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Dispersal of *Canarium euphyllum* (Burseraceae), a large-seeded tree species, in a moist evergreen forest in Thailand

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Abstract: We investigated the dispersal of a large-seeded tree species, *Canarium euphyllum* (Burseraceae), in the moist evergreen forests of the Khao Yai National Park in Thailand. By combining direct observations of fruit consumption in tree canopies (543 h) and the camera-trapping observations of fallen fruit consumption on the forest floor (175 camera-days), we identified the frugivore assemblage that foraged on the fruits of *C. euphyllum* and assessed their role in seed dispersal and seed predation. In the canopy, our results showed that seeds were dispersed by a limited set of frugivores, one pigeon and four hornbill species, and predated by two species of squirrel. On the forest floor, seven mammal species consumed fallen fruits. A combination of high rates of fruit removal and short visiting times of mountain imperial pigeons (*Ducula badia*) and hornbills (*Buceros bicornis*, *Aceros undulatus*, *Anorrhinus austeni* and *Anthracoceros albirostris*) led us to conclude that these large frugivorous birds provide effective seed dispersal for this tree species, in terms of quantity. These frugivorous species often have low tolerance to negative human impacts and loss of these dispersers would have severe deleterious consequences for the successful regeneration of *C. euphyllum*.

Key Words: camera trapping, frugivore, frugivory, ground squirrels, hornbills, imperial pigeons, rodents, seed dispersal, seed predation, squirrels

INTRODUCTION

Seed dispersal plays a critical role in the maintenance and the recovery of plant diversity in tropical forests (Terborgh *et al.* 2002), where dispersal relationships are extremely diverse. In general, fruits are eaten by a variety of animals, although certain fruit characteristics are more attractive to potential dispersers than others (Bollen *et al.* 2004a, Corlett 1996, Gautier-Hion *et al.* 1985, Kitamura *et al.* 2002). Among these characteristics, fruit (or seed) size is significantly related to the body size of consumers (McConkey & Drake 2002, Peres & van Roosmalen 2002, Wheelwright 1985). The maximum diameter of fruit (seed) swallowed by frugivorous birds is limited by their gape size, while there is no upper size constraint for mammalian frugivores as they are able to process fruit using their teeth and hands (Corlett 1998, Fleming *et al.* 1987). The seed dispersal of large-seeded plant species is therefore mostly dependent on large-bodied frugivores. Large frugivores are susceptible to extinction as a result of deleterious anthropogenic activities, and, consequently, large-seeded plant species are themselves vulnerable to extinction (Corlett 2002, Hamann & Curio 1999, McConkey & Drake 2002, Peres & van Roosmalen 2002).

Large frugivorous animals play an important role in seed dispersal and forest regeneration in Thailand (Brockelman 1985, Hardwick *et al.* 1997, Kitamura *et al.* 2002). Most field studies related to seed dispersal

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by large frugivores in Thai forests have focused on the interaction between focal plant species and their fruit consumers (Kitamura *et al.* 2002, 2004a; McClure 1974, Poonswad *et al.* 1998a) or the feeding ecology and dispersal role of frugivores, for example, civets (Rabinowitz 1991), hornbills (Kitamura *et al.* 2004b, c; Poonswad *et al.* 1998b), and gibbons (Bartlett 2003, Whitington & Treesucon 1991). The current study focuses on interactions between vertebrate frugivores and the large-seeded plant *Canarium euphyllum* (Burseraceae) in the moist evergreen forests of the Khao Yai National Park in Thailand.

Canarium trees produce drupaceous fruits that are dispersed by birds and mammals in tropical rain forests from Africa to the Pacific (Kochummen 1972). Large birds such as imperial pigeons and hornbills serving as the principal dispersers of *Canarium* trees in the Philippines (Hamann & Curio 1999, Heindl & Curio 1999), Borneo (Leighton 1982), India (Datta & Rawat 2003, Kannan 1994), and Cameroon (French & Smith 2005). In addition to birds, the sun bear (*Ursus malayanus*) in Borneo (McConkey & Galetti 1999) and the collared brown lemur (*Eulemur fulvus collaris*) in Madagascar (Bollen *et al.* 2004b) are also reported to be dispersers of this genus, while fallen fruits and seeds are consumed by terrestrial mammals such as rodents and deer (Blate *et al.* 1998, Chen *et al.* 2001, Gardner *et al.* 2000, Goodman & Sterling 1996, Yasuda *et al.* 2005). Most of these studies emphasized the importance of large frugivores as seed dispersal agents for this genus, however, most studies were conducted as a part of a particular animal's diet or represent brief observations of frugivores visiting *Canarium* fruit crops either in the canopy or on the ground. Therefore studies to date have been unable to establish the effectiveness, even in terms of quantity (Schupp 1993), of any frugivore seed dispersal for *Canarium* species, with the exception of McConkey & Galetti (1999), who followed the fate of *C. pilosum* seeds defecated by sun bears and subsequently determined seedling survivorship.

In this study, we examined the consumption of the fruit of the large-seeded *C. euphyllum* in a moist evergreen forest in Thailand to assess the role of frugivores as seed dispersers. Previously, we demonstrated that a limited number of frugivore species was considered as effective seed dispersers for a large-seeded tree, *Aglaia spectabilis* in Thailand (Kitamura *et al.* 2004a). By examining the disperser assemblage of another large-seeded tree species belonging to the different family at the same study site, we are able to examine further the importance of large frugivores for these large-seeded plants. The specific questions we address are: (1) What animal species are most important in the dispersal of *C. euphyllum* seeds and (2) which animals are the most important seed predators of *C. euphyllum*. To answer these questions, we made observations of fruit consumption and frugivore behaviour both in the canopy and on the ground below fruiting *C. euphyllum* trees over a period of 2 y.

STUDY SPECIES

This study was conducted in Khao Yai National Park (KY, 14°N, 101°E), Thailand. Further details of the study site are described elsewhere (Kitamura *et al.* 2005, Smitinand 1977). The genus *Canarium* comprises about 77 species and *Canarium euphyllum* Kurz is one of 12 species recorded in Thailand (Pooma 1999). In KY, it occurs as a canopy tree species, growing to about 35 m in height and 150 cm in diameter at breast height (dbh). In our study site, *C. euphyllum* was proved to be the 33rd ranked species in terms of number of individuals (nine individuals) among 105 plant species (1610 individuals in total) occurring in a 4-ha plot (Kitamura *et al.* 2005). Of these, only one *Canarium* tree was reproductive (S. Suzuki, unpubl. data). It is deciduous and produces inflorescences after the flush of new leaves during March–April. Fruit maturation takes 5–6 mo, usually occurring in August to September, but sometimes in November to December. Fruits are oblong drupes, 3.0–4.6 cm long and 1.7–2.8 cm wide ($n = 600$), ripening to blue-black. The stones are hard and woody, with three cells (often reduced to two or one). They are 1.8–4.0 cm long and 1.6–2.7 cm wide ($n = 600$), which makes them one of the largest seeds in KY (Kitamura *et al.* 2002).

METHODS

Fruit removal in the canopy

Frugivore activity and the depletion of fruits were monitored at two trees in November and December 2000 (Tree codes: GH10 and C294) and three trees during August to October 2001 (GH10, C130 and DCT). These four focal trees were 30 ± 4 m in height and 89 ± 42 cm in dbh (mean ± SD, respectively). Observations were made using binoculars from concealed positions that enabled views of as much of the focal tree canopy as possible. Watches usually took place between 06h00 and 18h00 and were conducted under almost all weather conditions except heavy rain. At first, we observed each focal tree in turn. After poor fruit crops of C294 in 2000 and C130 in 2001, we concentrated on observing GH10 in 2000, and GH10 and DCT in 2001. As a result, the total observation effort was biased to GH10.

For each individual frugivore that entered the focal tree, we recorded: (1) species, (2) times of arrival and departure, (3) the number of fruits handled (swallowed, dropped and predated), and (4) the number of seeds regurgitated. Mountain imperial pigeon (*Ducula badia*) commonly visited focal trees in flocks. When more than one individual arrived and fed at a focal tree at the same time, it was not possible to collect data accurately on all of them. Therefore, all data were collected on one focal individual, and only arrival and departure times were collected for feeding, non-focal individuals. Partial visits (those beginning or ending outside of the observation period) were excluded. Both median and mean values are reported; the former are not sensitive to extreme values, while the latter are useful for making comparisons with published data (Whitney *et al.* 1998).

We estimated the seed retention time of each focal animal. In previous studies (Holbrook & Smith 2000, Meehan *et al.* 2003, Westcott *et al.* 2005), feeding trials were usually conducted with captive frugivores to estimate the seed retention times, however, captive animals were not available in this study. Instead, we estimated the seed retention time as being the time when the last fruit was consumed in the previous feeding bout at the focal tree subtracted from the time when seed regurgitation was observed. After the departure of the focal animal, we searched for the regurgitated seeds and counted the number to confirm the observation. As the fleshy regurgitated seeds of *Canarium euphyllum* dropped by hornbills and mountain imperial pigeons retained a pink colour for a day, we were accurately able to determine the newly regurgitated seeds in the field. Since seed regurgitation by hornbills usually continued for 10–20 min, the median time was reported for each observation session. As watches were diurnal, visits by nocturnal canopy animals were not recorded, although we found no evidence of high levels of nocturnal fruit removal. Some flying squirrels might consume the fruits. Taxonomic nomenclature for mammals follows Srikosamatara & Hansel (1996) with partial corrections by Corbet & Hill (1992), and for birds follows Lekagul & Round (1991) with partial corrections by Kemp (1995).

We estimated the relative importance of each frugivore species in removing *C. euphyllum* fruits from the canopy by calculating the mean number of fruits eaten per visit and the total number of animals visiting the focal trees (Kitamura *et al.* 2004a). The fruits of *C. euphyllum* were rarely observed to drop without intervention of an animal, even on a strong windy day. Therefore we assumed that dropped fruits were mostly due to the handling behaviour by visiting animals. Since the purpose of this study was to elucidate the general pattern of each frugivore's behaviour as a seed disperser at the fruiting tree of *C. euphyllum*, the data from the 2 years for each frugivore species were combined for analysis. Pooling all the data might hide important variability among focal trees, but the sample sizes collected for most frugivore species were too small to test such variability. Other potential biases in the study were that repeated observations were made of the same animal individuals returning to collect more fruits, especially a pair of great hornbill at GH10.

Fruit removal on the ground

To determine the importance of frugivores in the removal of *C. euphyllum* fruits from below fruiting trees, we used an automatic photographic monitoring system (Sensor Camera Fieldnote, MARIF Co. Ltd., Japan). These cameras were tightly wrapped in thin transparent polypropylene bags to keep them dry and encased in unsealed plastic boxes. Yasuda (2004) reports the details of this system. Feeding trials were conducted at five trees in November and December 2000 (Tree codes: GH10, C294, C130, WB463 and DCT) and at two trees in September and November 2001 (GH10 and DCT). A sample of fruits was collected from the ground below the focal trees. In each trial, about 10 fruits were placed on a terrestrial feeding platform below the edge of the crown of the parent tree at 09h00. The removal of fruits from the feeding platform was recorded using an automatic camera system. The camera was equipped with an infrared sensor and an auto-quartz timepiece, so that the time of a visit by an animal was printed on the corresponding photograph (Yasuda 2004). Since the fruits of *Canarium euphyllum* were large enough to identify individually from the picture, we were able to count the number of fruits removed by each visitor. From the photographs taken by the camera system, the animal species that removed a particular sample could be identified, though several animals were either too fast or too slow to be detected by the sensor. Photographs were taken until either no fruits or film remained. Although we checked these cameras almost every day during the study period, in some cases, all of the film was finished within a day. Several fruits were consumed after the end of the film, thus we were not able to identify the fruit consumers in these cases. This undetermined fruit removal was categorized as 'unknown' (see Table 4). After the samples disappeared, the trial was repeated for at least 1 wk throughout the fruiting period.

RESULTS

Fruit removal in the canopy

In total, 543 h of observations (109 ± 97 h per tree per y, mean ± SD) were conducted during the study period. Direct observations indicated that a small assemblage of five bird species and two squirrel species (Table 1) consumed the fruits of *C. euphyllum*. Other frugivorous birds such as the hill myna (*Gracula religinosa*) and green-eared barbet (*Megalaima faiostricta*) sometimes visited focal trees, but were never observed to consume fruits.

Table 1. Frugivores visiting *Canarium euphyllum* in the canopy, body weight (kg), number of visiting animals (n) and their duration of visit (median, mean, minimum and maximum). Probability is from a Kruskal–Wallis test to reveal the variability of the duration of visits between individual trees in individual years within a species.

			Duration of visit (min)		
Frugivore species	Body weight (kg)	Visits (n)	Median	Mean (range)	P value
Birds					
Buceros bicornis, great hornbill	2.2–3.0	61	16	44 (1–278)	0.048
Aceros undulatus, wreathed hornbill	2.0–2.5	259	16	41 (1–284)	0.002
Anorrhinus austeni, brown hornbill	0.8–0.9	65	10	13 (1–29)	0.414
Anthracoceros albirostris, oriental pied hornbill	0.7–0.8	97	8	13 (1–42)	0.088
Ducula badia, mountain imperial pigeon	0.5–0.6	1918	8	13 (1–220)	0.035
Mammals					
Ratufa bicolor, black giant squirrel	1.4	40	80	90 (7–257)	0.037
Callosciurus finlaysonii, variable squirrel	0.3	33	24	25 (1–73)	0.328

Complete feeding observations were available for only a subset of all the visitations to focal trees by frugivores (but were usually >50% for most species, but <10% for *Anorrhinus austeni* and *Ducula badia*). There were significant differences in the durations of visits to focal trees in individual years for all species except *A. austeni* and *Callosciurus finlaysonii* (Table 1). The median visit length by frugivores was short except for that of *Ratufa bicolor*; however, extended visits (>1 h) were occasionally observed for *Buceros bicornis*, *Aceros undulatus* and *D. badia*. The extended visits of these three species were mainly due to long resting times, in contrast to the two squirrel species that, during their visits, ate continuously.

Frugivorous birds fed on ripe fruits and rarely attempted to feed on unripe green ones. Both squirrel species, in contrast, predated the seeds of ripe and unripe fruits. There was some variability between bird species in the numbers of fruits consumed per visit and in the numbers of fruits they dropped (Table 2). There were also significant differences in the numbers of fruit eaten and dropped per visit between focal trees in individual years (Table 2). At GH10, hornbills were recorded to regurgitate seeds (three times for *A. undulatus* and twice for *B. bicornis*) during their extended visits. The median seed retention time in these species was relatively long (89, 55 and 72 min for *A. undulatus*; 97 and 81 min for *B. bicornis*). Seed regurgitation by *D. badia* was observed several times at GH10, but we were unable to determine seed retention times. Unlike seeds regurgitated by hornbills, fruit pulp remained on seeds regurgitated by *D. badia*, which only partially digested fruits. As such, seeds regurgitated by *D. badia* could be easily distinguished from those regurgitated by hornbills. None of these seeds regurgitated by birds was damaged physically.

Just five frugivorous bird species removed 60.5% of seeds from fruiting trees. They dropped 27.7% of seeds and regurgitated 0.5% of seeds at the focal trees. Squirrels were responsible for dropping and/or predating 11.4% of seeds. *Ducula badia* was the top seed disperser in terms of quantity (54.4%, Table 3), followed by *A. undulatus* (29.5%) and *B. bicornis* (8.5%).

Fruit removal on the ground

In total, 175 d of camera trapping (25 ± 22 d per tree per y, mean ± SD) were conducted during the study period and 347 *Canarium* fruits were used in this study. All the sample fruits in the trials disappeared from the feeding platform within 1 wk. We obtained a total of

Table 2. Number of eaten fruits and dropped fruits per visit by each species (median, mean, range). Probability is from a Kruskal–Wallis test to reveal the variability of the number of fruits eaten per visit between individual trees in individual years within a species. A dash means that sample sizes are not enough for statistical test. nd: no data.

		Number of eaten fruits (n)			Number of dropped fruits (n)		
Species	Samples (n)	Median	Mean (range)	P value	Median	Mean (range)	P value
Birds							
Buceros bicornis	22	6	7 (1–10)	0.019	2	2 (0–5)	0.019
Aceros undulatus	30	6	5 (1–11)	0.021	2	2 (0–7)	0.006
Anorrhinus austeni	2	3	3 (3–3)	–	3	3 (1–5)	–
Anthracoceros albirostris	20	2	2 (1–4)	–	4	5 (0–16)	–
Ducula badia	11	1	1 (1–2)	–	1	1 (0–1)	–
Mammals							
Ratufa bicolor	28	9	21 (2–87)	0.023	nd	nd	–
Callosciurus finlaysonii	7	7	5 (1–8)	–	nd	nd	–

Table 3. Relative dispersal importance of each frugivore species observed removing fruits of *Canarium euphyllum* in the canopy. 'Regurgitated' indicates the number of regurgitated seeds at the focal plants. None of the birds ever predated the seeds, however, both species of squirrel rarely dropped the fruits without predating the seeds.

	Estimated number of fruits handled (n)			
Species	Regurgitated	Dropped/Predated	Dispersed	Relative dispersal importance (%)
Birds				
Buceros bicornis	17	122	408	8.5
Aceros undulatus	16	483	1416	29.5
Anorrhinus austeni	0	195	195	4.1
Anthracoceros albirostris	0	529	170	3.5
Ducula badia	5	872	2615	54.4
Bird total	38	2201	4804	100.0
Mammals				
Ratufa bicolor	0	217	0	0.0
Callosciurus finlaysonii	0	686	0	0.0
Mammal total	0	903	0	0.0

1429 photographs (566 photographs in 2000 and 863 in 2001). Of these, 1099 photographs included 16 mammal and five bird species, and the remaining 330 photographs were without any animals. Seven species of mammal were recorded to consume fallen fruit (Table 4). These animals identified from photographs around the focal trees varied from one to five species in 2000 and two and five in 2002. The number of pictures taken of each frugivore species and their numbers of consumed fruits were positively correlated (Spearman rank correlation, $r = 0.991$, $P < 0.001$). The Indochinese ground squirrel (*Menetes berdmorei*) and red spiny rat (*Maxomys surifer*) were the dominant consumers in both years and were repeatedly recorded to visit the feeding platforms to collect fruits. Although we could not obtain the evidence of fallen fruit consumption by wild pig (*Sus scrofa*) and sambar deer (*Cervus unicolor*) from our camera trap, we sometimes observed that they ate fallen fruits on the ground below focal trees during our diurnal observations. Siamese fireback (*Lophura diardi*) and red jungle fowl (*Gallus gallus*) were also observed to consume the fragments of fruit pulp that had been attacked by squirrels or rodents, but never consumed the fallen fruit whole.

DISCUSSION

Dispersal of *Canarium euphyllum* in terms of quantity

As predicted from its large fruit and seed size and as reported elsewhere (Hamann & Curio 1999, Heindl & Curio 1999, Leighton 1982), only a small number of canopy frugivores consume *C. euphyllum* fruits in KY (Table 1). In other *Canarium* species, the number of frugivore species recorded in the canopy was four for *C. asperum* in the Philippine (Hamann & Curio 1999), two for *C. villosum* in the Philippines (Heindl & Curio 1999), and seven for *C. schweinfurthii* in Cameroon (French & Smith 2005). The disperser richness of *C. euphyllum* in this study, therefore, is relatively high compared with those of other known *Canarium* species. However, this richness is at the lower end of the range of values reported for other tropical trees. For example, *Virola calophylla* was consumed by 20 species of frugivores in Peru (Russo 2003), *V. sebifera* by seven in Panama (Howe 1981), *V. noblis* by eight in Panama (Howe & Vande Kerckhove 1981), *Casearia corymbosa* by 12 in Costa Rica (Howe & Vande Kerckhove 1979), *Cymbopetalum baillonii* by 20 in Mexico

Table 4. Fallen fruit consumers photographed by the automatic camera system. Species are listed in order of decreasing total number of removed fruits. Numbers in parentheses indicate the frequency (%). Neither wild boar nor sambar deer were recorded by this system but were observed to consume fallen fruits around the focal trees. nd: no data.

Species	Daily habit	Number of pictures	Number of removed fruits
Menetes berdmorei, Indochinese ground squirrel	Diurnal	440 (48.5)	106 (30.5)
Maxomys surifer, red spiny rat	Nocturnal	252 (27.8)	51 (14.7)
Callosciurus finlaysonii, variable squirrel	Diurnal	91 (10.0)	11 (3.2)
Leopoldamys sabanus, noisy rat	Nocturnal	80 (8.8)	6 (1.7)
Tragulus javanicus, lesser mouse deer	Diurnal + Nocturnal	33 (3.6)	3 (0.9)
Muntiacus muntjak, barking deer	Diurnal + Nocturnal	10 (1.1)	1 (0.3)
Rattus remotus, Sladens's rat	Nocturnal	1 (0.1)	1 (0.3)
Sus scrofa, wild boar	Diurnal + Nocturnal	nd	nd
Cervus unicolor, sambar deer	Diurnal + Nocturnal	nd	nd
Unknown		nd	168 (48.4)
Total		907 (100.0)	347 (100.0)

(Coates-Estrada & Estrada 1988), *Commiphora harveyi* by ten in South Africa (Bleher & Bohning-Gaese 2001), and *Aglaia spectabilis* by seven in Thailand (Kitamura *et al.* 2004a).

The disperser assemblage of *C. euphyllum* is relatively limited, however, the total percentage of seeds dispersed away from the trees as found for this species (61%) is comparable with other tropical tree species. The percentages reported in previous studies were 54% for *Virola calophylla* in Peru (Russo & Augspurger 2004), 76% for *Virola sebifera* in Panama (Howe 1981), 62% for *Virola noblis* in Panama (Howe & Vande Kerckhove 1981), 91% for *Casearia corymbosa* in Costa Rica (Howe & Vande Kerckhove 1979), 45% for *Cymbopetalum baillonii* in Mexico (Coates-Estrada & Estrada 1988), 71% for *Commiphora harveyi* in South Africa (Bleher & Bohning-Gaese 2001), and 40% for *Aglaia spectabilis* in Thailand (Kitamura *et al.* 2004a).

The effectiveness of frugivores in terms of seed dispersal has both qualitative and quantitative components (Jordano & Schupp 2000, Schupp 1993). The quantity of seeds dispersed by a given frugivore depends on the number of visits made to a fruiting plant and the number of seeds dispersed per visit. It depends on frugivore abundance, the reliability of visitations by the frugivore, and the importance of fruit in its diet; the latter is conditional on the number of seeds handled during each visit and their probability of being dispersed (Schupp 1993). The number of visits made by *D. badia* to fruiting trees was far greater than that of any other frugivore species (Table 1) such that, despite the small number of fruits eaten by *D. badia* per visit, the contribution of this species to the total number of fruits consumed in the canopy was great (Table 2). As both of the squirrel species were seed predators, *D. badia* was the principal consumer of *C. euphyllum* fruits in the canopy.

The length of visits and seed passage time are both important factors in determining whether a frugivore deposits a large proportion of seeds beneath the parent plant (Holbrook & Smith 2000, Howe 1977, Pratt & Stiles 1983, Wheelwright 1991, Whitney *et al.* 1998). We found that all bird species made short visits to fruiting trees (Table 1), and we rarely observed birds to deposit seeds while in focal trees (Table 3). Although we do not have sufficient data to estimate the regurgitation times for *D. badia*, the known seed regurgitation time for other *Ducula* species (*D. spilorrhoa spilorrhoa*) is 15 min (Meehan *et al.* 2003), that is longer than the short visit length of *D. badia* in this study (<8 min, Table 1). Our observations of the seed regurgitation times by hornbills (55–97 min) are consistent with previous results for some Asian hornbills (Kitamura *et al.* 2004a, Leighton 1982) as well as African hornbills (Holbrook & Smith 2000). These results support the findings that most frugivorous birds carry seeds away from the parent tree (Table 3). As most of the fruit crop was removed in the canopy, the number of fallen fruits on the ground was relatively small (about 28%, Table 3). Therefore, we consider *D. badia* to be the most effective seed disperser of *C. euphyllum* seeds in terms of quantity, followed by hornbills.

Fates of *Canarium euphyllum* seeds dispersed by animals

The effectiveness of seed dispersal is increasingly being demonstrated by studies that track the fates of deposited seeds through to the germination of seedlings or that look at the role of secondary dispersers in influencing the seed shadow (Andresen & Levey 2004, Forget *et al.* 2005, Hoshizaki *et al.* 1997, McConkey 2005, Russo 2005, Wang & Smith 2002, Wenny 2000). The quality of seed dispersal is contingent upon the treatment seeds receive and the quality of their subsequent deposition (Schupp 1993). Seed treatment includes the level, if any, of seed destruction and the alteration of germination rates; deposition quality depends on the distance, direction, habitat and microsite of seed dispersal, as well as the dispersal environment, i.e. the number and identity of co-dispersed species that could potentially compete at the seedling stage (Schupp 1993). Mountain imperial pigeons (*D. badia*) and hornbills do not defecate, but regurgitate large seeds such as those of *C. euphyllum*. As seed regurgitation by these birds in flight has rarely been observed and we found *C. euphyllum* seeds beneath different canopy trees such as large strangler figs (*Ficus* spp.) and dipterocarps (*Dipterocarpus gracilis*), we assume that birds usually deposit the seeds of *C. euphyllum* beneath the trees in which they perch.

Our study also revealed high levels of fruit consumption by terrestrial mammals below focal trees (Table 4). Camera trapping is a useful method for observing animals consuming fallen fruit (Miura *et al.* 1997, Yasuda *et al.* 2005), but there are two points, which highlight the limitations in its applicability to determining the effectiveness of potential seed dispersal in this study. First, we did not record the wild pig (*S. scrofa*) or sambar deer (*C. unicolor*), consuming fallen fruit despite their consumption of a number of fruits around focal trees. The preliminary feeding trial conducted with habituated sambar deer revealed that they consumed a considerable number of *C. euphyllum* fruits per visit and regurgitated intact seeds around the sleeping site (S. Kitamura, *pers. obs.*); our method might lead to the underestimation of the contribution of large terrestrial mammals to the depletion of *C. euphyllum* fruits on the forest floor. In addition, the continuous trials at the feeding platform may have led to an overestimation of the effects of certain mammals such as *Menetes berdmorei* and *Maxomys surifer*, which were repeatedly recorded within single trial periods. Secondly, we were unable to follow the fates of seeds. The consumption of fallen fruits and the dispersal by terrestrial

Table 5. Comparison of the frugivore assemblages of large-seeded plants in KY. The numbers in parentheses indicate the number of species in each frugivore group reported from KY. Data for *Aglaia spectabilis* are referred from Kitamura *et al.* (2004a) and the tolerance to human impacts are referred from Corlett (2002).

	Plant species			
Frugivore group	*Canarium euphyllum*	*Aglaia spectabilis*	Tolerance to human impacts	Effects on seeds
Hornbills (4)	4	4	Low	Disperser
Imperial pigeons (2)	1	1	Low	Disperser
Deer (2)	2	0	Low/Middle	Disperser
Mousedeer (1)	1	0	High	Disperser
Wild pig (1)	1	0	High	Predator
Squirrels (9)	3	2	High	Predator (Disperser?)
Rodents (7)	3	1	High	Predator (Disperser?)
Porcupines (2)	0	1	Middle	Predator
Total number of species	15	9		

animals may be important processes of seed dispersal in South-East Asia (Corlett 1998, Yasuda *et al.* 2000) as well as in KY (S. Suzuki, unpubl. data). We have previously reported the scatter-hoarding behaviour by *Maxomys surifer* for *Aglaia spectabilis* (Meliaceae) in KY (Kitamura *et al.* 2004a), but the effectiveness of this species was not clear. Our observations for *C. euphyllum* suggest that some stones of the fruits removed by *Menetes berdmorei* were scatter-hoarded around the fruiting trees. The seeds of most *C. euphyllum* stones were predated within 1 wk; however, some stones remained in the soil for 22 mo (S. Kitamura, unpubl. data). Several seedlings establish themselves around the fruiting trees of *C. euphyllum* each year in the rainy season, which suggests that some seeds beneath fruiting trees escape predation. To evaluate the fates of these dispersed seeds, further study is required to follow the fates of post dispersal seed survival in *C. euphyllum*.

Implications for conservation of large-seeded plants

In this study, we have shown that large-bodied frugivores in the species-rich Thai forests can provide effective seed dispersal services for a large-seeded tree, *C. euphyllum*. The exact dispersal agents of *C. euphyllum* are almost certain to be different in different seasons and in different parts of the species range. In KY, mountain imperial pigeons and hornbills seem to be potentially important seed dispersers. In most parts of tropical Asia, these species are the largest frugivorous birds (Corlett 1998, Leighton 1982) and share very similar diets, especially among large-seeded fruits (Hamann & Curio 1999, Heindl & Curio 1999, Kitamura *et al.* 2002). In terms of the number of frugivore species, the frugivore assemblage that consumes the fruits of *C. euphyllum* is diverse, compared with other large-seeded tree, *Aglaia spectabilis* (Table 5). Large, canopy-dwelling, frugivorous birds are one of the major seed-dispersal agents for this species as well as for *A. spectabilis*; however, terrestrial mammals such as deer also consume fruits and apparently disperse *Canarium* seeds.

The dispersers of *C. euphyllum* seeds have particularly low tolerance to the effects of deleterious human activities (Table 5), and thus this plant species is prone to the loss of its main seed dispersers in KY and elsewhere. Large frugivorous animals such as imperial pigeons and hornbills, as well as sambar deer, are declining in numbers in the fragmented forests of northern Thailand (Pattanavibool & Dearden 2002), and many other large frugivore species are considered to be vulnerable to extinction as a result of hunting pressure and habitat loss in Thailand (Lekagul & Round 1991, Poonswad 1993) and across South-East Asia (Bennett *et al.* 1997, Corlett 2002).

Tropical forest plants may persist in fragmented and degraded landscapes for decades or centuries, but they rarely contribute to future generations after their seed dispersers are extinct (Corlett & Hau 2000). Even if local extirpation of large frugivorous animals does not occur, imperial pigeons and hornbills may no longer provide effective seed dispersal, in both quantitative and qualitative terms, once they have been reduced to meagre numbers or driven to ecological extinction (Redford & Feinsinger 2001). The current faunal assemblages of South-East Asia are already diminished in many places (Sodhi *et al.* 2004), and it may be possible that some plant species rely on a very limited number of frugivorous species for the dispersal of their seeds (Corlett 2002). The results from other studies in tropics (Chapman & Onderdonk 1998, Cordeiro & Howe 2003, Ganzhorn *et al.* 1999, Marsh & Loiselle 2003) are consistent with the idea that a loss of dispersal agents depresses plant recruitment following forest fragmentation and hunting. In these circumstances, failed fruit–frugivore interactions may be expected to accelerate the losses of plant diversity from the landscape over the long term.

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