Review Article

Pollination of *Myristica* and other nutmegs in natural populations

Manju V. Sharma[1] and Joseph E. Armstrong[2*]

[1]Keystone Foundation, PB No 35, Groves Hill Road, Kotagiri, The Nilgiris, Tamil Nadu, India
<mann.vasu@gmail.com>
[2]School of Biological Sciences, Illinois State University, CB 4120, Normal, Illinois 61790-4120, USA.
*Corresponding Author: jearmstr@ilstu.edu

Abstract

Field studies of several species of *Myristica* (Myristicaceae) have produced a more detailed understanding of the pollination and reproduction of nutmeg, which had long been wanting. Nutmegs are dioecious tropical forest trees within the order Magnoliales. Nutmegs conform to the general pattern of dioecious tropical trees; they have small, inconspicuous flowers with a pollen reward system, and interact with a guild of small, generalist insects, predominately beetles, thrips and flies. Pollen is the only obvious reward, so pollination operates by deception and foraging errors. Fluctuations in floral displays may encourage foraging errors, and beetles have been found to be sensitive and responsive to such changes in floral displays. Natural populations of nutmegs are generally male-biased, although irregular flowering can shift sex ratios from season to season. Intersexual differences in microhabitat preference were found in some, but not all nutmeg species studied. Compared to their importance and prevalence in tropical forests, the nutmeg family remains both under-studied and difficult to study. Future work should focus on aspects of nutmeg reproduction such as pollen flow and fruiting success (or seed set) that may offer conservation insights.

Keywords: dioecious, foraging errors, generalist, male-biased populations, *Myristica,* pollen reward, pollination, nutmegs, tropical forests, mistake pollination

Cite this paper as: Sharma, M. V. and Armstrong, J. E. 2013. Pollination of *Myristica* and other nutmegs in natural populations. *Tropical Conservation Science.* Vol. 6(5):595-607. Available online: www.tropicalconservationscience.org

Introduction

Nutmeg, both a spice and a pantropical plant family, is important for three reasons. First, although not as valuable as in times past, nutmeg, the spice obtained from the seed, the ruminant endosperm of *Myristica fragrans* (and a few related species), and mace, another spice from the reddish aril of the same plant, are important crops, primarily in Indonesia and Grenada, and while spices are not essential things, our eggnogs and other confections would be much duller without them. Second, the nutmeg family occupies a phylogenetic position near the base of angiosperms, the flowering plants, and may give clues to their ancestral traits. Third, members of the nutmeg family are important components of wet, lowland tropical rain forests, and their fruit is an important part of the diet of many birds and primates. In one respect or another, the reproduction of nutmegs is central for understanding everything from nutmeg cultivation to rain forest function and conservation.

The nutmeg family, Myristicaceae, is nested within the Magnoliales, an order which consists of six families; the other five are Annonaceae, Degeneriacaeae, Eupomatiaceae, Himantandraceae, and Magnoliaceae. This order is part of the magnoliid clade, a sister group to all other angiosperms except the basal ANA grade [1]. Some 15 genera and over 300 species comprise the nutmeg family. *Myristica* is the largest genus with about 100 species. The Myristicaceae is geographically widespread, pantropical, but genera are biogeographically restricted either to Central and South America, Africa and Madagascar, or Southeast Asia to Australia. Nutmegs are an ecologically important component of primarily lowland tropical forests, especially Amazonia [2-7]. Most nutmegs are dioecious trees or shrubs; some species of *Iryanthera* are monoecious [8-10]. Some species are canopy or even emergent trees, although many occupy the subcanopy and understory. Among those species that have been studied, *Myristica fatua* and *Gymnacranthera canarica* in the Western Ghats of southwestern India are dominant and endemic species in a few swamp forests, which are highly vulnerable habitats [11, 12]. *Myristica dactyloides,* endemic to Sri Lanka and India's Western Ghats, is a characteristic component, a dominant canopy species, of primary forests in mid and high elevation zones where it seems to prefer riverside habitats [13-15]. In Queensland, Australia, *Myristica insipida* is a subcanopy tree in a variety of forest communities up to about 900 m in elevation, where it is a common component in more mesic habitats [16].

The nutmeg of commerce or Banda nutmeg (*Myristica fragrans*) has been cultivated for centuries, first in Southeast Asia, and then in the Neotropics, but curiously little was known of its reproductive biology, including its pollination. Information provided in several books about tropical crops summed up the lack of knowledge. For example, pollination of nutmeg was effected by wind and small insects, perhaps even a wasp [17-19], a moth [20], unspecified small insects [21], or perhaps no pollination was required at all, although some strongly disagreed with that view [22]. The general reason for so much confusion is undoubtedly a combination of the small flower size, small pollinator size, and nocturnal flowering.

The dioecious nature of nutmegs has long been a problem for nutmeg cultivation, because while some male trees are needed for pollination, only female trees produce the cash crop [22]. Nutmegs germinate in a 1:1 sex ratio, but in plantations, seedlings are planted densely and after 6 to 7 years, when flowering finally reveals their sex, "excess" males are culled to a ratio of about 10 female trees to 1 male tree. Nutmeg growers were also confused by apparently "bisexual" trees, males that produced

some fruit [22]. Lastly, female trees produce many more flowers than fruit [22], and to nutmeg growers, the aborted flowers seem to be a waste. Was this because of inadequate pollination or some other biological problem?

The first scientific study of nutmeg flowering and pollination was carried out in commercial nutmeg plantations in lowland Kerala, India. Both beetle and thrip floral visitors were observed, but only one species of small beetle (Anthicidae) was a good candidate for being an effective pollinator [23]. This study provided little useful information about the pollinators of commercial nutmeg elsewhere, and since the study was not conducted in a natural forest community, the biology and pollinator interactions of wild nutmegs, the full diversity of pollinators, and the organization of natural nutmeg populations, remained unknown.

Beetles have long been considered important pollinators in families of the Magnoliales, but this overlooked other important pollinators even in the Annonaceae, which has been considered largely beetle pollinated [24-26]. In addition to beetles, flies and thrips are important pollinators for several genera of Annonaceae [26-30]. In Myristicaceae, thrips were reported as floral visitors of Neotropical species, and thrips, beetles, and flies have been found effecting pollination [31, 32]. These studies support the observation that thrips in general have been underestimated in importance as pollinators [33, 34]. For plants in the ANA grade (the three basal lineages of angiosperms), beetles, bees, and flies are important pollinators, and pollen rewards and floral deceit are common [35, 36]. Nutmegs not only have these features, but their small flower size, concave and enclosing perianths with small entrances, scented flowers, and nocturnal flowering, are all associated with beetle, thrip, and/or fly pollinators [34, 35-37]. The floral biology, the nature of pollination, and important pollinators of members of the nutmeg family have been elucidated by field studies of natural populations of several species of *Myristica*, and a review of these findings will form the basis for this report, although as we shall demonstrate, the nutmeg family remains under studied 45 years after Flach's 1966 report [22] summarizing knowledge of commercial nutmeg reproduction, during which time the study of tropical organisms has blossomed.

Sex and Spacing
Commercial nutmeg (*Myristica fragrans*) seedlings germinate in a 1:1 sex ratio, the result of purported sex chromosomes [22], but whether this is true for all nutmeg species remains unknown. In nature nothing close to a unitary sex ratio has been found, but this is not unexpected, considering that dioecy may allow for intersexual differences in resource use, longevity and survival, or aggregation for increasing pollination efficiency [38]. Female-biased ratios ranging from 10:1 to 20:1 in plantations do not seem to negatively affect fruit production, so even in such female-skewed populations pollen is not limiting, although lack of pollinators, both in number and species diversity, may affect fruit set [23]. However, the spacing of trees in a plantation is much closer than in nature. In Australia, the mean distance from male to nearest female for *Myristica insipida* was 9.6 (± 6.3) m and 19.4 (±14.4) m in two different forest communities, but these distances may represent clustering in mesic habitats [16]. In Amazonia, the average distance to the nearest flowering conspecific ranged from 57 to 147 m in four nutmeg species [10]. No one knows how nearest neighbor distances affect pollination, but it certainly depends upon the pollen vector.

Sex ratios for quite a few nutmeg species have been reported, and generally male trees outnumber female trees, although sometimes the differences are not statistically significant. A significant male-biased ratio of 1.57:1 was reported for one of the two populations of *Myristica insipida* in Queensland, Australia [16]. Two out of five Neotropical nutmeg species studied in central Amazonia in one flowering season had male-biased ratios (*Iryanthera macrophylla*: 2.6:1, and *Virola calophylla*: 3.3:1) [10]. In western Amazonia, of the 16 species in four genera (*Compsoneura*, *Iryanthera*, *Virola*, and *Otoba*) that were studied over four years, the number of male trees flowering exceeded the number of female trees flowering in most species in three out of the four years [39]. Cumulative sex ratios across years and tree sizes produced male-biased sex ratios ranging from 1.2:1 to 2.9:1, where enough individuals were tallied to make the count meaningful. Significantly male-biased populations were found in four species, one in each genus, in one, two, or three of the four years. Irregular flowering can dramatically alter functional sex ratios from year to year, as evidenced by significant female-biased ratios for two species of *Virola* in one of the four years.

Pollen/ovule ratios can be calculated by taking into account the intersexual differences in flower production and sex ratios. So far this has only been calculated for two species of *Myristica*, *M. dactyloides* in two different communities in southwestern India (P/O = 12,983 and 14,065) [40] and *M. insipida* in two different communities in Queensland, Australia (P/O = 16,219 and 19,003) [41], which seem quite similar at this point. The pollen grains per male flower were nearly identical in both studies, 5893 in the former and 5656 in the latter. These pollen-ovule ratios are on the order of three to four times the average P-O ratio for other obligate out-crossing plants [42]. These high ratios may well reflect the exclusive use of pollen as a floral reward.

In their study of Neotropical nutmegs, Queenborough et al. [39] found evidence of aggregation of sexes in four out of eight species. Another study of *Myristica insipida* in two different forest communities found no intersexual differences in nearest neighbors or in mean distances to nearest neighbors, suggesting no sexual aggregations. However in both communities this species was limited to mesic habitats produced by topography [16]. In these communities onset of flowering was irregular, but trees responded to an environmental cue and reached peak flowering 18-22 d following a rain event in excess of 100 mm [16].

Reports of truly monoecious trees in plantations of commercial nutmeg as well as bisexual flowers [22] have never been substantiated, but male trees of wild *Myristica insipida* do regularly produce a small number of female flowers and subsequently fruit [16]. In every case the female flower was the central or terminal flower of the inflorescence [43]. A higher frequency of female flowers on male trees among cultivated nutmeg may reflect a similar situation made more prevalent by selection to increase overall production. The only true monoecy in the family is found in *Iryanthera*.

Floral biology
Certain floral characteristics are found in *Myristica* and more generally among members of the nutmeg family, although many of the non-morphological features remain unknown for the majority of the family. Flowers tend to be small (< 1 cm), numerous, in small clusters, which along with a perianth color of white to cream to light green to yellow, or a fine, rusty-brown tomentum, renders them visually inconspicuous. A dully-colored perianth with small lobes provides little in the way of visual display, but

the flowers are highly fragrant when first open. The primary attractant signal is provided by floral odor, which in *Myristica fragrans* and *M*. *insipida* is a strong, pleasant, absolute scent [16, 23]. The apex of the stamina column (Fig. 1), the stigma, and the tips of the tepal lobes of *Myristica insipida* often show vital staining consistent with odor production, and although nectaries have been reported [18], the flowers contain no nectaries or other specialized rewarding structures [43, 44]. Floral scent in many other Magnoliales is often spicy-fruity or musky-pheromone, and in one sense these flowers can be considered fruit mimics; but from the insect perspective they are not deceptive when they provide nutritional rewards for adults and/or their larvae.

Fig. 1. Male flowers of *Myristica insipida* (a) and apex of androecial column of *M. dactyloides* (b) showing fully open anthers (bracket = 1 anther), pollen, and reddish color corresponding to osmophoric tissue. Bar = 1 mm.

In *Myristica fragrans* and *M*. *insipida* anthesis begins nocturnally. In these species the male flowers functioned from 12 to 48 hr, while female flowers functioned for 48 to 72 hr [41]. In *M. dactyloides* intersexual differences in floral longevity were reversed with male flowers lasting 7-9 d and female flowers lasting 4-5 d [32].   In all three species male trees produced more flowers per axillary inflorescence from 1.5:1 (*M. dactyloides*) to 2.1:1 (*M. insipida*); in both species insects responded to the larger displays at male trees with more visits [32, 45]. However the intersexual difference in flower number may vary considerably in other nutmeg genera. In Neotropical *Iryanthera hostmannii,* this ratio was reported to be 3:1 [46]. *Virola seibifera* had a 24:1 male to female flower ratio per inflorescence based on limited sampling and a greater intersexual difference in floral size than found in *Myristica* (n=6) [Armstrong, field notebook, 20 December 1998, unpublished data].

Unlike many flowers in the Magnoliales that have many floral parts, nutmegs have few floral parts: a single whorl of perianth, partly to almost completely fused, and either one whorl of stamens "fused" or adnate to a receptacular column bearing 3 to ~24 anthers [43, 44, 47] (Fig. 1) or a single pistil bearing a single ovule. In *Myristica* the flowers are urceolate with males being more slender and females broader [16, 23, 32 (See Fig. 1 [32]) (Fig. 1, 2). The perianth tissues are not fleshy as in many magnoliids and no evidence was found of visitors feeding on perianth tissues. After the tepal lobes open no other movement of floral parts takes place. The stigmas are wet, but produce no prominent exudates that might function as a food reward. At the end of anthesis the staminal column appears withered and the tips of the tepals and the stigma turn a dark reddish color (Fig. 2, 4). Pollen is the only reward present; female flowers require foraging errors to deliver pollen [23, 41, 45], a food-deception, automimicry commonly called "mistake pollination" [48], but a system much different from that found in *Eupomatia*, Magnoliaceae, or Annonaceae [41]. Unfortunately no floral odors of nutmegs have been analyzed, so no comparison to other magnoliids is possible. However it has been shown conclusively that beetles are sensitive and responsive to differences in the floral displays [45].
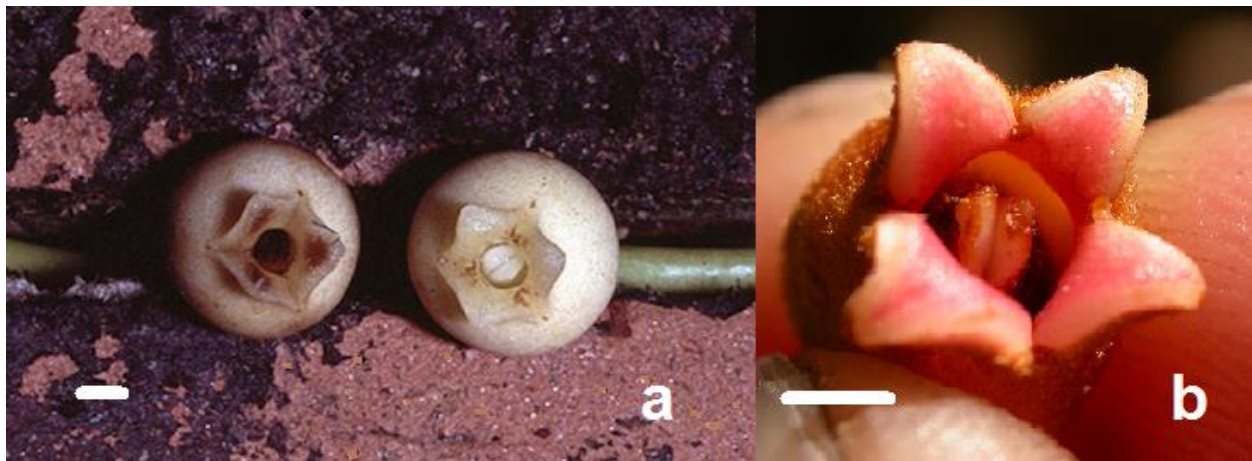

Fig. 2. Female flowers of *Myristica fragrans* (a) and *M. fatua* (b) showing perianths with three and four tepal lobes and a bilobed stigma just within the perianth opening. In *M. fragrans* the perianth opening is close around the stigma. The flower on the right is receptive; the flower to its left shows a post-receptive darkening of the stigma and tepal lobes. In *M. fatua* the almost bilabiate perianth opening provides much more access for insects to enter within the flower. The perianth is covered by a rusty tomentum. The bars are one mm long.

Insect Visitors and Pollinators

Prior research on commercial nutmeg indicated the primary pollinators to be beetles and thrips. For *Myristica insipida* in Queensland, Australia, nine beetle species belonging to five families were reported [45] and studies on *Gymnacranthera* and *Knema* species suggested Curculionids, Staphylinids and Chrysomelids as potential pollinators [49, 50]. While thrips were frequent floral visitors in *M. insipida* and captured in great numbers at male trees, the failure to find pollen-bearing thrips at female flowers and the responsiveness of beetles to differences in floral displays argued against thrips as an effective

pollinator during this study [45]. Thrips, on the other hand, were reported as pollinators for *Myristica dactyloides* [32], *Horsfieldia grandis* in Sarawak [48], and the Neotropical *Compsoneura sprucei* [31]. Detection of pollen on an insect's body is unfortunately the only real evidence of an insect's potential for pollination, but since thrips remove pollen from their bodies prior to flight [51], these studies may have underestimated their potential as pollinators. When the system being studied does not allow the researcher to manipulate pollinators and flowers to monitor pollen load, pollen deposition, and the resulting fruit set, determining the effectiveness of different floral visitors as pollinators is not possible. In some of these surveys of floral visitors, insects were not checked for pollen loads.

A recent study on *M. dactyloides* [32] revealed a whole spectrum of insects observed visiting the flower. In addition to thrips (Thysanopterans), which appeared to be the predominant pollinators (Fig. 3), and beetles (Coleoptera: Staphylinidae and Curculionidae), bees (Hymenoptera: Halictidae) and flies (Diptera: Syrphidae and Phoridae) were potential pollinators based on foraging behaviors and the presence of pollen loads on their bodies (Fig. 4). Until then, the only study that reported small diverse insects in a nutmeg pollinator guild was the one on Neotropical *Virola koschnyi* [31]. In *Myristica fatua*, thrips (Thysanoptera: Phlaeothripidae and Thripidae) and beetles (Coleoptera: Curculionidae, Cleridae, Cucujidae, Cantharidae and Silvanidae) were found to be potential pollinators [52].
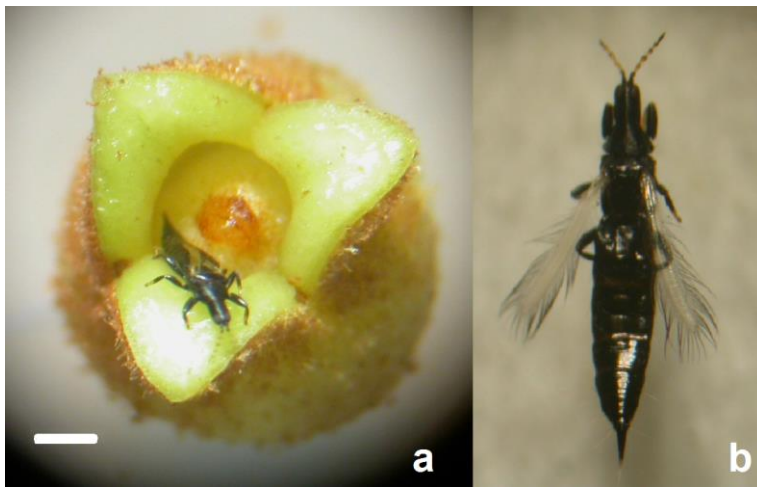
Fig. 3. Female flower of *Myristica dactyloides* (a) with thrip (b) exiting from perianth opening. Note bilobed stigma just below the perianth opening.

Based on Bawa et al. [31] and Givnish [53], *Myristica* conforms to a generalized, small-insect pollinator syndrome. Nevertheless, small differences in flower structure can greatly change how effective diverse insects are as pollinators. For example, in *Myristica fragrans* and *M. insipida* insect entry to female flowers is restricted by the tight fit of the perianth *around* the stigma, while flowers of *M. fatua* and *M. dactyloides* have a more open perianth easily entered by small insects [32] (Fig. 2, 3). Urn-shaped flowers also appear to provide a shelter with ambient temperature [54-56], and/or a site for agonistic

and mating activities for beetles [24, 25, 57]. Similarly, thrip larvae are frequently found within *Myristica* flower buds [32]. The usual beetle activities involved with cantharophily were largely lacking in *Myristica insipida,* thus highlighting the diversity among beetle pollination syndromes [41]. With beetles, pollination is often combined with feeding on stigmatic secretions, anthers and pollen, staminodia, and perianth parts (phytophagy) [50]. Clearly, considerable overlap of functional guilds exists on tropical tree species, and relatively small, simple flowers of trees such as nutmegs can interact with a range of potential insect pollinators [52].

Lastly, all nutmegs have a yellow to red aril associated with bird dispersal, and while bird dispersal of diverse nutmegs has been observed in many instances, this has been studied in detail only in *Virola* [58]. In Queensland, seed dispersal of *Myristica inspida* was a two-stage process where first fruit dehiscence presented the arillate seeds aloft, and then if not removed within 48 hrs, the fruit opened further dropping seeds to the ground where terrestrial birds could disperse them more locally [Irvine and Armstrong, unpublished data].
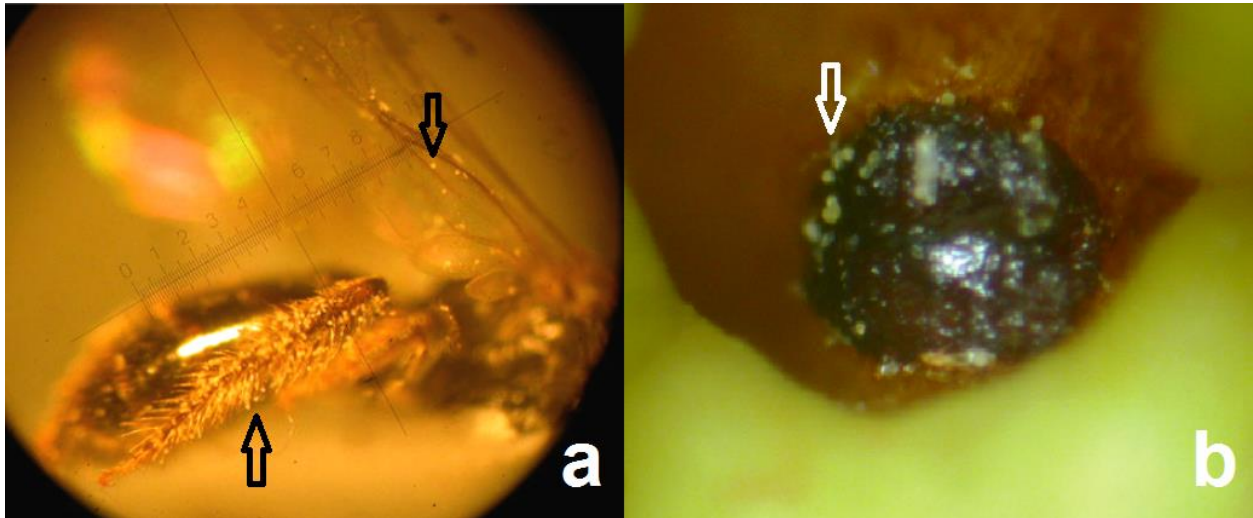

Fig. 4. Pollen loads (arrows highlight some of the many grains) on body and wings of a Halictid bee (a) and on the darkened, post-anthesis stigma (b).

Conclusions

The era of biological guesswork about the pollination of *Myristica* has ended with the cumulative understanding that, like most tropical dioecious trees [53, 59-62], the pollination of *Myristica* is effected by a loose mutualistic group of insects including beetles, flies, thrips, and even bees, in different proportions with different species and at different times and places. The "mistake" pollination of nutmegs is quite different from the pollination syndromes found in other families of the Magnoliales (Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae and Myristicaceae) in the topology of Soltis et al. [1, 25, 26, 63-67]. In terms of floral organization, the nutmegs with small,

unisexual, few-parted flowers and mistake pollination have more in common with some members of some ANA grade families (e.g., Amborellaceae), where unisexual flowers, pollen rewards, and food deceit are fairly common biologies [35]. A generalist entomophily involving beetles, thrips, micropterigid moths, as well as dipterans, and hymenopterans was proposed for ancestral angiosperms [68], and as more of the nutmegs are studied, this list is likely to describe their associated pollinators. While some general aspects of nutmeg floral biology may be retained from common ancestry with basal angiosperm ancestors, perhaps mistake pollination will prove to be a synapomorphy for Myristicaceae.

Just as greater sampling intensity may result in higher diversity of insects interacting with nutmeg flowers, more pollinator diversity is to be expected as studies of the nutmeg family continue. At this time the Myristicaceae remain very little studied, considering their importance and ubiquity in lowland tropical forests. Even for those species for which good data exist, field studies are snapshots in ecological time, and the effectiveness of diverse pollinators in such loose mutualistic guilds will vary depending upon natural cycles in populations and environmental variations that affect both plants and pollinators. Examples of this are presently limited, but one species of beetle, the most common floral visitor in an earlier study, was observed to be the least common of nine floral visitors in the same community on many of the same trees just four years later [45]. In light of studies of wild species of *Myristica*, the reproduction of commercial nutmeg should be reevaluated, especially in areas where nutmeg has been introduced and pollinators must be borrowed from native species, including native members of the Myristicaceae. Apart from differences in insect faunas among tree species and among continents, there could be an expected variation between primary and disturbed or secondary forests. Some canopy fauna such as Curculionid and Chrysomelid beetles, for instance, are susceptible to disturbances [69, 70].

Lastly Flach's [22] concerns about commercial nutmeg and its "sex" problem involved two components: the inability to determine the sex of seedlings and the abscission of a considerable percentage of the female flowers, which to growers represents lost crop. While the sexing problem remains, the abscission of female flowers has been biologically resolved, and although this understanding will not increase the nutmeg crop, it may ease growers' concern because such flower abscission is an inherent part of the floral biology, occurring even when hand-pollinated, because of the "over" production of female flowers for display/deceit purposes [38, 45, 71].

Implications for conservation

The challenges to furthering our understanding of nutmeg pollination are many. The paucity of studies on the reproductive biology of nutmegs is clear when only two authors, working over two decades apart, account for most of the detailed field studies of floral biology and pollinators. The primary reasons are fairly obvious to anyone who attempts to study nutmegs. Populations of Myristicaceae are known to display inconstant flowering, and gaps between flowering individuals and flowering years are significant [39]. Infrequency and inconstancy of flowering have stymied the second author's study of some Neotropical nutmeg species for more than a decade. The trees are large, generally inaccessible, and often found in low densities, making canopy research all the more difficult and time consuming, not to mention involving a certain amount of risk, such that long periods of observation and data gathering in the canopies of trees are virtually impossible. The flowers and floral visitors are small and require

diverse techniques and careful study to monitor their movements and observe whether, when, and how they move and carry pollen loads between male and female trees. Nutmegs are important components in some and common components in many tropical forests, but our knowledge of nutmeg reproduction remains quite limited, thus rendering futile many conservation strategies. Even further, commercial growers should be concerned about and should practice conservation of native rain forest in the vicinity of their plantations, where some of the tree species undoubtedly host the pollinators that make nutmeg cultivation possible and successful.

Acknowledgements

References

[1] Soltis, D. E., Smith, S. A., Cellinese, N., Wurdack, K. J., Tank, D. C., Brockington, S. F., Refulio-Rodriguez, N. F., Walker, J. B., Moore, M. J., Carlsward, B. S., Bell, C. D., Latvis, M., Crawley, S., Black, C., Diouf, D., Xi, Z., Rushworth, C. A., Gitzendanner, M. A., Sytsma, K. J., Qiu, Y.-L., Hilu, K. W., Davis, C. C., Sanderson, M. J., Beaman, R. S., Olmstead, R. G., Judd, W. S., Donoghue, M. J. and Soltis, P. S. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. *American Journal of Botany* 98: 704-730.

[2] Gentry, A. H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15: 1-84.

[3] Ribeiro, J. E L. S., Nelson, B. W., deSilva, M. F., Martins, L. S. S., and Hopkins, M. 1994. Reserva Florestal Ducke: Diversidade e composição da flora vascular. *Acta Amazonica* 24:19–30.

[4] Pascala, J.-P. and R. Pelissiera. 1996. Structure and floristic composition of a tropical evergreen forest in southwest India. *Journal of Tropical Ecology* 12 : 191-214.

[5] Spichiger, R., Loizeau, P. A., Latour, C., and Barriera, G. 1996.   Tree species richness of a South-Western Amazonian forest (Jenaro Herrera, Peru, 73º 40' W/5º 4' S). *Candollea* 51: 559-577.

[6] Pitman, N., Terborgh, J., Silman, M., Nunez, P., Neill, V.D., Ceron, C., Palacios, W. and Aulestia, M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82: 2101-2117.

[7] Valencia, R., Foster, R., Villa, G., Condit, R., Svenning, J.-C., Hernandez, C., Romoleroux,K., Losos, E. and Balsley, H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92: 214-229.

[8] Smith, A. C. 1937. The American species of Myristicaceae. *Brittonia* 2: 393-510.

[9] Rodrigues, W. A. 1980. Revisão taxonomica das espécies de Virola Aublet (Myristicaceae) do Brasil. *Acta Amazônica* 10: 1-127.

[10] Ackerly, D. D., Rankin-De-Merona, J. M. and Rodrigues, W. A. 1990. Tree densities and sex ratios in breeding populations of dioecious Central Amazonian Myristicaceae. *Journal of Tropical Ecology* 6: 239-248.

[11] Gamble, J. S. 1935. Flora of the Presidency of Madras. Vol. I to III. Adlard and Son Ltd., London.

[12] Krishnamoorthy, K. 1960. *Myristica* swamps in the evergreen forests of Travancore, In: Tropical Moist Evergreen Forest Symposium. Forest Research Institute, Dehradun, India.

[13] Ramesh, B.R. 1989. Evergreen forests of the Biligiri Rangan Hills, South India - Ecology, structure and floristic composition. PhD. University of Madras.

[14] Parthasarathy, N. 1999. Tree diversity and distribution in undisturbed and human- sites of tropical wet evergreen forest in southern Western Ghats, India. *Biodiversity and Conservation* 8: 1365-1381.

[15] Pascal, J.P. 1988. Wet evergreen forests of the Western Ghats of India: Ecology, Structure, Floristic Composition and Succession, French Institute, Pondicherry, India.

[16] Armstrong, J. E. and Irvine, A. K. 1989. Flowering, sex ratios, pollen-ovule ratios, fruit set, and reproductive effort of a dioecious tree, *Myristica insipida* (Myristicaceae), in two different rain forest communities. *American Journal of Botany* 76: 74-85.

[17] Nicholls, H. A. A. and Holland, J. H. 1929. *A text-book of tropical agriculture.* Macmillan and Co., London.

[18] Cobley, L. S. 1976. *Introduction to the botany of tropical crops.* 2nd edition. Longman, London.

[19] McIlroy, R. J. 1978. *An introduction to tropical cash crops.* Ibadan University Press, Ibadan, Nigeria.

[20] Deinum, H. 1949. Nootmuskaat en foelie. *Landbouwhogeschool Ind. Arch*. 2: 655-683.

[21] Purseglove, J. W. 1968. *Tropical Crops: Dicotyledons 2*. J. Wiley and Sons, New York.

[22] Flach, M. 1966. Nutmeg cultivation and its sex problem. *Mededelingen Landbouwhogeschool*, Wageningen 66:1–85.

[23] Armstrong, J. E. and Drummond, B. A. 1986. III. Floral biology of *Myristica fragrans* Houtt. (Myristicaceae), the Nutmeg of Commerce. *Biotropica* 18: 32-38.

[24] Gottsberger, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Plant Systematics and Evolution* 1:211–226.

[25] Gottsberger, G. 1988. The reproductive biology of primitive angiosperms. *Taxon* 37:630-643.

[26] Gottsberger, G. 1999. Pollination and evolution in Neotropical Annonaceae. *Plant Species Biology* 14, 143–152.

[27] Webber, A. C. and Gottsberger, G. 1995. Floral biology and pollination of *Bocageopsis multiflora* and *Oxandra euneura* in Central Amazonia, with remarks on the evolution of stamens in Annonaceae. *Feddes Repertorium* 106, 515-524.

[28] Momose, K., Nagamitsu, T. and Inoue, T. 1998. Thrips cross pollination of *Popowia pisocarpa* (Annonaceae) in a lowland dipterocarp forest in Sarawak. *Biotropica* 30, 444-448.

[29] Norman, E. M. 2003. Reproductive biology of *Deeringothamnus rugelii* and *D. pulchellus* (Annonaceae). *Taxon* 52, 547–555.

[30] Silberbauer-Gottsberger, I., Gottsberger, G. and Webber, A. C. 2003. Morphological and functional flower characteristics of New and Old World Annonaceae with respect to their mode of pollination. *Taxon* 52, 701–718.

[31] Bawa, K. S., Bullock, S. H., Perry, D. R., Coville, R. E. and Grayum, M. H. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* 72: 346-356.

[32] Sharma M. V. and K. R. Shivanna. 2011. Pollinators, pollination efficiency and fruiting success in a wild nutmeg, *Myristica dactyloides*. *Journal of Tropical Ecology* 27, 405–412.

[33] Kirk, W. D. J. 1984. Pollen-feeding in thrips (Insecta:Thysanoptera). *Journal of Zoology* 204, 107–117.

[34] Kirk, W. D. J. 1988. Thrips and pollination biology. In: *Dynamics of insect–plant interaction.* Ananthakrishnan, T. N. and Raman,A. (Eds.), pp. 129–135. New Delhi, India: Oxford and IBH.

[35] Thien, L. B., Bernhardt, P., Devall, M.S., Chen, Z.-D., Luo, Y.-B., Fan, J.-H., Yuan, L.-C. and Williams, J.H. 2009. Pollination biology of basal angiosperms (ANITA Grade). *American Journal of Botany* 96: 166-182.

[36] Endress, P. 2010. The evolution of floral biology in basal angiosperms. *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences* 365: 411-421.

[37] Jürgens, A., Webber, A. C. and Gottsberger, G. 2000. Floral scent compounds of Amazonian Annonaceae species pollinated by small beetles and thrips. *Phytochemistry* 55, 551–558.

[38] Opler, P. A. and K. S. Bawa. 1978. Sex ratios in some tropical forest trees. *Evolution* 32: 812-821.

[39] Queenborough, S. A., Burslem, D. F. R. P., Garwood, N. C. and Valencia, R. 2007. Determinants of biased sex ratios and inter-sex costs of reproduction in dioecious tropical forest trees. *American Journal of Botany* 94: 67-78.

[40] Sharma, M. V. 2009. *Pollination dynamics in a changing tropical forest landscape.* PhD Dissertation. University of London, London.

[41] Armstrong, J. E. and Irvine, A. K. 1989. Floral biology of *Myristica insipida* (Myristicaceae), a distinctive beetle pollination syndrome. *American Journal of Botany* 76: 86-94.

[42] Cruden, R.W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.

[43] Armstrong, J. E. and Tucker, S. C. 1986. Floral development in *Myristica* (Myristicaceae). *American Journal of Botany* 73: 1131-1143.

[44] Wilson, T. K. and Maculans, L. 1967. The morphology of the Myristicaceae. I. Flowers of *Myristica fragrans* and *M. malabarica*. *American Journal of Botany* 54: 214-220.

[45] Armstrong, J. E. 1997. Pollination by deceit in nutmeg (*Myristica insipida*, Myristicaceae): floral displays and beetle activity at male and female trees. *American Journal of Botany* 84: 1266-1274.

[46] Queenborough, S.A., Humphreys, A.M. and Valencia, R. 2013. Sex-specific flowering patterns and demography of the understorey rain forest tree *Iryanthera hostmannii* (Myristicaceae). *Tropical Conservation Science*. In press.

[47] Armstrong, J. E. and Wilson, T. K. 1978. Floral morphology of *Horsfieldia* (Myristicaceae). *American Journal of Botany* 65: 441-449.

[48] Baker, H. G. 1976. "Mistake" pollination as a reproductive system with special reference to Caricaceae. In: *Tropical trees: variation, breeding, and conservation*. Burley, J. and Styles, B. T. (Eds.), pp. 161-169. Academic Press, New York.

[49] Momose, K., Yumoto, T., Nagamitsu, T., Kato, M., Nagamasu, H., Sakai, S., Harrison, R. D., Itioka, T., Hamid, A. A. and Inoue, T. 1998b. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85: 1477-1501.

[50] Momose, K. 2005. Beetle pollination in tropical rainforests. In: *Pollination ecology and the rainforest - Sarawak studies.* Roubik, D. W., Sakai, S., and Hamid, A. A. (Eds.), pp. 104-110. Springer, Berlin.

[51] Williams, G. A., Adam, P., and Mound, L. A. 2001. Thrips (Thysanoptera) pollination in Australian subtropical rainforests, with particular reference to pollination of *Wilkiea huegeliana* (Monimiaceae). *Journal of Natural History* 35: 1-21.

[52] Sinu, P.A. and Sharma, M.V. 2013. Insect functional guilds in the flowering canopy of *Myristica fatua* in a lowland Myristica swamp, central Western Ghats, India. *Tropical Conservation Science.* In press.

[53] Givnish, T. J. 1980. Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. *Evolution* 34: 959-972.

[54] Bay, D. 1995. Thermogenesis in the aroids. *Aroideana* 18: 32-39.

[55] Seymour, R. and Schultze-Motel, P. 1997. Heat-producing flowers. *Endeavor* 21: 1527-1534.

[56] Bernhardt, P. 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Plant Systematics and Evolution* 222: 293-320.

[57] Goldbatt, P., Bernhardt, P. and Manning, J. C. 1998. Pollination of petalloid geophytes by monkey beetles (Scarabaeidae: Rutelinae: Hopliini) in southern Africa. *Annals of the Missouri Botanical Garden* 85: 215-230.

[58] Howe, H. F. 1981. Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. *The Auk* 98: 88-98.

[59] Bawa, K. S. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11:15-39.

[60] Givnish, T. J. 1982. Outcrossing versus ecological constraints in the evolution of dioecy. *American Naturalist* 119: 849-865.

[61] Beach, J. H. 1981. Pollinator foraging and the evolution of dioecy. *American Naturalist* 118: 572-577.

[62] Muenchow, G. E. 1987. Is dioecy associated with fleshy fruits? *American Journal of Botany* 74: 287-293.

[63] Thien, L. B. 1974. Floral biology of *Magnoli*a. *American Journal of Botany* 61: 1037-1045.

[64] Thien, L. B. 1980. Patterns of pollination in the primitive angiosperms. *Biotropica* 12: 1-13.

[65] Endress, P. 1984. The flowering process in the Eupomatiaceae (Magnoliales). *Botanische Jahrbücher für Systematik* 104: 297-319.

[66] Armstrong, J. E. and Irvine, A. K. 1990. Functions of staminodia in the beetle-pollinated flowers of *Eupomatia laurina*. *Biotropica* 22: 429-431.

[67] Dieringer, G., Cabrera, L., Larta, R. M., Loya, L., and Reyes-Castillo, P. 1999. Beetle pollination and floral thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). *International Journal of Plant Science* 160: 64-71.

[68] Bernhardt, P. and Thien, L. B. 1987. Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. *Plant Systematics and Evolution* 156: 159-176.

[69] Floren, A. and Linsenmair, K. E. 2003. How do beetle assemblages respond to anthropogenic disturbance? In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy.* Y. Basset, V. Novotny, S. E. Miller, R. L. Kiching (Eds.), pp. 190-197. Cambridge University Press, Cambridge.

[70] Speight, M. R., Intachat, J., Khen, C. V. and Chung, A. Y. C. 2003. Influences of forest management on insects. In: *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy.* Basset, Y., Novotny, V., Miller, S. E. and Kiching, R. L. (Eds.), pp. 380-393. Cambridge University Press, Cambridge.

[71] Bawa, K. S., Perry, D. R. and Beach, J. H. 1985b. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility mechanisms. *American Journal of Botany* 72:331–345.