

## POLLINATION SYSTEMS OF TREES IN KAKACHI, A MID-ELEVATION WET EVERGREEN FOREST IN WESTERN GHATS, INDIA<sup>1</sup>

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A long-term survey (1990–2000) of pollination modes of 86 tree species was carried out at Kakachi, a mid-elevation wet forest site in southern Western Ghats, India. Observations were made on 86 tree species. This comprises 80% of the total arboreal species present in the site. Approximately 75% of these species were specialized to a single pollinator group such as bee, beetle, or moth. Pollinators from diverse groups pollinate the remaining 25% of the tree species. Global comparison with other wet forest sites showed that diversity and specialized pollination modes observed in Kakachi bore closer resemblance to other lowland than montane forest sites described so far. However, the number of pollinators involved in pollination was comparable with montane sites. We examine the consequences that might have led to selection of the observed pollination modes in Kakachi. We discuss the conservation implications of these results.

**Key words:** India; pollination systems; Western Ghats; wet forest.

Tropical wet forests support a diverse assemblage of tree species, which are dependent on an equally wide array of animals for their pollination (Baker et al., 1983; Bawa, 1990). This has resulted in a highly complex set of interactions among them (Gilbert, 1980). Identifying pollination guilds or tree species assemblages with common pollination modes can delineate this complexity to some extent (Ibarra-Manríquez and Oyama, 1992). Further, comparisons of pollination modes in the different wet forest sites in the tropics can provide insights into the broad coevolutionary patterns between plants and their animal vectors (Howe, 1984) or perhaps cast light on such issues as the role of pollinators on angiosperm diversification (Bawa, 1995). Broad-scale community-level pollination studies also have wide application in ecosystem restoration (Johnson and Steiner, 2000; Kremen and Rickett, 2000). There is an increasing concern that human alterations of the ecosystem affect pollination systems, especially those that are relatively more specialized and dependent on a few pollinators (Bond, 1994). Specialized systems cannot be identified unless we conduct community-wide surveys of pollination systems.

Complete community-level characterization of pollination of any tropical forest site has not been successfully executed so far (Shatz, 1990). This kind of study could not be completed because much of the diversity of the plant species is contributed by the tall canopy trees in tropical forests that have remained inaccessible (Lowman and Nadkarni, 1995). Despite

this, Bawa and his co-workers (1985) have analyzed the pollination systems of 143 out of the estimated 2000 tree species in La Selva. Recently data on more species have been gathered from the same site (Kress and Beach, 1994). From the Old World tropics Momose et al. (1998) have reported the pollination systems of 270 species from Lambir, in Sarawak, Malaysia, a study that includes the shrubs, lianas, and epiphytes. A few studies have also been carried out in montane sites, which indicate distinct differences from lowland sites. Pollination systems in montane sites in general are less specialized than in lowland sites (Sobrevila and Arroyo, 1982; Tanner, 1982; also see Bawa, 1990). Today much of the lowland rain forest has been lost in South Asia, and what remains is the rain forest on the slopes of mountains that are inaccessible. These forests have been poorly studied, and much less is known about pollination modes and their organization.

In India, wet forests are restricted to the two global hotspots: one in the northeastern Himalayan region and the other in the Western Ghats. In Western Ghats the most luxuriant of wet forests are generally found in the mid-elevational range of 900–1300 m a.s.l in the Agasthyamalai hills in the southernmost tip. This region is rich in endemic flora and fauna and has been identified as an area of conservation importance (Ramesh et al., 1997). An earlier study on plant pollinators of the understory shrub community in the mid-elevation site in the Agasthyamalai region has shown that most plants are generalists and use diverse pollinator groups (Krishnan, 1994). Yet another study of the social bee guild, which was carried out in the same site, has shown some intricate relationships between social bees and their food plants (Devy, 1998). In this study, we report the results of a community-wide survey of pollination modes of the tree species from the same region. We compare the trends from this region with the existing data available from the other wet forest sites from both the Old and the New World tropics and contrast it with lowland and montane sites.

### MATERIALS AND METHODS

*Study site*—Western Ghats is a long chain of hills running parallel to the west coast of India for almost 1600 km. This study was conducted from 1990

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to 1996 at Kakachi (8°40' N and 77°30' E) in the southernmost part of Western Ghats. More data were collected in the following years (1997–2000) as a part of several other projects in the area since many tree species did not flower during the study period.

Elevation of Kakachi is about 1250 m a.s.l., and it receives an annual rainfall of over 3500 mm from both the southwest and northeast monsoons. The southwest monsoon is active during May to July, and the northeast monsoon during October to December. The study site is a part of the Kalakad-Mudanthurai Tiger Reserve. The vegetation is broadly classified as mid-elevation tropical wet evergreen forest and has been described in detail by Ganesh et al. (1996). Ganesh et al. (1996) list approximately 173 plant species that are composed of 42 canopy trees, 48 understory trees, 50 shrubs, 18 herbs, and 15 woody lianas. Emergents were distinctly absent in this forest, and the mean height of the trees ranges from 15 to 25 m.

*Cullenia exarillata*, *Palaquium ellipticum*, and *Aglaiia bourdillonii* are the dominant species in the site. Part of the flora flower annually, while others do not show predictable cycles (Devy, 1998). Field observations on pollinators of 86 tree species, which comprised both common and rare ones, were carried out within a 30-km<sup>2</sup> area. This included 67 of the 90 (74%) tree species recorded by Ganesh et al. (1996) and 20 other species not recorded in that study.

**Characterization of pollination modes**—Time of anthesis was determined for most tree species by direct observations of the flowering trees. For some species cut branches were placed in water and the anthesis time was recorded. Later this record was confirmed by field observations. For species with crepuscular or nocturnal anthesis, observations on visitors were carried out at night. For many tall trees, observations were made from temporary rafts erected with the help of tree climbers in the canopy (Fig. 1).

From the time of anthesis, continuous observations of visitors were done. The time spent on each species and the number of individuals sampled depended upon the behavior of pollinators. Often observations were conducted for 8–9 h over a 3-d period during peak flowering time. The number of species visiting the flowers was noted. For species for which continuous observations did not yield sufficient information, random checks were carried out. Pollinators that made negligible visits (<2%) were not considered in the analysis of pollination modes (see Herrera, 1989). If the ratio of visits by pollinators belonging to various groups such as moths, beetles, or bees were nearly equal, the species was considered generalized in its pollination mode. Pollination modes of all the tree species were characterized based on field observations, and no extrapolations were made based on flower structure or on visitors of related tree species. Wind pollination of species was confirmed by bagging experiments. One set of inflorescences was bagged with nylon wire mesh bags that would permit the flow of wind freely but restrict other visitors. The second set was covered by paper bags, which restricted both airflow and visitors (also see Bawa and Crisp, 1980). Observations of visitors were carried out for 2–3 consecutive years to determine any shift in pollinators between years. The prominent insect pollinators were collected and sorted according to morphological species using a microscope and later classified. In cases of species with small flowers or ones that did not open, approximately 50 flowers were collected from 2–3 trees and examined under the microscope to determine the presence of visitors. The vertebrate pollinators were identified to the species level. Among insects, the honey bees were identified up to species while others were classified into pollinator groups such as beetles, moths, butterflies, etc.

**Floral characters**—The flower colors were identified as white, cream, yellow, and others. The shape of the flowers were classified as tubular when the corollas had a narrow tube; brush-shaped if they had numerous stamens; cup-shaped if the center of the flower was deep where nectar was presented; chamber-shaped if flowers presented a hood and pollinators were not immediately visible; open if flowers disc-like (Figs. 1 and 2). The reward was classified as nectar, pollen, or floral tissue.

The phenology of tree species was classified as annually flowering species if they flowered every year; others that did not show any predictable cycles or had prolonged intervals were classified non-annually flowering species. The

data on phenology was obtained from the ongoing long-term study from the same site (T. Ganesh et al., unpublished data, Ashoka Trust, Bangalore, India). The relationship between the pollination modes and the flower characters were tested with *G* statistics using species numbers.

## RESULTS

**Pollinator spectra**—Over 50 species of anthophilous insects, which includes the social bees, beetles, moths, bugs, wasps, thrips, and flies, were encountered frequently. Social bees were composed of just two species: *Apis dorsata* and *Apis cerana*. *Apis florea*, which was encountered in the lower elevations, was distinctly absent here. Moths of various sizes, mostly belonging to the family Geometridae, visited the tree species. The carrion flies and the tiny fruit flies were recorded on six species. Among vertebrates, four nectarivorous birds, the little spider hunter (*Aracnothera longirostris*), the small sunbird (*Nectarinia minima*), the white eye (*Zosterops palpebrosa*), and the Nilgiri flowerpecker (*Dicaeum concolor*), visited the flowers. Although the birds were observed on flowers of tree species such as *Palaquium ellipticum* and *Elaeocarpus munronii*, they were only marginal visitors compared to the bees. However, birds seemed to play an important role in pollinating the epiphytic plants belonging to Loranthaceae and many ground herbs (M. S. Devy, unpublished data).

*Cynopterus sphinx*, the common frugivorous bat in the site, visited flowers. Among non-volant mammals, the giant squirrel (*Ratufa indica*), the flying squirrels (*Petaurista petaurista*), the lion tail macaque (*Macaca silenus*), and the brown palm civet (*Paradoxurus jerdonii*) were observed carrying pollen of *Cullenia exarillata* (Ganesh and Devy, 2000). Two rodents, the spiny dormouse (*Plantacantho lasiurus*) and a rat (*Rattus rattus*), visited a small treelet (*Helicia nilagirica* [Proteaceae]) at night (see <http://ajbsupp.botany.org/v90>).

**Frequency of pollination**—**Specialized mode**—Fifty-nine tree species, which comprised about 75% of the tree species studied, used a single group of insects such as bees, beetles, flies, or bugs as pollinators (Table 1, Fig. 3A). Of the tree species with a specialized mode, 35% were visited by only 1–2 species of pollinators. For 53% of the trees, about 3–4 species of pollinators were recorded. The remaining 10% of the tree species had 4–8 pollinators (Fig. 3B).

Social bees were important pollinators of trees (18%), followed by beetles (17%), flies (6%), and thrips (5%). Butterflies (5%) and moths (10%) together pollinated 15 of the tree species. Bees and beetles pollinated trees from various families representing diverse genera. Bats pollinated only *Syzygium mundagam* exclusively, although they played a larger role as disperser in the site (Ganesh, 1996). Other non-volant mammals pollinated just two species.

**Generalized mode**—About 25% (23/89) of the species were visited by a wide range of pollinator groups (Table 2). Small insects (<2 mm), including fruit flies, wasps, and moths, pollinated 15%, and large insects (5–8 mm) from various taxa, such as moths, beetles, and others, pollinated 10% of the trees species (Table 1).

**Pollination syndromes**—**Flower shape, color, and reward**—Flower shapes were related to the pollination systems (Table 3, *G* = 64.55, *df* = 30, *P* < 0.01). The social bees, which were more flexible in their floral choice, used flowers

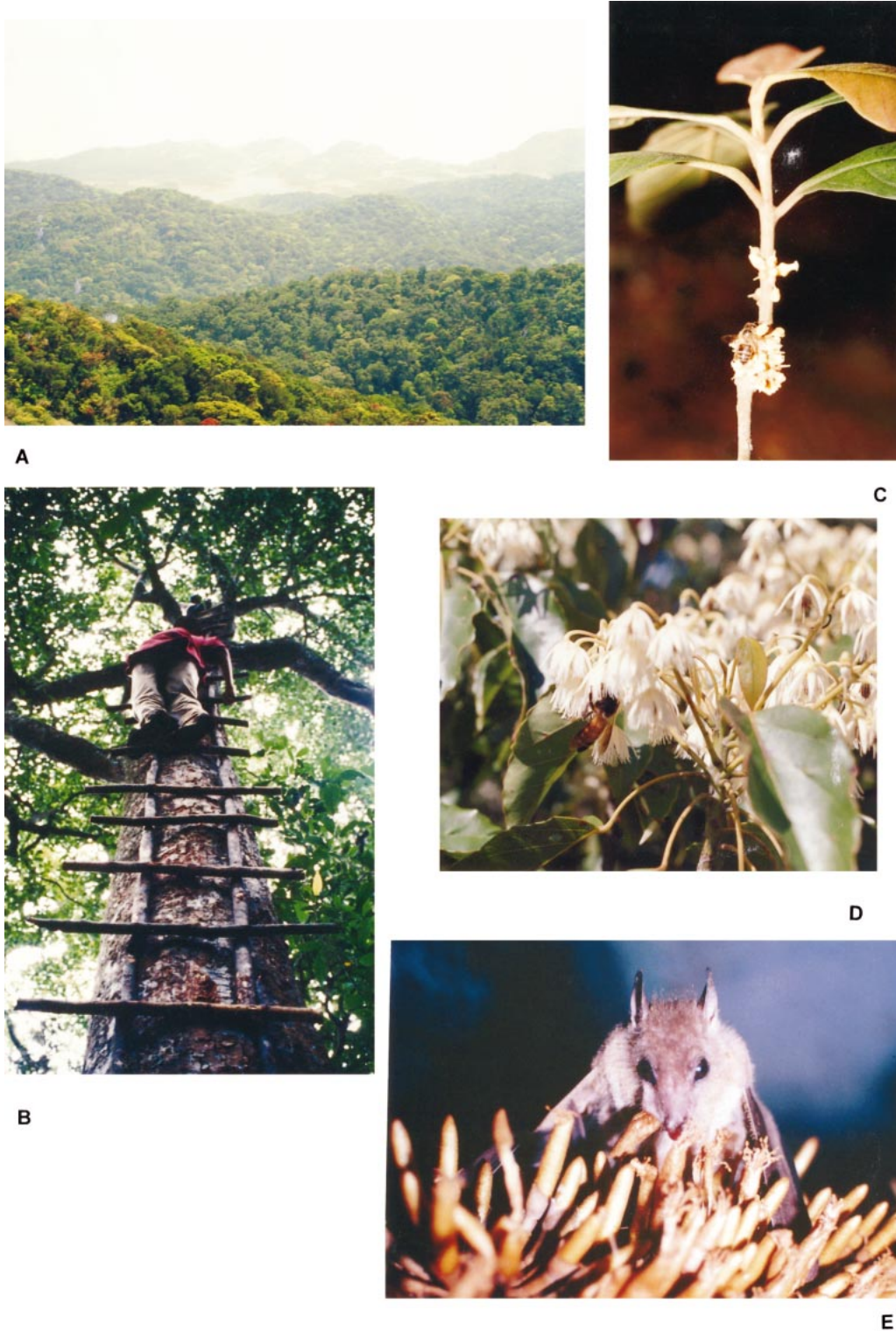


Fig. 1. (A) The rain forest site in the southern Western Ghats where this study was conducted. (B) Tree ladders used to access the canopy. (C) *Apis cerana* visiting *Isonandra lanceolata* flower. (D) *Apis dorsata* on *Elaeocarpus munronii*. (E) The bat pollinator *Cynopterus spinx* on tubular flowers of *Cullenia exarillata*.

of varying shapes from brush-shaped and open to short, tubular flowers. The beetles, flies, and thrips used flowers that were predominantly open. The longed-tongued butterflies and moths pollinated long tubular flowers. There was no relationship between the flower color and the pollination systems ( $G$

$= 19.3$ ,  $df = 22$ , ns). Most of the flowers present in the community were white or cream colored (Table 3).

The relationship between the reward and the pollination systems was significantly different ( $G = 170.52$ ,  $df = 30$ ,  $P < 0.01$ ). The social bees used species that offered pollen and

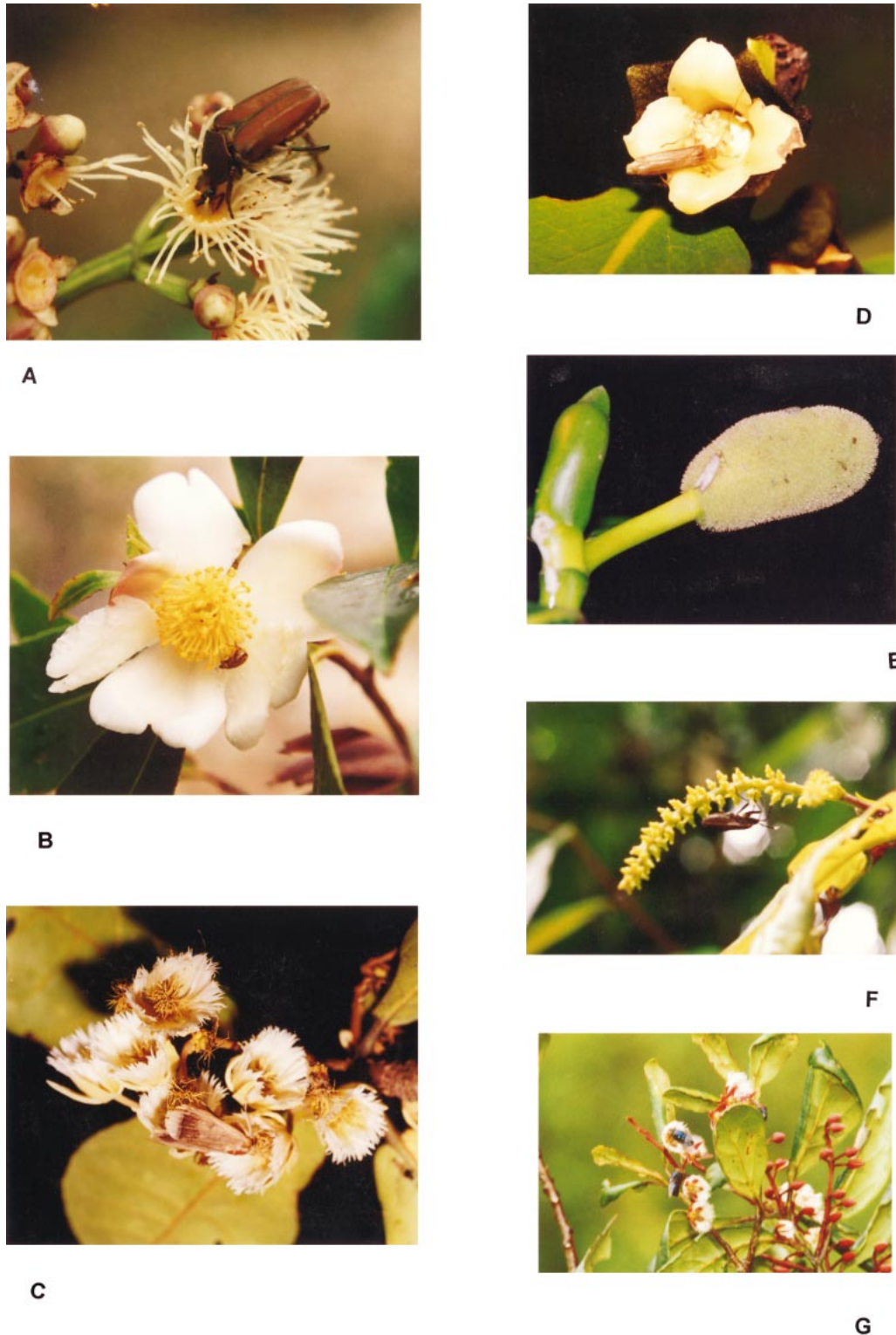


Fig. 2. (A) Large beetle on *Syzygium tamilnadensis*. (B) Large insects on *Gordonia obtusa*. (C) Moth on *Elaeocarpus tuberculatus*. (D) Beetle on *Diospyros malabarica*. (E) Moth on *Artocarpus heterophyllus*. (F) Beetle on *Antidesma menasu*. (G) Carrion fly on *Elaeocarpus serratus*.

nectar as a reward. Plants that offered only pollen as a reward characterized the beetle, thrip, and small insect guilds. The lepidopterans and the flies used species that offered only nectar as a reward.

The time of anthesis was significantly different for various pollination modes ( $G = 8.7$ ,  $df = 32$ ,  $P < 0.01$ ). The bat, beetle, moths, thrips, and few social-bee-pollinated species exhibited nocturnal anthesis. The rest of the species had diurnal

TABLE 1. Comparison of pollination modes between Kakachi and other wet sites.<sup>a</sup>

| Pollination modes | Kakachi     |            | Lambir <sup>b</sup> |            | La Selva <sup>c</sup> |            | Jamaica <sup>d</sup> |            | Venezuela <sup>e</sup> |            |
|-------------------|-------------|------------|---------------------|------------|-----------------------|------------|----------------------|------------|------------------------|------------|
|                   | No. species | Percentage | No. species         | Percentage | No. species           | Percentage | No. species          | Percentage | No. Species            | Percentage |
| Bees              |             |            |                     |            |                       |            |                      |            |                        |            |
| Large bees        | 0           | 0          | 10                  | 1          | 34                    | 28         | 0                    | 0          | 5                      | 13         |
| Small bees        | 16          | 18         | 41                  | 32         | 15                    | 13         | 0                    | 0          | 0                      | 0          |
| Beetles           |             |            |                     |            |                       |            |                      |            |                        |            |
| Beetles           | 15          | 17         | 35                  | 27         | 10                    | 8          | 0                    | 0          | 0                      | 0          |
| Moths             |             |            |                     |            |                       |            |                      |            |                        |            |
| Moths             | 9           | 10         | 1                   | 1          | 16                    | 13         | 2                    | 4          | 0                      | 0          |
| Butterflies       |             |            |                     |            |                       |            |                      |            |                        |            |
| Butterflies       | 4           | 5          | 0                   | 0          | 5                     | 4          | 0                    | 0          | 0                      | 0          |
| Wasps             |             |            |                     |            |                       |            |                      |            |                        |            |
| Wasps             | 2           | 2          | ND                  | ND         | 7                     | 6          | 0                    | 0          | 0                      | 0          |
| Flies             |             |            |                     |            |                       |            |                      |            |                        |            |
| Flies             | 5           | 6          | 1                   | 1          | 0                     | 0          | 0                    | 0          | 0                      | 0          |
| Thrips            |             |            |                     |            |                       |            |                      |            |                        |            |
| Thrips            | 4           | 5          | 0                   | 0          | 0                     | 0          | 0                    | 0          | 0                      | 0          |
| Bugs              |             |            |                     |            |                       |            |                      |            |                        |            |
| Bugs              | 1           | 1          | 0                   | 0          | 0                     | 0          | 0                    | 0          | 0                      | 0          |
| Diverse insects   |             |            |                     |            |                       |            |                      |            |                        |            |
| Small insects     | 13          | 15         | 27                  | 21         | 24                    | 20         | 47                   | 85         | 28                     | 77         |
| Large insects     | 9           | 10         |                     |            | 0                     | 0          | 0                    | 0          | 0                      | 0          |
| Bats/mammals      |             |            |                     |            |                       |            |                      |            |                        |            |
| Bats/mammals      | 3           | 3          | 5                   | 4          | 8                     | 7          | 0                    | 0          | 0                      | 0          |
| Birds             |             |            |                     |            |                       |            |                      |            |                        |            |
| Birds             | 0           | 0          | 7                   | 5.5        | 5                     | 4          | 2                    | 4          | 4                      | 10         |
| Wind              |             |            |                     |            |                       |            |                      |            |                        |            |
| Wind              | 5           | 6          | 0                   | 0          | 1                     | 1          | 6                    | 11         | 0                      | 0          |
| Total             | 86          |            | 127                 |            | 120                   |            | 55                   |            | 38                     |            |

<sup>a</sup> Frequencies of species in different pollination modes were recalculated in some sites to make them comparable with Kakachi. ND = no data.

<sup>b</sup> Momose et al. (1998); recalculated by excluding the epiphytes and lianas; small bees in Kakachi and Lambir mainly comprise the social bees.

<sup>c</sup> Kress and Beach (1994); tree species pollinated by >1 taxa of pollinator were scored under all pollinator groups; such cases were reallocated as generalized mode and removed from various pollination groups.

<sup>d</sup> Tanner (1982).

<sup>e</sup> Sobrevila and Arroyo (1982); small insects include small bees.

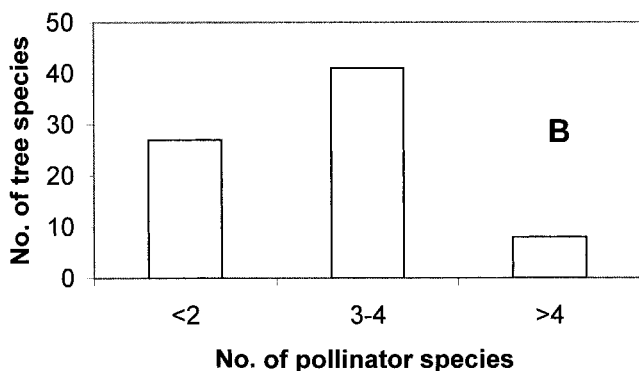
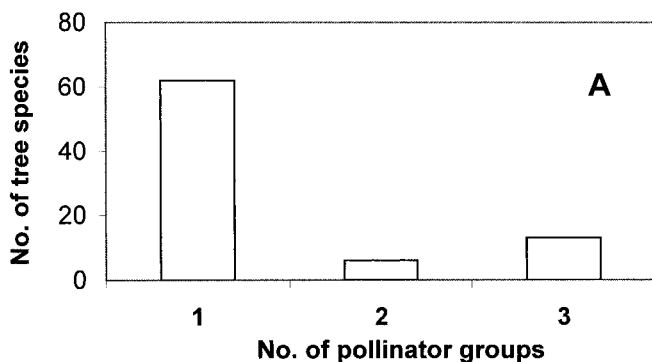


Fig. 3. Frequency distribution of species (A) pollinated by 1–3 pollinator groups and (B) pollinated by ≤2 pollinator species to >4 species.

anthesis. *Cullenia exarillata*, a mammal-pollinated species, was the only species that had an extended anthesis that lasted over a day and a night (Table 3; see also <http://ajb-suppl.botany.org/v90>).

*Influence of the phenology*—A long-term phenology of trees in the site in Kakachi has shown that a number of tree species have unpredictable flowering cycles. Some flower once every 2 yr and others at intervals of 3–4 yr. The pollination modes were independent of flowering cycles ( $G = 14.96$ ,  $df = 10$ , ns).

We further grouped the pollinator species such as thrips, flies, and social bees, which can multiply profusely, as r-selected species, and the slow breeders, such as moths, butterflies, bats, and mammals, were grouped as k-selected. The species pollinated by the r-selected pollinator species had a higher proportion of non-annual flowering species compared (76%) to those pollinated by k-selected species (Table 3,  $G = 4.8$ ,  $df = 1$ ,  $P < 0.01$ ). In almost all cases there was no shift in pollinator taxa between years. This includes tree species with

TABLE 2. Comparison of generalized and specialized modes of pollination.

| Site                   | Generalized |            | Specialized |            |
|------------------------|-------------|------------|-------------|------------|
|                        | No. species | Percentage | No. species | Percentage |
| Kakachi                | 22          | 26         | 65          | 74         |
| Lambir <sup>a</sup>    | 27          | 21         | 100         | 79         |
| La Selva <sup>b</sup>  | 28          | 22         | 97          | 78         |
| Jamaica <sup>c</sup>   | 47          | 82         | 10          | 12         |
| Venezuela <sup>d</sup> | 28          | 77         | 9           | 23         |

<sup>a</sup> Momose et al. (1998).

<sup>b</sup> Kress and Beach (1994).

<sup>c</sup> Tanner (1982).

<sup>d</sup> Sobrevila and Arroyo (1982).

TABLE 3. Flower characters and phenology of species in various pollination guilds.

| Pollination modes  | Color <sup>a</sup> |       |        | Shape <sup>b</sup> |      |         |        | Reward <sup>c</sup> |        |                   |        | Anthesis <sup>d</sup> |                       |           | Phenology <sup>e</sup> |            |
|--------------------|--------------------|-------|--------|--------------------|------|---------|--------|---------------------|--------|-------------------|--------|-----------------------|-----------------------|-----------|------------------------|------------|
|                    | Cream              | White | Others | Brush              | Open | Tubular | Others | Nectar              | Pollen | Nectar and pollen | Others | Diurnal               | Diurnal and nocturnal | Nocturnal | Annual                 | Non-annual |
| <b>Specialized</b> |                    |       |        |                    |      |         |        |                     |        |                   |        |                       |                       |           |                        |            |
| Bee <sup>f</sup>   | 9                  | 8     | 0      | 9                  | 4    | 4       | 0      | 0                   | 0      | 17                | 0      | 0                     | 0                     | 3         | 6                      | 11         |
| Beetle             | 0                  | 8     | 5      | 2                  | 8    | 0       | 3      | 0                   | 10     | 0                 | 3      | 2                     | 0                     | 11        | 7                      | 6          |
| Moth               | 0                  | 7     | 2      | 0                  | 3    | 5       | 0      | 9                   | 0      | 0                 | 0      | 0                     | 0                     | 9         | 5                      | 4          |
| Butterfly          | 0                  | 2     | 2      | 2                  | 1    | 1       | 0      | 4                   | 0      | 0                 | 0      | 4                     | 0                     | 0         | 4                      | 0          |
| Fly <sup>f</sup>   | 0                  | 5     | 0      | 1                  | 6    | 0       | 0      | 7                   | 0      | 0                 | 0      | 7                     | 0                     | 0         | 2                      | 5          |
| Thrip <sup>f</sup> | 0                  | 2     | 2      | 0                  | 4    | 0       | 0      | 0                   | 4      | 0                 | 0      | 0                     | 0                     | 4         | 1                      | 3          |
| Wasp               | 0                  | 0     | 0      | 0                  | 0    | 0       | 0      | 0                   | 0      | 0                 | 0      | 0                     | 0                     | 0         | 0                      | 0          |
| Bug                | 0                  | 2     | 1      | 0                  | 0    | 0       | 0      | 0                   | 2      | 0                 | 0      | 2                     | 0                     | 0         | 0                      | 2          |
| Wind               | 0                  | 1     | 1      | 2                  | 0    | 0       | 0      | 0                   | 0      | 0                 | 0      | 0                     | 0                     | 0         | 1                      | 1          |
| Bat/mammal         | 1                  | 1     | 0      | 1                  | 0    | 1       | 0      | 1                   | 0      | 0                 | 1      | 0                     | 1                     | 2         | 0                      | 1          |
| <b>Generalized</b> |                    |       |        |                    |      |         |        |                     |        |                   |        |                       |                       |           |                        |            |
| Small insects      | 0                  | 11    | 2      | 2                  | 7    | 0       | 0      | 0                   | 12     | 0                 | 0      | 10                    | 0                     | 0         | 5                      | 7          |
| Large insects      | 2                  | 1     | 1      | 1                  | 5    | 0       | 1      | 0                   | 7      | 0                 | 0      | 7                     | 0                     | 0         | 5                      | 2          |

<sup>a</sup>  $G = 64.55, P < 0.01.$

<sup>b</sup>  $G = 19.3, NS.$

<sup>c</sup>  $G = 170.52, P < 0.01.$

<sup>d</sup>  $G = 8.7, P < 0.01.$

<sup>e</sup>  $G = 4.8, P < 0.01.$

<sup>f</sup> R-selected species.

unpredictable flowering cycles as well as those that flowered every year. Monitoring of pollinators of tree species with unpredictable flowering cycles is still in progress.

DISCUSSION

**Generalized or specialized?**—Kakachi, a mid-elevation forest in southern Western Ghats, India, exhibits a great diversity of pollination modes. These modes can be distinguished into two groups. About 75% of the tree species were specialized to a single group of insects, such as bees or beetles. The other group, which comprised the remaining 25% of the species, were pollinated by insects coming from diverse groups. Remarkably, our inter-year observations also showed that there was no shift in the pollinator taxa between years in the specialized systems (M. S. Devy and T. Ganesh, unpublished data).

Recently, Waser et al. (1996) claimed that specialization may not be a dominant trend in the pollination systems, while Johnson and Steiner (2000), on the other hand, have argued that dichotomy between the generalized and specialized systems is a case of oversimplification. They point out that what we observe in natural systems is a continuum of pollination systems, with plant species pollinated by hundreds of pollinators at one end of the spectrum and species that are dependent on a single species at the other end. The pollinator and the disperser fauna in general were found to be depauperate in Kakachi compared with wet forests elsewhere (Ganesh, 1996; Devy, 1998; Ganesh and Davidar, 1999). Even the “generalized systems” in Kakachi did not have high diversity of pollinators, and at the most about 8–9 pollinator species were encountered. This still falls closer to the specialized system in the spectrum described by Johnson and Steiner (2000). Within the specialized modes, species pollinated by beetles and moths had 5–6 pollinator vectors visiting them, while the tree species pollinated by other groups were characterized by just 2–3 species of pollinators.

The lowland wet sites of both New and Old World forest

exhibit a high diversity of pollination modes. In contrast, the montane or high-elevation Neotropical forest in Venezuela and Jamaica show a paucity in pollination modes with a higher proportion of tree species being skewed to a generalized mode of pollination (Table 2). Kakachi maintained a high diversity of specialized pollination modes, although fewer pollinators were involved in the pollination of each of the guilds. Therefore, Kakachi appears to be an intermediary zone between the lowland forest and the high-elevation forests even in terms of pollination modes.

**Pollination syndromes**—The concept of “pollination syndrome” has appealed to many biologists, and they have used it to infer the pollinators of species without any field observations. The results of this study also demonstrate that it is difficult to predict the pollination systems based on floral characters alone (see also Momose et al., 1998). There was a considerable overlap of floral characters among the various pollination modes. The species pollinated by moths, thrips, and some beetle species opened during the night. There were instances in which *Apis dorsata*, a diurnal insect, was found visiting and pollinating tree species during the night (Devy, 1998; see also Dyer, 1985).

Assigning putative pollinators even to members of the same genera based on the observation of a few species may not always prove to be accurate. Species within a single genus could evolve characters that suit various pollinator taxa (Johnson, 1998). For example, even in Kakachi *Elaeocarpus tuberculatus*, which is pollinated by moths, exhibited nocturnal anthesis and a sweet odor, and *E. serratus*, pollinated by carrion flies, was characterized by diurnal anthesis and a dung odor. Other species, *E. munronii* and *E. venustus*, which also exhibited diurnal anthesis and emitted sweet odor, were pollinated by social bees. The floral structure of these species was very similar, and they exhibited only marginal difference in their size. On the other hand, species belonging to the genus *Litsea*, which share many traits, were all pollinated by honey

bees. Associating a pollination mode with a common suite of floral traits is difficult with the plant community of Kakachi. The basis of floral choice by various pollinator groups and the inter-year consistency seems unclear.

**Comparison with other wet forests**—Comparisons of the structure of the pollination modes show that the plant community of Kakachi shows closer resemblance to that of Lambir than to that of La Selva (Table 1). The bees play a larger role in Lambir and La Selva; they pollinate 39% and 41% of the arborescent species, respectively. In La Selva, diverse bee species, comprised of solitary, semi-social to social bees, were involved in pollination (Perry and Starett, 1980; Bawa, 1990). Although such diversity was not observed in Lambir, still many more species of social bees as well as solitary bees were involved in pollination in Lambir compared with Kakachi (Momose et al., 1998). The beetles are the second important group involved in pollination both in Kakachi and Lambir. However, the proportion of species pollinated by beetles is higher in Lambir (27%) than in Kakachi (17%). The bees and the beetles together pollinate more than 60% of the tree species in Lambir, which is almost twice that pollinated by bees and beetles in Kakachi (34%). A greater number of pollination modes were distributed among the tree species in Kakachi.

Vertebrate pollination is very rare in Kakachi, a trend that appears to be consistent with other tropical sites (Table 1). Wind pollination of trees in Kakachi is common among Euphorbiaceae members, and the proportion was similar to Jamaica but higher than in La Selva. Many of these are dioecious species that are found in gaps and edges of the forest (see also Bullock, 1994).

**Factors contributing to selection of pollination modes**—Many factors could contribute to the disparity or similarity observed in the distribution of pollination modes among wet sites. Among these, the geographical location and climatic factors of the site could be important contributors of selection in pollinator assemblages in a site (Bullock, 1995). Montane wet forests of Jamaica and Venezuela represent a low diversity of pollination modes, and insects from various groups are involved in the pollination of tree species in these forests (Table 1). Both these sites receive lesser rainfall than other lowland rain forest sites but are characterized by persistent cloud cover and low temperature, conditions that are not conducive to pollinator activity. The plant species in such conditions should take advantage of any visitors that visit the plants. Therefore, a more generalized mode of pollination in these sites could be more advantageous than a specialized mode (Sobrevila and Arroyo, 1982; Tanner, 1982; see also Bawa, 1990). Kakachi, at a mid-elevational range, has many specialized modes of pollination as in other lowland forest sites. Climatic conditions in Kakachi are more comparable to the lowland site of La Selva than to the other montane sites (Table 4). The cloud cover is restricted to a briefer period in Kakachi compared with other montane sites, allowing more favorable conditions for pollinator activity during a longer period of the year. Therefore, climate does not seem to be as much of a constraint in Kakachi as it may be in other montane sites that lie in higher elevations.

The flora or taxonomical status of tree species of an area also can have a profound effect on the distribution of species among various pollination modes (Bullock, 1995). Neotropical lowland sites are dominated by Fabaceae, whose flowers are

TABLE 4. Comparison of climatic conditions of Kakachi with other wet sites.

| Site                   | Elevation (m, a.s.l.) | Rainfall (mm) | Mean temperature (°C) |
|------------------------|-----------------------|---------------|-----------------------|
| Lambir <sup>a</sup>    | 150–250               | 2700          | 25.6                  |
| La Selva <sup>b</sup>  | 137                   | 3962          | 25.8                  |
| Jamaica <sup>c</sup>   | 2550                  | 2500          | 13                    |
| Venezuela <sup>d</sup> | 1749                  | 944           | 17.5                  |
| Kakachi                | 1250                  | 3500          | 20.5                  |

<sup>a</sup> Nakagawa et al. (2000).

<sup>b</sup> Sanford et al. (1994).

<sup>c</sup> Tanner (1982).

<sup>d</sup> Sobrevila and Arroyo (1982).

largely adapted to pollination by large bees (Bawa, 1990; Kress and Beach, 1994). This could have contributed to the dominance of the bee-pollinated guild in the site. The dipterocarps that dominate the Malaysian forests have high species diversity but low generic diversity, so the flowers bear close resemblance to one another. It has been suggested that the dipterocarp guild pollinated by thrips is the most dominant in the site (Appanah and Chan, 1981; Appanah, 1990; see also Bawa, 1990). The beetles replace the thrips in Lambir, a neighboring zone that shares many species with peninsular Malaysia (Sakai et al., 1999). Similarly, the Australian lowland wet forests are dominated by Myrtaceae, whose members are suspected to be beetle pollinated, making this guild perhaps the dominant one there (Irvine and Armstrong, 1990). Kakachi has relatively low tree species diversity, yet most of the genera present in the site are represented by only one or two species (94%), and very few have more than three species (6%), making the community taxonomically diverse (Ganesh et al., 1996). It is difficult to attribute the lack of domination of any single pollination mode in Kakachi simply to the high taxonomic diversity of the site. Certain genera in Kakachi are represented by species with diverse pollination modes, while others show some convergence (see <http://ajbsupp.botany.org/v90>); and therefore, one should not assume that domination of certain genera in Kakachi should lead to dominance of certain pollination modes. The manifestations of different patterns, even within old tropics, demonstrate that many of these interactions may have evolved to suit the conditions at a very local scale.

Other biotic factors, such as the phenology of the food plants, could favor the selection of certain pollination modes. Pollination by social bees, thrips, and beetles is more common in the southeast Asian lowland forest (Appanah and Chan, 1981; see also Momose et al., 1998). It has been suggested that selection of these modes may be due to the ability of these pollinator taxa to cope with the unpredictability of flowering schedules, which can vary from intervals of 2 to 12 yr there. For instance, species of chrysomelid beetles in Lambir have been recorded feeding on nonfloral parts during prolonged gaps between flowering. On the other hand, *Apis dorsata*, another important pollinator, was found to migrate into the forests only during mass flowering years (Momose et al., 1998; Itioka et al., 2001). Thrips, known for their high fecundity, increase their populations during outbursts of mass flowering years and thereby meet the pollination demand of the species (Appanah and Chan, 1981). Similarly, a long-term phenological study at Kakachi has shown that non-annual flowering nature is common among tree species (T. Ganesh et al., un-

published data; Devy, 1998). In Kakachi, pollinators such as the honey bees, which have the ability to multiply quickly along with sporadic flowering, pollinate a higher proportion of tree species with non-annual flowering cycles (Devy, 1998). Besides honey bees, the thrips and the flies, which also have higher fecundity compared to the other pollinator group, pollinate a higher proportion of non-annual flowering species (Table 3).

**Conservation implications**—Kakachi is characterized by a high diversity of pollination modes; however, a very low number of pollinator species was encountered within each guild compared with other lowland sites. We have also observed that during many mass flowering years there was exceptionally low fruit set in certain tree species mainly due to pollinator deficit (Ganesh and Devy, 2000). Above all, multiple-year observations have shown strong consistency in the pollinator taxa involved in the pollination of the tree species. The relationship between the pollinators and the food plants in Kakachi is more intricate compared to other tropical wet sites. Therefore, consequences of disturbance could be far more drastic in Kakachi, distorting such relationships and leading to cascading local extinction of the food plants and their pollinators.

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