Research Article

Phenology, seed dispersal and regeneration patterns of *Horsfieldia kingii*, a rare wild nutmeg

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Abstract
We present observational data on the flowering and fruiting patterns, seed dispersal, seedling recruitment and survival of a dioecious Myristicaceae species, *Horsfieldia kingii,* that occurs in the tropical forests of Arunachal Pradesh. *Horsfieldia* is rare (1 tree ha^{1}) with a scattered distribution; *Horsfieldia* trees did not flower every year, and flowering was staggered from April to July. Peak ripe fruit availability of *Horsfieldia* is from February to March. Failure of fruiting occurred in most years, and only 0-33% of sampled trees bore ripe fruits. Initiation of hornbill breeding coincides with the ripe fruit availability of this species. The percentage of hornbill nests in which nesting is initiated each year varies from 50 to 100% of nests, and our results show a significant positive relationship between the percentage of hornbill nests that are active in a given year and the contribution of the species to hornbill diet (n = 6 years). However, the overall contribution to the breeding season diet of hornbills is very low because of poor fruit availability in most years, resulting in limited seed dispersal at nests. Recruitment and survival of *Horsfieldia* seedlings below parent trees and hornbill nest trees were low; however, seedling survival was marginally higher at nest trees, suggesting that dispersal by hornbills even in a spatially contagious manner may be critical for this species. However, current recruitment of *Horsfieldia* at hornbill nests (2010) is significantly lower than at parent trees. This species appears to be seed-limited, while dispersal limitation may play a secondary role in determining its abundance.

Keywords: hornbills; *Horsfieldia kingii*; flowering pattern; fruiting pattern; Myristicaceae; seed predation; seedling survival, recruitment

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Introduction

Interactions between animals and plants have been an important evolutionary driver in both groups of organisms in tropical forests, where tree diversity is higher [1] and herbivore pressure is greater [2,3], and animal-dispersal of seeds is much greater [4, 5]. Dispersal is particularly important for plants, because the probability of recruitment is higher away from the parent and other conspecifics [6-8]; animal-dispersed trees tend to be dispersed farther and have less aggregated distributions than species dispersed by other means [9]. Therefore, trees produce fruits with bright attractive colors and high resource content [4] to encourage dispersal by animals, and many seeds can only germinate following passage through an animal’s digestive tract [10]. The pantropical Myristicaceae are a classic example of an animal-dispersed tree family, with large seeds enclosed in a brightly-colored nutrient-rich aril. In this paper, we examine phenology and regeneration in a classic animal-dispersed tropical tree species, and ask how interactions with animals determined variation in recruitment and abundance.

The supra-annual fruiting of many tree species, as well as periods of general fruiting failure, are documented features of tropical lowland forests [11-16]. The dependence on insect pollinators and the prevalence of a dioecious breeding system with male-biased sex ratios [17-20] have consequences for the flowering and fruit production patterns of many species, which can often be pollination-limited [18]. Flower abscission and abortion of unripe fruits resulting in low fruit set are common and affect subsequent seed availability, with further consequences for frugivore consumption, seed dispersal, and recruitment.

A number of studies have examined how processes such as phenology [16, 21], dispersal [7, 9], and abiotic and biotic neighborhoods [7, 8, 22] influence the distribution and regeneration of tree species. However, many of these are conducted at the community-level, and thus are heavily biased by information from common species. To better understand the mechanisms governing rare species, focused studies are required. We studied a rare species from the animal-dispersed tree family, Myristicaceae, the large seeds of which are dispersed both by primates [30-32] and by an assemblage of large frugivorous birds including toucans and guans [23-26], hornbills and pigeons [27-29]. Most Myristicaceae are dioecious, a breeding system associated with small inconspicuous flowers, a generalist insect pollination syndrome and frugivorous seed dispersal [33]. Further, many species of Myristicaceae are rare, occurring at densities of <1 reproductive tree/ha [34], although they do attain higher abundances in some areas [35]. India has 4 genera and 18 species; several species found in the Western Ghats and the Andaman Islands are dominant species in dipterocarp-forests and swampy habitats [36-39]. However, floristic studies from Eastern Himalaya sites have reported low densities of Myristicaceae species of < 1 to 2 trees/ha [40-42].

We present observational data from two different study periods (1997-1999 and 2009-2011) on the flowering and fruiting patterns, seed dispersal, seedling survival, and recruitment patterns of *Horsfieldia kingii,* which occurs in the tropical forests of Arunachal Pradesh, north-east India.

We quantified the arrival of seeds of *Horsfieldia* at hornbill nests (a primary seed deposition site during the breeding season) over the two study periods to characterize the extent of seed dispersal. We also measured the recruitment and monitored seedling survival of the species at nest sites and below parent trees, where recruitment and survival are expected to be low due to Janzen-Connell effects [2, 3]. We asked the following questions: 1) What is the extent of annual variation in flower/fruit production? 2) Does failure of fruiting in this species affect hornbill breeding? 3) Does this affect seed arrival at hornbill nests? 4) What are the patterns of recruitment and survival at nests and at parent trees?

Methods

Study site

The study was conducted in Pakke Wildlife Sanctuary and Tiger Reserve (862 km^2, 92°36’ – 93°09'E and 26°54 – 27°16'N) in the foothill forests of western Arunachal Pradesh, in the Eastern Himalaya, a global biodiversity hotspot [43]. The park is surrounded by contiguous forests on most sides and bounded by rivers in the east, west, and north. The terrain is undulating and hilly, with altitude ranging from 150 m to about 2,000 m above sea level. The area has a tropical and subtropical climate, with cold weather from November to February. It receives rainfall from the southwest monsoon (May-September) and the northeast monsoon (December-April). October and November are relatively dry. May and June are the hottest months. The monsoon lasts till September, but occasional rains occur throughout the year. The southwest monsoon is responsible for more than three-quarters of the annual rainfall. Thunderstorms occasionally occur in March-April. The average annual rainfall is 2,500 mm. The mean (± SD) maximum temperature was 29.3ºC ±4.2 and the mean minimum temperature was 18.3º ± 4.7, based on data from 1983 to 1995 recorded by the Tipi Orchid Research Centre. The vegetation of the reserve is classified as Assam Valley tropical semi-evergreen forest 2B/C1 [44]. The forests are multi-storied and rich in epiphytic flora, woody lianas and climbers. Major emergent species include *Tetrameles nudiflora* (Datiscaceae), *Ailanthus grandis* (Simaroubaceae) and *Altingia excelsa* (Hamamelidaceae). The lower elevation forests are dominated by *Polyalthia simiarum* (Annonaceae), *Pterospermum acerifolium* (Sterculiaceae), *Sterculia alata* (Sterculiaceae), *Stereospermum chelonoides* (Bignoniaceae), *Ailanthus grandis* and *Duabanga grandiflora* (Sonneratiaceae). Evergreen species include several middle-story trees in the Lauraceae and Myrtaceae. Subtropical broadleaved forests occur at higher elevations, while bamboo, cane and palms are common near perennial streams. Along larger streams and rivers, there are patches of tall grassland. The intensive study site (*ca.* 12 km^2) was located in the southeastern part of the park in the lower elevation moist deciduous and semi-evergreen forests (150 - 600 m).

Study species

Horsfieldia kingii (Hook.f.) Warb. is a dioecious evergreen tree, generally 10-12 m in height. The branches are usually crowded on top of the trunk and somewhat horizontal. The small staminate and pistillate flowers of the *Horsfieldia* genus are similar to species of *Myristica* and *Knema* [45]. The fruits are solitary, supported by a persistent perianth with a pericarp that is thick and leathery. The cream-colored ovoid seed is enclosed by a bright yellow entire aril. In north-east India, fruiting has been reported to be in June [46]. The fruits dehisce on ripening. The fruit and seed are edible and used as a substitute for betel nut. The density of *Horsfieldia* in the study area was 1.14 trees/ha (21 plots of 0.25 ha each) and the variance to mean ratio was 7.2 [47-49].

Flowering and fruiting patterns of Myristicaceae species

We used data from two long-term phenology censuses. In the first census, we extracted data for *Horsfieldia kingii* (*n* = 6 trees) from a community-level phenology study where all stems >30 cm girth at breast height in twenty-one 0.25 ha plots were monitored once a month between February 1997 and July 1999 [49]. For each tree, flowers, unripe fruit, semi-ripe fruit and ripe fruit were scored as 1 if present and as 0 if absent. In the second census, we tagged 20 *Horsfieldia kingii* trees in August 2009 (adding four more in December 2010) along trails, and monitored these as above until December 2012. We could not accurately determine the sex of tagged individuals by examining the small flowers, but if the individual bore ripe fruit for several years, we assigned the sex as female.

Contribution of Myristicaceae species to hornbill diet (1997-2000)

The breeding season of the three species of hornbills in the area (Great Hornbill *Buceros bicornis*, Wreathed Hornbill *Rhyticeros undulatus* and Oriental Pied Hornbill *Anthracoceros albirostris*) spans several weeks from March (entry into the nest by the female) to July (female and chick emergence). Ripe fruits of *Horsfieldia* are usually available from February to April. Hornbill diet in the breeding season was determined from observations of male visits and food delivery to the nest. The male hornbill delivers fruits to the female and chicks at the nest, and seeds subsequently regurgitated by the female and chicks are ejected out of the nest cavity, resulting in seed deposition below nests. Some seeds are also regurgitated and dropped by the male hornbill when he perches at the nest tree during his visits. This concentration of seeds below nests is called a midden. We used a combination of two methods, middens and nest watches, to quantify the diet of hornbills at 23 nests between 1997 and 2000. The area of the seed rain was marked and periodically cleared of leaf litter, and the regurgitated seeds were collected and counted. The disadvantage of the midden method is that some regurgitated seeds are removed or preyed upon by rodents and insects; however, most nests were checked every 2-3 days, minimizing this possibility. In 1997 and 2000, diet was determined from both methods, while in 1998 and 1999 diet was determined solely from seed counts at middens.

Seed arrival at hornbill nests (2010-2011)

In 2010, seed arrival (or seed dispersal by hornbills) was sampled at five hornbill nests (three Wreathed Hornbill and two Great Hornbill) during the breeding season of hornbills from March to mid-July (19 weeks), using seed traps instead of direct counts on the ground. All nest trees were *Tetrameles nudiflora*, a wind-dispersed emergent tree that is the main species used in the area by hornbills for nesting [47]. The 2010 breeding season commenced in the first to third week of March with nest entry dates between 3 and 28 March.

In 2011, we monitored six nests (three Wreathed Hornbill, one Great Hornbill, two Oriental Pied Hornbill) and nest entry occurred by the first to second week of April. We used the first six weeks of data on seed rain up to the beginning of May, as fruiting of *Horsfieldia* was low and finished by May.

Seed rain (regurgitated dispersed seeds) at hornbill nests occurs within a 2 - 5 m radius, with maximum seed rain occurring on the ground in front of the nest cavity. Two seed traps of 1m^2 were set up directly below the cavity of each nest in the area where maximum seed rain occurred. The seed traps were made of fine nylon mesh and strung to poles that were raised 1.5 m above the ground. Seed rain was monitored weekly with counts of seeds of each species falling into the traps at each nest. Given that most of the seed rain falls in a small concentrated area below the nest, two seed traps of 1 m^2 per nest were adequate to sample the seed rain at hornbill nests.

Hornbill nesting

We have a long-term hornbill nest-monitoring program (1997-2000 and 2003 to present) at the study site. Prior to the breeding season, regular visits were made to known nests every year during February-March to determine whether nesting had been initiated (visits by hornbill pairs, inspection and cleaning, followed by female entry and cavity sealed). Nest trees in which nesting had been initiated were checked occasionally throughout the breeding season to monitor whether the nest had remained active. Nesting attempts were defined as the number of nest trees in which nesting was initiated out of the total known nest trees in that year. Towards the end of the breeding season (mid-June to August), we visited all active nests every two to three days to obtain information on nest exit dates, nesting success, and number of chicks fledged. Overall nesting success was defined as the percentage of initiated nests that fledged young.

We used these data to examine the relationship between the percentage of hornbill nests where nesting was initiated (active) in a given year and: a) percentage of *Horsfieldia* fruits in diet, b) percentage ripe fruit availability of *Horsfieldia*, and c) average non-fig diet species richness in same year using Spearman's rank correlation. We used data for six years (1997-2000 and 2010-2011) where we had corresponding data on fruiting phenology. We also examined the relationship during twelve years between percentage of active nests and total rainfall in the previous six months before the initiation of breeding. Rainfall data at a sub-divisional level were downloaded from the Indian Institute of Tropical Meteorology, Pune [ftp://www.tropmet.res.in/pub/data/rain/iitm-subdivrf.txt].

Recruitment at hornbill nests and parent trees

In 1998, seedlings and saplings were enumerated in 5-m radius plots (plot area: 78. 57 m^2) around six *Horsfieldia* parent trees and in similar-sized plots in front of the cavity below six nest trees of two hornbill species (two Great Hornbill nests and four Wreathed Hornbill nests). We enumerated all seedlings/young saplings (≤ 50 cm), larger saplings (≥ 50 cm to ≤1 m) and poles (≥ 1 m to 3 m) of all hornbill food plant species at six nests.

In 2010, seedlings and saplings were counted below five different female *Horsfieldia* parent trees in 5-m radius plots. We also quantified the recruitment in 5-m radius circular plots in front of the cavity of 21 hornbill nest trees (eight Wreathed Hornbill, seven Great Hornbill, six Oriental Pied Hornbill). We enumerated all seedlings/young saplings (≤ 50 cm), larger saplings (≥ 50 cm to ≤1 m) and poles (≥ 1 m to 3 m) of all hornbill food plant species at 21 nests.

Seedling survival: hornbill nests and parent trees

A total of 38 *Horsfieldia* seedlings were tagged below four parent trees of *Horsfieldia*, and 26 seedlings were tagged below five hornbill nest trees. All seedlings were tagged and numbered consecutively. Seedlings were monitored from October 1998 to July 2000 (22 months). The seedling cohorts that were tagged below nest trees and parent trees in 1998 were monitored about 2-4 months after germination. Towards the end of March 1999, due to the occurrence of a fire, 15 seedlings (13 at nests and two at parents) died.

Results

Flowering and fruiting patterns: 1997-1999 and 2009-2011

The GBH of trees monitored for phenology is given in Table 1. Of six trees monitored for phenology in 1997-1999, three trees never bore flowers or fruit, one tree was recorded flowering but never with fruit, while the remaining two bore ripe fruit and were considered as females. Out of 24 sample trees monitored for phenology during 2009-2012, three never flowered or fruited. Eight trees flowered but were not seen to bear fruit and may possibly be male, while 13 trees flowered and bore fruit (though five of these trees were only seen with unripe fruit). These 13 trees are considered to be female.

Horsfieldia kingii: In 1997, flowering was noted between May and June, while flowering was not recorded in 1998 and 1999 (n = 6). In 2009-12, a few individuals with flowers were seen in other months, but the peak flowering was noted in June and July in 2010 and between April and June in 2011 (Fig. 1).

Table 1. Fruit characteristics, tree density, dispersion pattern, and size of trees monitored for phenology.

Species	Mean fruit weight (g)	Mean fruit size (mm)	Mean seed size (mm)	Tree density ha) (Mean ± SD)	Variance to mean ratio (index of clumping)	Mean GBH (cm)
Horsfieldia kingii	9.1	35.8 X 21.6	35.7 X 20.2	1.1 ± 2.9	7.2	107.3 (1997-1999) 121.8 (2010-2011)

Unripe fruits were recorded from August 1997 to February 1998. In the later study period, unripe fruits of *Horsfieldia* (5%) were noted in September 2009, while in 2010-11, unripe fruits were noted from August 2010 to February 2011, with a peak in January 2011. In 2011-12, unripe fruit availability was recorded from August 2011 till March 2012, with a peak in September 2011 (37.5% of trees).

Ripe *Horsfieldia* fruits were available from February to May, with peak ripe fruiting in February to March. Ripe fruits of this species were only recorded in 1997 and 1998 (16.67% in both years), while in 1999 there was a failure of fruiting (Fig. 1).

Phenology monitoring of *Horsfieldia* was initiated from August 2009, by which time the fruiting season was over, but casual observations suggested that fruiting was low in 2009. In 2010, fruiting was again low (10%) in April, and delayed fruiting from July to October was noted on one individual (n = 20 trees) (Fig. 1). In 2011, very low ripe fruit availability was noted from February to March (4.2%). In 2012, ripe fruit availability was noted from February to March with a high of 33.33% of *Horsfieldia* trees in ripe fruit.

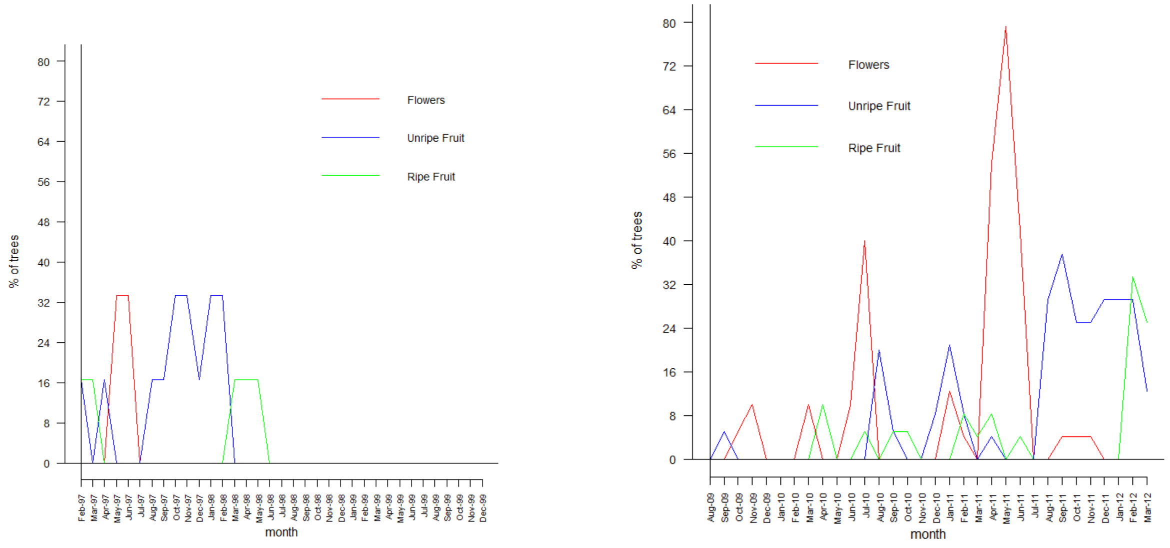

Fig. 1. Flower, unripe fruit and ripe fruit availability patterns of *Horsfieldia kingii* in (a) 1997-1999 (n = 6 trees) and (b) August 2009 - March 2012, (n = 24 trees).

Contribution of Horsfieldia to hornbill diet

Thirty-five non-fig species were recorded during four breeding seasons (1997-2000) at 23 nests (ten Wreathed Hornbill, nine Great Hornbill, four Oriental Pied Hornbill nests). Although 35 species were recorded in the diet, 98% of the non-fig fruit diet was contributed by 16 species. Overall, in 23 nests over four breeding seasons, *Horsfieldia kingii* formed only 1.05% (± 1.25) of the diet in terms of number of fruits delivered at nests and was ranked 11 among the total 35 species in the diet. The contribution of *Horsfieldia* varied from 0.02 to 2.88% of non-fig diet in different years and was dependent on ripe fruit availability (Fig. 2). In 1999, there was a failure of fruiting of this species with no ripe fruit recorded on our sample trees. Six hornbill nests were monitored in 1999 and no *Horsfieldia* fruits were delivered at four hornbill nests, while it formed a negligible part of the diet at two other nests.

Horsfieldia formed 1.49% of the non-fig diet of the Great hornbill, 0.98% of the diet of Wreathed hornbill and 0.24% of the diet of Oriental Pied hornbill. The latter may be an underestimate, as Oriental Pied Hornbill nests were only observed in 1999 and 2000 when there was low fruiting of *Horsfieldia*.

Seed rain at hornbill nests (2010-2011)

We compared the seed rain between 2010 and 2011 for the first six weeks from onset of nesting (March-end till May). A total of 2,010 seeds of nine hornbill food plant species were recorded at the five hornbill nests in the breeding season of 2010. Five species were deposited at all nests (*Polyalthia simiarum*, *Aglaia spectabilis*, *Cryptocarya amygdalina*, *Chisocheton cumingianus, Dysoxylum binectariferum*), while four species were recorded at some nests. No *Horsfieldia* were recorded in seed traps set up below nest trees in 2010. In 2011, eleven hornbill food plant species were recorded in the seed rain at six nests until the first week of May. *Horsfieldia* fruits formed 0.97% of the total seed rain in 2011.

During the several years of data on seed rain, the mean contribution of *Horsfieldia* seeds to the total seed rain at hornbill nests was very low, with negligible seed rain in 1999 and none in 2010, when there was a failure of fruiting (Fig. 2).

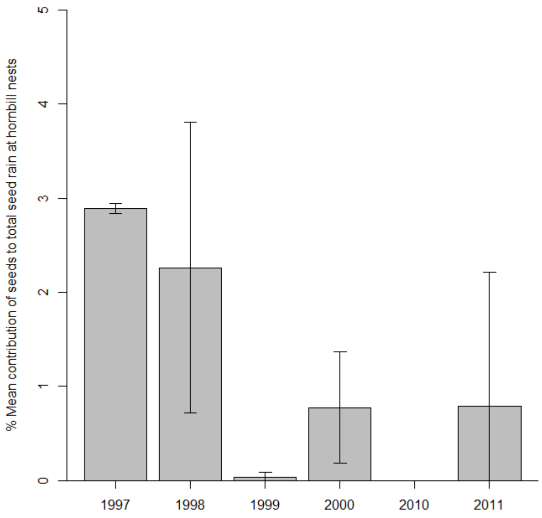

Fig. 2. Mean contribution (± SD) of *Horsfieldia* seeds to total seed rain at hornbill nest trees during the breeding season. Data is from seed counts on the ground below 23 hornbill nest trees (1997-2000) and from seed traps below 11 hornbill nest trees in 2010-2011.

Hornbill nesting and fruiting of Horsfieldia

The percentage of nests that were active (where nesting was initiated) was variable in most years (50-90%), with relatively low percentages of nesting in 1999, 2005, 2010, and 2011, when nesting was initiated in only 50-63% of nest trees (Table 2). The total rain in the previous six months (September to February) prior to initiation of breeding season was also low in these years (Table 2), but there was no significant relationship ($r_s = 0.30$, $p > 0.05$, $n = 12$ years).

Table 2. Annual variation in hornbill nesting attempts, success and in fruit consumption and ripe fruit availability.

Year	Number of nests monitored	Percentage of active nests (%)	Percentage nesting success (%)	Percent *Horsfieldia* contribution to diet	*Percent ripe fruiting *Horsfieldia*	Mean non-fig diet species	**Total rain before breeding season (mm)
1997	2	100	50	2.89	16.7	8	511
1998	19	84	81	2.26	16.7	15	487
1999	16	50	100	0.03	0	7	369
2000	17	65	100	0.77	0	13	576
2003	9	67	100	*ND*	*ND*	*ND*	441
2004	29	76	*ND*	*ND*	*ND*	*ND*	539
2005	36	58	62	*ND*	*ND*	*ND*	635
2006	46	70	87	*ND*	*ND*	*ND*	422
2007	11	90	80	*ND*	*ND*	*ND*	639
2008	23	65	100	*ND*	*ND*	*ND*	585
2009	30	70	96	*ND*	*ND*	*ND*	373
2010	30	63	89	0	10	7	304
2011	31	55	70	0.97	8	7	405
2012	33	84	93	-	33	-	261

* Maximum fruiting in a given month
** Rainfall over a previous six-month period (September to February)
ND: No data

Although the sample size was low, there was a significant positive relationship between percentage of active nests in a given year and the percentage of *Horsfieldia* contribution in the diet ($r_s = 0.916$, $p < 0.05$, $n = 6$, Fig. 3), but not the percentage of ripe fruiting *Horsfieldia* trees ($r_s = 0.802$) or the average non-fig diet richness in that year ($r_s = 0.354$).

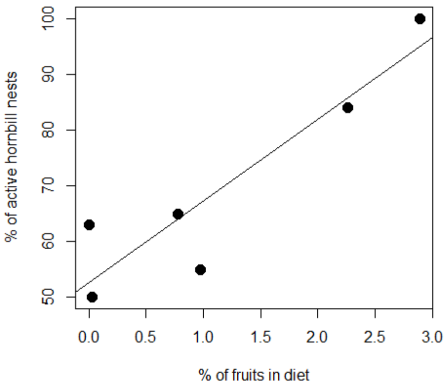

Fig. 3. Scatterplot showing the relationship between percentage of active hornbill nests and percentage of *Horsfieldia* contribution to the diet (n = 6 years).

Recruitment of Horsfieldia at hornbill nests and parent trees

Seedling density at parent trees ranged from 0 to 5.32 individuals/m^2 with an average density of 0.9184/m^2 (n = 6). However, if a single plot with unusually high recruitment of 5.32/m^2 is removed, the mean density at parent trees was much lower (0.0382/m^2 ± SD 0.045). The mean density of *Horsfieldia* recruits at nest trees was 0.0573/m^2 ± SD 0.043. However, there was no significant difference in densities between nest and parent trees (Mann-Whitney U test = 9, p = 0.329, n = 5, Fig. 4).

In 2010, seedling density around parent trees was 0.0254/m^2 ± SD 0.0238 (n = 5). Mean seedling/sapling density around 21 nest trees was 0.0061/m^2 ± SD 0.0153, ranging from 0 to 0.0509/m^2. Recruit density was significantly higher at parent trees than at nest trees (Mann-Whitney U test = 20.5, p = 0.034, Figure 4). In 2010, regeneration of 19 hornbill food plant species was recorded below hornbill nests, with 11 species comprising 95% of the total recruitment; *Horsfieldia* seedlings/saplings comprised only 0.84% of total recruitment at 21 hornbill nests with no *Horsfieldia* recruitment at 17 hornbill nests. The densities of seedlings/saplings and poles were very low (< 0.004/m^2) below nest trees in 2010 (Fig. 5).

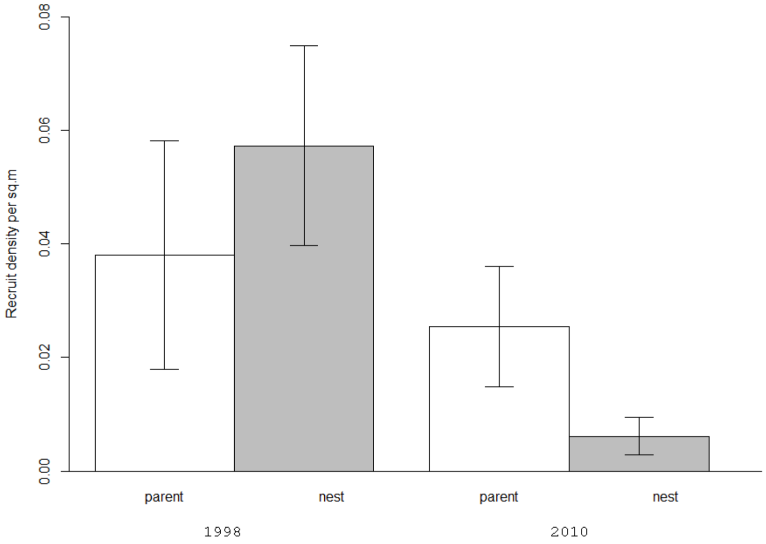

Fig. 4. Total recruitment below parent trees and hornbill nest trees of *Horsfieldia kingii* in 1998 and 2010 (n = 5 parent trees in 1998 and 2010, n = 6 nest trees in 1998, n = 21 nest trees in 2010). Error bars represent standard error of the mean.

Seedling survival: hornbill nests and parent trees in 1998

The pattern of mortality of seedlings of *Horsfieldia* at nest and parent trees over 22 months was similar until the sixth month (Fig. 6). At nest trees, due to an unusual fire event, 50% of the total seedlings died at 5-6 months in March 1999. However, following this, there was no further mortality of remaining seedlings, with 19% survival by the end of the 22-month monitoring period (Fig. 6). At parent trees, by the end of the sixth month, 26% of seedlings had died, which increased to 92% by one year, and by the 20th month, all seedlings had died.

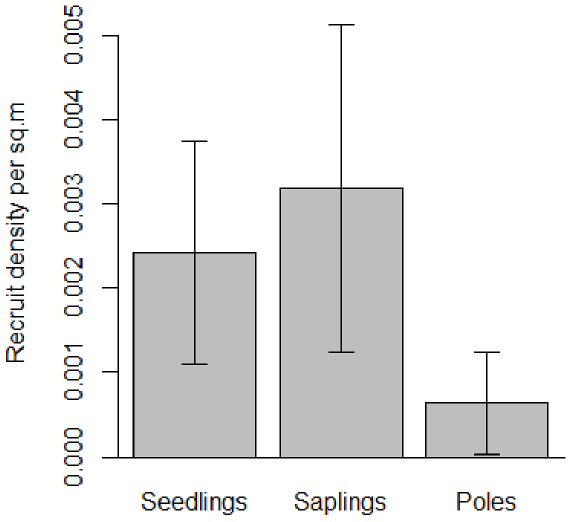

Fig. 5. Recruitment of seedlings, young and large saplings of *Horsfieldia kingii* below hornbill nest trees in 2010 (n = 21 trees). Recruitment was measured in 5 m radius plots in front of the hornbill nest cavity in 2010. Errors bars represent standard error of the mean.

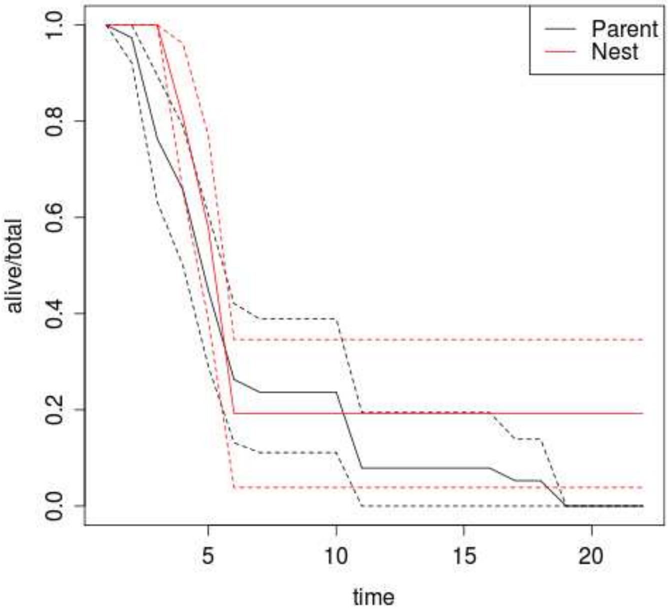

Fig. 6. Survival of tagged seedlings of *Horsfieldia* at hornbill nests (n = 4 trees, 38 seedlings) and parent trees (n = 5 trees, 26 seedlings) monitored for 22 months from October 1998 to July 2000. The dashed lines represent the 95% confidence intervals that are based on 100,000 bootstrap samples of the data at each time period.

Discussion

The flowering and fruiting patterns of *Horsfieldia* show considerable annual variation, with failure of fruiting or very low fruit availability in some years. Although we did not measure pollination rates, the poor fruit set may be partly due to pollination failure [18]. Estimates of tree density of *Horsfieldia* in the study area range from 0.54 trees/ha [50] to 1.14 trees/ha [49], and it has a scattered distribution, with mean nearest neighbor distance between adult trees estimated to be 131 m [50]. The distances between male and female trees are likely to be even greater, potentially affecting pollination rates [34]. Although the sample of trees for *Horsfieldia* was small in the earlier study period, no flowering was

recorded in 1998 and 1999, while fruit production failed in 1999. *Horsfieldia* fruits ripen along with the arillate capsular dehiscent fruits of three other Meliaceae during February to May [47]. There was a general failure of fruiting in 1999 when many arillate large-seeded fruits of Meliaceae also did not bear fruit [49], suggesting a more widespread phenomenon, such as supra-annual cycles in fruiting patterns.
In 2010, with a larger sample of *Horsfieldia* trees, we found a very unusual pattern: a few trees had ripe fruit in April, while some trees were found with unripe and ripe fruits later in the season from July to September. 2011 was also a low fruiting year, with only 4-8% of trees in ripe fruit. After three years of very low fruiting, 33% of trees were recorded to be fruiting in February-March 2012. Although we did not measure seed production, the inter-annual variation with years of zero or low fruiting and 17-33% trees in fruit in other years suggests that *Horsfieldia* is possibly a mast fruiting species.

There was poor fruit availability for hornbills in the breeding season of 1999, especially of non-fig fruits, which may have resulted in lower nesting. In 1999, breeding attempts by Wreathed hornbills (more of a non-fig fruit specialist than the Great hornbill) may have been fewer because of a lower fruit availability in the preceding non-breeding season (which may have been tied to poor rainfall [49]). Phenological data are not available for 2005; therefore the reasons for lower nesting in 2005 cannot be determined. In the later study period, there was low fruiting of *Horsfieldia* and other important non-fig hornbill food plant species in the breeding seasons of 2010 and 2011 when the percentage of active nests was relatively low (55-63%). Nesting success is generally high in hornbills, with 80-100% of active nests being successful (chicks fledging at the end of the season). 2005 and 2009 were the only years that nesting success was relatively low, with 63% and 70% of active nests being successful.

Large avian frugivores (hornbills and Mountain Imperial pigeons) consume the aril and regurgitate the seeds. They are the primary consumers and dispersers of *Horsfieldia*, and ripe fruit availability (February to April) coincides with the early part of the breeding season of hornbills (March to August). Although the species is ranked among the top fifteen species in the diet of hornbills [49], its overall contribution to the breeding season diet (1997-2000, 2010-2011) was low because ripe fruits were not available every year. Fruiting of *Horsfieldia* was absent or very low in 2010-2011, resulting in very limited seed rain of the species at hornbill nests. The species is also not recorded at all monitored hornbill nests due to the patchy availability of fruiting trees for foraging hornbill males. This patchy availability is reflected in the fact that out of 23 nests monitored in four years, there was low seed rain of *Horsfieldia*, which was recorded in only 17 nests, while in 2010, there was no seed rain at nests. Recruitment of seedlings and saplings from earlier years also reflected this with zero recruitment in 17 out of 21 nests in 2010. Poor fruit availability results in limited seed dispersal or seed rain at hornbill nests in most years. However, seeds that fall beneath nest trees are also vulnerable to predation by rodents. Recent studies have established the high levels of predation by rodents on *Horsfieldia* seeds [50, 51].

A combination of seed limitation and dispersal limitation (due to spatially contagious seed deposition) results in low recruitment at nest trees compared to other food plant species. Among eight important hornbill food plant species, *Horsfieldia* had the lowest seedling density around parent trees and nest trees [49]. Recruitment around nest trees was marginally higher than at parent trees in 1998, and we found that seedling survival was marginally higher at nest trees than parent trees, suggesting that dispersal by large avian frugivores is critical for this species, although recruitment remains poor.

Contrary to expectations, however, when we re-quantified recruitment around a larger sample of nest trees in 2010, nest trees were found to have significantly lower recruitment of the species than parent trees. The variability in seed deposition at nest trees and in seed and seedling survival possibly results in an inconsistent pattern of recruitment.

The sporadic and supra-annual fruiting of the species and limited set of dispersers, combined with overall high seed predation at parent trees and even at certain deposition sites by its main dispersers, are probable factors in the rarity of this species in the wild. The abundance and distribution patterns of this species appear to be shaped by several interacting factors such as irregular flowering and fruiting patterns and sporadic and limited seed dispersal, further compromised by high seed predation and poor recruitment and survival.

This species exhibits high variability in flowering and fruiting patterns, with several years of complete failure in flower/fruit production, but when available, they are consumed and dispersed by a limited set of dispersers. *Horsfieldia* is subject to heavy seed predation, and seed rain and recruitment are poor around aggregated dispersal sites such as hornbill nest trees relative to other food species that are also dispersed at nests (Fig. 7). Survival of seedlings was found to be higher at nest trees, suggesting that dispersal may confer an advantage despite the high seed predation at these spatially clumped seed deposition sites. However, the spatial and temporal variation in seed rain results in overall poor recruitment at nest trees.

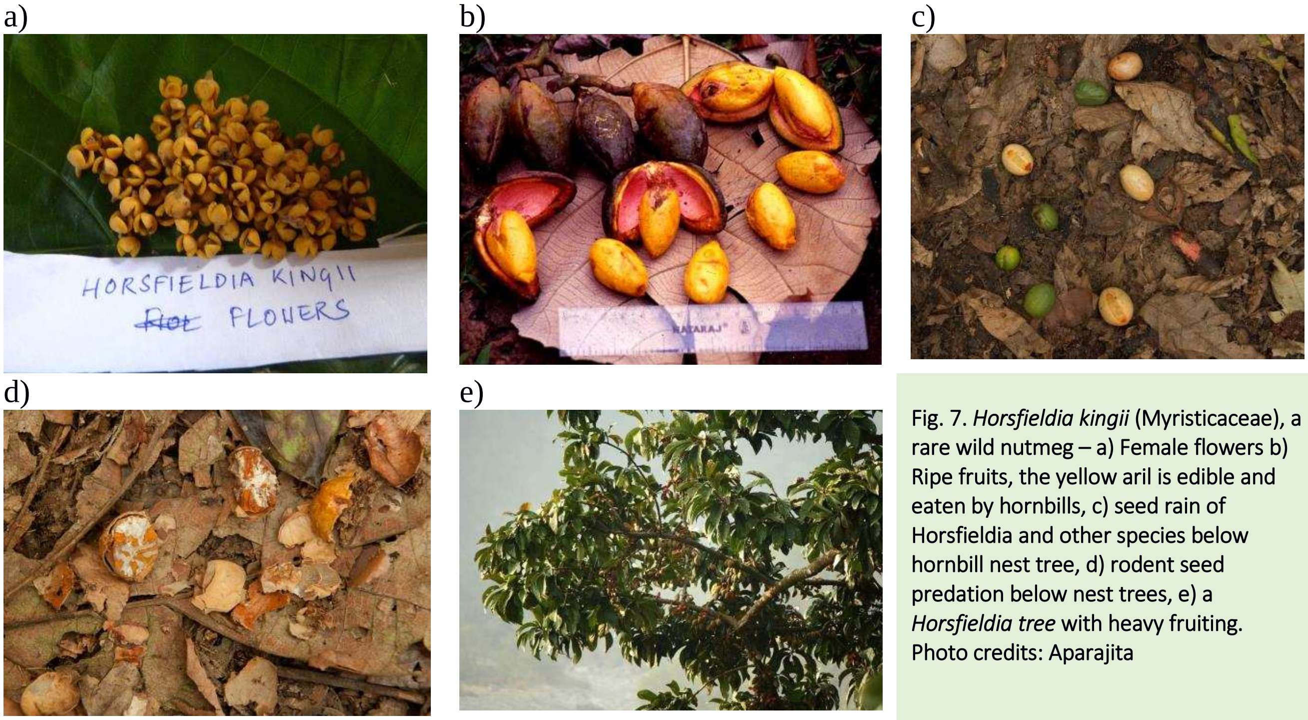

Fig. 7. *Horsfieldia kingii* (Myristicaceae), a rare wild nutmeg – a) Female flowers b) Ripe fruits, the yellow aril is edible and eaten by hornbills, c) seed rain of Horsfieldia and other species below hornbill nest tree, d) rodent seed predation below nest trees, e) a *Horsfieldia tree* with heavy fruiting. Photo credits: Aparajita

Based on our results, we hypothesize that the abundance and distribution of *Horsfieldia* are shaped primarily by biotic factors and that *Horsfieldia* is seed-limited and dispersal-limited (due to spatially contagious seed deposition), resulting in poor recruitment and low adult tree densities.

Future studies should focus on determining the factors causing the sporadic and supra-annual fruiting, with no fruit set in some years; on determining the pollination system of this species; and on understanding the flowering schedules of male and female trees and the inter-sex differences in size and abundance. The consequences of a skewed sex ratio and large distances between adults of opposite sexes for successful pollination also need to be examined. Further studies of inter-annual variation in seed production are needed to determine whether the species is a mast fruiting species [21]. Seed predation is an important factor affecting seed survival [50, 51], but further studies are required to understand the role of abiotic factors in determining the recruitment and adult tree distribution of this species.

Implications for conservation

The low tree densities, sporadic and supra-annual fruiting, skewed sex ratios and possible pollination limitation may result in low fruit and seed availability of this species with small effective breeding populations. The dependence of this species on a small assemblage of large avian dispersers, combined with high seed predation rates and poor recruitment and survival, may result in population declines, placing these tree species at greater risk from anthropogenic disturbances such as hunting (especially of large vertebrates in north-east India), deforestation and climate change.

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