

# PLANT-POLLINATOR INTERACTIONS IN TROPICAL RAIN FORESTS

*K. S. Bawa*

Department of Biology, University of Massachusetts, Boston, Massachusetts 02125

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## INTRODUCTION

Plant-pollinator interactions in tropical lowland rain forests (TLRF) offer unique opportunities to address several problems of current evolutionary and ecological interest. First, conspecifics of many tree species are spatially isolated and self-incompatible or dioecious (11, 16, 24, 36, 61). Thus selection for long-distance pollen flow may be more intense in TLRF than in any other community (78), making it possible to study the patterns of pollen flow that perhaps are not observed anywhere else. Second, in tree species longevity combined with intense pressure from competitors, predators, and pathogens as well as abiotic agents places a high premium on genetic recombination (78, 91), which may also select for larger pollen (and seed) shadows not generally encountered in other communities. Third, the high species richness of TLRF correlated in part with the richness of pollination mechanisms (3, 5, 11, 25) offers an unusual opportunity to examine the role of plant-pollinator interactions in plant speciation (33, 133). Fourth, the wide range of specialization in plant-pollinator interactions at various taxonomic levels provides rich material for an assessment of factors promoting coevolution (47). Fifth, the ubiquitousness of biotic pollination in almost all plant species in TLRF (80) makes it a unique community to study the effects of plant-pollinator interactions in the structure and organization of communities. Finally, the multitude of plant-pollinator interactions permits an analysis of the role of mutualistic interactions in maintaining stability in complex communities (57).

The question of community stability, apart from its theoretical importance, is a central issue in conservation biology.

It should be noted at the outset that the unusual importance of studying pollination systems in TLRF is matched by unusual difficulties encountered in gathering basic information. Canopy trees that define the structure and properties of TLRF present, because of their height, logistical difficulties for empirical and observational work not generally found in other ecosystems (100, 108, 110). Furthermore, in a given TLRF, hundreds of plant species together with thousands of pollinator species form a complex web of relationships difficult to unravel without a concerted effort lasting many years. Although a wealth of information exists about certain systems, e.g. figs and fig wasps (81, 152) and orchids and orchid bees (1, 41, 42), the data for a particular species assemblage are not from one site. One of the few exceptions is Stile's data set for *Heliconia* species and their hummingbird pollinators (135, 137). Much of the available information about pollination systems in TLRF at the level of particular "guilds" or communities is from scattered studies undertaken at sites throughout the tropics.

Plant-pollinator interactions in TLRF have been used as paradigms to study coevolution (47), gene flow (11, 24, 79), evolution of plant sexual systems (16, 20), and community stability (74) and can be thus reviewed in several different contexts. Here I first recapitulate the diversity of pollination systems in TLRF, based on recent work in the lowlands of Central America. The focus, unless specified otherwise, is on *lowland* rain forests. Montane forests are considered in a separate section; coastal mangrove forests are excluded due to the paucity of data (149). I then discuss plant-pollinator interactions in the context of gene flow and speciation, two topics central to the issue of species richness of tropical communities. I conclude with a brief commentary on the effects of disruption in plant-pollinator interactions on community stability and the maintenance of biodiversity, two topics, again, of much current interest.

The paper complements two other recent reviews of the subject (22, 90). Related topics that have been lately reviewed particularly in the context of tropical wet forests are: flowering phenology (18, 29), plant reproductive systems (24, 90), harvest of floral resources (82), pollinator specialization and coevolution (47, 74, 75), and the role of pollinators in the evolution of sexual systems of plants (16, 20).

## MODES OF POLLINATION

### *Diversity*

The diverse range of pollination systems found in angiosperms can be encountered in its entirety in most TLRF. It is well known that wind pollination is

rare, but not absent in TLRF (21). On the basis of studies on trees (25), I estimate that approximately 98% to 99% of all flowering plant species in TLRF are pollinated by animals. Biotic pollen vectors range all the way from one- to two-millimeter-long fig wasps (152) to flying foxes with a wingspan of two meters (38). Although flowers may receive a wide range of visitors, members of only one or two main classes, usually of the same order, act as effective vectors (25, 128). The subject of specialization and constancy is treated elsewhere in the paper. In the discussion below, reference to a particular pollinator implies that it is the primary pollen vector for a given plant species (or a group of plant species). The commentary is concerned with the ecological aspects of various pollination systems, rather than with the evolution of particular morphological, anatomical, or behavioral traits associated with various plant-pollinator interactions. Prance (115) describes detailed case studies for many of the major pollination modes considered below.

**POLLINATION BY VERTEBRATES** Bats, some nonflying mammals, and birds are the only pollen vectors known among vertebrates.

*Bats* Examples of bat pollination can be found in many families, but this mode of pollination is particularly common or well studied in the Bombacaceae (13, 14, 43, 98), and the genera *Passiflora* in the Passifloraceae (125, 126), *Parkia* in the Mimosaceae (73), and *Bauhinia* in the Caesalpiniaceae (66). Of the two orders of Chiroptera to which bats belong, only Microchiroptera, in which nectarivory is of relatively recent origin, are found in the neotropics; Megachiroptera, some of which are exclusively vegetarian, are restricted to the old world (13).

The number of plant species pollinated by bats or the number of bat species involved as pollen vectors is not known for any tropical wet forest. In a tropical lowland dry deciduous forest with approximately 150 tree species, 7 species of bats were found to carry pollen of 13 species of trees over a one-year period (65). Several species of bats apparently serviced a given plant species, and a particular bat species utilized the nectar and pollen of many plant species.

The floral syndromes of pollination by bats are well documented (13). In general, flowers open at dusk or soon after, are large, white or pale yellow in color, have a musky odor, and produce large quantities of nectar. However, in some species, flowers are small (3–5 mm across), but borne in dense clusters (135). In a community-wide study, Opler found the highest amount of nectar in a bat-pollinated species (107). On a per flower basis, bat pollination is perhaps energetically most expensive, but its benefits may be in the form of a long pollen shadow because bats forage over long distances (65, 132).

Bat-pollinated species may flower massively for a few days or bear a few flowers every day for several months (65).

*Nonflying mammals* Sussman & Raven (143) have presented circumstantial evidence for pollination of several tree species in Madagascar by lemurs, especially in areas where bat-pollination is absent or rare. They are uncertain about any specific adaptations involved in pollination by nonflying mammals and consider the system to be a relict that has survived from ancient times in certain areas. Janson et al (77) have also implicated nonflying mammals, e.g. opossums, kinkajous, and monkeys, in the pollination of several tree species such as *Cieba pentandra*, *Ochroma pyramidale*, and *Quararibea cordata* (all in the Bombacaceae) in an Amazonian forest. However, two of these three species (*C. pentandra* and *O. pyramidale*) are known to be bat-pollinated, and the nonflying mammals, the presumed pollinators, do destroy a number of flowers. The evidence for the effective transfer of pollen by nonflying mammals is indirect and weak.

Substantial evidence for pollination by nonflying mammals in tropical wet forests exists only for *Mabea occidentalis* (Euphorbiaceae), a small tree in the Central American lowland forests. The red woolly opossum, *Caluromys derbianus*, is a common visitor to the inflorescences of *M. occidentalis*, the flowers of which are also visited by noctuid and pyralid moths, Cerambycid beetles, Trigona bees, and bats (135). However, the inflorescences are "clearly adapted" to pollination by bats (135).

Pollination by rodents has been implicated for an epiphytic species of *Blakea* (Melastomataceae) in a Costa Rican montane forest (96), but the example remains to be explored in detail.

Clearly, the nectar-rich flowers or inflorescences with nocturnal anthesis, pollinated by moths or bats, are exploited by nonflying mammals. Inevitably, these mammals will be found visiting the night-blooming flowers and moving from one plant to another. However, such observations are not enough to suggest that the nonflying mammals transfer significant amounts of pollen from one plant to another. The contributions of these flower visitors to fruit and seed set must be measured against the frequent damage to the flowers they presumably pollinate (77). However, the availability of such flowers may be an important factor in the life cycle of nonflying mammals, if the flowers provide critical resources during periods of drought or low fruit abundance. The nature of interactions between nonflying mammals and flowers, and the consequences of these interactions for both mammals and plants, remain unexplored.

*Birds* In Central America, hummingbirds constitute the major group of bird pollinators. Pollination by hummingbirds is common in Acanthaceae,

Bromeliaceae, Gesneriaceae, Marantaceae, Musaceae, Rubiaceae, and Zingiberaceae. In a Costa Rican lowland rain forest with approximately 1800 flowering plant species, hummingbirds have been recorded to collect nectar regularly from 42 species and occasionally from another 27 species (137). None of the species in this community has been observed to be pollinated by nonhovering birds; however, several species of *Erythrina* in Central America are known to be pollinated by passerine birds (48, 103, 134, 148).

Stiles (136, 137) has reviewed the ecology of hummingbird pollination in a TLRF, and Feinsinger (46) in a montane rain forest. In the lowland forest, nine species of *Heliconia* are pollinated by nine species of hummingbirds, but there is no species specificity; each species of *Heliconia* is visited by more than one species of hummingbird, and each hummingbird species visits more than one species of *Heliconia* (136). Flowering patterns of *Heliconia* species are staggered in time (137). The staggered blooming has been attributed to competition for pollinators (137, 139), but the idea remains debatable (37, 111a, 140).

Although a very large number of birds pollinate many plant species in the old-world tropics, much of the available information is anecdotal and descriptive (2, 112–115). Coevolution between flower-visiting birds and flowers on a global basis has been reviewed by Stiles (138).

**POLLINATION BY INVERTEBRATES** The vast majority of plant species in tropical rain forests are pollinated by insects.

*Bees* Among insects, bees constitute perhaps the most important group in number and diversity of plant species pollinated. In the neotropical lowland rain forests, the vast majority of species in many common families such as Burseraceae, Euphorbiaceae, Clusiaceae, Fabaceae, Flacourtiaceae, Lecythidaceae, Melastomataceae, Orchidaceae, and Sapotaceae are pollinated by bees. The bee pollination system is particularly predominant in canopy trees (25).

The number and diversity of bee species that act as pollen vectors is equally great (122). Approximately 70 species have been recorded to visit the flowers of a single tree of *Andira inermis* (52) in a seasonal forest and 26 species as visiting the flowers of *Dipteryx panamensis* (104) in an aseasonal forest in Costa Rica. Both tree species are in the Fabaceae.

In general, based on size, two types of bees may be distinguished: medium to large-sized bees of the families Andrenidae, Apidae, Anthophoridae, Halictidae, and Megachilidae; and the small-sized bees in Apidae (tribe Apini), Halictidae, and Megachilidae (25). The former appear more prevalent on the canopy flowers and the latter on the understory flowers. The medium- to large-sized bees constitute a very heterogeneous group. The brightly

colored orchid bees of the tribe Euglossini in Apidae tend to forage singly or in small groups, primarily in the understory and subcanopy. In contrast, many anthophorids forage in large aggregations, mainly, but not entirely, in the canopy (G. W. Frankie, personal communication). Species pollinated by these bees often flower massively.

The diversity of bee-pollinated trees is so large that no generalizations can be made with respect to flower morphology or flowering pattern. Bee flowers, especially those that are pollinated by small bees can be relatively small and inconspicuous, and white, pale, or green in color. Flowers pollinated by medium-sized to large bees, may however be relatively large, brightly colored, and morphologically specialized as in many species of the Bignoniaceae, Fabaceae, Melastomataceae and Orchidaceae. Flowering may extend from a few days in some species to several months in others (54).

*Moths* Moth pollination is particularly prevalent in the Rubiaceae (25, 63). The heavily scented, white or pale flowers with narrow floral tubes and nocturnal anthesis in many species of such families as Apocynaceae, Meliaceae, Mimosaceae, and Solanaceae suggest that moths are also important pollen vectors in these groups. Moth-pollinated trees are mostly found in the understory and subcanopy.

Pollinating moths may be distinguished into two broad categories: (a) the large sphinx moths and (b) small moths in the Noctuidiae, and possibly in other families. Virtually nothing is known about the biology of the interactions that the latter group have with tropical trees. Even for sphinx moths, the available information is largely derived from Gottsberger's (58) work in Brazil, Nilsson and associates' investigations in Madagascar (104), and Haber & Frankie's (63) comprehensive study of sphinx moth-pollinated plants in a dry deciduous forest of Costa Rica.

The flowers pollinated by sphinx moths are generally white or pale yellow in color with deep corolla tubes; the flowers open in the late afternoon or after dark, are sweet scented, and offer nectar as the main reward to the moths (44, 63). Two types of flowers may be distinguished: tubular flowers with narrow corolla tubes terminated by four to six corolla lobes, and brush type of flowers with reduced corolla and many exerted stamens (63).

Although sphinx moth-pollinated plants may be found to flower at all times of the year, Frankie and coworkers (50, 63) have observed peak flowering during the wet season. They explain this seasonality by saying the plants serve as sources of food not only for adults but also for the larvae. The larvae depend upon leaves which in the case of most plant species in the dry deciduous forest are borne only during the wet season. The sphinx moth-pollinated species may flower in highly synchronous episodes lasting only four to five days, or they may bloom for as long as ten months (63; see also 32).

Moth pollination system is one of the most common but the least studied systems in tropical lowland rain forests.

**Beetles** Beetles constitute an important group of pollen vectors, next in importance perhaps only to bees and moths. Beetle pollination is particularly common in Annonaceae, Araceae (127, 155, 156), Cyclanthaceae (26), Lauraceae, Myristicaceae (10, 76), and Palmae (27, 67, 68, 102). The beetles involved are diverse, from weevils two millimeters in length to scarabs that are two centimeters long (26, 27, 127).

Very little is known about the ecology of interactions between beetles and flowers. Recent studies on aroids (155, 156), Cyclanthaceae (26), palms (27), and *Myristica* (9) are among the most well-documented cases of beetle pollination. Beach (26, 27) has shown the complex nature of interactions among beetles and other flower visitors such as fruit flies and weevils in the pollination of *Pejibaye* palm. Flowers pollinated by beetles range from small as in the Myristicaceae (9) to several centimeters across as in the Annonaceae (127). Flowers when small may be borne on large inflorescences that in the Araceae are enclosed by bracts (156). Nocturnal anthesis is characteristic of the system, which is driven by strong odors (127).

Recent studies in Australian rain forests indicate that in some communities up to one quarter of all plant species may be pollinated by beetles (76). Beetles pollinate plants of all life forms and in all the strata of the forests in such communities. The Australian studies suggest that overall beetles may be third in importance, after bees and moths, in the number of plant species that they pollinate in rain forests.

**Butterflies** Many species of butterflies are common visitors to the flowers of a diverse array of species with brightly colored corollas (or other appendages), especially in the Boragiaceae, Rubiaceae, and Vochysiaceae. However, this pollination system is among the least studied in tropical rain forests.

**Wasps** The mutualistic relationship between the cosmopolitan genus *Ficus* and wasps is well known and has been a subject of some recent reviews (81, 152). Apart from the agaonid wasps, a diverse array of wasps are found among the insects visiting generalized flowers of such taxa as Anacardiaceae, Burseraceae, Simaroubaceae, and others. However, the extent to which such species transfer pollen is not known. Curiously, the type of specialized relationship found between fig wasps and figs has not been reported for other wasps and plants or other insects and plants in tropical lowland rain forests.

**Large Flies** Fly pollination appears to be widespread in Sterculiaceae (115, 154). Many species of *Aristolochia* (115) and *Rafflesia* (28) are also pollinated by flies. Little is known about the ecology of fly pollination. Beaman et

al's (28) recent study of *Rafflesia* represents one of the few well-documented examples.

*Other insects* Pollination by thrips has been reported in some species of Myristicaceae (25) and Dipterocarpaceae (6). Curiously, although ants are abundant in TLRF and are known to pollinate plants in other regions (71, 86), pollination by ants is unknown in TLRF.

In summary, there are groups of species pollinated by the same class of pollinators, but little is known about the structure of these groups and the factors that influence the number and the diversity of the interacting species. Another general feature is the presence of a large number of species with a relatively generalist mode of pollination among trees. Such species with small, white, pale yellow or green, shallow flowers may account for up to 31% of all species, and most seem to be collectively pollinated by a diverse array of small insects (25). What selects for specialized and generalized modes of pollination in the same community? The two modes might differ with respect to energetic costs, including the cost of defending flowers from predators and nectar robbers. They might also differ with respect to reliability of pollination, distances over which pollen is dispersed, and the manner in which they influence male and female components of fitness.

### *Spatial Distribution*

The distribution of various pollination systems in TLRF appears to be nonrandom (25). In particular, systems based on medium-sized to large bees and small diverse bees primarily occur in the canopy, and those based on hummingbirds sphingid moths, and beetles in the understory (Table 1, see also 25). Enough data to evaluate the distribution of other systems do not exist. The vegetation in tropical forests is often differentiated into more than two vertical strata. Indeed, Kress & Beach (90) have organized data on plant-pollinator interactions under three strata. As our knowledge of plant-pollinator interactions at the community level increases, it may be feasible to find evidence for nonrandom distribution at a finer vertical scale.

The nonrandom distribution of plant-pollinator interactions may be expected on the basis of vertical stratification of animal communities in general (130). Plant taxa, particularly at the generic and the familial levels, are also often distributed in particular strata. Examples include dipterocarps, which occur primarily in the canopy, and the Rubiaceae, which are generally confined to the subcanopy or understory. Although the associations between a particular plant taxon and a particular pollinator vector could also contribute to the observed patterns, the origin of spatial correlations of such associations remains unexplained. It should be interesting to determine the extent to which

**Table 1** Frequencies of different pollination systems

Pollination type	Forest stratum	
	Canopy <sup>1</sup> Percent of species (N)	Subcanopy & Understorey <sup>2</sup> Percent of species (N)
Bat	3.8 (2)	3.6 (8)
Hummingbird	1.9 (1)	17.7 (39)
Medium-sized to large bee	44.2 (23)	21.8 (48)
Small bee	7.7 (4)	16.8 (37)
Beetle	—	15.5 (34)
Butterfly	1.9 (1)	4.5 (10)
Moth	13.5 (7)	7.3 (16)
Wasp	3.8 (2)	1.8 (4)
Small diverse insect	23.1 (12)	7.7 (17)
Wind	—	3.2 (7)
TOTAL	100% (52)	100% (220)

<sup>1</sup>Data from Bawa et al (25).<sup>2</sup>Data from Kress and Beach (90).

plants and pollinators reciprocally influence their abundance in various vertical strata.

The diversity of pollination systems seems to be the highest in the understorey (25). This might simply be a reflection of the diversity of plant species in that stratum. The significance of this observation is explored in another section.

### *Tropical-Temperate Zone Comparisons*

There are four major differences between pollination systems of TLRF and the north temperate zone forests. First, in aseasonal TLRF, pollination at the community level occurs throughout the year, though there may be well-defined peaks in flowering during certain times of year (51). By contrast, flowering in the north temperate zone is mostly confined to late spring and summer (118). Second, flowers of plants in TLRF generally last a day or two, whereas the mean longevity of flowers in the north temperate zone communities may extend to 7 days (116). Unpredictable conditions for pollination due to uncertain weather have been cited as one of the factors influencing longer flower longevity of the temperate zone plants (116). Third, pollination by vertebrates is almost nonexistent in forest communities in the north temperate zone, though birds and rodents constitute an important group of pollinators in the temperate zone Australia (49, 124) and in south Africa (15, 124). Finally, the proportion of wind-pollinated plants steadily increases as one moves from the equatorial region, reaching 80–100% among trees in some of the northernmost latitudes (119).

### *Tropical Montane Rain Forests*

Pollination systems in tropical montane rain forests appear to differ from those in the lowland rain forests in at least two respects. First, pollination by hummingbirds in the neotropics is more common in the montane than in the lowland rain forests (39, 47). For example, in a cloud forest of Costa Rica with 600 flowering plant species, hummingbirds have been observed to visit flowers of 100 species (47); a comparable figure for a lowland rain forest is less than 70 out of 1800 species of flowering plants (137). Second, the pollination system involving small generalist insects also appears to be more widespread in cloud forests (131, 145). Low temperatures in montane forests may limit the activity of bees and may explain their displacement by the hummingbird (39) and the generalist insect pollination system.

The number of bat species in all feeding guilds is known to decrease with an increase in altitude (59a). However, it is not known if the tropical montane forests have disproportionately fewer species of bat-pollinated plants than the lowland forests.

Montane forests also differ from the lowland forests with respect to sexual and breeding systems (Table 2). Proportionately, many more tree species are self-compatible in high altitude forests (69, 131, 145). Unpredictable weather conditions for pollination in the generally cold and wet environments in montane forests have been invoked to explain the high incidence of self-compatibility. Lack of strong selection for outcrossing or direct selection for homozygosity could also explain the preponderance of self-compatibility. However, the proportion of dioecious species in montane forests is similar to or exceeds that found in TLRF (131, 145). The prevalence of two somewhat opposite modes of reproduction in the same community defies an easy

**Table 2** Distribution of self-compatible, self-incompatible, and dioecious tree species in tropical lowland and montane rain forests.

Forest Type	Percentage self-compatible <sup>1</sup> species	Percentage self-incompatible <sup>1</sup> species	Percentage dioecious species <sup>2</sup>	References
Tropical lowland rain forest, Costa Rica	20	80	23	24
Montane forest, Venezuela	62	28	31	131
Montane forest, Jamaica	85	15	21	145

<sup>1</sup> Expressed as percentage of hermaphroditic species tested for self-incompatibility.

<sup>2</sup> Expressed as percentage of all tree species.

explanation. The preponderance of dioecious species in montane forests may not necessarily be due to selection for outcrossing in these ecosystems, but may be due to other advantages associated with dioecy (16, 17).

Finally, the individual flowers in montane forests on an average last 2–8 days more than in lowland rain forests (141); the longer life span is consistent with the notion of unpredictability in pollination, a possibility suggested above.

### *Southeast Asian Lowland Rain Forests*

The aseasonal southeast Asian rain forests are well known for the irregular, supraannual flowering at the community level (4). These forests also differ from most neotropical rain forests in having members of a single family, Dipterocarpaceae, dominating the canopy (12). Another unusual feature in some of these forests is that many species of the dominant genus *Shorea* may be pollinated by thrips (6). The thrips complete their life cycle during the flowering of congeneric sympatric species. Species of *Shorea* in south Asia are pollinated by bees, *Apis dorsata* and *A. indica* (40). The impact of irregular, supraannual flowering on the stability of the pollinator fauna, thrips and nonthrips remains unexplored. The temporal fluctuations in the abundance of pollinators may be responsible for the evolution of apomixis, which has been reported in some trees in southeast Asian rain forests (62, 85).

### *Global Patterns*

Do rain forests in different parts of the world differ with respect to the proportion of various pollination systems? Such differences might be expected on the basis of differences in geographical distribution of plants and animals. For example, hummingbirds which dominate the bird pollination systems in the neotropics are confined to the new world. Although other birds serve as pollen vectors in the old world tropics, their role in terms of species pollinated is not as well documented as in Central American forests. Bats have coevolved with plants over a much longer geological time scale in the paleotropics than in the neotropics, and completely vegetarian bats, as mentioned earlier, are confined to the old world (13). But we do not know whether the proportion of plants pollinated by bats in the paleotropics is greater than in the neotropics. Irvine & Armstrong (76) suggest that the frequency of beetle pollination is much greater in Australian than in Central American forests, but the latter have not been completely surveyed and the reported differences may be a sampling artifact. Finally, for bees, the most dominant pollen vectors in all TLRF, Roubik (122) reports similar patterns for the old and the new world tropics with respect to the proportion of species numbers in major families.

## SPECIALIZATION

The issue of specialization is critical to the discussion of the role of plant-pollinator interactions in speciation and community stability, as we note later.

On the basis of existing evidence, species in tropical lowland rain forests may be distinguished into three categories. To the first category belong species like figs that are extremely specialized in their pollinator requirements and the pollinating fig wasps which are very host specific (117, 152). However, the type of specific interaction exemplified by figs and fig wasps appears rare in tropical lowland rain forests.

The second category is exemplified by orchids and orchid bees and other plants that, as a taxonomic group, are pollinated by a particular assemblage of animals. Many species of orchids in the neotropics are pollinated by male euglossine bees (41, 42, 123). Each species of orchid may be visited by one or two species (1, 47). Similarly bees of any one species of euglossines may visit as many as nine different species of orchids, but most confine their visits to only one or two species. However, the euglossine bees also gather resources from many other plant species. (47). Similarly a majority of 20 species of *Dalechampia* (Euphorbiaceae) are pollinated by female euglossine bees only, and each species is visited by one or two species of the bees (7, 8).

Preliminary observations suggest that the type of specialization exemplified by orchids and orchid bees also exists in other plant-pollinator groups. For example, each of the five species of angraecoid orchids in Madagascar is pollinated by one species of hawkmoth, *Panogena lingens* (104). Several species of the Araceae and Annonaceae are pollinated by one or two species of scarab beetles (155; G. Schatz, personal communication).

At the next level of decreasing specialization are examples like the *Heliconia* and the hummingbirds. The nine sympatric species of the genus *Heliconia* (Musaceae) in a tropical lowland rain forest are visited by nine species of hummingbirds (136). Although as many as eight species have been recorded visiting one species of *Heliconia*, most species are predominantly visited by one or two species of hummingbirds. A group of species in Lecythidaceae are pollinated by euglossine bees, and the geographic ranges of both groups are known to coincide (101). In bat-pollinated species, evidence from tropical dry deciduous forests suggests that a given plant species is visited by several species of bats (65) though examples exist of a plant species being pollinated by a particular species of bat (59).

A large number of species in tropical lowland rain forests are pollinated by medium-sized to large bees, as mentioned earlier. Current data from several tree species in the Fabaceae indicate that flowers of most species, though displaying great morphological complexity for pollination by a specific group

of bees, are visited by a large number of bee species. For example, as stated earlier, Perry & Starrett (109) reported 19 species of bees visiting the flowers of a single large canopy tree of *Dipteryx panamensis*. In a dry deciduous forest, Frankie et al (52) captured 70 species of bees on the flowers of *Andira inermis*, also a large tree. Even though the diversity of bee species is very high, it is possible that only one or a few species constitute the effective group of pollinators.

To the third category belong species that apparently have a generalist mode of pollination. These species bear small flowers in which pollen and nectar are accessible to a wide range of small insects, such as bees, butterflies, beetles, flies, and wasps which collectively visit the flowers (25). It is not known if the visitors differ in their effectiveness as pollinators. In one such species, *Calathea ovandensis*, ten species of Hymenoptera and Lepidoptera were found to visit flowers, but Schemske & Horvitz (128) showed that one species of Hymenoptera was responsible for 66% and another species for 14% of all fruit set; collectively five species of Hymenoptera accounted for 99% of the fruit set. Even species that appear to exploit a wide range of pollen vectors may thus in practice be pollinated effectively by only one or two species.

In general, the type of specialized, almost one-to-one relationship that exists between figs and fig wasps is an exception rather than the norm in the tropics (47). Nonetheless in a majority of species, pollination systems are specialized to the extent that a given plant species is pollinated by one or a few species belonging to the same taxonomic group (e.g. euglossine or other bees, hummingbirds, scarab beetles, bats, etc). A further level of specialization may exist, but studies to evaluate the relative effectiveness of various flower visitors in achieving pollen dispersal and pollen deposition are lacking.

## POLLEN FLOW

Tropical forest plants with their diverse patterns of dispersion and modes of pollination provide an ideal material to compare the effectiveness of various pollinators in long-distance pollen flow. Nevertheless, little is known about dispersal of pollen in TLRF. Several lines of evidence, however, suggest that pollen flow in tree species may be extensive. First, most species are either self-incompatible or dioecious (11, 16, 24, 36, 61). Apomixis is known in some species of the south-east Asian Dipterocarp forests (62, 85), but the true extent of apomixis within individuals and species or among populations has not been determined. Second, studies based on mark-recapture techniques indicate that bees (52, 79) and hawkmoths (93) forage over long distances and have the potential for pollen flow among widely spaced conspecifics. Third, direct observations of flight patterns also reveal that some pollinators—bats, for example—forage over distances of many kilometers (65, 132). On the

other hand, territorial hummingbirds move pollen over restricted distances, though nonterritorial hummingbirds forage over long distances (92). Data derived from the studies of sexual systems, breeding systems, and flight patterns of pollen vectors, however, provide an estimate only of potential pollen flow. Realized pollen flow may not correspond with potential flow; there is evidence that in some species crosses involving conspecifics that are many hundred meters apart yield more fruits than among individuals that are relatively close to each other (89).

Genetic markers offer considerable promise in understanding the patterns of realized pollen flow in tropical rain forests (23, 31, 105, 106). Recent studies of mating systems based on progeny arrays of individual trees, utilizing genetic markers, have revealed a high degree of outcrossing and indicated potential for extensive pollen flow in several large canopy trees (21, 95, 96). Similarly, analysis of the population genetic structure of several species indicates low values for gene flow among populations (64). Both electrophoretic markers (105, 106) and the DNA "fingerprinting" (121) have the potential in the future considerably to enhance our understanding of pollen flow within and among populations.

The linkage of conspecifics by means of pollen flow over a large area in canopy and subcanopy tree species does not negate the possibility of restricted pollen flow and the potential for local genetic differentiation due to inbreeding in other taxa. In contrast to trees, many herbs and shrubs in TRLF are self-compatible; also the frequency of dioecy in the understory plants is only half of that encountered in tree species (90). It has been suggested that pollen flow in understory plants may be generally restricted (90), and that such taxa, especially in montane forests, may be largely inbred (131, 145). Many herbs, especially epiphytes, are also patchily distributed. Localized gene dispersal due to limited pollen flow in such species could result in subdivision of the populations. However, the neighborhood size that determines the potential for subdivision within a population is a function of both the distance over which pollen is dispersed and the density of individuals (153). Although pollen flow in understory plants may be localized, such plants, because of their small size, have much higher densities than canopy trees. Thus, the reduction in neighborhood size relative to those in trees may not be as great as expected from gene flow alone.

Fedorov (45) argued that a main contributor to the origin and maintenance of many closely related species in the humid tropics may be inbreeding combined with drift. In the absence of population genetic data, it is difficult to evaluate the validity of this argument. However, results of two population genetic studies are consistent with the notion of inbreeding and genetic drift in understory plants. A preliminary survey of genetic variation in some species of *Piper*, one of the most species-rich understory genera in Costa Rica, shows

little genetic diversity within populations (70) and indicates inbreeding. Similarly, low levels of genetic variation within populations, but high levels among populations, in a species complex of shrubs in the Gesneriaceae have been revealed (144). Autogamy and self-compatibility seem prevalent in several other taxa of herbs and shrubs, e.g. Maracaviaceae (56), Ericaceae (97), and Melastomataceae (120). Gentry (55) provides indirect evidence for the importance of drift and inbreeding as factors in speciation of many tropical plants.

In summary, although there is considerable evidence for outcrossing and long-distance pollen flow in several species, some data suggest that many taxa, primarily herbs and shrubs, may be highly inbred.

## POLLINATION AND SPECIATION

To what extent do plant-pollinator interactions contribute to species richness of TLRF? Although the role of pollinators as isolating mechanisms is well known (60, 142), the part that plant-pollinator interactions might have played in speciation in tropical communities has not been adequately evaluated (72). As I have argued elsewhere (19), ecological interactions between plants and animals by themselves or in combination with other factors may promote speciation in several ways. The following arguments are from Bawa (19).

First, a founder population can be reproductively isolated from the parental species if it interacts with a pollinator that has no or little interaction with the ancestral species. Geographical ranges of plants and their pollinators are often dissimilar (G. Stiles, personal communication). Thus, plants with a slightly variant floral morphology may be exposed to a different assemblage of pollinators. The floral variants in small, isolated, founder populations may be "fixed" not necessarily by genetic drift but by a new set of pollinators.

Second, differentiation of plant populations with a variant floral morphology may also lead to differentiation of host-specific pollinators; plant-pollinator interactions do lead to cospeciation more often than other kinds of mutualisms (133, 147). There is no direct evidence for cospeciation of plants and their pollinators from tropical rain forests, but it is suspected to have occurred in figs and pollinating fig wasps (117, 151).

Third, West-Eberhard (150) has argued that under selection for success in intraspecific competition (including competition for mates), characters important in the outcome of competition can undergo quick change, leading to rapid population divergence and speciation. Thus, the combined effects of plant-pollinator coevolution and sexual selection can accelerate speciation. West-Eberhard suggests that competition for mates via pollinators in groups with extremely specific pollinators could be a significant diversifying force in plant evolution. Apparently, in plants, the floral variants may arise first as a result

of sexual selection and then rapidly spread and be isolated by specific pollinators.

Fourth, plant-pollinator coevolution in combination with sexual selection in pollinators rather than in plants, as in the previous example, may enhance the rate of population divergence and hence speciation (87). Kiester et al (87) suggest that in orchids, sexual selection in euglossine bees, based on variation in their mating behavior due to variation in chemical odors collected from flowers, may lead to genetic instability in bee populations. This instability in conjunction with the selection by the orchid bees on floral characters may result in explosive cospeciation.

Finally, genetic drift, alone, or in conjunction with inbreeding combined with coevolution and sexual selection in plants or pollinators, or both, should accelerate speciation. Both West-Eberhard (150) and Kiester et al (87) assign a major role to drift in their models which consider the combined effects of coevolution and sexual selection in speciation. It is generally accepted that inbreeding has the potential to cause rapid population divergence (153).

The validity of the arguments above depends upon the prevalence of high specificity between plants and pollinators, sexual selection, genetic drift in plants, and inbreeding. I have already reviewed the evidence of plant-pollinator specificity as well as genetic drift and inbreeding in tropical rain forests. A review of sexual selection is beyond the scope of this paper, but arguments for the operation of sexual selection in tropical plants have been made before (16, 32).

Overall, specificity in plant-pollinator coevolution is critical in promoting continued cycles of speciation (87). Accordingly, high specificity should be positively correlated with species richness at various taxonomic levels. *Ficus* is the largest genus in the Moraceae. It also has the most specialized mode of pollination in the family. Locally, *Ficus* usually has a greater number of species than any other genus of the Moraceae. In the neotropics, many genera in such families as the Annonaceae, Lauraceae, and Rubiaceae display high specificity as well as considerable species richness. However, specificity in plant-pollinator interactions may not be a characteristic feature of all the species-rich genera because factors other than plant-pollination coevolution also play a role in speciation (133).

## COMMUNITY STABILITY

Stability, as defined here, refers to the ability of all populations to return to equilibrium following perturbation (111). It has been generally asserted that the abundance of obligate mutualisms in tropical rain forests makes such communities prone to instability (53, 99). Another viewpoint is that the evolution of obligate mutualisms requires stringent conditions, and such

mutualisms are relatively rare in natural communities (74). According to this viewpoint, mutualistic interactions often involve a diverse array of species. For example, a given species of plant may be pollinated by a wide variety of animals, and conversely a particular pollinator species may use floral resources of a wide variety of species. Selective pressures exercised by interacting species on each other are thus highly diffuse and often asymmetrical. As a result, removal of one of the interacting species is not likely to have a significant effect on the stability of the system. Obviously specificity to a large extent determines the effect of the disruption of a mutualistic interaction on community stability.

The disruption of a mutualistic interaction can influence stability in two ways. First, the effect may be direct, as, for example, the loss of one of the interacting partners in species-specific interactions may lead to the extinction of the other. Second, the effect may be indirect. For instance, the loss of a fig species and its pollinating wasp species may also lead to a loss of the nonpollinating wasp species that parasitize the pollinating species. Such an effect, referred to as the ripple effect (147), can extend through a large part of the community, depending upon the number of interacting species and the strength of the interactions. Apart from specificity, the importance of a species as a critical resource may be a primary determinant of the consequences of a disruption in plant-pollinator mutualism. Fluctuations in populations of keystone mutualists (57, 146) that provide resources when other resources are scarce or not available are expected to have a drastic effect on the community. Fig trees are presumed to be keystone resources because they provide fruits to a large number of primates and birds when the overall abundance of fruits in the community is low (146). A disruption of the pollination system in figs thus has consequences not only for figs and pollinating and nonpollinating fig wasps, but also for a large segment of the frugivore community. The disappearance of species like figs then could have a ripple effect throughout the community. Gilbert (57) and Howe (74) provide other examples.

There are two major problems in assessing how community stability may be influenced by a breakdown in plant-pollinator interactions. First, our understanding of the way in which pollinators interact with plants is very elementary. Flowers not only provide food to the pollinators but also act as sites of mating and predator avoidance (129). Furthermore, vegetative parts of the plants whose flowers are used as sources of food or mating sites by adults may provide food for the larvae. Adults may thus use a wide variety of species as sources of pollen and nectar, but only one species as a larval host. The extinction of this larval host will result in the extinction of the pollinator species and may also affect the host species serviced by the pollinator; but these effects may not be anticipated if the focus of attention is the interaction

between the adults and the flowers. Second, although a number of qualitative models have explored the impact of perturbations in plant-pollinator interactions on community stability (30, 57) there is no formal treatment of the subject.

The effect of habitat fragmentation on plant-pollinator interactions and consequently on community stability is another area of increasing concern. Insect abundance as well as diversity is known to decrease with a decrease in the size of the habitat (88). Furthermore, by altering light regimes and other microclimatic conditions (94) edge effects may also influence the composition and foraging of pollinators. Changes in composition and abundance of specific pollinators in small forested areas have been shown to result in lowered seed set in plants (84).

Small, isolated habitats may also lack habitat heterogeneity to support pollinator populations all year round. Nectarivorous bats on a diurnal basis (132) and moths on a seasonal basis (83) have been shown to utilize resources from distinct habitats, often involving different vegetation types or zones, separated by several kilometers. Clearly, plant-pollinator interactions can be severely disrupted in small, isolated, fragments of vegetation. The consequences for plants may be not only lowered reproductive output, but also altered patterns of pollen flow. Gene flow among small fragmented habitats via pollen (and seed) may be curtailed. The resulting inbreeding may further decrease fruit set. Changes in pollination and mating systems may thus act synergistically to lower reproductive output. However, the effects of such changes as manifested themselves in decreased regeneration may remain obscure for a long time.

## CONCLUDING REMARKS

Plant-pollinator interactions provide model systems to address a wide variety of ecological and evolutionary questions. Here I have briefly explored their role in microevolution and speciation of tropical forest plants, community structure, and community stability. Basic information about the natural history of plant-pollinator interactions in tropical lowland rain forests is obviously limited. Nevertheless, enough is known that precise, testable, hypotheses can be formulated. Among the subjects reviewed here, the following require special attention.

First, it is apparent that there are well-defined "guilds" of pollinators with an associated set of "host" plants in TLRF. A detailed study of these "guilds" and of the plants with which they interact, along the lines of Stiles' (136, 137) work on hummingbird—plant interactions, is essential for understanding the structure and organization of a particular class of plant-pollinator interactions and their relative role in maintaining the overall organization of the whole community.

Second, empirical studies are needed to determine the specificity of plant-pollinator interactions. Flowers of tropical forest plants receive a diverse array of visitors, but only a few act as effective pollinators. Schemske & Horvitz's (128) study provides a model for similar work on other species. The determination of specificity is critical to our notions of community stability and to evaluate the degree of coevolution between plants and their pollinators.

Third, pollination systems in plants are known to be the primary determinants of population genetic structure (95). The diversity of pollination systems combined with diverse patterns of dispersion and distribution of plants provides a novel material for comparative evaluation of the roles of pollinators and plant density in the genetic structure and microevolution of plant populations. Information on pollen flow and population genetic structure are also critical to the adequate conservation and management of forest genetic resources.

Fourth, in order to understand the role of plant-pollinator interactions in speciation, one needs to study such interactions in genera with a large number of sympatric species (19). It is particularly important to investigate the origin of variation in floral characters involved in sexual selection, especially in peripheral populations where incipient speciation is likely to occur (34, 35).

Fifth, the effect of forest fragmentation on plant-pollinator interactions is likely to assume special significance as efforts to conserve biodiversity in nature reserves continue to gain momentum. Extreme fragmentation and isolation of habitats can drastically affect major mutualistic interactions (83). The maintenance of biodiversity in fragmented reserves would require a knowledge of the dynamics of the key mutualistic interactions. In the vast majority of tropical rain forest reserves, virtually nothing is known about the basic plant-pollinator (and other plant-animal) interactions.

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#### Literature Cited

1. Ackerman, J. D. 1983. Specificity and the mutual dependency of the orchid-euglossine bee interaction. *Biol. J. Linn. Soc.* 20:301-14
2. Ali, S. A. 1932. Flower birds and bird flowers in India. *J. Bombay Nat. Hist. Soc.* 35:573-605
3. Appanah, S. 1981. Pollination in Malaysian primary forests. *Malaysian For.* 44:37-42
4. Appanah, S. 1985. General flowering in the climax rain forests of South-East Asia. *J. Trop. Ecol.* 1:225-40
5. Appanah, S. 1990. See Ref. 22
6. Appanah, S., Chan, H. T. 1981. Thrips: the pollinators of some dipterocarps. *Malaysian For.* 44:234-52
7. Armbruster, W. S. 1986. Reproductive interactions between sympatric *Dalechampia* species: are natural assemblages "random" or organized? *Ecology* 67:522-33

8. Armbruster, W. S., Webster, G. L. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. *Biotropica* 11: 278-83
9. Armstrong, J. E., Drummond, B. A. 1986. Floral biology of *Myristica fragrans* Houtt. (Myristicaceae), the nutmeg of commerce. *Biotropica* 18:32-38
10. Armstrong, J. E., Irvine, A. K. 1989. Floral biology of *Myristica insipida* R. Br. (Myristicaceae), a distinctive beetle pollination syndrome. *Am. J. Bot.* 76: 86-94
11. Ashton, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* 1:155-96
12. Ashton, P. S. 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. *Annu. Rev. Ecol. Syst.* 19:347-70
13. Baker, H. G. 1973. Evolutionary relationships between flowering plants and animals in American and African tropical forests. In *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, ed B. J. Meggers, E. S. Ayensu, D. Duckworth, pp. 145-59. Washington, DC: Smithsonian Inst. Press
14. Baker, H. G., Cruden, R. W., Baker, I. 1971. Minor parasitism in pollination biology and its community function: the case of *Cieba Acuminata*. *Bioscience* 21:1127-29
15. Baker, H. A., Oliver, E. G. H. 1967. *Ericas in Southern Africa*. Cape Town: Purnell
16. Bawa, K. S. 1980. Evolution of dioecy in flowering plants. *Annu. Rev. Ecol. Syst.* 11:15-39
17. Bawa, K. S. 1982. Outcrossing and the incidence of dioecism in island floras. *Am. Nat.* 119:866-71
18. Bawa, K. S. 1983. Patterns of flowering in tropical plants. In *Handbook of Experimental Pollination Biology*, ed. C. E. Jones, R. J. Little, pp. 394-410. New York: Van Nostrand, Reinhold
19. Bawa, K. S. 1989. Mating systems, genetic differentiation and speciation in tropical rain forest plants. *Biotropica*. (In review)
20. Bawa, K. S., Beach, J. H. 1981. Evolution of sexual systems in flowering plants. *Ann. Mo. Bot. Gard.* 62:254-74
21. Bawa, K. S., Crisp, J. E. 1980. Wind pollination in the understorey of a rain forest in Costa Rica. *J. Ecol.* 68:871-76
22. Bawa, K. S., Hadley, M., eds., 1990. *Reproductive Ecology of Tropical Forest Plants*. Camforth, England: Parthenon
23. Bawa, K. S., O'Malley D. M. 1987. Estudios genéticos y de sistemas de cruzamiento en algunas especies arbóreas de bosques tropicales. *Rev. Biol. Trop.* 35(Suppl. 1):177-88
24. Bawa, K. S., Perry, D. R., Beach, J. H. 1985. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and self-incompatibility mechanisms. *Am. J. Bot.* 72:331-45
25. Bawa, K. S., Perry, D. R., Bullock, S. H., Coville, R. E., Grayum, M. H. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination mechanisms. *Am. J. Bot.* 72:346-56
26. Beach, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). *Am. J. Bot.* 69:1074-81
27. Beach, J. H. 1984. The reproductive biology of the peach or "Pejibaye" palm (*Bactris gasipaes*) and a wild cogener (*B. perschiana*) in the Atlantic lowlands of Costa Rica. *Principes* 28:107-19
28. Beaman, R. S., Decker, P. J., Beaman, J. H. 1988. Pollination of *Rafflesia* (Rafflesiaceae). *Am. J. Bot.* 75:1148-62
29. Borchert, R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* 15:81-89
30. Boucher, D. H., ed. 1985. *The Biology of Mutualisms: Ecology and Evolution*. London: Croom & Helm
31. Buckley, D. P., O'Malley, D. P., Apsit, V., Prance, G. T., Bawa, K. S. 1988. Genetics of Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.: Lecythidaceae). I. Genetic variation in natural populations. *Theor. Appl. Genet.* 76:923-28
32. Bullock, S. H., Bawa, K. S. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. *Ecology* 62:1494-1504
33. Burger, W. C. 1981. Why are there so many kinds of flowering plants? *Bioscience* 31:572-81
34. Carson, H. L. 1985. Unification of speciation theory in plants and animals. *Syst. Bot.* 10:380-90
35. Carson, H. L. 1987. The genetic system, the deme, and the origin of species. *Annu. Rev. Genet.* 21:405-23
36. Chan, H. T. 1981. Reproductive biology of some Malaysian Dipterocarps. III. Breeding systems. *Malaysian For.* 44:28-34
37. Cole, B. J. 1981. Overlap, regularity and flowering phenologies. *Am. Nat.* 117:993-97
38. Cox, P. A. 1984. Chiropterophily and ornithophily in *Frecycinetia* (Panda-

- naceae) in Samoa. *Plant Syst. Evol.* 144:277-90
39. Cruden, R. W. 1972. Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. *Science* 176:1439-40
  40. Dayanandan, S., Attygalla, D. N. C., Abegunasekera, A. W. W. L., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S. 1990. See Ref. 22
  41. Dodson, C. H. 1975. Coevolution of orchids and bees. In *Coevolution of Animals and Plants*, ed. L. Gilbert, P. Raven, pp. 91-99. Austin: Univ. Texas Press
  42. Dressler, R. L. 1968. Pollination by euglossine bees. *Evolution* 22:202-10
  43. Equiarte, L., Rio, C. M., Arita, H. 1987. El nectar y el polen como recursos: el papel ecologica de los visitantes a las flores de *Pseudobombax ellipticum* (H.B.K.) Dugand. *Biotropica* 19:74-82
  44. Faegri, K., van Der Pijl, L. 1971. *Principles of Pollination Ecology*. Oxford: Pergamon. 248 pp.
  45. Fedorov, A. A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. *J. Ecol.* 54:1-11
  46. Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol. Monogr.* 48:269-87
  47. Feinsinger, P. 1983. Coevolution and pollination. In *Coevolution*, ed. D. J. Futuyma, M. Slatkin, pp. 282-310. Sunderland, Mass.: Sinauer
  48. Feinsinger, P., Linhart, Y. B., Swarn, L. A., Wolfe, J. A. 1979. Aspects of the pollination biology of three *Erythrina* species on Trinidad and Tobago. *Ann. Mo. Bot. Gard.* 66:451-71
  49. Ford, H. A., Paton, D. C., Forde, N. 1979. Birds as pollinators of Australian plants. *N.Z. J. Bot.* 17:509-19
  50. Frankie, G. W. 1975. Tropical forest phenology and pollinator plant coevolution. In *Coevolution of Animals and Plants*, ed. L. E. Gilbert, P. H. Raven, pp. 282-310. Austin: Univ. Texas Press
  51. Frankie, G. W., Baker, H. G., Opler, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62:881-919
  52. Frankie, G. W., Opler, P. A., Bawa, K. S. 1976. Foraging behavior of solitary bees: implications for outcrossing of a neotropical forest tree species. *J. Ecol.* 64:1049-57
  53. Futuyma, D. J. 1973. Community structure and stability in constant environments. *Am. Nat.* 107:443-46
  54. Gentry, A. 1974. Flowering phenology and diversity in Bignoniaceae. *Biotropica* 6:64-68
  55. Gentry, A. 1982. Neotropical floristic diversity: phylogeographical connections between Central and South America. Pleistocene climatic fluctuations or an accident of Andean orogeny? *Ann. Mo. Bot. Gard.* 69:557-93
  56. Gentry, A. 1989. See Ref. 72, pp. 113-34
  57. Gilbert, L. E. 1980. Food web organization and conservation of neotropical diversity. In *Conservation Biology*, ed. M. E. Soule, B. A. Wilcox, pp. 11-34. Sunderland, Mass.: Sinauer
  58. Gottsberger, I. S., Gottsberger, G. 1975. Über Sphingophile Angiospermen Brasiliens. *Plant Syst. Evol.* 123:157-84
  59. Gould, E. 1978. Foraging behavior of Malaysian nectar-feeding bats. *Biotropica* 10:184-93
  - 59a. Graham, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *J. Mamm.* 64:559-571
  60. Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3:82-97
  61. Ha, C. O., Sands, V. E., Soepadmo, E., Jong, K. 1988. Reproductive patterns of selected understorey trees in the Malaysian rain forest: the sexual species. *Bot. J. Linn. Soc.* 97:295-316
  62. Ha, C. O., Sands, V. E., Soepadmo, E., Jong, K. 1988. Reproductive patterns of selected understorey trees in the Malaysian rain forest: the apomictic species. *Bot. J. Linn. Soc.* 97:317-31
  63. Haber, W. A., Frankie, G. W. 1989. A tropical hawkmoth community: Costa Rican dry forest Sphingidae. *Biotropica* 21:155-72
  64. Hamrick, J. L., Loveless, M. D. 1989. Genetic structure of tropical tree populations: associations with reproductive biology. In *The Evolutionary Ecology of Plants*, ed. J. H. Bock, Y. B. Linhart, pp. 129-49. San Francisco: Westview
  65. Heithaus, E. R., Fleming, T. H., Opler, P. A. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology* 56:841-54
  66. Heithaus, E. R., Opler, P. A., Fleming, T. H. 1974. Bat activity and pollination of *Bauhinia pauletia*: plant-pollinator coevolution. *Ecology* 55:412-19
  67. Henderson, A. H. 1985. Pollination of *Socratea exorrhiza* and *Iriartia ventricosa*. *Principes* 29:64-71
  68. Henderson, A. H. 1986. A review of pollination studies in the *Palmae*. *Bot. Rev.* 52:221-59

69. Hernandez, H. M., Abud, Y. C. 1987. Notas sobre la ecología reproductiva de arboles en un bosque mefófilo de montaña en Michoacán, México. *Bol. Soc. Bot. Mex.* 47:5-35
70. Heywood, J. S., Fleming, T. H. 1986. Patterns of allozyme variation in three Costa Rican species of *Piper*. *Biotropica* 18:208-13
71. Hickman, J. C. 1974. Pollination by ants: a low energy system. *Science* 184:1290-92
72. Holm-Nielsen, L. B., Nielsen, I. C., Basslev, H., eds. 1989. *Tropical Forest: Botanical Dynamics, Speciation and Diversity*. New York: Academic. 380 pp.
73. Hopkins, H. C. 1984. Floral biology and pollination ecology of the neotropical species of *Parkia*. *J. Ecol.* 72:1-23
74. Howe, H. F. 1983. Constraints on the evolution of mutualisms. *Am. Nat.* 123:764-77
75. Howe, H. F., Westley, L. C. 1988. *Ecological Relationships of Plants and Animals*. New York: Oxford Univ. Press.
76. Irvine, T. K., Armstrong, J. E. 1990. See Ref. 22
77. Janson, C. H., Terborgh, J., Emmons, L. H. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica* 13 (Suppl.): 1-6
78. Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104:501-28
79. Janzen, D. H. 1971. Euglossine bees as long distance pollinators of tropical plants. *Science* 171:203-5
80. Janzen, D. H. 1975. *Ecology of Plants in the Tropics*. London: Edward Arnold
81. Janzen, D. H. 1979. How to be a fig. *Annu. Rev. Ecol. Syst.* 10:13-51
82. Janzen, D. H. 1985. The natural history of mutualisms. See Ref. 30, pp. 39-99
83. Janzen, D. H. 1987. Insect diversity of a Costa Rican dry forest: why keep it, and how? *Biol. J. Linn. Soc.* 30:343-56
84. Jennersten, O. 1988. Pollination in *Dianthus deltooides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. *Conserv. Biol.* 2:359-66
85. Kaur, A., Ha, C. D., Jong, K., Sands, V. E., Chan, H. T., et al. 1978. Apomixis may be widespread among trees of the climax rain forest. *Nature* 270:440-41
86. Kevan, P. G., Baker, H. G. 1983. Insects as flower visitors and pollinators. *Annu. Rev. Entomol.* 28:407-53
87. Kieffer, A. R., Lande, R., Schemske, D. W. 1984. Models of coevolution and speciation in plants and their pollinators. *Am. Nat.* 124:220-43
88. Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715-25
89. Koptur, S. T. 1984. Outcrossing and pollinator limitation of fruit set; breeding systems of neotropical Inga trees (Fabaceae: Mimosoideae). *Evolution* 38:1130-43
90. Kress, W. J., Beach, J. H. 1990. Flowering plant reproductive systems at La Selva Biological Station. Ms.
91. Levin, D. A. 1975. Pest pressure and recombination systems in plants. *Am. Nat.* 109:437-51
92. Linhart, Y. B. 1973. Ecological and behavioral determinants of pollen dispersal in hummingbird pollinated *Heliconia*. *Am. Nat.* 107:115-23
93. Linhart, Y. B., Mendenhall, J. A. 1977. Pollen dispersal by hawkmoths in a *Lindenia rivalis* Benth. population in Belize. *Biotropica* 9:143
94. Lovejoy, T. E., Bierggaard, R. O. Jr., Rylands, A. B., Malcolm, J. R., Quintela, C. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. In *Conservation Biology*, ed. M. E. Soule, pp. 257-85. Sunderland, Mass: Sinauer
95. Loveless, M. D., Hamrick, J. L. 1984. Ecological determinants of genetic structure in plant populations. *Annu. Rev. Ecol. Syst.* 15:65-90
96. Lumer, C. 1980. Rodent pollination of *Blakea* (Melastomataceae) in a Costa Rican cloud forest. *Brittonia* 32:512-17
97. Luteyn, J. L. 1989. See Ref. 72, pp. 297-307
98. Marshall, A. G. 1983. Bats, flowers and fruit: evolutionary relationships in the old world. *Biol. J. Linn. Soc.* 20:115-35
99. May, R. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton Univ. Press
100. Mitchell, A. 1982. *Reaching the Rain Forest Roof: A Handbook on Techniques of Access and Study in the Canopy*. Leeds, UK: Leeds Philos. Lit. Soc.
101. Mori, S. A. 1989. See Ref. 72, pp. 319-32
102. Mori Urpi, J. 1982. Pollination en *Bac-tris gasipaes* H.B.K. (Palmae). *Rev. Biol. Trop.* 28:153-74
103. Neill, D. A. 1988. Experimental studies on species relationships in *Erythrina* (Leguminosae: Papilionoideae). *Ann. Mo. Bot. Gard.* 75:886-969
104. Nilsson, L. A., Jonsson, L., Ralison, L., Randrianjohany, E. 1987. Angeraceoid orchids and hawkmoths in Central Madagascar: specialized pollination

- systems and generalist foragers. *Biotropica* 19:310-18
105. O'Malley, D. M., Bawa, K. S. 1987. Mating system of a tropical rain forest tree species. *Am. J. Bot.* 74:1143-49
  106. O'Malley, D. M., Buckley, D. P., Prance, G. T., Bawa, K. S. 1988. Genetics of Brazil nut (*Bertholletia excelsa* Humb. Bonpl.: Lecythidaceae). 2. Mating system. *Theor. Appl. Genet.* 76: 929-32
  107. Opler, P. A. 1983. Nectar production in a tropical ecosystem. In *The Biology of Nectaries*, ed. B. Bentley, T. Elias, pp. 30-79. New York: Columbia Univ. Press
  108. Perry, D. R. 1978. A method of access into the crown of emergent and canopy trees. *Biotropica* 10:155-57
  109. Perry, D. R., Starrett, A. 1980. The pollination ecology and blooming strategy of a neotropical emergent tree, *Dipteryx panamensis*. *Biotropica* 12:307-13
  110. Perry, D. R., Williams, J. 1981. The tropical rain forest canopy: a method for providing total access. *Biotropica* 13:283-85
  111. Pimm, S. L. 1986. Community stability and structure. In *Conservation Biology*, ed. M. E. Soule, pp. 309-30. Sunderland, Mass: Sinauer
  - 111a. Poole, R. W., Rathcke, B. J. 1979. Regularity, randomness, and segregation in flowering phenologies. *Science* 203:470-71
  112. Porsch, O. 1934. Säugetiere als Blumenbesucher und die Frage der Säugetierblume. I. *Biol. Gen.* 10:657-85
  113. Porsch, O. 1935. Säugetiere als Blumenbesucher und die Frage der Säugetierblume. II. *Biol. Gen.* 11:171-88
  114. Porsch, O. 1936. Säugetiere als Blumenbesucher und die Frage der Säugetierblume. III. *Biol. Gen.* 12:1-21
  115. Prance, G. T. 1985. The pollination of Amazonian plants. In *Key Environments: Amazonia*, ed. G. T. Prance, T. E. Lovejoy, pp. 166-91. Pergamon
  116. Primack, R. B. 1985. Longevity of individual flowers. *Annu. Rev. Ecol. Syst.* 16:15-37
  117. Ramirez, W. 1970. Host specificity of fig wasps (Agaonidae). *Evolution* 24:680-91
  118. Rathcke, B., Lacey, E. P. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16:179-214
  119. Regal, R. J. 1982. Pollination by wind and animals: ecology of geographic patterns. *Annu. Rev. Ecol. Syst.* 13:497-24
  120. Renner, S. 1986. The neotropical epiphytic Melastomataceae: phylogeographic patterns, fruit types and floral biology. *Selbyana* 9:104-11
  121. Rogstad, S. H., Paton, J. C. II, Schaal, B. A. 1988. M 13 repeat probe detects DNA minisatellite-like sequences in gymnosperms and angiosperms. *Proc. Natl. Acad. Sci. USA* 85:9176-78
  122. Roubik, D. W. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge: Cambridge Univ. Press. 514 pp.
  123. Roubik, D. W., Ackerman, J. D. 1987. Long term ecology of euglossine orchid bees (Apidae: Euglossini) in Panama. *Oecologia* 73:321-33
  124. Rourke, J., Wiens, D. 1977. Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by non flying mammals. *Ann. Mo. Bot. Gard.* 64:1-17
  125. Sazima, M., Sazima, I. 1978. Bat pollination of the passion flowers, *Passiflora mucronata*, in southeastern Brazil. *Biotropica* 10:100-9
  126. Sazima, M., Sazima, I. 1987. Additional observations on *Passiflora mucronata*, the bat-pollinated passion flower. *Cienc. Cult.* 39:310-12
  127. Schatz, G. 1990. See Ref. 22
  128. Schemske, D. W., Horvitz, C. C. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* 225: 519-21
  129. Simpson, B. B., Neff, J. L. 1981. Floral reward, alternatives to pollen and nectar. *Ann. Mo. Bot. Gard.* 68:301-22
  130. Smith, A. P. 1973. Stratification of temperate and tropical forests. *Am. Nat.* 107:671-83
  131. Sobrevila, C., Arroyo, M. T. K. 1982. Breeding systems in a montane tropical cloud forest in Venezuela. *Plant Syst. Evol.* 140:19-38
  132. Start, A. N., Marshall, A. G. 1976. Nectarivorous bats as pollinators of trees in west Malaysia. In *Tropical Trees: Variation, Breeding and Conservation*, ed. J. Burley, B. T. Styles, pp. 141-50. New York: Academic
  133. Stebbins, G. L. 1981. Why are there so many species of flowering plants? *Bioscience* 31:573-77
  134. Steiner, K. E. 1979. Passerine pollination of *Erythrina megistophylla* Diels. (Fabaceae). *Ann. Mo. Bot. Gard.* 66: 490-502
  135. Steiner, K. 1981. Nectarivory and potential pollination by a neotropical marsupial. *Ann. Mo. Bot. Gard.* 68: 505-13

136. Stiles, F. G. 1975. Ecology, flowering phenology and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285-10
137. Stiles, F. G. 1978. Temporal organization of flowering among the hummingbird food plants of a tropical wet forest. *Biotropica* 10:194-10
138. Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. *Ann. Mo. Bot. Gard.* 68:323-51
139. Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird pollinated plants in a tropical forest. *Science* 196:1177-78
140. Stiles, F. G. 1979. Reply to Poole and Rathcke. *Science* 203:471
141. Stratton, D. A. 1989. Longevity of individual flowers in a Costa Rican cloud forest: ecological correlates and phylogenetic constraints. *Biotropica* 21:308-18
142. Straw, R. M. 1956. Floral isolation in *Penstemon*. *Am. Nat.* 90:47-63
143. Sussman, R. W., Raven, P. H. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. *Science* 200:731-36
144. Sytsma, K. J., Schaal, B. A. 1985. Genetic variation, differentiation and evolution in a species complex of tropical shrubs based on isozymic data. *Evolution* 39:582-93
145. Tanner, E. V. J. 1982. Species diversity and reproductive mechanisms in Jamaican trees. *Biol. J. Linn. Soc.* 18:263-78
146. Terborgh, J. 1986. Keystone plant resources in the tropical forest. In *Conservation Biology*, ed. M. E. Soule, pp. 330-44. Sunderland, Mass: Sinauer
147. Thompson, J. N. 1982. *Interaction and Coevolution*. New York: Wiley
148. Toledo, V. M. 1977. Pollination of some rain forest plants by nonhovering birds in Veracruz, Mexico. *Biotropica* 9:262-67
149. Tomlinson, P. B., Primack, R. B., Bunt, J. 1979. Preliminary observations of floral morphology in mangrove Rhizophoraceae. *Biotropica* 11:256-77
150. West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Q. Rev. Biol.* 58:155-83
151. White, M. J. D. 1978. *Modes of Speciation*. San Francisco: Freeman
152. Wiebes, J. T. 1979. Coevolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* 10:1-12
153. Wright, S. 1969. *Evolution and the Genetics of Populations*, Vol. II. Chicago: Univ. Chicago Press
154. Young, A. M. 1982. Effects of shade cover and availability of midge breeding sites on pollinating midge populations and fruit set in two cocoa farms. *J. Appl. Ecol.* 19:47-63
155. Young, H. J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *Am. J. Bot.* 73:931-44
156. Young, H. J. 1990. See Ref. 22

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