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Longevity of Individual Flowers in a Costa Rican Cloud Forest: Ecological Correlates and Phylogenetic Constraints

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ABSTRACT

The mean individual flower longevity (MFL) was determined for 110 species at Monteverde, Costa Rica. Taxonomic constraints at the family level were the most important determinant of flower longevity. Family membership explained 73 percent of the variance in floral longevity compared to 2.6 percent among genera within families. There were trends in flower longevity associated with various ecological factors hypothesized to be important: bee-pollinated species had lower MFL than hummingbird and moth-pollinated species; MFL was negatively correlated with plant size (trees < shrubs < herbs); large flowers persisted longer than small flowers; MFL was higher in species with over 50 ovules per flower than in species with few ovules. However, when correlations due to taxonomic relatedness were eliminated, none of the ecological factors had a significant effect on flower longevity. There was no difference in MFL in two climatically distinct communities surveyed. The overall mean flower longevity (2.7 days) falls midway between that of tropical lowland species (1 day) and montane species (4–8 days) and thus is consistent with global patterns described by Primack (1985).

THE LONGEVITY OF INDIVIDUAL FLOWERS has rarely been considered as part of plant life history strategy, even though it may have important effects on reproductive biology. Flower longevity (the time between anthesis and senescence of the corolla) can affect visitation by pollinators and may have genetic effects by influencing the level of inbreeding (Primack 1985). Insofar as there is a cost of maintaining a flower, it will affect the reproductive energy budget. The seasonal flowering phenology of tropical plants at the population or community level has received much attention (Daubenmire 1972; Frankie *et al.* 1974, 1983; Opler *et al.* 1980; Bawa 1983) as have descriptions of the floral biology of individual species (Gentry 1974, Webb & Bawa 1983, Koptur 1983, Hopkins 1984). The studies focusing on the phenology of individual flowers have concentrated on sex allocation and the relative timing of male and female functions (Thomson & Barrett 1981, Lloyd & Yates 1982, Devlin & Stephenson 1985, Webb & Littleton 1987). A few studies have noted floral longevity as part of other work (Arroyo *et al.* 1981, Webb & Bawa 1983, Koptur 1983, Hopkins 1984), but it has only rarely been studied systematically or seen as a potentially evolving plant character (Kerner 1895, Primack 1985, Dobkin 1987).

Primack (1985) summarized the literature on floral longevity and found several striking patterns. Temperate species tend to have flowers that persist longer than tropical species, spring wildflowers in the temperate zone persist longer than summer flowers, and plants from high elevations have longer-lived flowers than those from low elevations. In general, mean flower longevity increased in cooler and more mesic habitats. There are several possible explanations for these patterns. Flower longevity may be influenced by the probability of receiving sufficient pollinator visits. When pollinators are scarce or unpredictable (*e.g.*, due to differences in efficiency among pollinator species or unfavorable climatic conditions—Cruden 1972) there may be selection for increased floral longevity (see Kerner 1895). Similarly, under conditions of pollen limitation, species with many ovules per flower may require a longer period to achieve maximum seed set than species with few ovules to fertilize. However, selection for male function in hermaphrodite flowers may favor a protracted period of pollen donation (Harder & Thomson 1988) and diminish the importance of ovule number effects. Flower longevity may also be influenced by metabolic considerations. When transpirational costs are high (dry climates) or when energetic investment costs (Ball 1932, Bookman 1983) are low (small flowers) one would expect shorter mean floral longevity. Primack (1985) hypothesized that genetic costs may select for decreased flower longevity. Longer floral longevity will increase the number of open flowers on any given day and thus increase the probability of geitonogamous inbreeding in self-compatible species.

In many cases pollination may trigger corolla senescence. Although such a strategy seems logical and many field botanists consider pollination-induced senescence to be common, there is little published data from natural populations to support this. In controlled conditions, flowers of *Petunia hybrida* (Gilissen 1977), *Digitalis purpurea* (Stead & Moore 1979) *Rhododendron* spp. (Gori 1983), and some orchids (Arditti & Flick 1976) wilt and abscise more rapidly after pollination as compared to unpollinated controls (see also Dobkin 1987). Similar effects have been

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found in natural populations of *Lobelia cardinalis* (Devlin & Stephenson 1984) and *Lysimachia quadrifolia* (Primack 1985) and *Faramea occidentalis* (pers. obs.). Motten (1986) found decreased floral longevity after pollination in several species of temperate herbs.

In this study I report data on the floral longevity of species in two adjacent plant communities along a climatic gradient in Costa Rica. My specific predictions were as follows. 1) Following Primack's (1985) observation of increased flower longevity in cooler and more mesic habitats, I predicted greater MFL in the cloud forest species compared to the adjacent lower montane moist forest (see Study Area and Methods). Since bees are less likely to forage during periods of inclement weather than hummingbirds (Cruden 1972), I predicted that any difference in MFL due to climatic differences in the two communities would be greater for insect-pollinated species than for hummingbird-pollinated species. 2) Assuming that "getting pollinated" is the primary determinant of flower longevity, I predicted greater MFL in species having many ovules per flower, and an emphasis on female function (longer female phase in dichogamous species and greater MFL in females of dioecious species). Note, however, that this hypothesis ignores potentially important selection on male reproductive success. 3) Energetic considerations predict greater MFL in species with large flowers due to the greater investment in floral structures, all else being equal. Finally, I compared species with different pollination syndromes, growth habit, and number of simultaneously open flowers for differences in flower longevity.

STUDY AREA AND METHODS

The study was conducted near Monteverde, Costa Rica, on the western slope of the Cordillera de Tilaran. The vegetation can be divided into two distinct communities: a cloud forest along the crest of the continental divide at elevations from 1500 to 1650 meters and a drier, partially deciduous forest at the lower elevations, in and below the town of Monteverde (1400 to 1500 meters). These communities are classified as premontane wet forest and lower montane moist forest, respectively (Feinsinger 1976, after Holdridge 1967). The cloud forest community included both the elfin forest and the transitional forest communities (Lawton & Dryer 1980). The two communities studied are climatically distinct; the cloud forest is cooler and receives more precipitation than the lower montane forest. The differences are particularly apparent during the end of the dry season in April. Floristically the communities are also distinct, sharing few species, even though they may be separated by less than a kilometer. Further descriptions of the study site are given by Buskirk & Buskirk (1976), Feinsinger (1976), and Lawton & Dryer (1980).

I collected phenological data through daily censuses of marked flowers. I attempted to census every species flowering during the months of April and May 1984, but flowers of most canopy species were not accessible. Thus the sample is biased towards understory species. Flowers were marked as buds using a variety of methods. Large flowers were tagged individually with numbered jeweler's tags; for smaller-flowered species, I tagged inflorescences, and flowers were identified by coding them with small black dots of india ink on their petiole or corolla. When flowers were especially numerous, this was supplemented with a map of the inflorescence. For each flower I recorded the date of opening and the date of senescence. Senescence was defined as when the corolla had fallen off or when it could be dislodged by vigorous shaking or a light tug. There was usually little doubt about when a flower was senescent. I recorded flower longevities to the nearest day; flowers lasting less than a day were classified as one-day flowers. All censuses were made on natural, open-pollinated flowers and thus measure the realized flower longevity. If pollination-induced senescence is a general phenomenon, the observed flower longevities may be partially determined by variation in pollinator service as well as intrinsic plant "strategies."

Plants were broadly classified into three pollination classes (bees and other small insects, lepidopterans, and hummingbirds) based on observations of floral visitors, general pollination syndromes, and supplemented with data from Murray *et al.* (1987). Since all floral visitors are not necessarily pollinators, this classification must be regarded as only an approximation of the true pollination categories. In addition, I classified plants (trees, shrubs, herbs, and lianas) by habit, flower size, ovule number, and the number of other open flowers on the same plant. Flower size was based on the maximum length or width of the corolla and was divided into five categories (0.5, 1, 2, 4, and 4+ cm). I counted ovules on a subset of species and used the median count from five flowers. When published information was available, or when families had a constant ovule number (*e.g.,* Lauraceae always have one ovule), this information was also included. The total number of open flowers on a plant was estimated visually and categorized as 0–5, 5–15, 15–50, 50–100, or 100+ flowers.

The basic observation for all statistical analyses is the mean flower longevity for the species. Although numerous observations for each species were made, species are represented by a single datum. I was unable to transform these data to normality, so all statistical tests were done with the non-parametric Kruskall-Wallis (K-W) test (Procedure NPAR1WAY, SAS Institute). Nested analysis of variance (SAS procedure GLM) was used to estimate the variance components for families and genera. Since the maximum longevity of unpollinated flowers may more accurately indicate underlying plant strategies when pollinator-induced senescence is important, I also performed the statistical tests on the maximum individual flower

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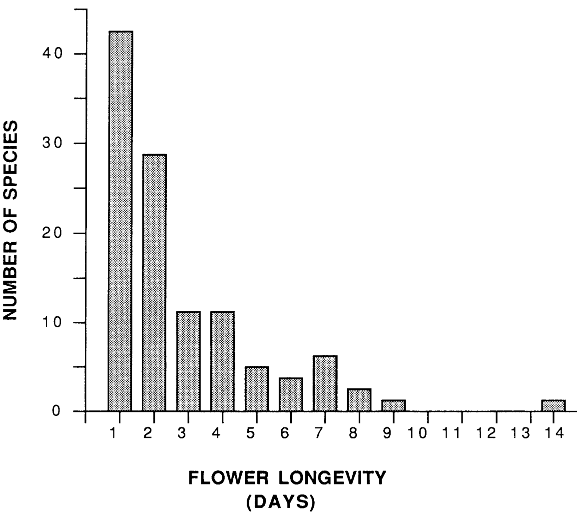

FIGURE 1. The distribution of individual flower longevities at Monteverde, Costa Rica.

longevity within each species. There is no way of knowing how many of these flowers were pollinated; the maximum flower longevity is the closest approximation to unpollinated flowers in the absence of data from bagged inflorescences.

RESULTS

I determined the flower longevity for 110 species, representing 35 families and 71 genera (Appendix). Sixty–nine of these were cloud forest species and 36 were from the lower, moist forest community. There was little overlap among habitats—only five species occurred in both communities. A total of 1963 flowers were censused. The mean flower longevity (MFL) for all species combined was 2.73 days; MFL ranged from 1 day (in 43 species) to 14 days in *Bomarea hirtella* (Fig. 1).

Table 1 shows descriptive statistics for flower longevity classified by some potentially important ecological variables. Using this approach several trends are apparent. Hummingbird-pollinated flowers persist longer than bee– or lepidopteran-pollinated species (3.8 days vs 2.0–2.8 days; Table 1). Within hummingbird-pollinated species, there was no significant difference in MFL among species pollinated by long-billed hummingbirds (4.66 days) and short-billed hummingbirds (2.91 days, K-W = 1.99, ns) following the classification of Murray *et al.* (1987). The effect of pollinator type on MFL differed in the two communities. There was no difference among pollinators in the moist forest species (K-W = 0.79; df = 2, Table 1), whereas in the cloud forest community there were highly significant differences (K-W = 14.73; df = 2; $P = 0.0006$). Among the cloud forest species, hummingbird-pollinated plants had greater MFL than plants pollinated by bees and lepidopterans (Table 1). Bird-pollinated species had higher MFL in the cloud forest than in the lower montane moist forest, and the MFL of bee-pollinated species was lower in the cloud forest, a pattern opposite to predictions.

The growth habit of a species also appears to have an effect on flower longevity (Table 1). Trees had short flower longevities, averaging less than two days, followed in order by shrubs, herbs, and lianas. Since only three species of lianas were included, their long MFL may be an artifact. Flowers larger than four cm persisted over twice as long as species with smaller flowers (4.8 vs 2 days, Table 1). Female function appeared to be an important determinant of MFL. Species with over 50 ovules per flower had MFL twice as long as fewer ovuled species (Table 1). In the three dioecious species, females had flowers lasting on average three days longer than flowers of males (Appendix 1). Similarly, in all eight dichogamous species for which I have data on the relative lengths of female and male phases ($P < 0.01$, signs test) the female phase was longer than the male phase. However, I do not know that the stigmas were receptive throughout this period and these observations come from only two families (Appendix 1). Mean flower longevity was heterogeneous across plants with varying numbers of other open flowers (K-W chisq = 16.6; $P = 0.003$), but the highest MFL was for intermediate sizes. Finally, there was no significant difference in MFL in the two communities surveyed (2.78 vs 2.47 days, Table 1).

TAXONOMIC CONSTRAINTS:—By far the most important factor influencing flower longevity was taxonomic affiliation (Table 2). Family means explained 73.2 percent of the variation in flower longevity compared to only 2.6 percent among genera within families. Since many families were represented by only a single species, I repeated the analysis using only common families (families with five or more species sampled). Among common families, family means explained 80.6 percent of the variance in MFL vs 6.0 percent among genera within families. The Gesneriaceae and Lobeliaceae were common families with consistently long flower longevities while the Melastomataceae and Rubiaceae tended to have much shorter-lived flowers (Table 2).

Although these data are the result of a nearly complete survey of understory species blooming during April and May, families are not evenly represented in these data. Nineteen families were represented by only a single species, while in the most common family, Rubiaceae, 24 species were surveyed. This non-random distribution among families may account for some of the apparent differences in flower longevity (Table 1). If nothing else, the strong family effect shows that species within a family are not independent observations, which leads to excessively liberal

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TABLE 1. *Effects of various ecological factors on mean flower longevity (MFL, days) and maximum flower longevity. Results using all species; correlations due to taxonomic effects are not controlled.* N *refers to the number of species surveyed in each category. The non-parametric Kruskal-Wallis (K-W) test was used since the data were not normally distributed.*

	N	Mean flower longevity	Range	Average maximum flower longevity		
Community:						
Cloud forest	69	2.77	1.0–14.0	3.64		
Moist forest	36	2.47	1.0–8.0	3.72		
		K-W = 1.06		K-W = 0.64		
					MFL	
					Cloud	Moist
Pollinator class:						
Bees	56	1.99	1.0–8.0	2.77	1.8	2.6
Lepidopterans	9	2.82	1.0–6.6	4.22	2.2	3.6
Hummingbirds	34	3.80	1.0–14.0	5.00	4.3	2.5
		K-W = 10.26**		K-W = 11.22**	K-W = 14.73***	K-W = 0.79
Habit:						
Lianas	4	4.57	4.0–7.0	5.25		
Herbs	21	4.01	1.0–14.0	5.28		
Shrubs	62	2.68	1.0–8.0	3.16		
Trees	23	1.94	1.0–6.2	3.04		
		K-W = 8.42*		K-W = 6.57		
Flower size (cm.):						
0.5–1.0	38	2.18	1.0–8.0	3.10		
1.0–2.0	42	2.03	1.0–4.6	2.98		
2.0–4.0	12	2.79	1.0–6.7	3.92		
4.0+	18	4.78	1.0–14.0	6.00		
		K-W = 10.21*		K-W = 8.13*		
Number of ovules:						
1–5	21	1.60	1.0–8.0	2.23		
5–50	6	1.98	1.2–3.5	2.66		
50+	13	3.40	1.0–7.0	4.61		
		K-W = 8.57*		K-W = 7.04*		
Number of open flowers:						
0–5	8	1.45	1.0–2.0	2.00		
5–15	14	5.69	1.0–14.0	7.14		
15–50	26	2.47	1.0–7.0	3.19		
50–100	26	2.48	1.0–8.0	3.76		
100+	36	1.92	1.0–7.4	2.81		
		K-W = 16.6**		K-W = 16.0**		

* = $P < 0.05$ ** = $P < 0.01$ *** = $P < 0.001$.

statistical tests. Using family membership as a covariate, (analyzing the deviations from family means), is not appropriate since many of the ecological effects are confounded with taxonomic relationships. For example, all of the Lobeliaceae in this survey were hummingbird-pollinated herbs with large flowers; all of the Melastomataceae were bee-pollinated species with small flowers; all of the Acanthaceae were hummingbird-pollinated. One can not tell if differences in flower longevity are due to ecological factors or taxonomic constraints.

Instead, I collapsed these data to one observation per family using the mean floral longevity. In cases where a family contained several different pollination systems or growth habits I computed separate means for each level of the classification variable of interest. For example, to look at the effect of pollination system, I took the mean for all species in a family that shared the same type of pollinator. Since all the Lobeliaceae in this data set were hummingbird-pollinated, those six species were treated as only one evolutionarily independent observation. On the other hand, since the Rubiaceae contained species with several different pollination systems, the bee, moth, and hummingbird-pollinated Rubiaceae were treated as three independent observations. The same was done for the other

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TABLE 2. *Mean flower longevity (MFL, days), by family, for species at Monteverde, Costa Rica. Family membership explained 73% of the variance in mean flower longevity. Families are listed in order of increasing MFL.*

Family	Number of species	Mean flower longevity	Range
Caprifolaceae	1	1.00	—
Fabaceae	1	1.00	—
Lamiaceae	1	1.00	—
Symplocaceae	1	1.10	—
Melastomataceae	9	1.23	1.00–1.75
Costaceae	2	1.25	1.00–1.50
Myrtaceae	3	1.27	1.10–1.50
Meliaceae	1	1.30	—
Verbenaceae	1	1.35	—
Malvaceae	3	1.37	1.00–2.00
Rubiaceae	24	1.37	1.00–3.00
Heliconiaceae	2	1.50	1.00–2.00
Ericaceae	3	1.83	1.30–2.80
Myrsinaceae	1	2.00	—
Phytolacaceae	1	2.00	—
Acanthaceae	5	2.14	1.11–2.88
Solanaceae	14	2.16	1.00–4.10
Erythroxalaceae	1	2.17	—
Boraginaceae	3	2.17	1.00–4.16
Dilleniaceae	2	2.34	1.80–2.89
Sapindaceae	1	2.44	—
Polygalaceae	1	2.60	—
Loranthaceae	1	3.12	—
Gentianaceae	2	3.50	1.00–6.00
Clethraceae	1	3.50	—
Onagraceae	1	3.90	—
Lauraceae	1	4.00	—
Clusiaceae	1	4.20	3.90–4.50
Apocynaceae	1	4.31	—
Gesneriaceae	10	4.50	2.00–7.00
Nyctaginaceae	2	5.60	2.90–8.00
Flacourtiaceae	1	6.20	—
Asclepiadaceae	1	6.61	—
Lobeliaceae	6	7.00	5.00–9.40
Amaryllidaceae	1	14.00	—

variables, using the mean value of flower longevity for each combination of family and the classification variable of interest. In contrast to using the raw values, this technique errs on the conservative side; since it is conceivable, for example, that the several bird-pollinated Lobeliaceae each independently experienced selection for long MFL and might therefore be evolutionarily independent observations.

Using only one observation per family, none of the ecological variables had a statistically significant effect on flower longevity (Table 3). The probability of the null hypothesis being true was greater than 0.05 in all cases. This may reflect true equivalence of the ecological factors or it may just reflect the low power resulting from reduced sample sizes. The rank order of flower longevities is similar to that in the raw data, and many of these trends coincide with predicted differences in flower longevity. As above, bee-pollinated flowers had the shortest mean longevity (2.35 days), 40 percent shorter than hummingbird and lepidopteran pollinated flowers (3.8 days). However, the difference between hummingbird and lepidopteran flowers was much reduced. Once again trees had shorter MFL than shrubs and herbs (2.2 vs 3.0, 3.3 days), and large flowers persisted longer than small flowers (4.2 vs 2.5 days). Again, there was a non-significant trend for increasing flower longevity with ovule number and cloud forest species averaged slightly longer than species from the lower montane moist forest (Table 3).

Using the maximum flower longevity instead of MFL (on the assumption that it represents the longevity of unpollinated flowers) did not change the statistical conclusions for any test (Tables 1, 3). The ecological trends followed those for MFL, but again they could not be distinguished from zero when taxonomic effects were controlled.

DISCUSSION

These data are consistent with the global patterns of floral longevity described by Primack (1985). The overall mean floral longevity of 2.7 days in this cloud forest community is intermediate between tropical lowland species (one day flowers) and montane species (4–8 days). However, differences among habitats were not distinguishable in the two adjacent communities in this more local survey. The ecological differences between the communities are great enough to alter the floristic composition, but apparently did not influence MFL.

A major result of this study is the strong effect of taxonomic affiliation on MFL. Primack shows that several families may have different MFL in different environments (tropical vs temperate) but he does not explicitly test the importance of phylogenetic history. It is clear from the present study that, at least within a local area, family membership may be the most important determinant of flower longevity. The fact that most of the variation in MFL occurred among families rather than among genera or species suggests that phylogenetic constraints at the family level may be important and may limit the evolution of MFL. Kochmer and Handel (1986) found similar phylogenetic constraints on the seasonal flowering phenology of various temperate plant species.

The general problem of controlling phylogenetic effects in a comparative survey of this sort is difficult and there is no completely satisfactory solution. Felsenstein (1985) made great progress when he outlined a method of weighting each comparison by the time since divergence of the taxa. However, his method requires a complete phylogeny of the group, which in a large survey is usually not available. Instead we must usually be satisfied with crude approximations to put upper and lower bounds on the

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TABLE 3. *Mean and maximum flower longevity associated with ecological factors. Taxonomic effects are controlled by using the mean MFL for each family × character combination. None of the Kruskal-Wallis (K-W) tests were significant at* $P < 0.05$.

	N	Mean flower longevity	MFL range	Average maximum flower longevity	MFL	
					Cloud	Moist
Habitat:						
Cloud forest	20	3.21	1.0–14.0	4.42		
Moist forest	19	2.93	1.0–6.6	4.08		
		K-W = 0.11		K-W = 0.15		
Pollinator class:						
Bees	24	2.35	1.0–5.6	3.38	2.2	2.2
Hummingbird	11	3.81	1.0–14.0	4.69	2.1	4.2
Lepidopteran	4	3.72	1.8–6.6	4.95	4.2	2.8
		K-W = 2.03		K-W = 1.42	K-W = 2.90	K-W = 0.79
Habit:						
Lianas	2	3.85	5.3–5.3	4.83		
Herbs	14	3.33	1.0–14.0	4.26		
Shrubs	16	3.00	1.0–6.0	4.03		
Trees	15	2.24	1.0–6.2	3.66		
		K-W = 3.84		K-W = 1.42		
Flower size (cm):						
0.5–1.0	17	2.77	1.0–6.6	4.17		
1.0–2.0	15	2.19	1.0–4.2	3.17		
2.0–4.0	6	2.74	1.2–5.2	3.75		
4.0+	10	4.24	1.0–14.0	5.01		
		K-W = 1.06		K-W = 0.52		
Number of ovules:						
1–5	8	1.72	1.0–7.7	2.23		
5–50	4	1.94	1.0–3.5	2.50		
50+	9	3.38	1.0–6.6	4.50		
		K-W = 4.20		K-W = 3.04		
Number of open flowers:						
0–5	4	1.36	1.0–1.7	1.75		
5–15	7	5.40	1.0–14.0	6.46		
15–50	12	2.62	1.0–6.6	3.34		
50–100	10	3.31	1.0–6.2	5.21		
100+	17	2.28	1.1–5.1	3.50		
		K-W = 6.38		K-W = 7.17		

significance tests. The analysis of raw data is a liberal test due to the automatic correlations among closely related taxa, and the comparison of family means errs on the conservative side due to potential independent selection for MFL.

Most of my *a priori* hypotheses were not supported statistically by these data. I could detect no difference in MFL between the two communities surveyed, even though they show distinct climatic differences in the late dry season when these data were collected. Furthermore, the interaction between community and pollinator type was opposite to predictions. I found no evidence to support the inbreeding avoidance hypothesis. However, this hypothesis only predicts decreased MFL in self-compatible species, and data on compatibility were not available for the species I studied. The inclusion of an unknown number of self-incompatible species in my sample may explain the lack of pattern with respect to the number of open flowers.

Several recent papers have argued that the evolution of floral displays may be more closely dependent on pollen donation (male reproductive success) than female reproductive success (Sutherland & Delph 1984, Stanton *et al.* 1986). In this study, the greater duration of both the female flowers in dioecious species and the female phase in dichogamous species, and the trends for increasing MFL in species with many ovules are consistent with the hypothesis that the evolution of flower longevity in these species resulted from maximization of female reproductive

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success. Evidence for pollination-induced senescence would also support the hypothesis that flower longevity is influenced primarily by female function.

The trends of increased MFL in large, hummingbird-pollinated flowers of herbs and shrubs suggest possible factors that may influence the evolution of individual flower phenologies at Monteverde. However, the strong taxonomic constraints at the family level imply that MFL is not an evolutionarily labile trait in these communities. The observed patterns probably result from historical selection pressures which may or may not correlate with the current ecological patterns of flower longevity.

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APPENDIX 1. *Mean (MFL, days) and maximum observed flower longevity for 110 species at Monteverde, Costa Rica. Also shown are classifications by community ("Com": C = cloud forest, M = moist forest, B = both), pollination syndrome ("Pol": B = bee, H = hummingbird, L = lepidopteran), habit ("Hab.": T = tree, S = shrub, H = herb, V = liana), flower size ("Size": 1 = 0–1, 2 = 1–2, 3 = 2–4, 4 = 4+ cm), number of open flowers ("Nfl": 1 = 0–5, 2 = 5–15, 3 = 15–50, 4 = 50–100, 5 = 100+) and number of ovules ("Ov": 1 = 1–5, 2 = 5–50, 3 = 50+). Lengths of male and female phases in dioecious or dichogamous flowers are shown when available. Species names were determined as closely as possible from collections in the herbarium at the Monteverde Cloud Forest Reserve and from discussions with resident botanists.*

Species	*N*	MFL	Max	Com	Pol	Hab	Size	Nfl	Ov	
Acanthaceae										
Dicliptera iopus	9	1.1	2	C	H	S	3	1	1	
Hansteinia blepharorachis	34	2.9	4	C	H	S	3	2	1	
Justicia aurea	1	2.0	2	C	H	S	2	1	1	
Justicia oerstedii	65	2.0	5	B	H	H	3	1	1	
Razisea spicata	34	2.7	5	C	H	S	4	2	1	
Amaryllidaceae										
Bomarea hirtella	6	14.0	14	C	H	H	4	2	—	
Apocynaceae										
Tabernaemontana sp.	22	4.3	5	M	L	T	3	4	—	
Asclepiadaceae										
Asclepias curassavica	35	6.6	8	M	L	H	1	3	3	
Boraginaceae										
Cordia spinosa	42	1.0	1	C	—	S	1	4	1	
Cordia sp.	11	1.4	2	C	—	S	1	4	1	
Tournefortia sp.	25	4.2	6	C	—	S	1	4	—	
Caprifoliaceae										
Vibernum costaricana	39	1.0	2	M	B	S	1	3	1	
Clethraceae										
Clethra lanata	10	3.5	4	M	B	T	1	5	2	
Clusiaceae										
Tovomita nicaraguensis	9	4.2	6	M	B	S	2	4	1	(♂3.9; ♀4.5)
Costaceae										
Costus wilsonii	5	1.0	1	B	H	H	4	1	—	
Costus montanus	4	1.5	2	C	H	H	4	1	—	
Dilleniaceae										
Sarauia veraguensis	9	2.9	4	C	B	T	2	4	3	
Sarauia sp.	20	1.8	2	C	B	T	2	4	—	
Ericaceae										
Cavendishia crassifolia	10	1.4	3	C	H	T	3	5	3	
Satyria warzewiczii	14	1.3	3	C	H	T	3	5	—	
Vaccinium sp.	8	2.8	3	C	B	S	1	5	3	
Erythroxalaceae										
Erythroxalon amplum	23	2.2	3	M	—	S	1	5	1	
Flacourtiaceae										
Xylossma qhichensis	22	6.2	14	M	—	T	1	4	—	
Gentianaceae										
Symbolanthus pulcherrimus	4	6.0	8	C	H	S	4	2	—	
Unknown sp.	7	1.0	1	C	B	H	2	3	—	
Gesneriaceae										
Besleria formosa	26	2.6	5	C	H	S	2	4	—	
Besleria solanoides	13	4.1	5	M	H	S	2	4	3	
Besleria triflora	14	4.6	5	C	H	S	2	4	3	
Besleria sp.	14	2.0	3	C	H	S	2	3	—	
Capanea grandiflora	14	4.9	6	C	H	V	3	3	—	(♂1.8; ♀3.4)

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APPENDIX 1. *Continued.*

Species	*N*	MFL	Max	Com	Pol	Hab	Size	Nfl	Ov	
Columnea magnifica	4	7.0	7	C	H	V	4	2	—	(♂2.3; ♀4.0)
Drymonia conchocalyx	3	4.0	4	C	H	V	3	2	—	(♂2.0; ♀2.5)
Kohleria strigosa	7	6.7	9	C	H	S	3	2	—	(♂2.0; ♀4.7)
Monopyle maxonii	9	4.3	5	C	B	H	2	2	—	
Solanofera calycosa	7	4.9	6	C	H	S	4	3	—	
Heliconiaceae										
Heliconia monteverdensis	18	2.0	2	C	H	H	4	1	1	
Heliconia tortuosa	24	1.0	1	B	H	H	4	1	1	
Lamiaceae										
Salvia tiliaefolia	32	1.0	1	C	B	H	1	3	1	
Lauraceae										
Ocotea sp.	1	4.0	4	C	B	S	1	5	1	
Leguminosae										
Erythrina lanceolata	5	1.0	1	M	H	T	4	4	—	
Lobeliaceae										
Burmeistera cyclostgmata	6	8.0	8	C	H	H	4	2	—	(♂2.0; ♀6.0)
Burmeistera parviflora	8	9.4	13	C	H	H	4	2	—	(♂3.0; ♀7.0)
Burmeistera sp.	5	5.6	7	C	H	H	4	2	—	
Centropogon costaricae	5	7.0	10	C	H	H	4	3	—	(♂2.5; ♀4.5)
Centropogon solanifolius	8	7.0	14	C	H	H	4	2	3	(♂3.3; ♀5.0)
Lobelia laxiflora	9	5.0	6	M	H	H	4	3	3	
Loranthaceae										
Gaiadendron punctatum	16	3.1	4	C	B	S	2	5	—	
Malvaceae										
Hampia appendiculata	14	1.1	2	M	B	T	2	5	—	
Malvaviscus palmanus	1	2.0	2	C	H	S	4	3	1	
Pavonia rosea	10	1.0	1	M	B	H	2	1	1	
Melastomataceae										
Arthrostema ciliata	14	1.0	1	M	B	H	4	2	3	
Conostegia oerstediana	8	1.8	2	C	B	T	2	5	—	
Conostegia xalapensis	20	1.6	3	M	B	S	2	5	—	
Conostegia sp.	15	1.0	1	C	B	T	2	5	—	
Miconia sp. 1	12	1.0	1	C	B	T	1	5	—	
Miconia sp. 2	16	1.0	1	C	B	T	1	5	—	
Monochetum floribundum	12	1.0	1	C	B	S	2	3	—	
Monochetum linearifolium	5	1.0	2	C	B	S	2	3	—	
Unknown sp.	20	1.7	2	C	B	S	1	5	—	
Meliaceae										
Cedrella tonduzii	23	1.3	3	M	B	T	1	5	—	
Myrsinaceae										
Ardissia conpressa	19	2.0	5	M	B	T	2	5	1	
Myrtaceae										
Myrcia splendens	26	1.1	1	M	B	T	2	5	—	
Unknown sp. 1	27	1.2	2	M	B	T	2	5	2	
Unknown sp. 2	16	1.5	2	M	B	T	2	5	—	
Nyctaginaceae										
Neea amplifolia	58	5.2	8	M	B	S	1	5	1	(♂2.9; ♀7.4)
Torrubia costaricana	133	6.1	10	M	B	S	1	4	1	(♂4.1; ♀8.0)
Onagraceae										
Fuchsia jumenzii	18	3.9	5	C	B	S	2	3	3	
Phytolacaceae										
Phytolacca rivinoides	21	2.0	5	C	B	H	1	5	—	

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APPENDIX 1. *Continued.*

Species	*N*	MFL	Max	Com	Pol	Hab	Size	Nfl	Ov
Polygalaceae									
Monnina sylvatica	34	2.6	4	B	B	H	1	5	1
Rubiaceae									
Cephaelis axillaris	11	1.0	1	C	—	S	1	3	—
Cephaelis elata	12	1.0	1	C	H	S	1	5	—
Coussarea sp.	39	1.0	1	M	L	S	3	5	1
Faramea occidentalis	39	2.6	8	M	L	S	2	4	1
Gonzolagunia rosea	23	1.0	1	C	B	T	2	5	2
Guettarda poassana	31	1.7	3	C	L	T	2	5	1
Hamelia patens	10	1.5	2	M	H	S	3	4	3
Hoffmania sp. 1	29	1.3	2	C	B	S	1	4	1
Hoffmania sp. 2	5	1.0	1	M	B	S	1	4	1
Hoffmania sp. 3	13	1.0	1	C	B	S	1	4	1
Palicourea galleotiana	24	1.0	2	M	H	S	2	4	—
Palicourea laziorachis	18	1.0	2	C	H	S	2	5	1
Palicourea macrocalyx	18	1.9	3	C	B	S	2	4	1
Palicourea montivaga	15	1.0	1	C	—	S	2	5	—
Psychotria sp. 1	11	1.0	1	C	—	S	1	4	—
Psychotria sp. 2	19	1.0	2	M	—	S	1	4	—
Psychotria sp. 3	19	1.5	2	M	—	S	1	4	—
Psychotria sp. 4	18	1.2	2	C	B	S	1	3	—
Psychotria accuminata	11	1.0	1	M	B	S	1	3	—
Psychotria grandicarpa	15	1.0	1	C	B	S	1	3	1
Psychotria tonduzii	13	1.5	2	C	—	S	1	3	—
Rondeletia calycosa	22	2.6	4	C	L	S	2	5	—
Rondeletia torresii	18	3.0	3	C	L	S	2	5	—
Xerococcus congestus	7	1.0	1	C	B	S	1	3	3
Sapindaceae									
Matayba apetella	9	2.4	4	C	B	T	2	5	—
Solanaceae									
Acnistus arborescens	22	3.1	4	M	B	T	2	5	2
Cestrum sp.	50	2.3	3	C	L	S	3	5	—
Cestrum fragile	17	1.3	3	C	L	S	2	5	—
Lycianthes sp.	15	1.6	2	C	B	S	2	4	—
Lycianthes synanthera	21	1.8	3	M	B	S	2	4	—
Solanum sp. 1	24	1.9	3	M	B	S	1	3	—
Solanum sp. 2	6	3.5	4	M	B	S	1	3	—
Solanum americanum	8	1.3	2	C	B	S	1	3	2
Solanum fasioloides	8	1.0	1	C	B	S	2	2	—
Solanum hispidum	17	2.4	3	C	B	S	2	5	3
Solanum nudum	5	1.8	2	M	B	S	1	3	—
Solanum siparunoides	15	2.4	4	C	B	V	2	3	—
Solanum trizygum	9	4.1	5	M	B	S	1	3	—
Witheringia cocoloboides	19	1.8	3	C	B	S	2	4	2
Symplocaceae									
Symplocos limoncillo	19	1.1	2	M	B	T	2	5	1
Verbenaceae									
Verbena sp.	42	1.4	2	B	B	H	1	3	—

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