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COPING WITH THE EPIPHYTIC EXISTENCE: POLLINATION STRATEGIES

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ABSTRACT. Populations of epiphytic flowering plants are often composed of scattered individuals or small, hyperdispersed clusters. These characteristics create conditions for pollination somewhat different from that encountered by many terrestrial plants. For example, plant distribution and size constraints imposed by the epiphytic habit may have limited floral apparency or competitiveness for adequate pollinator service. To cope with these problems, epiphytes employ one of several specialized pollination strategies which involve deception, or exclusive or unique rewards. Each of the specialized strategies is probably most efficient for diffusely distributed species and may have either a terrestrial or an epiphytic origin. In one system, plants produce few flowers per day for long periods. The blossoms contain a high quality reward which is exclusively accessible to large traplining pollinators. In another, pollinator attraction is based on deceit which by-passes constraints directly imposed by pollinator foraging energetics. The deception may exploit sexual, feeding or egg-laying behaviors of their pollinators. A third strategy employed by many neotropical epiphytes is pollination by male euglossine bees. The flowers produce fragrances which serve as specific attractants and perhaps precursors to sex pheromones of the bees. Pollination occurs when male bees arrive and collect the fragrance compounds. All three strategies are not unique to epiphytes. Both terrestrials and epiphytes with shared size and dispersion constraints seem to have more specialized pollination biologies than their more densely populated and floriferous neighbors. The dispersion-specialization hypothesis generates testable predictions, some of which are presented.

Epiphytic flowering plants possess an incredible array of morphological, anatomical and physiological adaptations associated with the stresses imposed by their habitat (Madison, 1977). Although considerable vegetative diversity exists among epiphytes, much evolution of species-rich groups has been attributed to adaptive radiation via zoophilous pollination mechanisms (Pijl & Dodson, 1966; Ashton, 1984). Nevertheless, the role of pollination biology in the evolution and adaptation of epiphytes is rarely mentioned in the literature (e.g., Richards, 1952; Johansson, 1974; Madison, 1977; Benzing, 1981; Lüttge, 1985; but discussed in Benzing & Atwood, 1984). If pollination biology is of special significance to the evolution of epiphytic groups, then there should exist patterns in pollination strategies that relate to shared environmental conditions. I shall attempt to identify common pollination strategies among epiphytes and those factors that may affect their evolution. Does the epiphytic habit impart unusual constraints on plant–pollinator interactions? If so, then how do epiphytes cope with these conditions?

CONSTRAINTS

The relatively small size of epiphytes may limit flower production. Consequently, floral displays may be insufficiently large to compete for pollinator attentions on the same basis as the more floriferous trees, shrubs and lianas. There are several ecological reasons for small plant size. Obviously, the weight of a large epiphyte could be more than a phorophyte (live plant substrate) could bear without falling or breaking. Secondly, resources might be better allocated towards sexual reproduction rather than vegetative structures for plants growing in an unstable, ephemeral habitat (Schaffer, 1974; Benzing, 1976) in which bark exfoliates, branches are shed, and trees die. Epiphytes attached to tree trunks and major limbs may be old, but others, especially twig epiphytes, grow on short-lived substrates where life expectancy is brief. Precocious flowering is one way epiphytes may cope with the vagaries of their substrate, even if it means smaller, suboptimal floral displays (Schemske, 1980). Epiphyte size may also be limited because many are stressed (Janzen, 1975; Benzing, 1984; Montalvo & Ackerman, 1986) and lack resources (nutrients, water, light) for rapid growth and maintenance of large plant bodies. Indeed, some of the more bizarre vegetative structures of epiphytes are special adaptations for water and nutrient procurement (e.g., Benzing, 1976; Janzen, 1974a).

A second probable constraint on the pollination biology of epiphytes is their distribution within a community. Plant dispersion affects the availability of pollinator rewards which can have a profound influence on the evolution of pollination strategies (Janzen, 1971; Regal, 1977; Stiles, 1978a; Augspurger, 1981; Burger, 1981; Ackerman, 1986). Characteristics of the phorophyte can strongly influence vertical and hori-

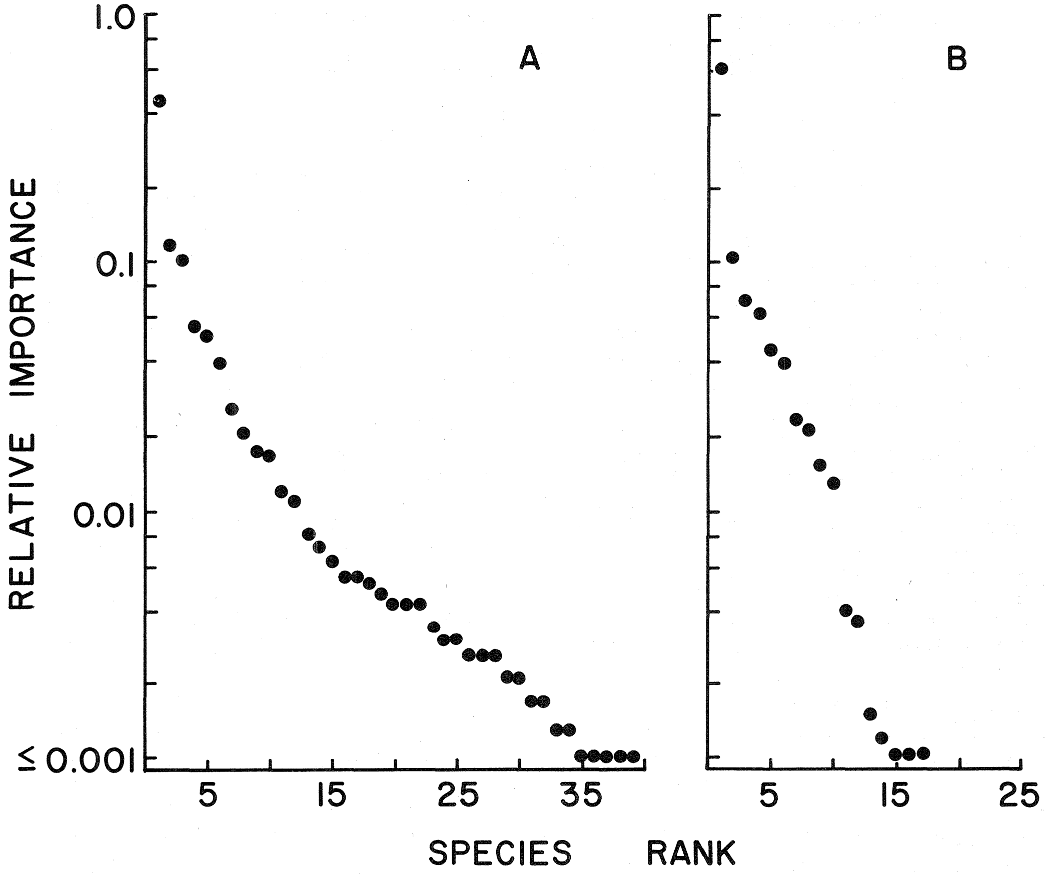

FIGURE 1. Relative abundance of epiphyte species at two cloud forest sites in Colombia. Data are from Sugden (1979) and include only mature, angiosperm epiphyte species. For each location, the species are ordered from left to right on the horizontal axis by their abundance ranks. The vertical axis delineates the proportion of the epiphyte community represented by each species. A, epiphyte community of Sierra Nevada de Santa Marta. Density of individuals on the horizontal plane is 1.67 per square m. B, epiphytes of the Serrania de Macuira. Density is 5.45 individuals per square m.

zontal plant dispersion. Dispersion patterns of epiphyte populations are variable but rarely do they appear dense and regularly distributed (Grubb et al., 1963). Even in cloud forests where epiphyte loads are particularly heavy, most species of the epiphyte community are scattered (Sugden, 1981). Furthermore, most species are relatively rare in these dense communities. Sugden (1979) found that a small fraction of the species present in two Colombian cloud forests accounted for approximately two-thirds of the total individuals present (FIGURE 1).

Differences in horizontal dispersion patterns of epiphytes between communities may be affected by both biotic and abiotic factors. Climate may play a major role in southern Nigeria where Sanford (1968) found that single species dominance per tree and per site was found only in the driest forests. Disturbance may substantially affect epiphyte communities too. The tropical forest is a dynamic, frequently disrupted environment where species have little opportunity to establish large, dense populations (Hubbell, 1979; Pickett, 1980; Brokaw, 1982; Thorington et al., 1982).

Biotic interactions such as dispersal properties may also affect horizontal dispersion. Wind or bird-dispersed epiphytes were randomly distributed in a cacao plantation of regularly spaced, even-aged trees, whereas ant-dispersed or associated species were aggregated (Madison, 1979). Dispersion characteristics are further complicated by phorophyte specificity (Johansson, 1974) which may be caused by physical and chemical characteristics. *Bursera simaruba* (L.) Sarg. (Burseraceae) carries few epiphytes, probably because of the mode by which its bark exfoliates (pers. obs.). Mexican oaks with high phenolic content in their bark are generally epiphyte-free because of inhibitory effects on seed germination (Frei & Dodson, 1972; Frei, 1973).

Vertical heterogeneity in epiphyte dispersion patterns have been noted by Johansson (1974) and Sugden (1979) and, like the distribution of cryptogamic epiphytes, it may be related to substrate characteristics and stratification of light, nutrient and water availability (Barkman, 1958). Again, disturbance can play an important role. Tree trunks and large limbs are much more stable habitats than canopy twigs. Vertical distribution of epiphytes may be important in pollination interactions because pollinator foraging behavior can be height-dependent (Levin & Kerster, 1973; Frankie & Coville, 1979; Paulus & Gack, 1980 cited by Dafni, 1984; but see Roubik et al., 1982).

Vascular epiphytes exhibit a large diversity of dispersion patterns. Pollination strategies are likely to be variable and reflect the complexities of epiphyte dispersion, but we may also expect that the more common strategies would be particularly efficient or effective for widely dispersed, low density populations.

SPECIALIZATION

Because of size and dispersion characteristics, epiphytes would appear to be weak competitors for the same pollinator services as larger arboreous neighbors. However, strong selection may exist for more specialized pollinator relationships to circumvent poor apparency or competition for pollination to draw pollinators to widely dispersed flowers. Thus, pollination strategies of epiphytes should be somewhat more specialized than those of more floriferous trees and shrubs, and specialization may be related to dispersion patterns.

Supporting evidence for this hypothesis is meager, but most available data are consistent. At the community level, the diversity of pollination mechanisms found in canopy trees of a lowland Costa Rican forest was relatively less than that found in the subcanopy and also among epiphytes, although the epiphytes were not yet fully quantified (Bawa et al., 1985). This pattern may reflect differences in specialization of plant–pollinator interactions where the canopy trees have more generalized floral biologies.

Additional support comes from species-level comparisons. Of two Brazilian aroids, the diffusely distributed species, *Philodendron selloum* C. Koch, has a highly specialized floral biology whereas the densely distributed species, *P. bipinnatifidum* Schott, has a relatively generalized pollination system (Gottsberger & Amaral, 1984). Among hummingbird-pollinated *Heliconia* (Heliconiaceae) in Costa Rica, some species occur in early successional habitats and rapidly form clonal populations or large clumps. These species have high rates of flower and nectar production and are pollinated and defended by aggressive, territorial birds. Another group of *Heliconia* do not form large stands and individuals tend to be dispersed. The morphologically exclusive flowers have floral tubes that are accessible to only long-billed hermits (Stiles, 1978a). All *Heliconia* have relatively elaborate pollination systems, but those species that form sparse populations are seemingly more specialized.

In the following discussion, evidence is presented that suggests pollination strategies employed by epiphytes appear specialized and seem particularly suited for overdispersed populations. In the neotropics, three of the more common and better known strategies are trapline, deception and euglossine pollination.

Trapline Pollination

Most epiphytes of Bromeliaceae, Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae, Rubiaceae and others (rarely in Orchidaceae) are likely traplined. Documentation, though, is scarce, yet the occurrence of trapline pollination may be inferred from floral morphology and flowering behavior because the syndrome is well established for terrestrial herbs, vines, lianas and shrubs (Janzen, 1971; Feinsinger, 1976; Ackerman, 1985). Characteristically, these plants bloom for long periods and maintain a consistent daily production of a few, often conspicuous and fragrant flowers. A high quality pollinator reward is produced and protected from exploitation by all but a few pollinator and robber species (Janzen, 1974b). The reward is usually nectar or pollen, but oils, resins and perhaps fragrances are important in some families (Armbruster & Webster, 1979; Simpson & Neff, 1981; Armbruster, 1984; Renner, 1984; Ackerman, 1985).

Traplining pollinators are robust animals, commonly long-billed birds, bats, large bees and hawkmoths (e.g., Frankie & Baker, 1974; Linhart & Mendenhall, 1977; Feinsinger & Colwell, 1978). They develop foraging routes that incorporate scattered, but predictable, high yield, resource stops. Pollinators may follow the same routes daily (Janzen, 1971), but under certain conditions, their foraging bouts may be quite plastic (Ackerman et al., 1982). Nevertheless, trapliners are generally strong fliers and probably important long-distance pollen vectors for very scattered individuals of epiphyte populations (Janzen, 1974b).

Because of highly desirable and predictable rewards, pollinator visits to trapline plants are to a certain extent, density-independent. Within some critical range of densities and rewards, visits to scattered individuals must become energetically feasible. Trapline pollination may therefore release competition for pollination between epiphytes and larger, more generalist flowering plants with large floral displays (Bawa, 1983). Nevertheless, some competition for pollination may have influenced flowering times of some species. In lowland central Panama, most traplined nectar-hosts pollinated by euglossine bees flowered during the mid-wet season even though their pollinators were more abundant during the dry and early wet seasons. During seasons of high bee abundance, alternative nectar resources with larger floral displays were in peak flower: the lianas, trees and shrubs (Ackerman, 1985). Competition for pollination, although not the only plausible explanation (cf. Stiles, 1978b), could have produced and maintained the phenological segregation of the two plant groups.

Competition for pollination via interspecific pollen transfer is likely to have generated character divergence and speciation (cf. Rathcke, 1983; Waser, 1983). It may have had a large role in the evolution of epiphyte pollination systems. Because a trapliner can incorporate numerous species in a given foraging bout, interspecific pollinations could occur and thereby limit conspecific pollinations and reproductive success. However, Haber (in Janzen, 1983: 633) noted that when traplining hawkmoths visit several plant species, pollen from the different plants is deposited on distinct regions of the pollinator's body. Though untested, the assemblage of specific pollen deposition sites may be a consequence of character divergence mediated by selection pressures caused by interspecific pollen transfers. Clearly, we need thorough studies of pollen loads on both pollinators and stigmas, and of fitness consequences of interspecific pollinations (see Kress, 1983a; Kohn & Waser, 1985).

Traplined plants are often diffusely distributed (e.g., Feinsinger, 1976; Stiles, 1978a) but they do remain attractive to pollinators when growing in dense populations (Ackerman et al., 1982; Busby, pers. comm.). However, pollinator foraging behaviors, pollen flow characteristics and consequently breeding systems may change (Handel, 1985). In dense populations, pollinator movement between plants may, for example, be shortened and pollen flow distances reduced. The probability of geitonogamous pollinations could increase, especially if the high population density was a result of clonal propagation, a common phenomenon among epiphytes. Seed production would still occur because many traplined plants (tropical forest herbs and probably epiphytes) are self-compatible (Grove in Bawa et al., 1985). Selection for physiological incompatibility mechanisms would be low for species which are normally sparsely distributed and produce few flowers at a time (Kress, 1983b). When these species form dense populations, inbreeding depression can occur (e.g., Schemske, 1983), which may exert strong selection for developing incompatibility mechanisms or against extensive clumping. Since neither of these features appear to be prevalent among traplined plants, terrestrial or epiphytic, the incidence of high flower density and consequently geitonogamy is probably too unusual to strongly influence selection. Thus, the frequency of traits associated with trapline pollination probably increased in populations because they offset the disadvantages of small, local population sizes. As a result, trapline pollination may lose some of its advantages in dense plant populations (cf. Rabinowitz, 1981).

The evolution of floral traits in traplined plants may have been a result of several different sources of selection other than competition for pollination. In some cases, resources may limit fruit and seed production so that the evolution of floral traits may be driven by sexual selection (e.g., Stephenson & Bertin, 1983). In other situations, mutualistic interactions could be important. For example, a group of plant species can maintain populations of long-lived pollinators with sequential flowering phenologies (Stiles, 1977). Effective mutualism, though, is likely an outcome and not a cause of sequential flowering times of sympatric species (Waser & Real, 1979).

Deception Pollination

The second specialized pollination strategy common to epiphytes employs deception in which the flowers offer little or no pollinator reward. This is particularly common among orchids, terrestrial and epiphytic, but is also known in other families, mostly among terrestrial herbs, vines and occasionally trees (Gentry, 1974; Baker, 1976; Dafni, 1984). Deception mechanisms involve different types of mimicry and the best known are those based on the reproductive or food foraging behaviors of their pollinators (Pijl & Dodson, 1966; Ackerman, 1986).

Deception that capitalizes on the reproductive behaviors of pollinators sometimes involves mimicry of insect brood sites. Pollination occurs when female insects visit a succession of flowers to lay their eggs on what appears to be an appropriate substrate for larvae. Although the best documented cases involve terrestrial species (e.g., *Paphiopedilum*: Atwood, 1985; *Epipactis*: Ivri & Dafni, 1977), some epiphytes may be involved as well. Good candidates are *Dracula* (Orchidaceae) species, whose flowers reportedly mimic fungi, the larval substrate of fungus gnats (Sciaridae, Mycetophilidae; Vogel, 1978a), and some Araceae (Dafni, 1984).

Mate mimicry, better known in its extreme manifestation as pseudocopulation, is also more thoroughly documented for terrestrial orchids, especially the European *Ophrys* (Kullenberg & Bergström, 1976) and several Australian genera (Stoutamire, 1975, 1983). However, reliable preliminary observations indicate that some neotropical epiphytes may be "pseudocopulated" as well, e.g., *Trichoceros* (Pijl & Dodson, 1966), and *Oncidium henekenii* Schomb. ex Lindl. in Hispaniola (Dod, 1976). Flowers that employ mate mimicry to attract pollinators are similar to pollinator mates in some critical characteristics that elicit mating behaviors by stimulating the visual, tactile and olfactory senses of their pollinators. The deception may be sufficiently complete that pollinating insects may attempt to copulate with the flowers (Stoutamire, 1983).

Deception also operates when flowers mimic pollinator food resources. Self-mimicry probably occurs in the monoecious terrestrial and epiphytic begonias (Begoniaceae). Stigmas of female flowers are similar to the stamens of male flowers. Pollinating bees probably visit the males to collect pollen and occasionally mistake a female for a pollen flower (Vogel, 1978b).

Many food-deceptive plants do not have specific models and only appear as "likely" food plants to naive pollinators (Gentry, 1974; Ackerman, 1981b; Little, 1983). The epiphytic *Cochleanthes lipscombiae* (Rolfe) Garay (Orchidaceae) had two sources of uninitiated pollinators: 1) recently emerged, young bees who presumably had not yet established foraging routes, and 2) bees that were exploring additional resources during a period of rapid turnover in the flowering of their nectar hosts (Ackerman, 1983a).

Deception pollination systems can be complicated. For *Cochleanthes lipscombiae,* some level of specific model-mimicry may also operate. The orchid shares pollinators, phenology, geography, habitat and general floral appearance with the traplined liana, *Clitoria javacensis* HBK (Leguminosae; Ackerman, 1983a). Combining the bases for attraction may not be uncommon. The very large orchid genus *Epidendrum* is primarily a food-deceptive group, and most species are pollinated by moths and butterflies. Floral fragrances may be pheromone-like and attract only one sex (Wagner, 1973; Adams & Goss, 1976), but the pollination event actually involves feeding behavior, the extension of the tongue and probing for non-existent nectar.

Visitation frequencies and reproductive success of species with deception pollination systems may be frequency-dependent. Reproductive success should be inversely related to flower densities and mimicry should be less effective when the relative frequency of models is low. In fact, because of these effects we would expect deception flowers, like those that are traplined, to work best for species with diffuse populations (e.g., epiphytes). Unfortunately, such ecological relationships are rarely studied (Bierzychudek, 1981; Dafni & Ivri, 1981a, 1981b; Ackerman, 1986).

The evolutionary loss of pollinator rewards in deceptive epiphytes and terrestrials presumably occurred without the loss of reproductive success. This shift most likely occurred in hyperdispersed populations, such as those common to epiphytes. Reward flowers below a critical density would not meet the energetic needs of their pollinators and consequently would receive no more than a few cursory visits. Variants lacking a reward still would receive a few exploratory, pollinator visits. Resources previously used for reward production could be reallocated to produce more flowers, mature more fruit or improve longevity, if resources were limiting (Ackerman & Montero Oliver, 1985; Ackerman, 1986). In these cases, fruit and seed set may sometimes be pollination limited, but fruit production over the lifetime of the individual may be resource limited, a condition which may occur for the epiphytic orchid, *Ionopsis utricularioides* (Sw.) Lindl. (Montalvo & Ackerman, 1986). Hand pollinations increased fruit set over natural levels but the higher fruit set affected subsequent growth and flowering. Nutritional constraints imposed on epiphytes are well known (e.g., Benzing, 1981) and suggest that ultimate resource limits to sexual reproduction may occur.

Male Euglossine Pollination

Epiphytes throughout the tropics probably employ trapline and deception pollination strategies. However, some geographic regions have unique pollination systems. In the neotropics, a large number of epiphytes are pollinated by male euglossine bees as they collect floral fragrances. About 600 species of orchids, mostly epiphytes, and some terrestrial and epiphytic members of the Araceae, Gesneriaceae and other families produce floral fragrances that serve as both an attractant and reward for the male bees (Dodson et al., 1969; Williams & Dressler, 1976; Armbruster & Webster, 1979; Croat, 1980; Dressler, 1982; Williams, 1982). Many of the orchids are quite specialized and well known for their bizarre flowers, exotic fragrances and complex pollination mechanics. The bees possess specialized structures for collection and storage of the fragrance compounds and perhaps convert the chemicals to sex pheromones (Williams & Whitten, 1983). The plants are clearly dependent on the bees for pollination but thus far there are no data indicating that the bees are dependent on the flowers for fragrances (Ackerman, 1983b; Armbruster, unpubl.; Roubik & Ackerman, unpubl.).

Both male euglossine and trapline pollination are based on reward systems. They seem common among hyperdispersed epiphytes, but pollinator foraging behavior is probably distinct between the two modes. With a few possible exceptions (e.g., *Dalechampia,* Euphorbiaceae: Armbruster & Webster, 1979; *Peristeria elata,* Orchidaceae: pers. obs.), most male euglossine-pollinated species do not produce flowers daily for long periods of time as is typical of traplined plants. Although individual flowers may last for long periods of time, when pollinated, they cease fragrance production and become unavailable for repeat visits. Unlike nectar, fragrances are probably not nutritional requirements (Ackerman & Montalvo, 1985), and the frequency by which the bees must collect a particular compound is unknown. The need for collection may be irregular and the foraging behavior may be opportunistic.

Similar to traplining pollinators, male euglossines may carry pollen from different fragrance species on different parts of their bodies (Ackerman, 1983b). Differential placement of pollen by fragrance flowers may be a result of competition via interspecific pollen transfer. Closely related, sympatric species, though, do not share pollinators (Dressler, 1968; Ackerman, 1983b) because the initial stages of reproductive isolation probably occur through evolutionary changes in attraction specificity of the floral fragrance (Williams & Dodson, 1972). A slight change in a floral fragrance may attract a very different group of bees. However, higher taxa are often distinguished on the basis of floral characteristics associated with pollination mechanics (e.g., Catasetinae: Dodson, 1975; Zygopetalinae: Dressler, 1981). These taxonomic categories do share pollinators which suggests that interspecific pollen transfer may have served as a strong selection force for differential pollen placement and for generating supraspecific evolution (Dressler, 1981).

Because individuals can, by means of their floral fragrance, draw pollinators from a kilometer or more away (Ackerman, 1981b), pollen flow distances may be great (Williams & Dodson, 1972). In fact, euglossine bee pollination, like trapline and deception strategies, may not be a very efficient system for large, dense populations. In Panama, a large clonal population of a robust terrestrial plant, *Spathiphyllum friedrichsthalii* Schott (Araceae), was pollinated by numerous species of fragrance-foraging euglossines and pollen-foraging stingless bees (Montalvo & Ackerman, unpubl.). The male euglossine visits were daily but few, and the bees visited only a small fraction of the available fragrance producing spadices. Visitations by male euglossine bees may be somewhat independent of the number of available inflorescences in the population. Consequently, a few plants may attract as many euglossine bees as a clump of numerous plants. In any case, the euglossine pollination strategy seems well suited for neutralizing the constraints of small plant size, uncertainty and dispersion imposed by the epiphytic habitat.

CONCLUSIONS

Although only a few scattered reports on epiphyte pollination systems exist, epiphytes appear to have employed relatively specialized pollination strategies. The epiphyte habitat imposes two constraints that may have profoundly influenced the evolution of these strategies: plant size and plant dispersion. The former is usually small and affects floral display size and reward production. The latter is often hyperdispersed and influences pollinator foraging behavior. The three well-known pollination strategies of neotropical epiphytes (traplining, deception and male euglossine pollination) are solutions to these problems but none is unique to epiphytic plants. The different strategies have some similar characteristics which may be explained by the dispersion–specialization hypothesis. In essence, it states that those species with small floral displays and populations of scattered individuals should have specialized floral biologies.

Autecological studies of epiphyte dispersion and pollination are clearly needed for all epiphyte groups but they should reach beyond the task of describing and cataloging plant–pollinator interactions. Epiphyte pollination obviously cannot be studied without epiphytes, but ecological and evolutionary processes can be examined using more accessible terrestrial species with analogous floral and dispersion characteristics. Employing a combination of terrestrial and epiphytic systems, the rather complex dispersion–specialization hypothesis can be tested at various levels.

A first approach would be to determine if specialization is related to floral display and plant dispersion. If the hypothesis is correct, then the relationship should hold for comparisons of related sympatric species with very different displays or dispersion patterns. Life forms with similar pollination mechanisms or strategies should have similar display and dispersion characteristics.

If the dispersion–specialization relationship exists, then predictions concerning the mechanisms for the evolution and maintenance of the system may be tested. For example, specialized pollination strategies of species that have characteristically diffuse populations may be less effective under crowded conditions perhaps because of inbreeding depression (Schemske, 1983). Conversely, the pollination strategies of those plants normally found in large, dense populations should be less effective in hyperdispersed populations because of competition for pollination.

The pollination problems and solutions of epiphytes are not necessarily unique. In fact, some of the specialized pollination strategies may have evolved among terrestrial ancestors that had similar size and dispersion constraints as epiphytes today (Ackerman, 1983c; Benzing & Atwood, 1984). Nevertheless, pollination biology does appear to be of special significance to the evolution of epiphytic groups.

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