]
H. sucosa	*Callosciurus* sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	P. melalophos	Leaf monkey	5.8	Krau, Malaysia	[103]
	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
	A. comatus	Hornbill	1.4	Budo Sungapi Padi, Thailand	[57]
	Aceros corrugates	Hornbill	1.6	Budo Sungapi Padi, Thailand	[57]
	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	R. undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
	Presbytis femoralis	Leaf monkey	7.3	Pasoh, Malaysia	[58]
	Hystrix brachyura	Porcupine	8	Pasoh, Malaysia	[58]
H. superba	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
	Macaca nemestrina	Macaque	8.9	Pasoh, Malaysia	[58]
	Leopoldamys sabanus	Rodent	0.4	Pasoh, Malaysia	[58]
	Maxomys surifer	Rodent	0.2	Pasoh, Malaysia	[58]
	Lariscus insignis	Squirrel	0.2	Pasoh, Malaysia	[58]
	Varanus bengalensis	Lizard	7	Pasoh, Malaysia	[58]
H. tomentosa	*Trachypithecus obscurus*	Leaf monkey	7	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	Callosciurus sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	A. corrugates	Hornbill	1.6	Budo Sungapi Padi, Thailand	[57]
	A. galeritus	Hornbill	1.1	Budo Sungapi Padi, Thailand	[57]
	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	Buceros vijil	Hornbill	2.9	Budo Sungapi Padi, Thailand	[57]
	R. undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
H. wallichii	*A. galeritus*	Hornbill	1.1	Kutai, Indonesia	[45]
Horsfieldia sp.CH051	*P. melalophos*	Leaf monkey	5.8	Krau, Malaysia	[103]

	M. fascicularis	Macaque	4.5	Krau, Malaysia	[103]
	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
Horsfieldia sp.FR001	*Helarctos malayanus*	Bear	46	Sungai Wain, Indonesia	[111]
Knema attenuata	*Ocyceros griseus*	Hornbill	0.3	Indira Gandhi, India	[112]
K. attenuata	*Paradoxurus jerdoni*	Civet	4	Kalakad Mundauthurai, India	[113]
	Semnopithecus entellus	Leaf monkey	13.8	Maharashtra, India	[114]
	Macaca silenus	Macaque	7.5	Indira Gandhi, India	[115]
K. cinerea	*A. albirostris*	Hornbill	0.8	Pakke, India	[108]
	B. bicornis	Hornbill	2.5	Pakke, India	[108]
	R. undulatus	Hornbill	2.7	Pakke, India	[108]
	D. badia	Pigeon	0.6	Pakke, India	[108]
	Hylobates lar	Gibbon	6	Krau, Malaysia	[103]
	Symphalangus syndactylus	Gibbon	12.4	Krau, Malaysia	[103]
	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
	Hylobates moloch	Gibbon	5.7	Gunung Halimun, Indonesia	[116]
	Presbytis comata	Leaf monkey	6.5	Gunung Halimun, Indonesia	[116]
	Trachypithecus auratus	Leaf monkey	7.1	Gunung Halimun, Indonesia	[116]
	M. tonkeana	Macaque	12	Lore Lindu, Indonesia	[110]
	P. pygmaeus	Orangutan	57.5	Ketambe, Indonesia	[94]
	P. pygmaeus	Orangutan	57.5	Ketambe, Indonesia	[94]
K. conferta	*H. klossii*	Gibbon	5.8	Siberut, Indonesia	[95]
K. curtisii	*Callosciurus* sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
K. elegans	*H. lar*	Gibbon	6	Khao Yai, Thailand	[117]
	A. austeni	Hornbill	0.9	Khao Yai, Thailand	[10, 59, 98]
	A. albirostris	Hornbill	0.8	Khao Yai, Thailand	[10, 59, 98]
	B. bicornis	Hornbill	2.5	Khao Yai, Thailand	[10, 59, 98]
	R. undulatus	Hornbill	2.7	Khao Yai, Thailand	[10, 59, 98]
	D. badia	Pigeon	0.6	Khao Yai, Thailand	[10]
	C. finlaysonii	Squirrel	0.3	Khao Yai, Thailand	[10]
	Hylobates pileatus	Gibbon	8.4	Khao Yai, Thailand	[118]
	Paradoxurus hermaphroditus	Civet	3.2	Khao Yai, Thailand	[51]
	Muntiacus muntjak	Deer	24	Khao Yai, Thailand	[51]
	M. surifer	Rodent	0.2	Khao Yai, Thailand	[51]
	C. finlaysonii	Squirrel	0.3	Khao Yai, Thailand	[51]
	Viverra zibetha	Civet	6.3	Khao Yai, Thailand	[71]
	H. lar	Gibbon	6	Khao Yai, Thailand	[71, 119]
	Atherurus macrourus	Porcupine	6	Khao Yai, Thailand	[71, 119]

K. erratica	*A. nipalensis*	Hornbill	2.4	Huai Kha Khaeng, Thailand	[97]
K. furfuracea	*T. obscurus*	Leaf monkey	7	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	Callosciurus sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	A. comatus	Hornbill	1.4	Budo Sungapi Padi, Thailand	[57]
	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	B. rhinoceros	Hornbill	2.8	Budo Sungapi Padi, Thailand	[57]
	R. undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
K. glauca	*Callosciurus* sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
K. glaucescens	*P. pygmaeus*	Orangutan	57.5	Sungai Wain, Indonesia	[94]
K. globularia	*T. obscurus*	Leaf monkey	7	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	Callosciurus sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	A. corrugates	Hornbill	1.6	Budo Sungapi Padi, Thailand	[57]
	A. galeritus	Hornbill	1.1	Budo Sungapi Padi, Thailand	[57]
	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	R. undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
K. hookeriana	*Callosciurus* sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	H. lar	Gibbon	6	Krau, Malaysia	[103]
	S. syndactylus	Gibbon	12.4	Krau, Malaysia	[103]
	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
	A. galeritus	Hornbill	1.1	Budo Sungapi Padi, Thailand	[57]
	M. nemestrina	Macaque	8.9	Pasoh, Malaysia	[58]
	Sus scrofa	Pig	70	Pasoh, Malaysia	[58]
	Trichys fasciculata	Porcupine	2.5	Pasoh, Malaysia	[58]
	L. sabanus	Rodent	0.4	Pasoh, Malaysia	[58]
	M. surifer	Rodent	0.2	Pasoh, Malaysia	[58]
	L. insignis	Squirrel	0.2	Pasoh, Malaysia	[58]
K. intermedia	*P. rubicunda*	Leaf monkey	6	Tanjung, Indonesia	[101]
K. latericia	*H. malayanus*	Bear	46	Sungai Wain, Indonesia	[111]
	P. pygmaeus	Orangutan	57.5	Gunung Palu, Indonesia	[120]
	A. cassidix	Hornbill	2.4	Tangkoko DuaSudara, Indonesia	[63, 96]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	R. undulatus	Hornbill	2.7	Kutai, Indonesia	[45]

	M. fascicularis	Macaque	4.5	Bukit Timah, Singapore	[121]
	P. pygmaeus	Orangutan	57.5	Mentoko, Indonesia	[94]
	P. pygmaeus	Orangutan	57.5	Meratus, Indonesia	[94]
K. latifolia	*Hylobates muelleri×agilis*	Gibbon	5.7	Barito Ulu, Indonesia	[122]
K. laurina	*P. pygmaeus*	Orangutan	57.5	Danum Valley, Malaysia	[123]
	M. fascicularis	Macaque	4.5	Bukit Timah, Singapore	[121]
	A. nipalensis	Hornbill	2.4	Huai Kha Khaeng, Thailand	[124, 125]
	B. bicornis	Hornbill	2.5	Huai Kha Khaeng, Thailand	[124, 125]
	Presbytis thomasi	Leaf monkey	6.7	Ketambe, Indonesia	[126]
	P. pygmaeus	Orangutan	57.5	Ketambe, Indonesia	[94]
K. pallens	*A. galeritus*	Hornbill	1.1	Kutai, Indonesia	[45]
K. percoriacea	*H. muelleri×agilis*	Gibbon	5.7	Barito Ulu, Indonesia	[122]
K. pseudolaurina	*T. obscurus*	Leaf monkey	7	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	Callosciurus sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
K. scortechinii	*M. nemestrina*	Macaque	8.9	Pasoh, Malaysia	[58]
	Tragulus kanchil	Mousedeer	2.3	Pasoh, Malaysia	[58]
	H. brachyura	Porcupine	8	Pasoh, Malaysia	[58]
	Rhinosciurus laticaudatus	Squirrel	0.2	Pasoh, Malaysia	[58]
	Tupaia glis	Tupai	0.2	Pasoh, Malaysia	[58]
Knema sp.CH052	*Calyptomena viridis*	Broadbill	0.1	Krau, Malaysia	[103]
	Hornbill 6 spp.	Hornbill	NA	Krau, Malaysia	[103]
	P. melalophos	Leaf monkey	5.8	Krau, Malaysia	[103]
	Callosciurus prevostii	Squirrel	0.4	Krau, Malaysia	[103]
Knema sp.FR002	*H. malayanus*	Bear	46	Sungai Wain, Indonesia	[111]
Knema sp.GI001	*H. agilis*	Gibbon	6	Krau, Malaysia	[104]
Knema sp.GP	*P. pygmaeus*	Orangutan	57.5	Gunung Palu, Indonesia	[94]
Knema sp.KA001	*P. pygmaeus*	Orangutan	57.5	Danum Valley, Malaysia	[123]
Knema sp.KO001	*A. nipalensis*	Hornbill	2.4	Huai Kha Khaeng, Thailand	[124, 125]
Knema sp.ME	*P. pygmaeus*	Orangutan	57.5	Meratus, Indonesia	[94]
Knema sp.SW	*P. pygmaeus*	Orangutan	57.5	Sungai Wain, Indonesia	[94]
Knema sp.US	*P. pygmaeus*	Orangutan	57.5	Ulu Segama, Malaysia	[94]
Knema sp.VC001	*A. nipalensis*	Hornbill	2.4	Huai Kha Khaeng, Thailand	[97]
	Rhyticeros subruficollis	Hornbill	2.1	Huai Kha Khaeng, Thailand	[97]
Knema sp.YH001	*A. galeritus*	Hornbill	1.1	Bukit Barisan Selatan, Indonesia	[99]
Knema sp.YH002	*B. rhinoceros*	Hornbill	2.8	Bukit Barisan Selatan, Indonesia	[99]
	R. undulatus	Hornbill	2.7	Bukit Barisan Selatan, Indonesia	[99]

Myristica andamanica	*Ducula aenea*	Pigeon	0.5	NA	[127]
M. beddomii	*M. silenus*	Macaque	7.5	Indira Gandhi, India	[115]
M. ceylanica	*Aceros waldeni*	Hornbill	1.1	North Negros, Philippines	[11]
	Penelopides panini	Hornbill	0.5	North Negros, Philippines	[11]
	A. waldeni	Hornbill	1.1	North Negros, Philippines	[128]
M. cinnamomea	*P. pygmaeus*	Orangutan	57.5	Ulu Segama, Malaysia	[94]
	M. nemestrina	Macaque	8.9	Pasoh, Malaysia	[58]
	H. brachyura	Porcupine	8	Pasoh, Malaysia	[58]
	T. fasciculata	Porcupine	2.5	Pasoh, Malaysia	[58]
	M. surifer	Rodent	0.2	Pasoh, Malaysia	[58]
	R. laticaudatus	Squirrel	0.2	Pasoh, Malaysia	[58]
	V. bengalensis	Lizard	7	Pasoh, Malaysia	[58]
M. dactyloides	*Semnopithecus johnii*	Leaf monkey	11	Kalakad Mundauthurai, India	[129]
	M. silenus	Macaque	7.5	Kalakad Mundauthurai, India	[129]
	Platacanthomys lasiurus	Rodent	0.8	Kalakad Mundauthurai, India	[129]
	Ratufa indica	Squirrel	2	Kalakad Mundauthurai, India	[129]
	O. gingalensis	Hornbill	0.2	Sinharaja, India	[105]
	G. ptilogenys	Myna	0.2	Sinharaja, India	[105]
	Viverricula indica	Civet	3	Sinharaja, India	[105]
	Herpestes fuscus	Mongoose	2.7	Sinharaja, India	[105]
	F. layardi	Squirrel	0.1	Sinharaja, India	[105]
	O. griseus	Hornbill	0.3	Indira Gandhi, India	[112]
	M. silenus	Macaque	7.5	Indira Gandhi, India	[130]
M. elliptica	*A. comatus*	Hornbill	1.4	Budo Sungapi Padi, Thailand	[57]
	A. galeritus	Hornbill	1.1	Budo Sungapi Padi, Thailand	[57]
	R. undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
	M. nemestrina	Macaque	8.9	Pasoh, Malaysia	[58]
	H. brachyura	Porcupine	8	Pasoh, Malaysia	[58]
	T. fasciculata	Porcupine	2.5	Pasoh, Malaysia	[58]
	L. sabanus	Rodent	0.4	Pasoh, Malaysia	[58]
	M. surifer	Rodent	0.2	Pasoh, Malaysia	[58]
	Maxomys whiteheadi	Rodent	0.6	Pasoh, Malaysia	[58]
	R. laticaudatus	Squirrel	0.2	Pasoh, Malaysia	[58]
	V. bengalensis	Lizard	7	Pasoh, Malaysia	[58]
M. fatua	*R. plicatus*	Hornbill	1.6	Crater Mountain, PNG	[131]
M. guatteriifolia	*Rhyticeros everetti*	Hornbill	1.1	Sumba, Indonesia	[132]
M. hypargyraea	*Ducula pacifica*	Pigeon	0.4	Eua, Tonga	[70]
	Pteropus tonganus	Flying fox	0.6	Eua, Tonga	[62]
	Prosopeia tabuensis	Parrot	0.2	Eua, Tonga	[62]

	Rattus spp.	Rodent	0.2	Eua, Tonga	[62, 133]
M. iners	*Callosciurus* sp.	Squirrel	NA	Budo Sungapi Padi, Thailand	(S. Kitamura, unpublished data)
	A. comatus	Hornbill	1.4	Budo Sungapi Padi, Thailand	[57]
	A. galeritus	Hornbill	1.1	Budo Sungapi Padi, Thailand	[57]
	B. bicornis	Hornbill	2.5	Budo Sungapi Padi, Thailand	[57]
	B. rhinoceros	Hornbill	2.8	Budo Sungapi Padi, Thailand	[57]
	R. undulatus	Hornbill	2.7	Budo Sungapi Padi, Thailand	[57]
M. lowiana	*P. pygmaeus*	Orangutan	57.5	Sebangau, Indonesia	[100]
	P. pygmaeus	Orangutan	57.5	Tuanan, Indonesia	[94]
M. maingayi	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
	M. nemestrina	Macaque	8.9	Pasoh, Malaysia	[58]
	T. kanchil	Mousedeer	2.3	Pasoh, Malaysia	[58]
	T. fasciculata	Porcupine	2.5	Pasoh, Malaysia	[58]
	L. sabanus	Rodent	0.4	Pasoh, Malaysia	[58]
	T. glis	Tupai	0.2	Pasoh, Malaysia	[58]
M. malabarica	*S. entellus*	Leaf monkey	14.5	Maharashtra, India	[114]
	M. silenus	Macaque	7.5	Indira Gandhi, India	[130]
M. maxima	*R. undulatus*	Hornbill	2.7	Bukit Barisan Selatan, Indonesia	[99]
	P. pygmaeus	Orangutan	57.5	Sungai Wain, Indonesia	[94]
M. muelleri	*Ptilinopus magnificus*	Pigeon	0.2	Laceys Creek, Australia	[134]
	Ptilinopus superbus	Pigeon	0.1	Laceys Creek, Australia	[134]
	Ducula spilorrhoa	Pigeon	0.5	Laceys Creek, Australia	[134]
M. subalulata	*Manucodia chalybatus*	Bird of Paradise	0.2	Crater Mountain, PNG	[131]
	Parotia lawesii	Bird of Paradise	0.2	Crater Mountain, PNG	[131]
M. venisa	*H. muelleri×agilis*	Gibbon	5.7	Barito Ulu, Indonesia	[122]
M. villosa	*P. pygmaeus*	Orangutan	57.5	Kinabatangan, Malaysia	[94]
	P. pygmaeus	Orangutan	57.5	Sungai Wain, Indonesia	[94]
M. warburgii	*R. plicatus*	Hornbill	1.6	Wide Bay, New Britain, PNG	[106]
Myristica sp.AL001	*D. aenea*	Pigeon	0.5	NA	[127]
Myristica sp.AL003	*Ducula bicolor*	Pigeon	0.5	NA	[127]
Myristica sp.AL004	*D. badia*	Pigeon	0.6	NA	[127]
	A. nipalensis	Hornbill	2.4	NA	[135]
Myristica sp.AL005	*B. bicornis*	Hornbill	2.5	NA	[135]
Myristica sp.BB001	*Diphyllodes magnificus*	Bird of Paradise	0.2	Mt. Missim, PNG	[136]
	Manucodia keraudrenii	Bird of Paradise	0.2	Mt. Missim, PNG	[136]
	Paradisaea raggiana	Bird of Paradise	0.2	Mt. Missim, PNG	[136]

	P. lawesii	Bird of Paradise	0.2	Mt. Missim, PNG	[136]
Myristica sp.BB002	*Cicinnurus magnificus*	Bird of Paradise	0.1	Varirata, PNG	[21]
	M. chalybatus	Bird of Paradise	0.2	Varirata, PNG	[21]
	P. raggiana	Bird of Paradise	0.2	Varirata, PNG	[21]
	P. magnificus	Pigeon	0.2	Varirata, PNG	[21]
	Ptilinopus pulchellus	Pigeon	0.1	Varirata, PNG	[21]
	P. superbus	Pigeon	0.1	Varirata, PNG	[21]
Myristica sp.CH053	*Hornbill 6spp*	Hornbill	NA	Krau, Malaysia	[103]
	P. melalophos	Leaf monkey	5.8	Krau, Malaysia	[103]
	C. prevostii	Squirrel	0.4	Krau, Malaysia	[103]
Myristica sp.CH054	Squirrel	Squirrel	NA	Krau, Malaysia	[103]
Myristica sp.GI003	*D. pacifica*	Pigeon	0.4	NA	[37]
Myristica sp.GI004	*Ducula latrans*	Pigeon	0.6	NA	[37]
Myristica sp.KET	*P. pygmaeus*	Orangutan	57.5	Ketambe, Indonesia	[94]
Myristica sp.KN	*P. pygmaeus*	Orangutan	57.5	Kinabatangan, Malaysia	[94]
Myristica sp.LM001	*A. galeritus*	Hornbill	1.1	Kutai, Indonesia	[45]
Myristica sp.LM002	*A. comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	A. corrugates	Hornbill	1.6	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	B. rhinoceros	Hornbill	2.8	Kutai, Indonesia	[45]
Myristica sp.LM003	*A. comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	B. rhinoceros	Hornbill	2.8	Kutai, Indonesia	[45]
	R. undulatus	Hornbill	2.7	Kutai, Indonesia	[45]
Myristica sp.LM004	*A. comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	R. undulatus	Hornbill	2.7	Kutai, Indonesia	[45]
Myristica sp.LM005	*A. comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	A. malayanus	Hornbill	1	Kutai, Indonesia	[45]
	R. undulatus	Hornbill	2.7	Kutai, Indonesia	[45]
Myristica sp.ML006	*A. comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	A. corrugates	Hornbill	1.6	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	A. malayanus	Hornbill	1	Kutai, Indonesia	[45]
	B. rhinoceros	Hornbill	2.8	Kutai, Indonesia	[45]
Myristica sp.ML007	*A. comatus*	Hornbill	1.4	Kutai, Indonesia	[45]
	A. galeritus	Hornbill	1.1	Kutai, Indonesia	[45]
	B. rhinoceros	Hornbill	2.8	Kutai, Indonesia	[45]

	R. undulatus	Hornbill	2.7	Kutai, Indonesia	[45]
Myristica sp.PA001	*H. lar*	Gibbon	6	Ketambe, Indonesia	[137]
Myristica sp.RK001	*B. bicornis*	Hornbill	2.5	Indira Gandhi, India	[46]
	O. griseus	Hornbill	0.3	Indira Gandhi, India	[46]
	D. badia	Pigeon	0.6	Indira Gandhi, India	[46]
Myristica sp.SM001	*D. bicolor*	Pigeon	0.5	NA	[138]
Myristica sp.TN	*P. pygmaeus*	Orangutan	57.5	Tuanan, Indonesia	[94]
Myristica sp.US	*P. pygmaeus*	Orangutan	57.5	Ulu Segama, Malaysia	[94]
Myristicaceae sp.AZ001	*Trachypithecus phayrei*	Leaf monkey	7.4	Lawachara, Bangladesh	[139]
Myristicaceae sp.BL001	*Nomascus concolor*	Gibbon	6.8	Wu Liang, China	[140]
Myristicaceae sp.DE001	*Trachypithecus vetulus*	Leaf monkey	8.2	Panadura, Sri Lanka	[141]
Myristicaceae sp.DU001	*Pygathrix nigripes*	Leaf monkey	10.7	Phuoc Binh, Vietnam	[142]
Myristicaceae sp.FA001	*N. concolor*	Gibbon	6.8	Dazhaizi, China	[143]
Myristicaceae sp.FR001	*Ptilinopus iozonus*	Pigeon	0.1	Brown River, PNG	[144]
	P. magnificus	Pigeon	0.2	Brown River, PNG	[144]
	P. superbus	Pigeon	0.1	Brown River, PNG	[144]
	P. pulchellus	Pigeon	0.1	Brown River, PNG	[144]
	Ducula rufigaster	Pigeon	0.5	Brown River, PNG	[144]
Myristicaceae sp.FU001	*Presbytis potenziani*	Leaf monkey	6.4	Betumonga, Indonesia	[145]
Myristicaceae sp.GI002	*D. aenea*	Pigeon	0.5	NA	[37]
Myristicaceae sp.GO001	*D. aenea*	Pigeon	0.5	NA	[146]
Myristicaceae sp.GO002	*D. pacifica*	Pigeon	0.4	NA	[146]
Myristicaceae sp.GO003	*D. bicolor*	Pigeon	0.5	NA	[146]
Myristicaceae sp.GO004	*D. spilorrhoa*	Pigeon	0.5	NA	[146]
Myristicaceae sp.GR001	*Macaca mulatta*	Macaque	9.9	Baimaxueshan, China	[147]
Myristicaceae sp.GU001	*P. thomasi*	Leaf monkey	6.7	Gunung Leuser, Indonesia	[148]
Myristicaceae sp.IS001	*Hoolock hoolock*	Gibbon	6.5	Lawachara & Chunati, Bangladesh	[149]
Myristicaceae sp.KET	*P. pygmaeus*	Orangutan	57.5	Ketambe, Indonesia	[94]
Myristicaceae sp.KO001	*T. auratus*	Leaf monkey	7.1	Pangandaran, Indonesia	[150]
Myristicaceae sp.KR001	*Macaca radiata*	Macaque	5.3	Marakkanam, India	[151]
Myristicaceae sp.KU001	*Trachypithecus pileatus*	Leaf monkey	11.4	Pakke, India	[152]
Myristicaceae sp.KU002	*Macaca munzala*	Macaque	15	Zemithang, India	[153]
Myristicaceae sp.LE001	*Rhinopithecus avunculus*	Leaf monkey	11.3	Khau Ca, Vietnam	[154]
Myristicaceae sp.LI001	*Trachypithecus poliocephalus*	Leaf monkey	8.1	Fusui, China	[155]
Myristicaceae sp.MA001	*Nasalis larvatus*	Leaf monkey	15.6	Kinabatangan, Malaysia	[156]
Myristicaceae sp.MI001	*Semnopithecus ajax*	Leaf monkey	14.9	Machiara, Pakistan	[157]
Myristicaceae sp.OB001	*Macaca nigra*	Macaque	7.7	Tangkoko DuaSudara, Indonesia	[158]
Myristicaceae sp.RA001	*P. nigripes*	Leaf monkey	10.7	Seima, Cambodia	[159]
Myristicaceae sp.SM001	*R. plicatus*	Hornbill	1.6	Wide Bay, New Britain, PNG	[106]

Myristicaceae sp.SU001	*Macaca cyclopis*	Macaque	5.5	Jentse, Taiwan	[160]
Myristicaceae sp.TM001	*Macaca arctoides*	Macaque	10.3	Khao Krapuk, Thailand	(T. Maruhashi, unpublished data)
Myristicaceae sp.WO001	*Trachypithecus delacouri*	Leaf monkey	8.4	Van Long, Vietnam	[161]
Myristicaceae sp.WU001	*H. hoolock*	Gibbon	6.5	Nankang, China	[162, 163]
Myristicaceae sp.ZH001	*Trachypithecus francoisi*	Leaf monkey	5.9	Nonggang, China	[164]
Myristicaceae sp.ZH002	*Macaca assamensis*	Macaque	9.1	Nonggang, China	[165]