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Intersexual mimicry and flowering phenology facilitate pollination in a dioecious habitat specialist species, *Myristica fatua* (Myristicaceae)

Shivani Krishna · Hema Somanathan

Abstract *Myristica fatua* is a dioecious specialist species restricted to the endangered, freshwater *Myristica* swamp forests in the Western Ghats, India. Earlier studies have alluded to pollination by deception in members of the *Myristica* genus, and thus we examined the pollination ecology comprising floral biology, flower production, flower visitors, and reproductive success in *M. fatua* and inferred the potential strategies that could permit such deception in this habitat specialist tree. Male flowers provide pollen rewards for an extended period of time while female flowers are rewardless and both sexes are visited by generalist insects, mainly by honeybees and stingless bees. Bee visits were significantly more frequent and longer on male than on female flowers as bees collected pollen from male flowers. We found that flower production patterns create a preponderance of males compared to females in the swamp populations.

Using a model of honeybee color vision, we found the distance between the color loci of male and female flowers and based on minimum visual angle subtended by these flowers, we suggest that the two floral sexes cannot be discriminated by bees. Bees are likely deceived by the perceptual similarity of rewardless female flowers to pollen-offering male flowers and pollination is the consequence of foraging errors made by pollinators that encounter largely male–rarely female flower mosaics as they forage among clump-distributed *M. fatua* trees in the swamp habitat.

Keywords Bakerian mimicry · Bees · Deceit · *Myristica* swamps · Pollen rewards · Western Ghats

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Introduction

Rewards form the basis of plant–pollinator relationships and most angiosperms signal to their pollinators honestly using a variety of floral features informing the location and quality of rewards. Thus, angiosperms in general invest heavily in both rewards and floral signals. For instance, the cost of nectar production is estimated to range from 3.3 to 37% of daily photosynthates (Southwick 1984; Harder and Barrett 1992), while these resources could instead be allocated to fruit production (Pyke 1991). Some plants have evolved mechanisms to avoid costs associated with producing floral rewards and instead resort to

dishonest signaling in which signals displayed are not associated with rewards. Dishonest signaling apart from possibly conserving resources could also facilitate outcrossing in cases where pollinators visit few flowers and spend little time on rewardless plants (Jersáková et al. 2006). For deceit systems to be successful, negative frequency-dependent selection is essential in which rewardless mimics overlap spatially and temporally with their rewarding models, while occurring at lower frequencies (Ågren et al. 1986; Ferdy et al. 1998; Castillo et al. 2002; Johnson et al. 2003; Internicola et al. 2008). Such deception has repeatedly evolved in angiosperms (Renner 2006), but has been extensively studied only in the Orchidaceae (food deception and sexual deception; Jersáková et al. 2006; Gaskett 2011).

Flower constancy and directed movement of pollinators between conspecifics are important in all animal-pollinated species, more so in dioecious species, since pollinators have to deliver pollen from male to female trees (Bawa 1980a; Beach 1981). Despite the criticality of inter-sex movement, in more than 65% of dioecious species, one sex, usually females produce little or no rewards and instead they deceive pollinators by bearing semblance to rewarding male flowers (Bawa 1980b; Willson and Ågren 1989; Ågren and Schemske 1991). Such intraspecific mimicry between the sexes of a species is synonymously referred to as Bakerian mimicry (Baker 1976; Little 1983; Dafni 1984; Renner 2006), automimicry, intersexual mimicry, or intraspecific Batesian mimicry (Dafni 1984). Examples include species in the family Caricaceae such as *Jacaratia dolichaula* (Bawa 1980b) and *Carica papaya* (Baker 1976), the genus *Begonia* belonging to Begoniaceae (Ågren and Schemske 1991; Schemske and Ågren 1995; Le Corff et al. 1998), and *Ficus carica* belonging to the Moraceae family (Soler et al. 2012).

The ancient nutmeg family, Myristicaceae, has a pantropical distribution with five genera and 300 species in tropical Asia. Unlike its sister family Magnoliaceae, which has large bisexual flowers, species of Myristicaceae are characterized by their small, unisexual flowers (Armstrong and Tucker 1986; Sauquet et al. 2003). While most previous studies have reported Myristicaceae to be largely a beetle-pollinated family (Armstrong and Drummond 1986; Armstrong and Irvine 1989), some *Myristica* species have generalized insect pollination (Sharma and Shivanna

2011). Studies on *Myristica insipida*, a sub-canopy tree in Australia (Armstrong 1997), *M. dactyloides*, in the Western Ghats, India (Sharma and Shivanna 2011), and a review of the *Myristica* genus by Sharma and Armstrong (2013) suggest pollination by deception with pollen rewards in males and no known rewards in females. Species within this genus are typically characterized by their inconspicuousness and high pollen-to-ovule ratios (Sharma and Armstrong 2013). With this background, we examined the pollination ecology, specifically the presence of deceptive pollination in *Myristica fatua var. magnifica* (Bedd.) Sinclair (Myristicaceae), a dioecious tree species in the Western Ghats, India. None of the previous studies have systematically evaluated the presence of deceptive pollination in this plant family. A previous study of insect guilds on flowering *M. fatua* trees using canopy sticky traps revealed species of beetles and thrips as potential pollinators (Sinu and Sharma 2013). Thus, apart from the predictions of being a generalist system, the pollination biology of *Myristica fatua*, a tree that occurs in specialized *Myristica* swamp forests, is not well known. It is crucial to understand the pollination ecology of this species as it has been categorized as endangered (IUCN 2000) and recent studies have shown that climate change scenarios through modified hydrological regimes could result in population declines in this swamp specialist species (Priti et al. 2016). Moreover, *M. fatua* seeds are also dispersed by large frugivorous birds such as hornbills and threatened primates such as *Macaca silenus* and *Trachypithecus johnii* (Krishna and Somanathan 2016) and secondarily dispersed by freshwater crabs (Krishna and Somanathan 2014). Thus, insights into the reproductive biology of specialists such as *M. fatua* are considered critical. We examined the mechanism of pollination in *M. fatua* by asking the following questions: (1) What are the rewards offered by male and female flowers (for example, pollen, nectar, temperature)? (2) Who are the major visitors of *M. fatua* flowers and do they behave differentially at male and female flowers? (3) What is the natural level of fruit set in this species? Since the success of deception would depend on low frequency of rewardless flowers compared to rewarding flowers, we asked if (4) male flowers more abundant than female flowers and if (5) fruit set is affected by sex ratios and distance between male and female trees?

Methods

Study system and species

Myristica fatua var. magnifica is a habitat specialist species limited to lowland freshwater *Myristica* swamp forests, which are dominated by *Myristicaceae* members (Chandran and Mesta 2001) and are globally restricted to the Western Ghats of India. They occur in small swamp patches (0.1–20 ha) confined to valleys along streams flowing through evergreen, semi-evergreen, or moist deciduous forests (Chandran et al. 1999; Roby et al. 2014; Krishna and Somanathan 2014, 2016). The best representatives of this ecosystem occur in our study region, i.e., Kulathupuzha reserve forest (8°51N, 77°5E) in the southern Western Ghats. *Myristica fatua* is a sub-canopy tree (20–25 m in height) and produces small, urceolate, creamish-white colored monocarpellate flowers and large capsules with a single seed enclosed in a brightly colored aril. We studied floral biology and pollinator visitation in two swamp patches, namely Marappalam (MP) and Pullumala (PM), using custom-built ladders and platforms at a height of 22–25 m to access flowers and conduct observations in the canopy. Flowering phenology was recorded in four swamps, MP, PM, and two more swamps, namely Munnamchal (MC) and Emponge (EG). Spatial distribution of individual trees was studied by mapping trees in four swamps (< 5 ha), MP, PM, and in two more swamps, i.e., Valiyapacha (VP) and Ambalathupacha (AP). In addition to these four swamps, sex ratios were recorded in swamps (> 5 ha) MC, Dalikarikkam (DK), Neerattuthadam (NT), and Chettadi (CT).

Floral traits and rewards

We quantified male and female flower sizes by measuring the diameter of the corolla aperture, length and width of petals, and depth of the corolla tube in male and female flowers ($N = 30$ each). Anthesis and flower longevity were measured by tagging mature flower buds (both open and bagged treatments) and monitoring flowers every 3 h for changes in corolla and anther condition until senescence. We determined pollen productivity on freshly opened male flowers ($N = 10$) by collecting pollen from anthers using a fine needle onto a gridded microscopic slide and counting the pollen numbers under a light microscope after staining with basic fuchsin jelly. As microcapillary tubes yielded no nectar, we used Diastix® strips (Bayer Diagnostics, India) that could be dabbed on the internal and external surfaces of flowers to detect the presence of sugars. Furthermore, to test if flowers produced heat as a reward, as is often suggested in beetle-pollinated flowers (Bernhardt 2000), a probe thermometer (Tolexo^R) was inserted into male and female flowers ($N = 10$ flowers each) every 3 h at night from 1800 to 0600 h.

Spectral reflectances of petals of male and female flowers ($N = 5$ each) were measured using a spectrophotometer (Maya 2000, Ocean Optics, USA). Preliminary observations indicated that flowers were visited by a suite of small-sized insects, including honeybees and stingless bees (*Apis cerana* and *Tetragonula* spp.), which were the dominant visitors at both male and female flowers. Therefore, the chromatic properties of male and female petals were determined using the receptor noise-limited model (RNL, Vorobyev et al. 2001) of honeybee color vision.

The RNL model is a color vision model assuming that color detection and discrimination thresholds are set by noise in photoreceptors. As photoreceptor sensitivities are highly conserved among hymenopterans (Peitsch et al. 1992) and since such values are not yet available for *A. cerana* or *Tetragonula* spp., we used the spectral sensitivity values of the Western honeybee (*Apis mellifera*) photoreceptors (Menzel and Backhaus 1991; see also Hempel de Ibarra et al. 2014). Distance between the color loci of averaged male and female flower spectra was calculated using this model, and distances less than 2.3 RNL units indicate that bees cannot distinguish between the two stimuli (Vorobyev et al. 2001).

Flowering phenology, flower production, and visitation

During yearly flowering from 2012 to 2016, we made observations of male and female flowering patterns (onset, duration, and intensity from December to June) in four swamps ($N = 30$ males, $N = 33$ females; 6–8 individuals/swamp). Trees were scored 1–4 in class intervals of 25%, based on the percentage of crown flowering, a common method used to score flowering intensity (where $1 = 1$–25%, $2 = 25$–50%, $3 = 50$–75%, $4 = 75$–100% flowers, Fournier 1974). Augspurger's index of flowering synchrony (Z, where

0 = total asynchrony and 1 = total synchrony; Augspurger 1983) was computed and compared to examine the differences in degree of synchrony within and between the sexes.

To estimate flower production, the number of flowers on segments of branches (length 0.5 m, $N = 15$ branches) of male and female trees ($N = 3$ each) were counted. It was not possible to accurately count the large number of flowers produced by tall male trees (height > 20 m) using binoculars from the ground. Hence, total flower production on male trees ($N = 75$) was estimated by counting the number of flowers in eight 50×50 cm quadrats (per tree) placed randomly on the forest floor under flowering trees. The number of flowers within the quadrat along with the area of the flowering crown gave a quantitative estimate of flower production in male trees. Since female flowers form fruit, a similar procedure would underestimate flower count. Instead, estimates were obtained by intermittent counts of flowers on branches of female trees ($N = 26$). Since the female trees produced fewer flowers, the flower numbers could be reliably estimated using binoculars from the ground.

Using custom-built canopy platforms at a height of 22–25 m, visitation observations were conducted both manually and by setting up video recorders (Sony HDR XR160E Handycam®) on three male and three female trees from 0600 to 1800 h; this amounted to 600 observation hours over 50 days (15-min observation sessions) across the 2013 and 2014 flowering seasons. These platforms were erected on trees such that two flowering trees of opposite sex were also visible from the platform itself. During the peak flowering period, diurnal observation sessions were alternated between male and female trees. Nocturnal visitation was observed for 60 h in February 2013 (peak flowering in male and female trees) from 1800 to 0500 h using a pair of night vision binoculars (US Night Vision, USA) to record the presence of nocturnal visitors, their identity up to taxonomic order level, and abundances. The time spent by individual visitors on male and female flowers was recorded using a stopwatch.

Sex ratios, distribution of sexes, and pollination success

All reproductive *M. fatua* individuals (diameter at breast height (dbh) > 10 cm, $N = 301$) in four swamp patches (MP, PM, VP, AP) were tagged, geo-referenced, and sexed during flowering and sex ratios were calculated. Sex ratios were also calculated in four other large-sized swamps (MC, DK, NT, CT), by counting the number of reproductive male and female trees in twenty plots (dimension 20×20 m). To examine spatial distribution, Clark and Evans test of dispersion (Clark and Evans 1954) was used. The test determines deviation from randomness either towards aggregation or regularity.

Pollination success was determined by estimating fruit set (flower:fruit ratio). Female trees ($N = 8$ per swamp) were marked in all eight swamps (MP, PM, VP, AP, MC, DK, NT, CT) and flowers on 8–10 tagged branches on each female tree were counted. At the end of the season, immature fruits were counted on these tagged branches. We examined fruit set on focal female trees in relation to sex ratios in all eight swamps and distance to the nearest male and nearest female, as well as the number of males and females within a 15 m radius using Spearman rank correlations in four of the main swamps (MP, PM, VP, AP).

To check for the possibility of apomixis, fruit set was examined by enclosing flowers ($N = 20$) in muslin bags to exclude insect visitors on two female trees. A minimal amount of pollen (< 4 grains) was collected from freshly dehisced anthers of two male *M. fatua* trees (< 40 m distance of focal trees) from within the swamp to perform hand pollinations ($N = 20$) following which flowers were bagged and fruit set was examined later. Lastly, on the same two female trees, flowers ($N = 60$) were tagged, left open for visits by pollinators and natural fruit set was measured.

All statistical analyses were performed in the base package, and spatial analysis was done using the package 'spatstat' (Baddeley and Turner 2005) of R 3.1.1 (R Core Team 2014). Results are presented as mean ± SD.

Results

Floral traits and rewards

Male flowers are borne in clusters of 8–10, while female flowers occur singly or in clusters of 2–3 (Fig S1 in Supplementary material). Corolla tube depth and diameter were slightly smaller in male flowers when compared to female flowers (Table 1). Stigmas are

Table 1 Characteristics of male and female *Myristica fatua* flowers and flowering patterns of male and female trees (mean ± SD)

Characteristics	Male	Female	Statistic (χ^2)
Mean corolla tube depth (mm)	5.02 ± 0.87	6.48 ± 0.33	8.90*
Mean corolla tube diameter (mm)	6.6 ± 0.64	6.58 ± 0.78	8.29*
Mean aperture diameter (mm)	4.7 ± 0.66	5.7 ± 0.88	15.04*
Mean width of the flower (mm)	4.48 ± 0.65	4.62 ± 0.35	0.62
Anthesis	1800–0600 h	1900–0300 h	
Longevity (h)	72	72–96	
Mean floral temperature (°C)	28.2	28.2	
Flowering months	Dec–Aug	Jan–Jun	
Flowering duration (mo)	9	6	
Mean flowering synchrony (Z)	0.98	0.89	
Display size (50 cm branch)	52.02 ± 30.7	2.87 ± 1.13	
Mean visitation time by diurnal visitors (sec)	22.7 ± 22.9	1.63 ± 0.59	

Differences in male and female floral traits are presented with Chi-square statistic derived from Kruskal–Wallis test (asterisk indicates statistical significance). Z denotes index of synchrony ranging from 0 to 1 (Augspurger 1983) for complete asynchrony to complete synchrony

bivalved, creamish in color, and resemble the fused anthers of male flowers. Both male and female flowers have 3–4 petals (Fig. 1a, b). The distance between the color loci of male and female flowers was 0.67 units, which is below the theoretical discrimination threshold of bee vision (Vorobyev et al. 2001, Fig S2 in Supplementary material).

Pollen is the only reward produced by male flowers. The number of pollen grains produced in male flowers was estimated to be 6198 ± 590 (range 5359–6736).

Glucose test strips did not reveal the presence of any detectable levels of sugars in male and female flowers. The temperatures within male and female flowers were similar and comparable to the temperature at night (27–29 °C) (paired Wilcoxon signed-rank test, male: $V = 190$, $P = 1$; female: $V = 136$, $P = 0.90$; Table 1), thus ruling out the presence of thermal rewards in these flowers. Overall, there was no evidence of any reward other than pollen in male flowers, while female flowers were rewardless.
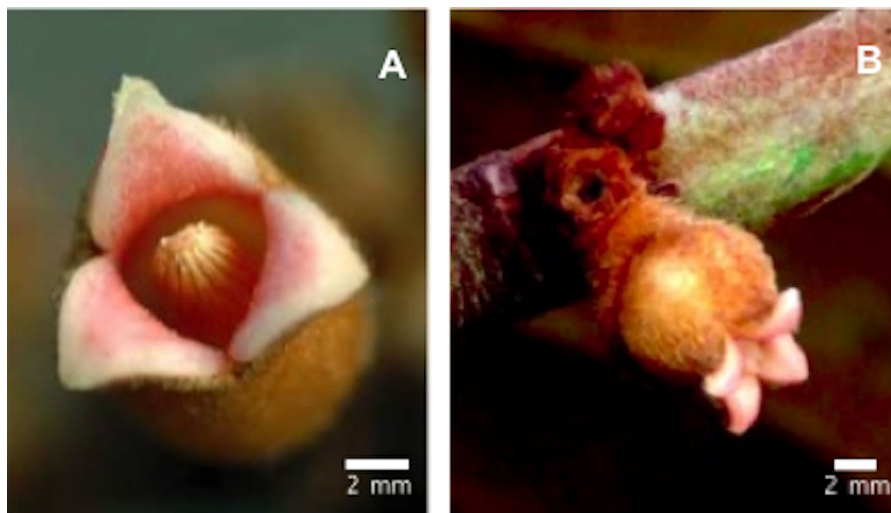
Fig. 1 **a** Male and **b** a female *Myristica fatua* flower

Timing of anthesis and floral longevity did not vary between bagged and open treated flowers (Kruskal–Wallis test, $\chi^2 = 0.029$, df = 1, $P = 0.86$). Male flowers opened at night (between 1800 and 0600 h ($N = 24$)) and lasted for 72 h ($N = 24$). Female flowers also opened at night (between 1900 and 0300 h ($N = 8$)) and lasted for 72–96 h ($N = 10$).

Flowering phenology, flower production, and visitation

Flowering in *M. fatua* extends from December through August (Fig. 2). Peak flowering in males was between January and June with more than 85% of trees flowering, while the flowering peak in female trees was in February and March. Male trees have prolonged flowering compared to female trees (Kruskal–Wallis test, $\chi^2 = 43.78$, df = 1, $P < 0.001$). The index of flowering synchrony (Z) ranged from 0.93 to 1 for males, and from 0.46 to 1 in females in the different swamps and did not differ significantly between the sexes (Kruskal–Wallis test, $\chi^2 = 0.22$, df = 1, $P = 0.63$). The duration of flowering differed significantly between males in the four swamp sites (Kruskal–Wallis test, $\chi^2 = 11.07$, df = 3, $P = 0.01$) as well as between female trees ($\chi^2 = 22.30$, df = 3, $P = 0.01$).

The mean number of flowers on male branch segments was significantly higher than the number of flowers on segments of female trees (Table 1). Total number of flowers produced by male trees ranged from 45 to 76402 (rounded to nearest integer) with a mean of 7784.29 ($\pm$ 12318.50) within a season. Thus, on average the total number of flowers produced by male trees was 30 times greater than female trees (253.11 ± 40.95).

We recorded visits by two social bee species, *Apis cerana* (46%) and a *Tetragonula* spp. (48%), while the remaining 6% of total visits to flowers were by solitary bees, hover flies, beetles, thrips, and moths. Beetles and moths were the only visitors observed at night. Both *A. cerana* and *Tetragonula* spp. actively collected pollen grains from male flowers and were also seen on female flowers. Therefore, we considered them to be major pollinators of *M. fatua*. Bee species visited male flowers much more often: 1199 visits were observed to male flowers versus only 19 visits to female flowers over a 50-day observation period. In all the 15-minute observation sessions on male trees, bees made 3–48 flower visits during their peak activity period, while on female trees, flower visits were absent in many of these sessions. Thus, the overall visitation rates to male (0.20 visits/flower) and female flowers (0.006 visits/flower) differed significantly (proportionality test, $\chi^2 = 18.3$, df = 1, $P < 0.001$). The two bee species spent significantly more time on male flowers than on female flowers (Kruskal–Wallis test, $\chi^2 = 50.5$, df = 1, $P < 0.001$, Table 1). The mean duration of visits was 22.7 s ($\pm$ 22.9, $n = 228$ visits) to male flowers and only 1.63 s ($\pm$ 0.59, $n = 19$ visits) to female flowers.

Fig. 2 Proportion of flowering male (dashed line, $N = 30$ trees) and female (solid line, $N = 33$ trees) individual *M. fatua* trees (combined across four swamps)
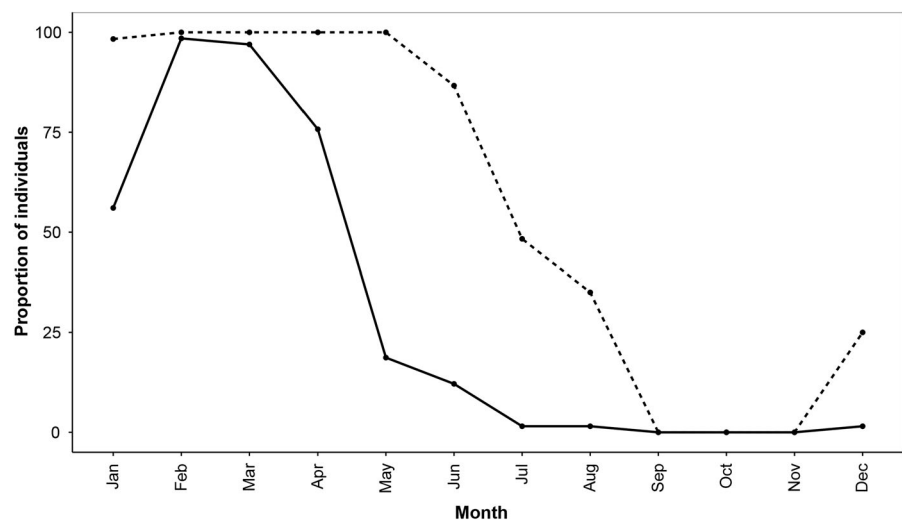
Sex ratios, distribution of sexes, and pollination success

Myristica fatua trees were strongly clustered within swamps with R-values for Clark and Evans tests for all the four swamps lower than 1 (R = 0.3–0.6). The mean nearest neighbor distances between *M. fatua* trees varied among the four mapped swamps ranging from 3.72 m (± 10.6; MP) to 15.45 m (± 29.6; AP). Of the eight swamps, six were male-biased, and was not significantly different from unity in the two other swamps (MP, MC). There were significant differences between swamps in fruit set across the eight swamps (Kruskal–Wallis test, χ^2 = 16.41, df = 7, P = 0.02, N = 8 trees/swamp). Post hoc tests showed that the two swamps VP and PM differed significantly (post hoc pairwise Wilcoxon test, VP–PM, P = 0.008) in their percent fruit sets. Distance to the nearest male or female tree, as well as the number of male and female trees within a 15 m radius, did not appear to influence fruit set on females either (Table 2). Mean fruit set on female trees was not correlated with the sex ratio of the swamp (Table 3, Spearman rank-correlation test, r = 0.11, P = 0.77).

Natural fruit set was 63.5% (± 4.25, swamp MP) and hand pollination did not increase fruit set (54.7 ± 15.7%). Bagged flowers from which pollinators were excluded did not set fruit.

Discussion

The floral features and pollen rewards in *M. fatua* are similar to the other species of *Myristica* genus (Sharma and Armstrong 2013). Males provided pollen rewards and females were rewardless conforming to pollination by deception. Species with intersexual

Table 3 Sex ratios (M:F) and mean percent fruit sets in eight study swamp sites

Swamp	Sex ratio	Fruit set (%)
AP	1.61	36.62
VP	2.84	16.26
MP	0.95	37.42
PM	2.02	63.82
CT	1.88	43.13
DK	1.56	33.39
MC	0.97	41.51
NT	1.88	34.45

mimicry systems are known to utilize a diversity of strategies for successful deceit such as chemical mimicry in case of *Ficus carica* (Grafen and Godfray 1991; Patel et al. 1995; Soler et al. 2012), phenological patterns in *Jacaratia dolichaula* (Bawa 1980b), or large size of mimics in *Begonia* species (Schemske and Ågren 1995). Our results suggest that fruit set in *M. fatua* was relatively higher in most of the study populations compared with the general trend for nectarless species, which have average fruit sets of < 15% (Tremblay et al. 2005). In *M. fatua*, the clustered spatial distribution of male and female trees restricted to patchy swamp habitat, low densities of female flowers when compared to male flowers, as well as the early and prolonged flowering of males are highly suited to the success of deceit as a strategy in which unrewarding female flowers mimic male flowers.

Myristica fatua did not set fruit apomictically, and while hand pollination did not increase fruit set, small numbers of pollen grains were sufficient for fruit set in this single-ovuled species. Our study shows that *M. fatua* is visited by several insect groups, of which

Table 2 Spearman correlations (correlation coefficient, r) showing relationship between fruit set of female trees and distance to the nearest male, female, and number of flowering males as well as females within 15 m radius in four swamps

Swamp	Distance to the nearest male	Distance to the nearest female	Number of flowering males (15 m radius)	Number of flowering females (15 m radius)
AP	− 0.35	0.39	0.24	0.09
VP	0.32	0.01	− 0.47	0.14
MP	− 0.7	0.5	0.67	0.46
PM	0.02	− 0.44	0.65	0.22

Asiatic honeybees and stingless bees are most common. This contrasts with reports of beetle pollination being the common state in the Myristicaceae family (Armstrong and Drummond 1986; Armstrong and Irvine 1989) and supports findings from a recent study also from the Western Ghats (India), which showed the predominance of generalization with thrips, beetles, and bees as potential pollinators in the congeneric *M. dactyloides* (Sharma and Shivanna 2011). In *M. fatua,* bees, flies, beetles, and thrips were found to collect pollen from male flowers. Generalized pollination systems are hypothesized to provide reproductive assurance by buffering plants from fluctuations in pollinator populations (Waser et al. 1996; Marten-Rodriguez and Fenster 2010). Such buffering is likely to be important in *M. fatua* since the fruit numbers are low and investment per seed is very high (mean seed weight = 20.9 ± 2.93 g; Krishna and Somanathan 2014), along with its restricted habitat requirements.

The several fold higher flower numbers on male trees along with male-biased or roughly equal sex ratios create a spatial and temporal preponderance of male flowers compared to females, and thus contribute to the success of deceit as a pollination strategy. Visitation rate to male flowers was much higher in comparison to females (0.006 visits/female flower vs 0.20 visits/male flower). Also, the two main bee pollinators spent significantly more time on male flowers to collect pollen (average 23 s per visit), while they alighted on rewardless female flowers only fleetingly (< 3 s). These differences in the number and duration of visits suggest that *M. fatua* is pollinated via foraging errors made by pollen-seeking visitors that are deceived into visiting rewardless female flowers. Similarly, in the congeneric *M. insipida*, deceit pollination via foraging errors of beetles was suggested due to intersexual differences in floral display (Armstrong 1997). Rewardless morphs or species occurring at low frequencies are often pollinated as a result of foraging errors of pollinators, resulting in mistake or chance pollination. Most rewardless orchids are known to rely on naïve insect visitors for successful pollination since experienced pollinators can learn to avoid the species entirely after few visits (Ackerman 1981; Dafni 1984; Smithson and Gigord 2003; Internicola et al. 2007; Internicola and Harder 2012). However, in other species (Johnson et al. 2003; Renner 2006) and in *M. fatua*, as foraging

bees encounter variable amounts of rewards in flowers (empty/partially empty male flowers or empty female flowers), and since they do not visually differentiate female flowers from males, negative reinforcement for female flowers is unlikely. Also, certain amount of errors in foraging is considered to be useful as a long-term strategy to keep track of changing resources in space and time (Deneubourg et al. 1987; Weidenmüller and Seeley 1999). Thus, both experienced and naïve pollinators may be involved in such pollination systems. Additionally, in *M. fatua,* conditioning of pollinators by early flowering male trees which produce pollen could facilitate visits to rewardless female flowers that open later in the season. This also suggests that male flowers could possibly be functioning as reliable pollen sources making it a less variable foraging environment. Additionally, the relatively lower flowering synchronization between female trees when compared to male trees, further depresses the numbers of rewardless flowers at any point of time and could prevent or minimize negative associative conditioning at rewardless female flowers in pollinators. Orchid species with generalized food deception were shown to have significant advantages for fruit set in individuals with long-lasting flowers than those that retain flowers for shorter periods (Primack 1985; Internicola and Harder 2012). However, in non-orchids such as *M. fatua,* asynchronous flower opening in females prolongs the flowering at the tree level and is likely to improve reproductive assurance.

The spatial configuration of male and female trees can influence pollinator movement and thereby fruit set in dioecious species (House 1993; Stacy et al. 1996; Somanathan and Borges 2000). Foraging distances of common pollinators of *M. fatua*, i.e., *Apis cerana* and *Tetragonula* spp., lie in the range of 200–500 m (Dyer and Seeley 1991; Raju 2009). The swamp habitat is an overall clustered space where the distances between male and female trees do not exceed 30 m and most of them lie within the range of 3–10 m; thus, it is likely that any effect of spatial proximity on fruit set was not detected. Similarly, in *Aralia nudicaulis* (Barrett and Thomson 1982) and *Jacaratia dolichaula* (Bullock and Bawa 1981), both of which are species with non-rewarding females, fruit set was not related to local sex ratios and distance to the nearest males.

Visual mimicry is important for bee pollinators in food deceptive systems (Roy and Raguso 1997; Galizia et al. 2005) and the close resemblance in spectral properties, shape, and size between female and male *M. fatua* flowers suggests that hymenopterans such as honeybees and stingless bees that have poor visual acuity and spatial resolution (Srinivasan and Lehrer 1988; Dafni et al. 1997; Vorobyev et al. 1997; Hempel de Ibarra et al. 2015) are unable to distinguish male and female *M. fatua* flowers on the basis of pattern, shape, size, or color, even when they are very close to the flower. The distance between the color loci of male and female flowers is below the threshold of discriminability and could result in a generalized response by bees towards male and female flowers. The size differences between male and female flowers are indiscriminable to bees even when they are very close to the flower (within 5 cm). The minimum visual angle subtended by individual male and female flowers on the eye of the bee (5.3°—males, 6.8°—females) is not sufficient for bees to detect flowers by color (Fig. S1 in Supplementary material). In the western honeybee (*Apis mellifera*), it has been shown that to detect stimuli that present both achromatic and chromatic contrasts, the object has to subtend a visual angle of at least 5°, while in the stingless bee, *Tetragonula carbonaria*, the minimum visual angle required is 9.5° (Giurfa et al. 1996; Vorobyev et al. 1997; Dyer et al. 2016). This suggests that individual male and female flowers of *M. fatua* cannot be detected by differences in size even when the bee is within landing distance, and thus they are likely to generalize between them, thus effecting pollination. So far, we have discussed visual discriminability of male and female flowers in the context of bees; however, in this generalist pollination system, other modalities such as scent could additionally be involved in mediating deceit pollination by beetles, thrips, or flies. While scent produced by *M. fatua* is not detectable for humans, whether floral scent detectable by insects is involved in this system in addition to visual mimicry remains to be investigated.

Pollination systems of habitat specialist species are predicted to be specialized or involve strategies such as enhanced attraction mechanisms that promote reproductive success (Miller-Struttmann 2013). However, in case of *M. fatua*, we speculate that investing resources in lipid-rich, brightly colored arils, and large and heavy seeds could possibly facilitate better

establishment than resources expended on producing nectar sugars which occurs under challenging abiotic conditions of the swamps that are flooded during the monsoons. Thus, it is tempting to hypothesize a possible relationship between survival in narrow abiotic conditions and rewardlessness. This is yet to be tested across such specialized habitats.

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