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EVALUATION OF CHARACTER DISPLACEMENT AMONG PLANTS IN TWO TROPICAL POLLINATION GUILDS[1]

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Abstract. In cloud forest at Monteverde, Costa Rica, two guilds of bird-pollinated plants exist; one guild pollinated by long-billed hummingbirds, primarily the Green Hermit (*Phaethornis guy*), and one guild pollinated by short-billed hummingbirds, primarily the Purple-throated Mountain-gem (*Lampornis calolaema*). Plants were assigned to guilds based on hummingbird visit patterns documented during >4000 plant-hours of field observations, and on identities of pollen grains collected from 600 mist-netted hummingbirds. Other studies indicated that pollination in these plants is often insufficient for maximum seed set. Each guild was examined for character displacement expected within a stable assemblage of plants structured by competition for pollination. (1) By comparing observed flowering phenologies with those obtained through a randomization procedure, we determined whether each species' phenology minimized overlap with the remainder of its guild. (2) We also examined complementarity between phenological displacement and morphological displacement in reproductive structures.

Neither guild exhibited pronounced character displacement. (1) In most cases, flowering phenologies were indistinguishable from those generated at random; the few statistically significant departures mostly indicated aggregation, rather than displacement, of flowering seasons. (2) In most cases, morphological similarity was independent of phenological similarity. The only statistically significant result among the studied species was a positive correlation, among long-flowered species only, between rarity and uniqueness of flowering season.

We do not conclude that this absence of expected pattern indicates that competition never occurs or that competition is an inconsequential ecological event. Rather, we attribute absence of pattern to the following aspects of biological variability, two of which we have demonstrated in other studies. (1) Within any one year, density-dependent competition for pollination is sporadic, and is not clearly related to flowering season or morphological similarity. (2) The nature of interspecific interactions varies among years, as neither the relative intensities of flowering nor the flowering seasons themselves are consistent from year to year. (3) The nature of interspecific interactions varies with changes in species composition, which occur over short distances. (4) The assemblage of species is probably not stable over long time spans; the species have Gleasonian ecologies that change distribution and abundance faster than natural selection or diffuse competition can screen out improper phenotypes or species, respectively.

Key words: character displacement; cloud forest; competition for pollination; Costa Rica; flowering phenology; hummingbirds; null models; pollination.

INTRODUCTION

During the past decade, many ecologists have reexamined apparent patterns in the phenotypic traits of sympatric species, patterns attributed to ongoing ecological processes (Strong et al. 1984, Diamond and Case 1986). The patterns most often debated involve character displacement among species in a guild (sensu Root 1967) or "taxon-guild" (Schoener 1986). The

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process most often held responsible is interspecific competition for shared, limited resources (Connell 1983, Schoener 1983). Among groups of plants that share animal pollinators or seed dispersers, interspecific competition for the services of animals could lead to displacement in the timing of flowering or fruiting (reviewed by Rathcke and Lacey 1985, Wheelwright 1985). Among species that flower simultaneously, competition could result in morphological character displacement that involves flower shape or placement of reproductive parts (Heinrich 1975, Waser 1983).

Before causal relationships between an ecological process and an interspecific pattern are invoked, the existence of pattern should be conclusively demonstrated (Simberloff 1983). In the past, the existence of pattern within pollination guilds was sometimes judged only by a visual inspection of flowering seasons (e.g., Heithaus 1974, Stiles 1977, Feinsinger 1978). Recently, more objective statistical techniques have been used to evaluate pattern (Poole and Rathcke 1979, Pleasants 1980, 1983, Thomson 1980, 1981, Fleming and Partridge 1984, Wheelwright 1985). These techniques have been applied to data from both temperate and tropical plant assemblages. Although a few data sets suggest regular spacing of flowering or fruiting seasons, most indicate phenologies that are random or even aggregated relative to those generated by the null model (Waser 1983, Fleming and Partridge 1984, Rathcke and Lacey 1985, Wheelwright 1985, Kochmer and Handel 1986).

Most data sets used in previous analyses are somewhat inappropriate for rigorous statistical tests of character displacement within guilds (Fleming and Partridge 1984). First, data were often collected in a qualitative manner only, such that statistical analyses can deal only with the spacing of flowering or fruiting "peaks," or the spacing of the midpoints of periods of "good flower." As Zimmerman (1984) and others have pointed out, however, flowers produced away from peak times may be at least as important in seed production and plant population dynamics as flowers produced at peak times. In addition, the variable shapes of seasonal flowering curves among species (e.g., Gentry 1974, Bawa 1983) may be biologically meaningful, so that neither the timing of peak flowering alone nor the entire span of flowering alone is likely to estimate biologically important aspects of flowering for all species. Second, as Fleming and Partridge (1984) and Primack (1985) point out, many data sets include only a subset of the guild under study (e.g., Stiles 1975, 1977, Fleming 1985, Wheelwright 1985) or include representatives of several overlapping guilds (e.g., Parrish and Bazzaz 1979, Rabinowitz et al. 1981). Third, in many studies it is misleading to erect a null model of random flowering and an alternate hypothesis of regularly dispersed peaks (cf. Harvey et al. 1983). Pollinator abundance may vary widely over the season, for reasons unrelated to flower abundance, such that the process of competition alone would lead to aggregation, rather than regularity, in flowering peaks (Rathcke and Lacey 1985). In addition, abiotic factors may render some seasons (e.g., winter at temperate or boreal latitudes, severe dry seasons in many tropical regions) less suitable for flowering than others, so that the null model for tests of competition-induced pattern should not necessarily be based on random flowering throughout the year (Stiles 1979, Cole 1981, Rathcke and Lacey 1985).

Much of the discussion of character displacement in flowering phenologies or other flowering traits involves hummingbird-pollinated plants (Heithaus 1974, Stiles 1977, 1979, 1981, 1985, Waser 1978*a*, Brown and Kodric-Brown 1979, Poole and Rathcke 1979, Waser and Real 1979, Cole 1981, Gleeson 1981, Fleming and Partridge 1984). In this paper we evaluate evidence for competition-induced pattern in two guilds of hummingbird-pollinated plants in cloud forest at Monteverde, Costa Rica. Plants were assigned to guilds objectively and without taxonomic limitations. We subjected quantitative phenological data collected over 2 yr to randomization techniques similar to those of Fleming and Partridge (1984) and Kochmer and Handel (1986). Comparisons of data with a null model of random flowering are reasonable, because (1) population densities of the hummingbird pollinators are remarkably stable over the year, and (2) the constantly wet conditions of the cloud forest understory provided no a priori basis for expecting some seasons to be better for flowering than others.

METHODS

Phenological data

The Monteverde Cloud Forest Preserve, near Monteverde, Provincia de Puntarenas, Costa Rica, contains ≈4800 ha of Lower Montane Rain Forest (Holdridge 1967) and similar life zones. Except for a single livestock trail and several footpaths, the Preserve has been influenced very little by human disturbance. The Preserve lacks exotic species except for a few ruderals restricted to the livestock trail. Although direct rainfall decreases from November to May, the trade winds that prevail during that season constantly bathe the cloud forest in which we worked with wind-blow mist. As a result, the forest interior never experiences a true "dry season." Lawton and Dryer (1980) provide details on climate and vegetation.

Phenological data were derived from monthly censuses of hummingbird-visited flowers. On the 1st d of each month from July 1981 through June 1983, we counted all bird-visited flowers on each of 10 study plots. Four plots located in closed-canopy, mature-phase forest ranged from 1600 to 1925 m^2, totalling 7280 m^2. Six plots, totalling 2300 m^2, encompassed gaps caused by treefalls that had occurred 1–3 yr earlier; these ranged from 132 to 544 m^2. Study plots are described in detail elsewhere (Feinsinger et al. 1987).

We collected data by walking slowly along a grid of trails in each plot, carefully counting all open flowers of all plant species known to be visited by hummingbirds, up to 10 m above the forest floor. Because hummingbirds that frequent understory plants also forage at several species of epiphytic Ericaceae in the canopy, one of us (Busby) collected data on ericad flowering using another method. One day each month, all fallen corollas of canopy and subcanopy Ericaceae known to be frequented by hummingbirds were counted along a 1.5 × 5000 m belt transect located near the other study plots. Because ericad flowers remain on the plant for ≈2 d, the number of fallen corollas should be proportional to the total number of viable flowers open the previous day. The number of freshly fallen flowers may underestimate the number of open ones; on the other hand, the corollas counted may actually have accumulated over several previous days, leading to overestimation. Because these methods differ radically from the censuses of open, viable flowers within study plots, we performed all analyses twice, once with data (including data on epiphytic Ericaceae within 10 m of, and visible from, the ground) obtained from the 10 study plots only, and once substituting the belt-transect Ericaceae data (corrected for area covered) for the Ericaceae data collected on plots.

Analysis of phenological overlap

At Monteverde, as elsewhere in the Neotropics, plants adapted for hummingbird pollination fall into two groups: those with long corollas, pollinated almost exclusively by long-billed hummingbirds such as most members of the hermit hummingbird subfamily (Phaethornithinae), and those with much shorter corollas, pollinated almost exclusively by hummingbirds with quite short, straight bills (Stiles 1981, Feinsinger 1983, Feinsinger et al. 1986). Based upon our familiarity with the system (4218 plant-hours of observations on hummingbird visits made during 1981–1982, and identification of ≈700 000 pollen grains collected from 600 hummingbirds mist-netted on study plots during 1981–1983), we could unequivocally assign nearly all species to one or the other guild. The few exceptions, plants visited frequently by both long- and short-billed hummingbirds, were sparsely flowering species whose inclusion in analyses for both guilds scarcely changed the results at all.

At long-flowered plants (including the few "ambivalent" species listed in Table 1), 68.2% of all pollinating visits came from a single hummingbird species, *Phaethornis guy* (the Green Hermit). Most remaining visits came from three other long-billed hummingbird species. At short-flowered plants adapted for hummingbird pollination, 96.9% of all pollinating visits came from *Lampornis calolaema* (the Purple-throated Mountain-gem; Feinsinger et al. 1986). Thus, flowering plants in either guild experience collective effects of several other species, such that competitive or facilitative relationships among species within each guild should be diffuse rather than pairwise. If competition were to induce character displacement, for example, each species would be phenologically displaced from the summed flowering of all other species in its guild ("guildmates") rather than from one "competitor" species at a time. Therefore, following Thomson and Rusterholz (1982) and Fleming and Partridge (1984), instead of pairwise overlaps we computed *n*-wise overlaps, or the overlap between each species and the summed flowering of all its guildmates.

Our approach used a procedure similar to that of Fleming and Partridge (1984) to compare observed *n*-wise overlaps with those generated by a series of randomizations. Observed 24-mo flowering curves for all species were started at random months within the 24-mo period, "wrapping around" to the beginning of the period as necessary. This method is analogous to mapping the observed phenological curves onto a 24-mo calendar at random. Overlap between each species and the summed phenology of all its guildmates was then computed using the proportional similarity index (symmetrical), or *PS* (Eq. 1), and the Levins (1968) index (asymmetrical), or *LI* (Eq. 2).

$$PS_{ij} = 1 - 0.5\left(\sum_{m} |p_{im} - p_{jm}|\right) \tag{1}$$

and

$$LI_{ij} = \sum_{m} (p_{im}p_{jm})/p_{im}^2, \tag{2}$$

where p_{im} is the proportion of species i's flowering that occurs in month m, and p_{jm} is the proportion of summed flowering by all of i's guildmates that occurs in month m. PS averages the overlap of i on j with that of j on i, whereas LI is the extent to which i is overlapped by j. For each set of randomly generated phenologies, both indices were calculated for each species i and the sum of its guildmates (j); then another set of randomly generated phenologies was generated. The procedure was repeated 100 times for each guild, with (one set) or without (a second set) the data on canopy Ericaceae from the belt transect. For each overlap index in each of the four sets of 100 runs, then, we ranked overlap values in ascending order, and noted how many values from randomly generated phenologies were greater or less than the observed overlap between species i and its combined guildmates j. To reject the null hypothesis of random flowering pattern, the observed overlap between species i and its combined guildmates j must be lower than that of 95% of the randomly generated values (indicating a divergent flowering season) or >95% of the randomly generated values (indicating a convergent flowering season).

Morphological data

One response to competition for pollination might be divergence in the location of reproductive parts

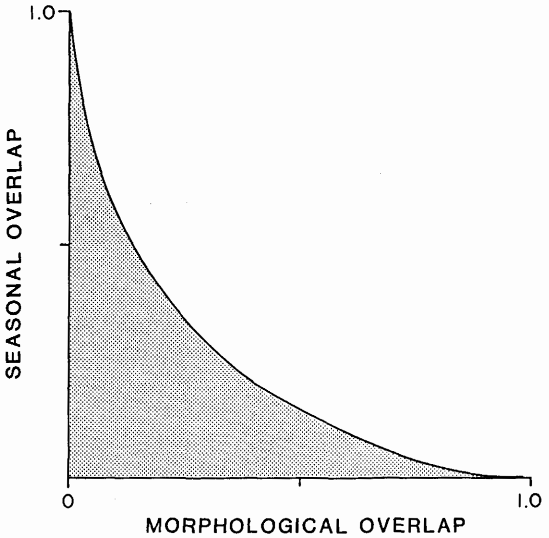

FIG. 1. A possible complementary relationship of phenological overlap to morphological overlap between pairs of plant species in the same guild. If competition has structured the guild, most species pairs would be expected to fall in the area below the curve.

among members of a guild. Such divergence would lessen the amount of pollen lost to inappropriate stigmas, or of inappropriate pollen deposited on stigmas, should pollinators visit a variety of simultaneously flowering species (Waser 1978*b,* Brown and Kodric-Brown 1979). For most species in both guilds, we measured distance from base of the flower (nectaries) to midpoint of anthers in a sample of at least 10 flowers taken from at least three plants. Data from 600 pollen loads taken from hummingbirds (P. Feinsinger, K. G. Murray, and C. A. Murcia, *personal observation*) indicate that the base-to-anthers distance is a reasonable estimate of the site where pollen is carried on hummingbirds, relative to the tip of the bill, even though loads on hummingbirds tend to be somewhat smeared and intermingled. For each species, we calculated mean and variance in base-to-anthers distance.

Comparison of phenological and morphological overlap

Morphological overlap between two guildmate plants is calculated as the area of intersection of the two frequency distributions of base-to-anther distances (cf. MacArthur 1972:42):

$$\alpha = e^{-\frac{|\bar{x}_1{}^2 - \bar{x}_2{}^2|}{\delta_1{}^2 - \delta_2{}^2}}. \qquad (3)$$

If interspecific competition has exerted a strong force on community structure, then species pairs with high overlaps along both morphological and phenological dimensions should be scarce relative to pairs with low overlaps along one or both dimensions (Fig. 1). For pairs of species with low phenological overlap the extent of morphological overlap should be irrelevant. Similarly, for pairs with low morphological overlap the extent of phenological overlap should be unimportant (at least in terms of interspecific pollen transfer—cf. Waser 1978*b,* 1983). The particular overlap values we calculated may not always accurately represent the potential impact of plants on one another's pollination success; thus, the values themselves are not an issue, only the relative locations of the points relating morphological to phenological overlap.

We assessed complementarity of displacement within each guild in two ways. First, for each guild we plotted the point representing phenological overlap, measured with *PS* (Eq. 1, with *j* a single other species) against morphological overlap (Eq. 3) for each possible pair of species. This provides a large sample size, but the pairs are not statistically independent; furthermore, any trends could be obscured by adding species that overlap little with any guildmates to species that overlap greatly with all their guildmates. Thus, within each guild we also created a separate plot for the overlaps between a given species *i* and each of its guildmates. On each plot, we divided the points into four quadrants using the method of Steele and Torrie (1960: 410), drawing a vertical line from the median *x* value and a horizontal line from the median *y* value. We then counted the points in the upper right-hand quadrant. A random dispersion of points (no complementarity) would, on average, provide the upper right quadrant with ¼ of the total; complementarity would produce a number much less than ¼ of the total (cf. Fig. 1). Using the corner test of association (Steele and Torrie 1960: 410), we examined the plot for each guild in total, and the separate plot for each long-flowered plant species. We had complete data on too few short-flowered species to test each separately for significance.

RESULTS

Flowering phenologies

Most hummingbird-pollinated plant species at Monteverde appear to flower independently of the times at which their guildmates flower. In Table 1, numbers indicate the rank of observed overlap (Eqs. 1 and 2) relative to 100 randomly generated overlaps. Thus, values <5 indicate observed overlaps less than those generated by the null model, values >95 indicate observed overlaps greater than those generated by the random model. Although the symmetrical index (Eq. 1) and asymmetrical index (Eq. 2) generated somewhat different values, both lead to the same general conclusions. In the long-flower guild (Table 1A), only the understory epiphyte *Guzmania nicaraguensis* (visited by short-billed as well as long-billed hummingbirds) and the common giant herb *Heliconia tortuosa* flowered in patterns that, in most comparisons, minimized overlap with their guildmates. In contrast, in most comparisons four species (*Poikilacanthus macranthus,* *Alloplectus tetragonus, Drymonia rubra,* and *Malvaviscus arboreus*) each overlapped with remaining long flowers more than expected from the null model. In the short-flower guild (Table 1B), no species we examined appeared to minimize overlap with other species, whereas *Burmeistera tenuiflora* overlapped with the remaining short flowers more than expected.

No relationship existed between unusual overlaps and length of flowering season. For example, *Guzmania* and *Poikilacanthus* both had very short flowering seasons, whereas *Heliconia, Drymonia,* and *Burmeistera* all had lengthy seasons. Results from analyses incorporating the belt-transect Ericaceae data were qualitatively similar to those from analyses restricted to the data set collected on the principal study plots.

We also examined each guild for a relationship between displacement in flowering phenology and rarity, reasoning that rare species might suffer the most from interspecific competition (leading to the most unique flowering seasons) or benefit the most from facilitation (leading to the most aggregated flowering seasons—Feinsinger 1983, Rathcke 1983). We measured "uniqueness" of flowering season as the numbers reported for the Levins (1968) index in Table 1, and measured flowering density in a species as the sum of all flowers counted on the 24 monthly censuses. In the short-flower guild, no correlation existed between rank in uniqueness and rank in rarity ($r_s = -0.0018$). In the long-flower guild, however, rare species tended to have more unique flowering peaks than common ones ($r_s = .5123$, $P < .05$).

Does morphological displacement complement phenological displacement?

Morphological displacement among species with similar phenologies did not compensate for the general absence of significant divergence in flowering times (Table 2). In most plots of morphological overlap against phenological overlap, pairs with high overlap along both dimensions (upper right-hand quadrant) were not scarce relative to pairs in other quadrants, whether a guild was examined in its entirety or individual species were compared with all their guildmates. Typically (Fig. 2), morphological overlap values were independent from phenological overlap values. Two long-flowered species, *Heliconia tortuosa* and *Columnea magnifica,* actually experienced a greater number of high pairwise overlaps along both dimensions than expected by chance, whereas only one species, *Malvaviscus palmanus,* experienced a significant trade-off between phenological and morphological overlap. Because these are multiple tests, one P value of .05 (in either direction) is expected by chance.

To ensure that the absence of complementarity was not an artifact of the quadrant technique, we also calculated Spearman rank correlations between morphological and phenological overlaps for all comparisons reported in Table 2. Negative correlation coefficients would indicate a trade-off between displacement in time and displacement in morphology. Results, however, closely paralleled those reported in Table 2: most correlations were close to zero or were positive, two (*Heliconia tortuosa* and *Guzmania nicaraguensis*) were significantly positive, and none was significantly negative.

Discussion

Within a stable assemblage of plants, consistent competition for pollination may result in nonrandom patterns among the species' flowering phenologies or floral morphologies, provided that no other constraints on those traits exist (Feinsinger 1983, Waser 1983, Rathcke and Lacey 1985). Character displacement leading to decreased phenological or morphological overlap could result from either (1) natural selection within the community against phenotypes with flowering seasons or morphologies that overlap those of other guildmates (e.g., Waser 1978*a*), or (2) selective establishment in the community of species with dissimilar phenologies and morphologies (e.g., Feinsinger 1978, 1983, Waser 1978*a,* Primack 1985). Pollination in the Monteverde cloud forest is often insufficient for maximum seed set and clearly relates to plant fitness (Feinsinger et al. 1986); W. H. Busby and S. Kinsman (*personal observation*) surveyed most species listed in Table 1 and found that many flowers received fewer compatible pollen grains than the number of ovules available for fertilization. In this study, we fully expected at least the short-flower hummingbird pollination guild, which has relatively little opportunity for morphological displacement (Feinsinger et al. 1986), to demonstrate displaced flowering phenologies. We expected the long-flower guild, which has much more opportunity for morphological displacement (Feinsinger et al. 1986), to demonstrate complementarity between phenological and morphological displacement. Indeed, even phenological convergence is possible among rare species with widely different morphologies (Feinsinger 1983). Yet neither the randomization analysis of phenologies alone nor the tests for complementarity revealed the expected patterns. Furthermore, among short-flowered plants no relationship existed between rarity and phenological convergence, while among long-flowered plants increasingly rare species flowered in increasingly divergent, not convergent, patterns.

In some animal pollination guilds, failure of plants to exhibit phenological regularity has been attributed to constraints imposed by climatic seasonality (e.g., Schemske et al. 1978, Stiles 1979, Cole 1981, Motten 1986) or seasonal variation in pollinator availability (e.g., Waser 1979, Rathcke and Lacey 1985). Neither of these constraints appears to operate in the Monteverde cloud forest. Unlike second-growth tropical habitats (Colwell 1973, Feinsinger 1976, Wolf et al. 1976, Feinsinger et al. 1985) or forest canopy (Feinsinger and Colwell 1978), the cloud forest understory does not

TABLE 1. Results of phenological overlap simulations for the two guilds of hummingbird-pollinated plants in the Monteverde cloud forest, based on 2 yr of data. Values reported are the percentage of cases in which the observed overlap between a particular species' flowering phenology and that of all other guildmates was greater than that obtained when all species' phenologies were scrambled randomly in time. Values <5 indicate lower overlap of actual flowering seasons than expected under the null hypothesis of randomly placed flowering seasons, those >95 indicate greater than expected overlap.

	Data from study plots only		Data from study plots and belt transects	
Species	Proportional similarity index	Levins' (1968) index	Proportional similarity index	Levins' (1968) index
A. Flowers visited primarily by long-billed hummingbirds				
Acanthaceae				
Justicia aurea Schldl.	73	92	74	91
Poikilacanthus macranthus Lindau	94	99	95	99
Razisea spicata Oersted	44	68	44	71
Bromeliaceae				
Guzmania nicaraguensis Mez & C. F. Baker ex Mez*	3	3	4	2
Pitcairnia brittoniana Mez*	13	54	10	56
Ericaceae				
Psammisia ramiflora Klotsch	16	9	61	82
Gesneriaceae				
Alloplectus tetragonus (Oerst.) Hanst.	100	100	100	100
Capanea grandiflora (Kunth) Decne ex Pl.*	62	46	64	50
Columnea magnifica Oersted	19	20	22	24
Columnea microcalyx Hanstein	93	93	92	93
Columnea lepidocaula Hanstein	30	36	33	38
Drymonia conchocalyx Hanstein	59	80	63	80
Drymonia rubra Morton	100	100	100	100
Heliconiaceae				
Heliconia tortuosa Grigg	1	1	1	1
Lobeliaceae				
Centropogon solanifolius Benth.	63	57	64	60
Malvaceae				
Malvaviscus palmanus Pittier & Donnell-Smith	95	99	94	99
Rubiaceae				
Ravnia triflora Oerst.	89	94	89	94
Zingiberaceae				
Costus barbatus Suess.	69	81	64	76
Renealmia thyrsoidea (R. & P.) Poepp. et Endl.	94	91	95	91
B. Flowers visited primarily by short-billed hummingbirds				
Acanthaceae				
Hansteinia blepharorachis (Leonard) Durkee	29	27	40	38
Dicliptera trifurca Oersted	78	75	100	93
Bromeliaceae				
Guzmania nicaraguensis Mez & C. F. Baker ex Mez*	63	35	55	26
Pitcairnia brittoniana Mez*	78	88	85	88
Ericaceae				
Cavendishia complectans Hemsley	70	50	71	62
Cavendishia crassifolia (Benth.) Hemsley	75	84	73	74
Gonocalyx pterocarpus (Donn. Sm.) Luteyn			10	15
Satyria warscewiczii Klotsch	67	71	73	49
Gesneriaceae				
Besleria formosa Morton	59	67	94	95
Besleria princeps Hanst.	20	15	16	10
Besleria triflora (Oerst.) Hanst.	60	60	52	64
Capanea grandiflora (Kunth) Decne ex Pl.*	88	82	95	90
Gasteranthus wendlandianus (Hanst.) Wiehl.	29	18	28	18
Lobeliaceae				
Burmeistera tenuiflora Donn. Sm.	100	100	100	100

TABLE 1. Continued.

Species	Data from study plots only		Data from study plots and belt transects	
	Proportional similarity index	Levins' (1968) index	Proportional similarity index	Levins' (1968) index
Rubiaceae				
Cephaelis elata Sw.	30	28	16	19
Palicourea lasiorrachis Benth. ex Oerst.	71	77	64	70
Palicourea macrocalyx Standl.	12	8	6	6

* Denotes species (*Guzmania, Pitcairnia*) whose pollen is carried primarily by long-billed hummingbirds, but sometimes by short-billed hummingbirds as well, or species (*Capanea*) whose pollen is carried primarily by short-billed hummingbirds but also by long-billed hummingbirds.

experience seasonal influxes of migrant hummingbirds (P. Feinsinger et al., *personal observation*). The major hummingbird pollinators (*Lampornis calolaema* and *Phaethornis guy*) are nonmigratory, and the population densities vary astonishingly little over the year (P. Feinsinger, W. H. Busby, and K. G. Murray, *personal observation*). At various times of the year, bursts of flowering in canopy Ericaceae occasion sudden declines in visit frequencies of *Lampornis* to understory flowers, but these dips are of short duration and are unpredictable in timing (W. H. Busby, *personal observation*). Furthermore, we could discern no climatic constraints on flowering seasons. Both the driest and wettest seasons are characterized by intense flowering of several species from both guilds (Linhart et al., *in press*). Although there is somewhat of a lull in production of short flowers from August through October, and in long flowers from May through August (Feinsinger et al. 1986: Fig. 3), these periods are not clearly related to climatic constraints.

Phylogeny may broadly constrain flowering phenologies of cloud forest plants to certain seasons, a pattern also noted in temperate floras (Kochmer and Handel 1986). For example, Acanthaceae listed in Table 1 flower primarily from late wet season to early dry season (September–March), Gesneriaceae flower primarily from early dry season through early wet season (November–June), and Rubiaceae flower primarily from mid dry season through mid wet season (March–September). Furthermore, related species elsewhere in Costa Rica and even in Trinidad and Tobago tend to flower within the same periods (cf. Stiles 1978, 1985, Feinsinger et al. 1982). Nevertheless, within these constraints natural selection due to competition could still adjust phenologies (or morphologies) to minimize overlap (Waser 1978*a*, 1979, 1983), and selective establishment of species from a phylogenetically diverse pool could lead to a complementary set of species, regardless of phylogenetic origins (Primack 1985, Kochmer and Handel 1986). Thus phylogenetic constraints, while restricting lability in flowering phenology and morphology of particular species (cf. Kochmer and Handel 1986), cannot alone account for the absence of pattern among the phylogenetically diverse guilds examined here.

Could selection for optimal timing of fruit and seed maturation override the expected selective forces on flowering phenologies, and thus be responsible for scarcity of pattern in the latter? Rathcke and Lacey (1985) point out that timing of fruit maturation, seed dispersal, and germination may be more critical to plant fitness than timing of flowering. Murray (1986) has shown that seasonal migrations of some frugivorous birds at Monteverde affect the rate of fruit removal from plants depending on them for seed dispersal, making some seasons better than others for fruit maturation. However, although most of the plants listed in Table 1 are adapted for seed dispersal by birds (Wheelwright et al. 1984), most are dispersed by nonmigratory as well as migratory species. Hence seasonal variation in dispersal success is probably minimal in most species. Furthermore, although early wet season may be optimal with respect to germination and seedling survival in some communities (e.g., Garwood 1983), data currently available suggest that timing of flowering and fruiting are not strongly interdependent (Rathcke and Lacey 1985, Skeate 1985). Thus, strong selective forces on fruiting phenology, even if they exist, need not affect flowering phenology. Also, even if seasonal constraints on fruiting and seed dispersal affected flowering phenologies, they would not explain the absence of a complementary relationship between flowering phenology and morphology (Table 2).

Having exhausted alternative explanations for the apparent lack of expected patterns in flowering phenology and floral morphology, we must turn to the premise of the process-and-pattern argument: that competition for pollination occurs consistently within a stable assemblage of plants. We suggest that neither consistent competition nor long-term stability characterizes many plant assemblages. Although competitive mechanisms certainly exist among the plant species considered here (P. Feinsinger, W. H. Busby, and H. M. Tiebout III, *personal observation*), other work at

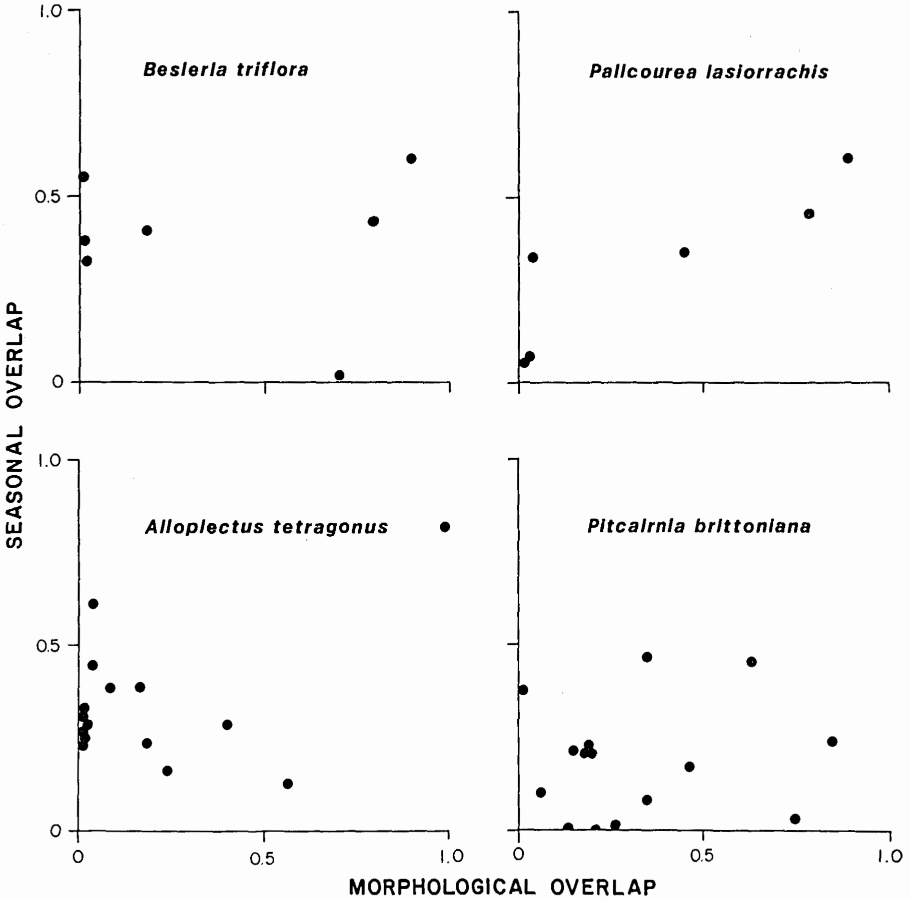

FIG. 2. Observed relationships between phenological overlap (measured with Eq. 1) and morphological overlap (Eq. 3) for four typical hummingbird-pollinated plant species from the Monteverde cloud forest. Each point represents the overlaps between the indicated species and one other species in the same guild.

Monteverde (Feinsinger et al. 1986) suggests that the expression of these mechanisms in the field may be quite sporadic. During 1982–1983, we examined the relationship between a plant's pollination success (defined as the number of conspecific, compatible pollen grains received by its stigmas) and the species composition of neighboring flowers. Among the four species examined (long-flowered *Razisea spicata* and *Drymonia rubra,* and short-flowered *Hansteinia blepharorachis* and *Besleria triflora*), we found evidence for negative density dependence only in the two short-flowered species, and even then only sporadically. *Besleria* did experience pronounced competitive effects at the ends of its flowering season, but not during its peak. The opposite was true for *Hansteinia.* Neither long-flowered species experienced negative density-dependent effects from other species during any of the three seasonal samples. In fact, one sample for each long-flowered species suggested that interspecific facilitation (Rathcke 1983, Thomson 1983), rather than competition, occurred regardless of the morphological similarity of neighbors. Thus, the reproductive consequences of flowering at the "wrong" time, or of having a morphology similar to that of neighbors, are not at all clear-cut.

In addition, the nature of interspecific interactions undoubtedly varies between years, as well as within years. Flowering phenologies of the plants we examined, like phenologies of other animal-pollinated plants (Stiles 1977, Rathcke and Lacey 1985), varied quite extensively and independently among the four years for which we now have data (Y. B. Linhart et al., *personal observation*). Thus, each year a given phenotype is likely to face a quite different array of interacting species (cf. Rathcke and Lacey 1985). Such temporally variable competitive environments permit the coexistence of species (or phenotypes) having traits that would be suboptimal in a stable environment (Chesson 1986, Chesson and Case 1986, Hubbell and Foster 1986).

Furthermore, the species composition of plant assemblages may not be sufficiently stable in time or space for competition, even if it were consistent, to sort

TABLE 2. Relationship between phenological overlap between species pairs, calculated as proportional similarity in distribution of flowering over time (Eq. 1), and morphological overlap in terms of anther placement (Eq. 3).

Species*	Number of pairs in upper-right quadrant† (high overlap on both axes)	Result of corner test
Long-flowered guild		
Acanthaceae		
Justicia aurea	3	NS
Poikilacanthus macranthus	3	NS
Razisea spicata	4	NS
Bromeliaceae		
Guzmania nicaraguensis	5	NS
Pitcairnia brittoniana	3	NS
Ericaceae		
Psammisia ramiflora	4	NS
Gesneriaceae		
Alloplectus tetragonus	4	NS
Columnea microcalyx	3	NS
Columnea magnifica	6	$P < .01$‡
Drymonia conchocalyx	3	NS
Drymonia rubra	3	NS
Heliconiaceae		
Heliconia tortuosa	6	$P < .005$‡
Lobeliaceae		
Centropogon solanifolius	3	NS
Malvaceae		
Malvaviscus palmanus	2	$P < .05$§
Rubiaceae		
Ravnia triflora	4	NS
Zingiberaceae		
Costus barbatus	4	NS
All long-flowered species pairs	29	NS
Short-flowered guild‖		
Acanthaceae		
Dicliptera trifurca	2	
Hansteinia blepharorachis	1	
Gesneriaceae		
Besleria triflora	2	
Besleria formosa	2	
Lobeliaceae		
Burmeistera tenuiflora	2	
Rubiaceae		
Cephaelis elata	2	
Palicourea lasiorrachis	2	
Palicourea macrocalyx	1	
All short-flowered species pairs	9	NS

* The list is smaller than that in Table 1 because complete morphological data could not be obtained for all species.

† Quadrants were determined by the method used for the corner test of association (Steele and Torrie 1960:410). After pairs deleted by quadrant method, total pairs for each species of long-flowered plant are 14; 6 for each short-flowered plant; 120 total long-flowered pairs; 28 total short-flowered pairs.

‡ More pairs than expected in upper right, counter to hypothesis.

§ Fewer pairs in upper right than expected.

‖ Number of pairs too few for corner test of association.

phenologies into a precise pattern. (1) Ranges of the species making up each guild do not coincide even within the Monteverde cloud forest; thus, each population interacts with an assemblage of guildmates whose species composition changes rapidly over space. (2) Davis (1986) provides evidence that rates of plant migration in eastern North America are species-specific and often very rapid in geological time, and there is no reason to expect markedly greater stability in Central American forests. Unless diffuse competition from extant species is sufficiently strong to prevent any sexual reproduction from occurring in a recent colonist population, the reshuffling of populations at any one site may simply be too rapid to allow the formation of pattern, whether by natural selection among co-occurring species, or by differential establishment success based on floral traits (see Colwell and Winkler 1984).

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