

DISTURBANCE AND PREDICTABILITY OF FLOWERING PATTERNS IN BIRD-POLLINATED CLOUD FOREST PLANTS¹

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Abstract. The distribution and flowering patterns of hummingbird-pollinated plants were compared from July 1981 to June 1983 in three patch types in cloud forest at Monteverde, Costa Rica. Study plots were: (1) four recent, large (1100–2500 m²) disturbances (“cutovers”) produced by cutting vegetation, (2) six recent, smaller (200–600 m²) disturbances caused by treefalls, and (3) four plots (1600–1800 m²) of canopied forest. Based on published literature dealing with communities that characterize different regimes of disturbance, we tested one assumption and two hypotheses. *Assumption:* Plant species composition differs among the three patch types. *Hypothesis 1:* Phenotypic specialization by plants for co-evolved interactions with hummingbirds will be lowest in large gaps, highest in forest, and intermediate in treefalls. *Hypothesis 2:* Predictability of flowering phenologies and nectar production will be lowest in large gaps, highest in forest, intermediate in treefalls.

Neither the assumption nor the hypotheses were supported by the results. The patch mosaic in this cloud forest was not associated with major differences in species composition of bird-pollinated plants. Most species studied were self-compatible. Most abundant in cutovers were species with long corollas, relatively specialized for attracting long-billed hummingbirds. Species with short corollas, which can be visited by many hummingbird species and some insects, were most abundant in treefalls and forest. Variation in phenological patterns showed no consistent trends among patch types. Predictability of flower and nectar production tended to be greatest in treefalls, which are foci of concentrated flowering activity by all species. Discrepancies between our results and previous studies can be ascribed to two facts. (1) Much of the literature dealing with ecological consequences of disturbance has dealt with large-scale anthropogenic disturbances such as old fields of the eastern USA, whereas we studied smaller, natural, or quasi-natural disturbances. (2) Studies of forest disturbance have focused on the tree layer, whereas we studied the understory herbs, shrubs, and epiphytes. Natural disturbance usually involves death and replacement of one or more trees, whereas individuals of other life forms may persist through the disturbance.

Key words: cloud forest; community structure; Costa Rica; disturbance; flowering; gaps; hummingbird-pollinated species; nectar production; patch dynamics; succession; treefalls.

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INTRODUCTION

To understand community organization, ecologists are paying increasing attention to the effects of spatial patchiness upon species composition and biotic interactions. This patchiness requires analysis from several perspectives. Initial studies often determine the causes of patchiness and analyze the distributions of individual species and species assemblages. These studies are then followed by analyses of changes in species composition. Finally, to understand what controls these species dynamics, attempts must be made to relate spatio-temporal patterns in species composition to specific traits and interactions of the species involved.

Many natural landscapes are irregular mosaics of patches, generated by disturbances varying in time of occurrence, severity, and extent (Aubréville 1938, Jones 1945, Watt 1947, Whittaker and Levin 1977, Connell 1978, Garwood et al. 1979, Whitmore 1982, Finegan 1984, Sousa 1984a, Pickett and White 1985). Species compositions often differ according to patch size and age. These differences are usually ascribed to traits of the component species that result in differential abilities to invade some patches or to persist in others. For example, many studies suggest that patches produced by extensive and severe disturbances provide new habitats whose physical conditions change unpredictably and rapidly (Caborn 1973, Lee 1978, Whitmore 1984, Collins et al. 1985). Into such areas arrive species whose traits often differ greatly from those of pre-disturbance species (Baker and Stebbins 1965, MacArthur and Wilson 1967, Whitmore 1984, Sousa 1984a). Such colonizing species are expected to be able to move about the landscape quickly and thus to be somewhat independent of specific mutualisms. In addition, because communities in these habitats have a low level of organization, they have low resistance to invasion by new species (Harper 1977). Therefore, in such postdisturbance sites, species composition changes rapidly, and species interactions and other features of biotic constancy (e.g., population size, phenology, flower and fruit production) may be highly variable.

In contrast, patches that have been undisturbed for some time include some species that have persisted for long periods. Population dynamics and reproductive success of these species are affected more strongly by biotic factors than by physical factors (MacArthur and Wilson 1967, Margalef 1968, Odum 1969). In fact, these species are expected to be relatively co-evolved, i.e., dependent upon other specific species for exploitation (e.g., Brown 1984, 1985), pollination, and fruit dispersal (Baker and Stebbins 1965, Parrish and Bazzaz 1979). Because of this interdependence, biotic conditions are expected to be relatively more constant than in recently disturbed habitats (Odum 1969). The theoretical formulation of these ideas and partial empirical support for them has led to wide acceptance in ecology of the existence of significant contrasts in species

composition and community organization between recently disturbed or "early successional" habitats and relatively undisturbed or "mature" habitats. Yet a need exists for (1) studies that will test specific predictions derived from these generalizations, and (2) tests of those ideas in a variety of disturbance mosaics, natural and anthropogenic.

The present study was conducted in montane cloud forest at Monteverde, Costa Rica. Montane wet forests of the Neotropics provide good examples of mosaic patterns of disturbance generated, in part, by their steep slopes, shallow waterlogged soils, and periodic earthquakes. In these forests, openings range from the small, relatively frequent gaps created by falling limbs or trees to less frequent, but much larger, landslides (Whitmore 1978, Garwood et al. 1979, Denslow 1980, Lawton and Dryer 1980, Lawton 1982). We tested (1) the assumption that the various patches making up the forest mosaic have different species compositions, and (2) predictions about several biological features of component species. We examined a subset of plant species and their hummingbird pollinators (see also Feinsinger et al. 1986). Hummingbirds and bird-pollinated plants are a common feature of montane ecosystems in the Neotropics, where hummingbirds are reliable pollinators because they can forage under the adverse conditions (often windy, cool and rainy) common to those elevations (Cruden 1972, Colwell 1973, Wolf et al. 1976, Terborgh 1977). As a result, many plant species are adapted to hummingbird pollination; for example, in the Monteverde cloud forest and nearby areas, almost 100 of some 600+ angiosperm species described to date are pollinated at least in part by hummingbirds. We consider these plants and their pollinators to be suitable for the empirical tests we performed, as there is no a priori reason to believe that the plant-hummingbird component is qualitatively different from other components of such a community (Stiles 1975, 1981, Feinsinger 1976, 1977, 1978, Feinsinger and Colwell 1978, Linhart and Feinsinger 1980, Schemske and Brokaw 1981, Kodric-Brown et al. 1984, Feinsinger et al. 1986).

OBJECTIVES AND PREDICTIONS

We analyzed three patch types of the habitat mosaic in the Monteverde cloud forest: (1) Forest, or undisturbed patches ($\approx 1/2$ ha) of canopied forest; (2) Cutovers, or recent, relatively large ($\approx 1/2$ ha) disturbances; and (3) Treefalls, or recent, smaller ($< 1/20$ ha) disturbances). All are described in detail below. Two different gap sizes were chosen because they represent examples of the two most common causes of disturbance in this forest: large gaps are usually produced by landslides, small gaps by treefalls. In addition, they tend to represent two different intensities of disturbance: larger gaps usually involve more intense disturbance, while smaller treefall gaps involve less severe disturbance

and provide an intermediate situation between large gaps and forest. Elsewhere, species composition and dynamics have been shown to vary both with gap size and amount of disturbance. We used these patch types to test one assumption and two general hypotheses with associated predictions.

Assumption: Different patches of the mosaic have different species compositions.

This assumption is based on extensive evidence gathered in other communities. The evidence for differential species composition between patches of different sizes and ages comes from studies of temperate forests (Jones 1945, Watt 1947, Runkle 1985), herbaceous communities (Watt 1947, Platt 1975, Grubb 1977), tropical forests (Aubréville 1938, Richards 1952, Hartshorn 1978, Denslow 1980, 1985, Whitmore 1982, 1984, Brokaw 1985a, b), and marine communities (Lubchenco and Menge 1978, Lubchenco and Gaines 1981, Sousa 1984b).

Hypothesis 1: Phenotypic specialization by plant species for co-evolved interactions with hummingbirds should be least in large disturbances and greatest in forest. Specifically, morphological traits and features of the breeding system are more "opportunistic" or "generalized" in large disturbances to ensure some reproduction, more "specialized" in forest, and intermediate in treefalls.

Prediction 1a: In cutovers we expect species whose flowers have relatively short (10–28 mm) corollas, which can be probed by many hummingbird species and some insect flower visitors, whereas species in forest are expected to have flowers with longer (> 30 mm) and more decurved corollas, which permit visits by only a few hummingbirds with appropriately shaped bills.

Prediction 1b: The proportion of self-compatibility will be highest among species in cutovers, lowest in forest, and intermediate in treefalls.

Contrasting attributes of early-arriving, "generalist" species and long-term persistent "specialist" species are discussed by Stebbins (1958), Baker (1965, 1974), Baker and Stebbins (1965), MacArthur and Wilson (1967), Margalef (1968), and Odum (1969). Some comparisons of "generalists" and "specialists" specifically involve flowering, pollination, and breeding systems (e.g., Stebbins 1958, Baker 1965, 1974, Baker and Stebbins 1965, Moldenke 1975, Wissel 1977, Ruiz Zapata and Arroyo 1978, Stiles 1978a, Lloyd 1979, Opler et al. 1980). They report that generalist, early-colonizing species often have relatively simple flowers that (1) can be visited by a wide variety of pollinators, (2) are self-compatible, and (3) are self-pollinated. In contrast, species of more stable, late successional habitats, where pollinators are thought to be available more predictably, (1) have flowers with more complex shapes or structures that restrict visits to specialized pollinators carrying relatively homogeneous pollen loads, and (2) are often self-incompatible.

Hypothesis 2: There will be greater temporal varia-

tion (i.e., less predictability) in the flowering phenology of species in large disturbances than in forest, with species in treefalls being intermediate.

Prediction 2a: Month-to-month variation in number of flowers for all species will decrease directionally from cutovers, to treefalls, to forest.

Prediction 2b: Variation in diversity of species in flower will show the same trend.

Prediction 2c: Temporal variation in total amounts of nectar resource available to pollinators will show the same trend.

Compared to forest understory, disturbed areas typically have high insolation, substantial diurnal and sometimes seasonal fluctuations in insolation, substantial fluctuation in air and soil temperatures, and sometimes significant nutrient influx (Caborn 1973, Lee 1978, Denslow 1980, Whitmore 1984, Collins et al. 1985). All these factors are known to affect flowering intensities (Barkham 1980, Collins et al. 1985, Pitelka et al. 1985). Therefore, both temporal and spatial heterogeneity in physical conditions can be expected to affect the flowering patterns of resident species. In recent disturbances there may be greater seasonal fluctuations in flower numbers and more rapid turnovers of species in flower than in undisturbed habitats. These expectations reflect, in general, discussions of the consequences of disturbance in Margalef (1968, 1969) and Odum (1969), *inter alia*. Elaborations and demonstrations of these expectations (Gómez-Pompa et al. 1976, Connell and Slatyer 1977, Bazzaz and Pickett 1980, Swaine and Hall 1983, Brokaw 1985a, b) have contributed to their general acceptance. In the context of plant-animal interactions, plants as food resources have been shown to be more variable and less predictable in recent, large disturbances than in later successional habitats both for insect herbivores (Southwood 1977, Brown and Southwood 1983, Brown 1984), and for insect pollinators (Parrish and Bazzaz 1979).

METHODS

Study site

The Monteverde region (10°18' N, 84°49' W) is at 1300–1800 m elevation in the Cordillera de Tilarán, Costa Rica. A steep climatic gradient exists between the lower elevations on the Pacific slope and the continental divide, a distance of ≈ 3 km, with the result that "life zones" (Holdridge 1967) are compressed, changing rapidly with elevation. Prevailing northeast winds help create an almost continuous cloud cover and heavy mist in the Monteverde Cloud Forest Reserve, which straddles the Continental Divide. Periodic high winds result in tree and limb falls. Vegetation and climate are described in detail elsewhere (Lawton 1980, Lawton and Dryer 1980).

The cloud forest merges with elfin forest on the crest of the Continental Divide. The formations in which we worked are termed Leeward Cloud Forest, Wind-

ward Cloud Forest, and Swamp Forest (Lawton and Dryer 1980). Canopy height is 12–20 m, with a very irregular shrub layer at 3–6 m and, in places with adequate light, an herb layer at 0–1 m. Vines and epiphytes are common at all levels.

We studied three types of patches:

1) Large, recent disturbances produced most commonly by landslides. We could not include landslides as sites of intensive research in our study, because of their physical instability. Therefore, we established four experimental plots (labeled "cutovers") of a size comparable to small landslides (1155, 1768, 1993, and 2442 m²). The vegetation in the area of these plots had been cut annually to a height of 20–40 cm for ≈ 10 yr prior to 1974. It was allowed to regrow 1974–1980, then was cut to <10 cm in January 1980, and recut (to ≈ 30 cm) in July 1980 and January 1981. In their physiognomy, these cutovers resembled the sides of a landslide, whose vegetation has been almost completely stripped off to a height of <1 m, but where in most places the soil is still in place. The resemblance of cutovers to landslides was enhanced by the presence of a denuded cattle trail (not included in the area reported above), down the center of each cutover. We also surveyed monthly the vegetation and hummingbirds on one nearby landslide to see whether its species composition resembled that of the cutovers. Our cutovers were very different from the typical anthropogenic disturbances in that they had not been plowed, burned, or grazed. Thus, while cutovers do not mimic landslides, they do resemble them in several critical characteristics (including area, species composition, and approximate intensity of disturbance).

2) Small, recent disturbances, typically produced by falls of single trees or by two to three trees joined by lianas, were termed "treefalls." They usually consist of a matrix of broken and tangled branches from the fallen tree and from the shrubs and herb layers below. We studied six of these gaps formed 1–3 yr prior to the onset of our study. Sizes of these treefalls were 132, 267, 423, 466, and 544 m².

3) Undisturbed forest, consisting of patches of closed-canopy forest with no treefalls during at least 50 yr, was designated as "forest." Our subjective estimate was based on the absence of undecomposed tree trunks on the forest floor, the presence of a relatively closed canopy produced by large trees, and estimates of frequencies of treefalls at Monteverde (Murray 1986). We chose four such plots, of sizes comparable to the cutovers (1600, 1850, 1905, and 1925 m²).

Field techniques

We studied plant species of the herb and shrub layers, and epiphytes up to 10 m above the forest floor. Except for the small, subcanopy tree *Symplocos tribracteata*, no trees are specialized for bird pollination at Monteverde. Canopy epiphytes were not included, as they, along with their pollinators, appear to comprise a sys-

tem somewhat differentiated from that of the clearings and forest understory (Feinsinger and Colwell 1978).

We surveyed the hummingbird-visited plants flowering in all 14 study plots from 1 July 1981 through 15 June 1983. During year 1 (1981–1982), surveys were made monthly. During year 2 (1982–1983), these same plots were surveyed fortnightly, once at the beginning and once in the middle of each month. During each survey, specific trails were followed in each plot, and the numbers of flowering plants and flowers for each species were recorded. In cutovers and forest, the trails were 5–10 m apart, running parallel to one another along the length of these plots. Each treefall contained a trail along the periphery of the plot, and one or more trails through the center. Distances between trails were small enough that all plants could be seen. Censuses were done simultaneously by several people and were usually completed in 1 d.

To determine the amount of nectar produced by the species studied, we recorded, for all species, (1) the number of days that flowers remained open, and (2) nectar production. Length of flower life was determined by counting the days between first opening of flowers and abscission. Nectar production was measured with microcapillary tubes using flowers covered with fine-mesh bags that prevented pollinator visitation. Sucrose content was measured with a refractometer, and the value obtained was converted to joules (Bolten et al. 1979).

Data analysis

Format.—At Monteverde, as in most neotropical sites, hummingbirds tend to fit into a few categories of bill sizes, body sizes, and associated foraging behaviors (Feinsinger and Colwell 1978, Stiles 1981, 1985, Feinsinger 1983, Feinsinger et al. 1986). Some hummingbirds with fairly large bodies (6–> 12 g at Monteverde) and relatively large, often decurved bills (≥ 28 mm) feed primarily at medium to long corolla (≥ 30 mm) flowers. Other species, with small bodies (2.6–6 g at Monteverde) and short bills (≤ 25 mm at Monteverde), often feed at short-corolla flowers adapted for bird pollination, but some also feed at flowers with long corollas by piercing the base of the corollas to reach the nectaries, and some feed at flowers adapted for insect pollination whenever the nectar is plentiful and easily available. Because of this differential usage of plant species adapted for hummingbird pollination, the plants were partitioned into three subsets: "Long" = species with long (>30 mm) corollas, predominantly pollinated by long-billed hummingbirds; "Short" = species with short (<30 mm) corollas, predominantly pollinated by short-billed hummingbirds; and "Insect" = species that are mainly insect pollinated but commonly visited by short-billed hummingbirds. The bird-pollinated subset included the long + short corolla species. The short-billed bird + insect-visited subset included short-corolla + insect species.

To detect differences among patch types with respect to specific pollination systems, many analyses were performed on subsets of the plant species (e.g., long or short). To allow for comparisons between years 1 and 2, data were analyzed separately for each year. To detect overall patterns, data for the years 1 and 2 were combined. In all preceding analyses, only the first-of-the-month data were used. Finally, the fortnightly data from year 2 only were analyzed using the changes in floral composition. To determine whether variation among patch types exceeded variation within patch types, analyses were performed with individual plots as units. To compare patch types, data for all plots within each patch type were summed. All analyses testing specific predictions used one-tailed tests. Other analyses used two-tailed tests.

Calculations performed.—To test the assumption that species compositions differ among patch types more than within patch types, we calculated (1) species frequency, (2) proportional similarity, and (3) coefficient of community.

Species frequency.—Relative abundance of flowers in each species was determined within the subsets noted above.

Proportional similarity.—Similarity of plots and patch types was evaluated with the proportional similarity index: $PS = 1 - 0.5 \sum |P_a - P_b| = \sum \min(P_a \text{ or } P_b)$, where P_x is the frequency of flowers of a particular species in plot or patch type x (Whittaker 1975).

To determine whether differences among patch types were significant, PS was first calculated between all pairs of plots in all three habitats, for each monthly or fortnightly survey. Then, for each survey, we combined all plots in a given patch type and compared patch types for the full set of plant species. Friedman's test, SPSS subprogram NONPAR Friedman (Hull and Nie 1981:230), was used to test the null hypothesis of equality of numbers of flowering plants per species in plots (1) within and (2) between patch types. Then, we compared the mean PS between patch type pairs. Mean PS between two patch types (e.g., cutover and forest) consisted of the average of all PS between pairs of individual plots of these two patch types (e.g., one plot in cutover and one in forest).

Coefficient of community.—We also made interhabitat comparisons with the Coefficient of Community (Whittaker 1975) using only the presence or absence of flowering species, in the same subsets of plant species used in PS above. A comparison of these results with proportional similarity indices permits us to detect whether interhabitat differences at the resource (i.e., flowers per species) level agree with differences at the taxonomic (i.e., flowering species) level.

To test Hypothesis 1, that morphological traits and other features of the reproductive biology were increasingly specialized from cutover to forest, flower sizes and breeding systems were compared in the three hab-

itats. Corolla length was determined by measuring the distance from the nectaries at the base of the corolla to the opening where a bird could insert its bill. Incompatibility relations were examined by performing controlled pollinations on most species. Details of these studies will be reported elsewhere by J. H. Beach.

To test Hypothesis 2, that predictability in (a) flowering phenologies and (b) resource availability increases from cutover to forest, phenologies (using the number of flowers per species) were determined from monthly censuses, and resource availability was calculated using length of flower life and nectar production. Then, we calculated (1) monthly (or fortnightly in year 2) turnover rates, (2) diversity of species in flower, and (3) month-to-month variation in overall production of flowers and nectar.

Turnover Rates measure the change in species composition of flowers from one survey to the next. The values can be used to measure changes in resource availability and the relative predictability of these changes. These rates are expressed as the turnover rate $TR = 1 - PS$, where PS is the proportional similarity of the flowering species in one given plot during two successive surveys. Note that this is different from the use of PS described above. Turnover rate was calculated for each plot of the three patch types and for the total habitat data (i.e., all plots within a given habitat) as well.

Turnover rates were used to analyze changes in the three patch types as follows. First, rates within and among habitats were compared, to determine whether intrahabitat heterogeneity was less than interhabitat variability. Then, to test Prediction 2a, we compared both (1) magnitude and (2) variation of rate in the three habitats. We predicted that both magnitude and variation would be greatest in cutovers, smallest in forests, intermediate in treefalls. Magnitude of TR between plots within patch types and between patch types was tested with Friedman's test. Variation in TR was tested to determine whether survey-to-survey changes were regular, and therefore predictable, or irregular and unpredictable. Variation between patch types was analyzed (following transformations, as necessary) in two ways: (1) The jackknife procedure (Sokal and Rohlf 1981) was used on the statistic $U = \ln(s_1/s_2)$ to test the equality of variances s_1 and s_2 of turnover rates in different habitats. (2) The homogeneity of variances in the three habitats was tested by Cochran's cv test, the Bartlett-Box F test, and the F_{\max} test in the same sets of turnover rates as the jackknife procedure above. Finally, to see whether rates changed in concern in different habitats, i.e., if month-to-month fluctuations in resource availability showed similar temporal patterns in the three habitats, Pearson product-moment correlations between habitats were calculated, following tests for normality.

Species diversity.—Another important aspect of hummingbird-flower communities is predictability in

diversity of resources available. We predicted that species diversity of flowers should show the greatest month-to-month variability in cutovers and least in forest (Prediction 2b). Species diversity was calculated using Simpson's (1949) index D , $D = 1 - \sum n_i(n_i - 1) / N(N - 1)$ where n_i is the number of individuals in the i th species and N is total number of all species (Pielou 1969, Poole 1974).

Diversity indices based on numbers of flowers per species per subset (i.e., $L + S$, L , etc.) were calculated for every survey in every plot. Because plots differed in area, and diversity is known to vary with area, interplot comparisons must be interpreted cautiously. Pearson product-moment correlation coefficients were calculated between diversity and plot area separately for each patch type. We also calculated temporal variation in diversity within plots. For each plot, the mean values and the coefficients of variation of the diversity indices for years 1 and 2 were calculated. Friedman's test was used to test the null hypothesis that all plots within a habitat type have equal diversity. We then compared this variation, averaged for all plots within a patch type, between the three patch types. For this comparison, the Kruskal-Wallis one-way ANOVA was performed on the coefficients of variation of the diversity indices.

Flower and nectar production.—To flower visitors, the attractiveness of a given area depends both on the total energy reward and the distribution of this reward among flowers. From Hypothesis 2 we predicted that both individual "packages" of reward (flowers) and total reward (energy in nectar) will vary most in cutovers and least in forest (Prediction 2c). Flower and energy production per plot and per habitat were calculated for years 1 and 2 separately for long-, then short-corolla species and the long + short subset with the addition of the insect-pollinated species *Gonzalagunia rosea*. This species was included because it is very common in cutovers, produces numerous flowers, and is frequently visited by hummingbirds (P. Feinsinger, *personal observation*). The numbers of flowers, and the available energy per plot and per habitat, were calculated for each monthly survey. Energy density (joules per square metre) was calculated for each plot and each habitat. Energy densities of the three patch types were compared by Friedman's test. Variability in total flower production and in energy production were also compared using the jackknife test (Sokal and Rohlf 1981).

RESULTS

Test of assumption of differences in species composition

Species compositions were very similar in the three patch types, and there were almost equal numbers of long-corolla (21) and short-corolla (17) species in the study plots (Table 1). Clearly, the assumption is not supported by the results.

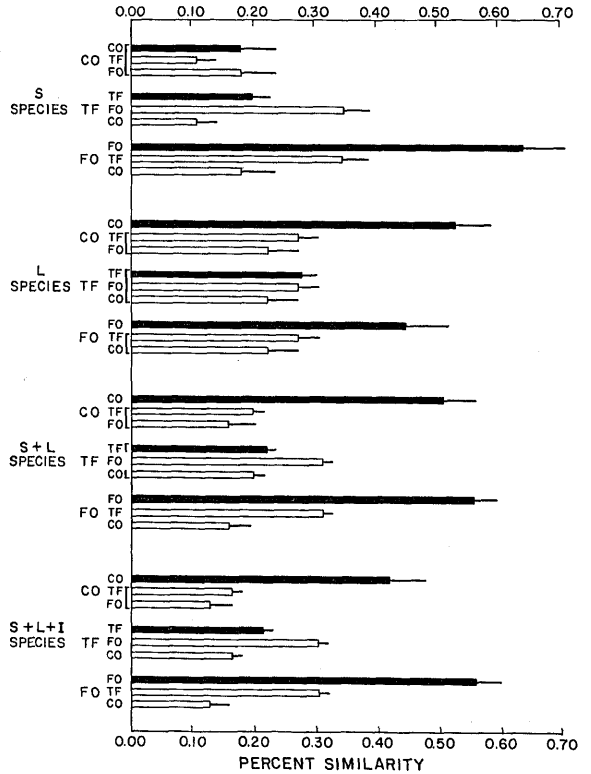


FIG. 1. Similarities of species in flower between plots in each of three patch types averaged over 2 yr (July 1981–June 1983) at Monteverde, Costa Rica. The similarities are expressed as mean values of Percent Similarity, with 95% confidence intervals shown as narrow lines extending to right of bars. Each mean value consists of mean of all individual similarity indices between pairs of plots of any two given patch types. The comparisons involve all species studied including those with long corollas (L), those with short corollas (S), and those with insect-adapted (I) flowers. The first set of bars involves S species only, the next set involves L species only, and the other sets involve combinations of species. Each group of bars involves three two-way comparisons. The first one consists of plots within cutovers (CO) compared to one another, then plots in CO compared to plots in treefalls (TF), then plots in CO compared to plots in forest (FO). For clarity, the within-patch-type plot comparisons are always shown as solid bars. In all cases, the assumption is that plots within patch type are more similar to one another than plots in two different habitats. Results of Friedman's test for the 2 yr combined are summarized by brackets to the right of habitat symbols. Within any subset, any two (or three) indices joined by a bracket are not significantly different from one another. If two patch types (e.g., CO and FO) are not significantly different from one another, but the intermediate (TF) is, this is indicated by a break in the bracket.

As noted above, we also assumed implicitly that a given patch type is homogeneous enough that plots are representative of that patch type; that is, variability among plots within a patch type is lower than variability among patch types. In Fig. 1, we summarize comparisons of PS within and among patch types. The implicit assumption of habitat homogeneity held true for plots in cutovers and forest, but not treefalls. Re-

TABLE 1. Hummingbird-visited species found in experimental plots at Monteverde, Costa Rica and their characteristics.

Family	Subset*	Flower life (d)†	Nectar energy (J/d)‡	Number of flowering months in patch types in 1982-1983		
				Cut-overs	Tree-falls	For-est
Acanthaceae						
<i>Dicliptera trifurca</i> Oersted	Short	1	61.3	7	3	1
<i>Hansteinia blepharorachis</i> (Leonard) Durkee	Short	2	10.2	10§	10	9
<i>Justicia aurea</i> Schldl.	Long	3	49.7	5	2	2
<i>Poikilacanthus macranthus</i> Lindau	Long	4	29.0	1	3	3
<i>Razisea spicata</i> Oersted	Long	2	27.3	7	6	5
Amaryllidaceae						
<i>Bomarea caldasii</i> (H.B.K.) Asch. & Graebner	Long	12	17.3	2§	0	0
Bromeliaceae						
<i>Guzmania nicaraguensis</i> Mez. & C. F. Baker	Long	1	68.8	1§	1	2
<i>Pitcairnia brittoniana</i> Mez.	Long	1	223.2	5§	4	4
<i>Tillandsia insignis</i> (E. Morr.) Sm. & Pittier	Short	1	20.1	2	1	0
Costaceae						
<i>Costus barbatus</i> Suess.	Long	1	148.4	7§	4	7
<i>Renealmia thyrsoides</i> (R. & P.) Poepp et Endl.	Long	1	162.5	0§	3	0
Ericaceae						
<i>Cavendishia complectans</i> Hemsley	Short	1	69.7	2§	3	5
<i>Cavendishia crassifolia</i> (Benth.) Hemsley	Short	1	115.4	0§	3	2
<i>Psammisia ramiflora</i> Klotsch.	Long	3	64.9	4§	6	3
<i>Satyria warszewiczii</i> Klotsch.	Short	1	30.5	2	2	0
<i>Vaccinium posanum</i> Donn. Sm.	Insect	1	38.6	0	1	0
Gesneriaceae						
<i>Alloplectus tetragonus</i> (Oerst.) Hanst.	Long	5	101.0	11§	12	9
<i>Besleria triflora</i> (Oerst.) Hanst.	Short	4	28.3	5§	10	11
<i>Besleria formosa</i> Morton	Short	3	40.4	0	7	3
<i>Besleria princeps</i> Hanst.	Insect	2		0	0	3
<i>Capanea grandiflora</i> (Kunth) Decne. ex Pl.	Long	3	274.3	0§	3	1
<i>Columnnea microcalyx</i> Hanst.	Long	6	10.4	5§	7	3
<i>Columnnea magnifica</i> Oersted.	Long	6	38.5	2§	8	6
<i>Columnnea lepidocaula</i> Hanst.	Long	7	9.8	0	5	1
<i>Columnnea</i> sp.	Short	4		0	0	1
<i>Drymonia conchocalyx</i> Hanst.	Long	2	174.2	8§	7	10
<i>Drymonia rubra</i> Morton	Long	3	169.9	9§	8	10
<i>Gasteranthus wendlandianus</i> (Hanst.) Wiehl.	Short	5	34.2	2§	3	1
Heliconiaceae						
<i>Heliconia tortuosa</i> Grigg	Long	1	462.6	12§	10	3
Labiatae						
<i>Salvia longimarginata</i> Briq.	Insect	1		0¶	5	0
Lobeliaceae						
<i>Burmeistera cyclostigmata</i> Donn. Sm.	Short	8	33.6	7§	11	7
<i>Burmeistera tenuifolia</i> Donn. Sm.	Short	8	33.6	4§	12	2
<i>Burmeistera microphylla</i> Donn. Sm.	Insect	8		0	2	0
<i>Centropogon solanifolius</i> Benth.	Long	7	42.7	11§	5	2
Loranthaceae						
<i>Gaiadendron punctatum</i> (R. & P.) G. Don.	Short	1?	52.4	0	1	0
Malvaceae						
<i>Malvaviscus palmanus</i> Pittier & Donn. Sm.	Long	3	64.6	12§	11	7
Rubiaceae						
<i>Cephaelis elata</i> Sw.	Short	1	47.7	1	10	11
<i>Gonzalagunia rosea</i> Standl.	Insect	1	18.8	12	0	0
<i>Palicourea macrocalyx</i> Standl.	Short	1	36.0	0	5	3
<i>Palicourea</i> sp.	Short	1	29.8	0	1	0
<i>Palicourea lasiorrhachis</i> Benth. ex. Oerst.	Short	1	22.9	2§	3	6
<i>Ravnia triflora</i> Oerst.	Long	7	6.7	2	5	4
Symplocaceae						
<i>Symplocos tribracteata</i> Almeda	Long	2	51.5	0	0	2

sults using the Coefficient of Community were similar. In contrast to patterns in cutovers and forests, treefall plots were so heterogeneous that they resembled forest plots significantly more than they resembled one another. Plots within forest were significantly more homogeneous and treefalls more heterogeneous than plots within cutovers. Analyses based on data of year 1 only (12 observations) or year 2 only (24 observations) are not shown, but were similar to each other and to the results for the two years combined.

Comparisons were also done for subsets of flower species. Results (Fig. 1) indicate that insect-pollinated species (primarily *Gonzalagunia* and *Salvia*), found mostly in cutovers, had little effect on the results. Once again, treefall plots resembled forest plots more than they resembled one another; the difference was significant in all comparisons except that involving long-flowered species. Comparisons among patch types show some important distinctions between the long- and short-flowered species. Cutovers were most homogeneous in terms of long species and least homogeneous in the short species; forest plots were most homogeneous in terms of short species, and in terms of all species combined.

Test of hypothesis that species in large disturbances are more opportunistic

The predictions associated with this hypothesis were not borne out. In this study, species were considered opportunistic if (1) they had short corollas, or (2) they were self-compatible. Both short- and long-corolla species were common in all habitats (Table 1). In addition, on the true landslide, 15 of 23 species recorded had long corollas (Table 1). In fact, long-corolla species contributed the majority of nectar resources in all habitats, and their proportional contribution was greatest in cutovers and the landslide (see Table 5). Most species, regardless of habitat, were self-compatible excepting the Rubiaceae, all of which were self-incompatible (J. H. Beach, *personal observation*).

Test of hypothesis that constancy in flowering phenologies and nectar production is associated with habitat type

None of the predictions was supported.

Variation in species composition of flowers (Prediction 2a)

Turnover rates were predicted to be highest in cutovers and lowest in forests. This was not borne out

(Fig. 2). Analyses for years 1 and 2 together showed no significant differences between habitats in long + short + insect, long + short, or short species; for long species only, cutovers had the lowest turnover rates and forests the highest. The difference was very pronounced ($P = .006$) in the direction opposite to the prediction; thus H_0 cannot be rejected. Data from the fortnightly surveys of year 2 showed a similar pattern. Turnovers for individual plots were analyzed separately and together for years 1 and 2; the null hypothesis (that there are not significant differences among plots within habitats) was borne out in 42 of the 48 comparisons made.

Contrary to predictions, variance in turnover rates was not highest in cutovers or lowest in forest (Fig. 2, Table 2). In addition, tests using Cochran's C , Bartlett's F , and F_{\max} to test homogeneity of variances also suggested the absence of a consistent pattern: for years 1 and 2 combined, the null hypothesis of no difference between patch types was accepted in 7 of 12 tests. Turnovers within subsets of long- and short-flowered species were not correlated significantly among patch types. Forests and treefalls were significantly correlated when most (long + short) or all (long + short + insect) species were considered (Table 3).

Changes in species diversity (Prediction 2b)

Variation in species diversity was not highest in cutovers or lowest in forest plots. Mean diversities were correlated significantly with area in cutovers (for the long + short + insect set, $r = 0.929$, $P = .035$), but not in treefalls ($r = 0.259$, $P = .310$) or forest ($r = 0.142$, $P = .429$).

Spatial and temporal diversity of species in flower varied tremendously (Appendix). In all plots, diversities were higher for long than for short species but the cvs were higher for short than for long species. The heavy blooming of insect-pollinated species, which occurred predominantly in the cutovers, accounted for these fluctuations. Thus, the diversity of the cutovers could be very low while the availability of flowers and nectar was actually exceptionally high. The cv of diversity was not significantly different among patch types.

Variation in Flower and Energy Production (Prediction 2c)

The variation in availability of flowers and energy was seldom greatest in cutovers and least in forest (Table 4). When all nectar-producing species (that is long + short + *Gonzalagunia*) were considered, pairwise com-

* Subset indicates whether a hummingbird-pollinated species has a long or short corolla or whether it is primarily insect pollinated.

† Flower life indicates the time a flower stays open before wilting.

‡ See Methods: Field Techniques for explanation of methodology of nectar determination.

§ These species were also found on a nearby landslide.

|| Nectar production not determined.

¶ Flowered in cutovers in year 1.

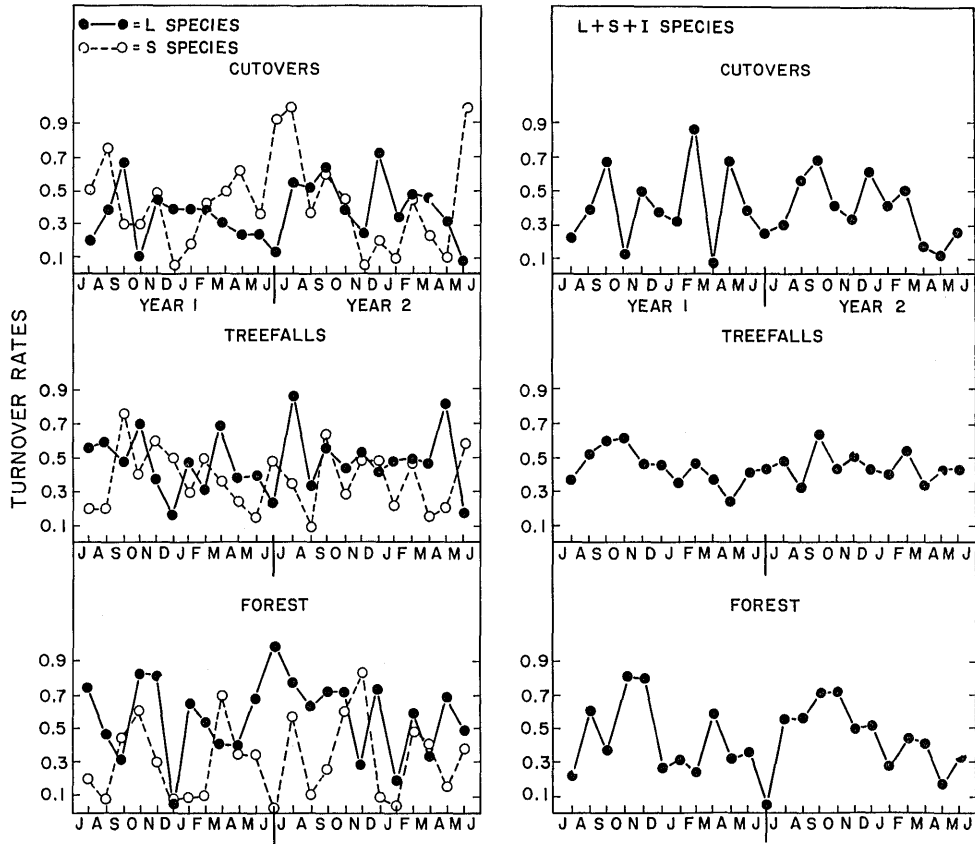


FIG. 2. Monthly variation in turnover rates of species in flower in cutover plots (CO), treefalls (TF), and forest plots (FO) in the cloud forest of Monteverde, Costa Rica. Year 1 is July 1981 to June 1982 and year 2 is July 1982 to June 1983. Turnover rates are shown separately for species with long corollas (L) and short corollas (S), and for all species studied (L + S + I). Differences in turnover rates between patch types are not significant for L + S + I species or for S species, but are significant for L species ($P < .006$). Variances of turnover rates are similar in CO and FO, and both patch types are significantly more variable than TF.

parisons of patch types showed very different patterns, depending on whether they were being compared with respect to variability of (a) total flowers present or (b) total energy available.

There were marked differences between patch types in flower production, energy production, density of flowers, and concentration of energy per plot (Table 5). Forest plots were by far the least floriferous and the least productive areas. In all patch types, long species produced the majority of the energy available to hummingbirds. Flowering was heavier in year 2 than in year 1.

DISCUSSION

Interhabitat comparisons of species composition

Disturbances in the cloud forest at Monteverde produce a mosaic of gaps of different sizes amid a canopied forest. The lack of canopy trees in the disturbed areas permits a greater light influx (Chazdon and Fetcher

1984) and more variable moisture and temperature conditions (Caborn 1973, Lee 1978, Denslow 1980, Collins et al. 1985). Different intensities of soil disturbance associated with tree uprooting or landslides also contribute to differences among patches (Richards 1952, Garwood et al. 1979). Despite differences in appearance and physical conditions, the patch types we studied showed no major differences in species composition (Table 1). Of the species we studied, the only species that were distributed differentially among patch types were as follows: (1) cutovers: *Bomarea caldasii* occurred only on cutovers and landslides; *Gonzalagunia* was characteristic of landslides, and of abandoned second-growth pastures at slightly lower elevations. *Centropogon*, *Dicliptera*, and *Justicia* were also found primarily in cutovers. (2) treefalls: one flowering individual each of *Vaccinium poasanum*, *Burmeistera microphylla*, and *Gaiadendron* was found there. At Monteverde, all are typically canopy epiphytes that periodically end up in treefalls created by their host

TABLE 2. Comparison of variances in turnover rates of flowering between pairs of patch types at Monteverde. Data from years 1 and 2 were analyzed using the jackknife procedure (Sokal and Rohlf 1981:795). t is given in parentheses for each comparison.

Data sets†	Pair of patch types‡ compared		
	CO/FO	CO/TF	FO/TF
S	CO = FO(1.07)	CO > TF(2.24)	FO = TF(1.28)
L	CO = FO(-1.36)	CO = TF(-0.13)	FO = TF(1.37)
L + S	CO = FO(-0.14)	CO > TF(3.39)*	FO > TF(3.64)*
L + S + I	CO = FO(0.04)	CO > TF(4.02)*	FO > TF(3.60)*

* $P < .05$. Critical value: $t = 2.07$ for $df = 22$.

† S = short-corolla flowers; L = long-corolla flowers; I = insect-pollinated flowers.

‡ Patch types are cutovers (CO), treefalls (TF), and forest (FO).

tree. *Palicourea* sp. was too uncommon to determine its habitat preference. *Renalmia*, found throughout the herb-shrub layer of the forest, flowered only in treefalls. (3) forest: *Symplocos* was the lone species we found restricted to the forest. Except for *Gonzalagunia*, *Justicia*, and *Dicliptera*, these species were relatively minor components of the flora of the three patch types studied.

The lack of major differences in flowering species composition among patch types occurs in many other understory plant species as well. A recent survey of insect-pollinated species in our plots revealed few differences in composition between treefalls and forests, although the cutovers did have several species characteristic of large second-growth areas (Y. B. Linhart, *personal observation*). This absence of pronounced differences is probably associated with (1) the fact that landslides and treefalls are so common that the forest is extremely dynamic; consequently, the boundaries between recent disturbances and canopied forest can change quickly. (2) Small disturbances have a small area-to-circumference ratio, which allows for rapid encroachment of plants from the forest boundary (Souza 1984a); as a result, treefalls often resemble adjacent forests in species composition and flowering patterns more than they resemble one another (Fig. 1). (3) The soil in treefalls can be turned over substantially but is seldom removed. As a result, its seed bank and the roots and stems of many understory plants remain in situ and regrowth can occur rapidly. We do not know in detail how landslides would compare with cutovers. The one landslide we surveyed contained many of the same major species found in the cutovers we studied (Table 1).

Because interhabitat differences in physical conditions within tropical forests are so commonly reflected in differential species compositions (e.g., Richards 1952, Denslow 1980, Whitmore 1982, Brokaw 1985a, b), we wondered whether the Monteverde cloud forest is unusual in that the uniformly cool, moist conditions produce no sharp differences in environmental conditions among habitats, specifically no excessive insolation or drought stress in recent disturbances. In May 1983,

several of the authors visited the La Selva Biological Station, a lowland site with a more marked differentiation between wet and dry seasons and a well-studied flora (Janzen 1983). We surveyed the distribution of hummingbird-pollinated species over natural disturbances (treefalls), man-made disturbances, and canopied forest. The relative frequency of natural disturbance is comparable between La Selva (Brokaw 1985b, D. and D. Clark, *personal communication*) and Monteverde. The terrain is much less steep at La Selva, hence landslides do not occur. Anthropogenic, repeatedly disturbed, "cutover" areas exist, but they are markedly different from those at Monteverde in (1) being larger (often 100×20 m or more), and (2) having been maintained as pastures or in second growth much longer. In terms of the bird-visited species, these "permanent" second-growth areas were characterized by dense, extensive stands of *Heliconia* spp. and many *Hamelia patens* shrubs, that were absent from forest. Species compositions of hummingbird-visited flowers were very similar in forest understory and natural disturbances (primarily treefalls), however. As at Monteverde, flower densities were higher in gaps than in understory. Our observations were confirmed by conversations with D. and D. Clark and D. Levey (*personal communication*), who had also noted that at La Selva the species compositions of shrubs, herbs, and epiphytes in natural disturbances differ little from those in forests. In March 1985, P. Feinsinger (*personal ob-*

TABLE 3. Pearson correlation coefficients r , and their significance levels for comparisons between turnover rates in species composition of flowers for pairs of patch types.†

	All species		Bird-pollinated species	
	FO	TF	FO	TF
CO	0.0434 $P = .422$	0.1157 $P = .299$	0.3608* $P = .045$	0.2449 $P = .130$
FO	...	0.3924* $P = .032$...	0.4633* $P = .013$

* $P < .05$.

† Patch types: CO = cutovers, TF = treefalls, and FO = forest plots.

TABLE 4. Comparison of variability in flower production and energy production in cutovers (CO), treefalls (TF), and forests (FO) at Monteverde. Years 1 and 2 were combined.

Characteristic	Species subset†	Pairs of patch types compared‡		
		CO/FO	CO/TF	FO/TF
No. flowers	S species	CO < FO*	CO = TF	FO = TF
	L species	CO = FO	CO > TF*	FO > TF*
	L + S + <i>Gonza.</i>	CO = FO	CO > TF*	FO > TF**
Energy (J)	S species	CO < FO*	CO = TF	FO = TF
	L species	CO < FO*	CO = TF	FO = TF
	L + S + <i>Gonza.</i>	CO > FO**	CO > TF**	FO = TF

* $P \leq .05$, ** $P \leq .01$.

† Data were analyzed separately for subsets of species, i.e., long-corolla (L) or short-corolla (S) species or L + S + *Gonzalagunia*, the most common insect-pollinated species.

‡ Variability was compared using the jackknife test (Sokal and Rohlf 1981:795).

ervation) also surveyed a cloud forest physiognomically similar to that of Monteverde, at Estación Biológica Coréa, Los Farallones de Cali, Colombia (elevation 2300–2600 m): there, bird-visited flowers and hummingbirds were distributed quite indiscriminately among forest, small gaps, and landslide-caused gaps. As at Monteverde, *Bomarea* spp. were exceptional, being restricted to the large gaps created by landslides.

Since there were no major differences in species composition among habitats, it is not surprising that the first hypothesis, dealing with expected differences in flower structure and breeding systems, was not borne out. Also, the distribution and relative abundance of long and short bird-pollinated species shows that, contrary to the prediction, flowering in cutovers is often dominated by long-corolla species, especially *Justicia*, *Alloplectus*, *Centropogon*, and *Malvaviscus*. In contrast, the most common flowering species in forests and some treefalls are often the short-corolla species *Besleria triflora*, *Cephaelis elata*, and *Palicourea lasiorrhachis*. This general pattern is underscored by comparisons of similarity values among plots within habitats and among habitats (Fig. 1). Values for long species are highest in cutovers, indicating that the plots in this habitat are

most consistent with one another in having long species in flower. In contrast, similarity values for short species are highest among plots within forest, suggesting that such species are more consistently distributed in this habitat. No clear explanation comes to mind to account for this pattern. Perhaps it is fortuitous to some extent and is associated with the habitat preferences of a few species (e.g., *Bomarea*, *Justicia*, *Cephaelis*, and *Besleria*). The result is useful as an antidote to the compelling arguments about the need for colonizing species to be opportunistic and for late successional species to be specialized in all features of their biology (Baker and Stebbins 1965, Odum 1969, Grime 1979, Parrish and Bazzaz 1979). It appears to contradict observed distributions of hummingbird-pollinated plants at La Selva, noted by Stiles (1975, 1978b). However, in his sample Stiles included large, abandoned cacao plantations and pastures as well as the chronically disturbed successional plots discussed above. As discussed below, we have reason to believe that significant differences may exist in the flora of the natural disturbances we studied and chronic human-generated disturbances.

The fact that the understory flora does not show patterns that follow predictions based on published information does not imply that there are no floristic

TABLE 5. Amount of nectar, expressed as density of energy, in cutovers (CO), treefalls (TF), and forest plots (FO) at Monteverde. Data are separated for long corolla (L), short corolla (S), and L + S + *Gonzalagunia*, the most common insect-adapted species fed upon by hummingbirds.

Flower subset	Year	Energy density (J/m ²)			Patch type comparisons*			
		CO	TF	FO	Significance	Homogeneous subsets		
Short	1	3.1	39.4	8.3	$P < .0001$	<u>CO</u>	<u>FO</u>	<u>TF</u>
	2	4.1	53.3	16.6				
	1 and 2	7.2	92.8	24.9				
Long	1	89.7	144.4	14.1	$P < .0001$	<u>FO</u>	<u>CO</u>	<u>TF</u>
	2	198.2	206.9	45.3				
	1 and 2	287.8	351.3	59.4				
L + S + <i>Gonza.</i>	1	101.0	183.9	22.4	$P < .0001$	<u>FO</u>	<u>CO</u>	<u>TF</u>
	2	219.4	260.2	61.9				
	1 and 2	320.4	444.1	84.2				

* Differences between patch types were tested by Friedman's test. Homogeneous subsets (pairs of patch types that do not differ significantly from one another) are linked by a horizontal line.

differences among patches, or that species characteristic of disturbed areas do not exist at Monteverde. Trees such as *Cecropia*, *Heliocarpus*, and *Trema*, and shrubs such as *Eupatorium*, *Phytolacca*, and several *Witheringia* and *Solanum* are characteristic of newly disturbed sites at Monteverde, such as landslides and cutovers. Presumably this is because they require freshly disturbed soil and/or abundant light to establish themselves (Richards 1952, Hartshorn 1980, Lawton and Dryer 1980, Murray 1986). In fact, these species can grow in such high density in large disturbances that they dominate both visually and in terms of biomass. However, they comprise but a small proportion of the flora, and a large number of the species found intermixed with these colonizers are much more catholic in their habitat tolerance. This dominance by a few species is one reason for the common impression that disturbances support principally pioneer species. Another reason has to do with the focus on the study of trees by tropical forest ecologists. In the tree stratum, pioneer species and genera of widespread distribution in the tropics have been readily identified (e.g., *Cecropia*, *Macaranga*, *Trema*, *Heliocarpus*, *Ochroma*, and others), and their mode of establishment and distribution are repeatedly contrasted to those of primary species (Aubréville 1938, Richards 1952, Denslow 1980, 1985, Whitmore 1982, Brokaw 1985a, b). In contrast, understory species have not been studied as thoroughly, and their presence is seldom quantified. In those communities where understory species have been noted, the distribution of herbs is also thought to show significant associations with gaps (Richards 1952, Hall and Swaine 1981, Collins et al. 1985). Shrubs are reported to be associated with gaps to a lesser extent than are herbs or trees (Aubréville 1947, Hartshorn 1978, Whitmore 1978, Denslow 1980), although some species are either restricted to or prefer gaps (Brokaw 1985a, Murray 1986).

The lack of specificity of distribution in the species of herbs and shrubs we have studied, and perhaps species elsewhere, may be due to the fact that understory species behave differently from trees during and after disturbance. Individual trees are typically uprooted or broken, and die shortly thereafter; they seldom resprout from the base or from roots. This results in replacement of dead individuals by nearby saplings, which often means that one species is succeeded by another. In contrast, while members of the understory vegetation are also broken up, they are seldom uprooted. In addition, many broken pieces of terrestrial or climbing epiphytic Gesneriaceae, or forest floor Rubiaceae or Acanthaceae at Monteverde, regenerate roots from stems remarkably quickly, whether stems are buried in soil or on the surface. Therefore, disturbance is often followed by abundant regrowth of established individuals rather than replacement, providing less opportunity for changes in species makeup.

Finally, it must be borne in mind that our work was

done in a forest subjected to relatively small, natural disturbances. This probably helps explain why our results are not congruent with "classical" ideas about successional and other changes in the composition and attributes of plant species in various types of patches. Many of these ideas involve attempts to generalize from studies of species that successfully colonize either islands or early successional habitats (e.g., Baker and Stebbins 1965). Information gained about insular colonization is not directly applicable to species dynamics in mainland patches (e.g., Platt 1975). Ideas about dynamics of early succession are shaped by the abundant literature on old fields and disturbed areas of the eastern USA and Europe. These areas have been disturbed repeatedly or modified for hundreds to thousands of years, and are considered to be good examples of large-scale disturbance. Under those conditions, there do indeed develop communities composed primarily of "weedy," "pioneer," or "colonizing" species whose characteristics fit the predictions we made originally. Even in such areas, however, many of the colonizing field species (e.g., those native to North America), were not, in fact, selected to colonize large disturbances but to maintain themselves in relatively persistent, open habitats, too marginal to develop closed canopy forests but subjected repeatedly to physical stress (Baker 1974, Marks 1983). Also, in the tropics (and probably elsewhere), repeatedly disturbed patches (usually anthropogenic) may differ from natural gaps because of changes in soil properties and depletion of native species from soil seed banks (Bazzaz and Pickett 1980, Belt 1985).

Predictability of flowering

The second hypothesis dealt with an expected gradient of increasing unpredictability of flowering patterns from cutovers to forests. It was based on the demonstration that disturbed areas have more variable insolation, moisture, and temperature conditions (Cahoon 1973, Lee 1978, Denslow 1980, Collins et al. 1985) than does forest understory. All these factors, including variation in temperature (Chabot 1978) and especially available light, are known to affect flowering (Whigham 1974, Chabot 1978, Barkham 1980, Pitelka et al. 1985) and nectar production (Hocking 1968, Zimmerman 1983), though there are constraints to the responses of some understory species (Collins et al. 1985). It should be stressed that Hypothesis 2 is independent of the assumption regarding differences in species composition, and of the predictions regarding flower specialization. That is, there could be few or no differences among habitats in either composition or specialization of species, but because of variation in physical conditions, differences in flowering phenology and resulting nectar availability could still occur. In actuality, though (1) turnover rates and variation in turnovers of species in flower showed few differences among habitats or patterns, contrary to Prediction 2a (Fig. 2, Table 2); (2) in terms of flower species diversity (Prediction

2b), both cutovers and forest were more heterogeneous than treefalls for short species, whereas cutovers are slightly less heterogeneous than other habitats for long species; (3) total production and variability in production of flowers and energy did not conform to Prediction 2c (Table 4). In summary, some patterns are discernible, but they are complex, and depend upon which subset of species is examined and which aspect of variability or unpredictability is considered.

In addition to providing tests of predictions based on published work, our results show some important patterns of spatial and temporal variation in flowering and food availability. (1) Despite similarities in species compositions, the habitats did not have similar flowering phenologies or flower production. Turnover rates of species in flower were not correlated. (2) Variances of turnover rates indicate that both cutovers and forest were often more variable than treefalls (Table 2, Fig. 2). Forests were probably so variable because many species have shorter flowering seasons there (Table 1). Cutovers may have been more variable because of the flowering flushes shown periodically by a few species such as *Justicia*, *Gonzalagunia*, or *Salvia*. (3) Despite marked differences in amount of flowering in the 2 yr of the study (Table 5), interhabitat differences in variability and predictability of flowering showed the same patterns in year 1 and year 2. (4) Dramatic interhabitat differences occurred in the production of flowers and nectar (Table 5). The relatively low level of flowering in forest understory and concentration of flowering in treefall gaps has long been noted by students of tropical biology (e.g., Aubréville 1938, Richards 1952, Wallace 1962, Belt 1985, Brokaw 1985b). This phenomenon is probably associated with the increase in light availability in gaps, allowing for higher levels of photosynthesis and the anticipated buildup of nutrients necessary for flowering and fruit production (Chazdon and Fetcher 1984). The effect of such differences in light availability upon intraspecific variation in flowering has been demonstrated previously (Barkham 1980, Pitelka et al. 1985). Cutovers did not show as high a density of flowering as did treefalls. This may result from the presence of many more individuals and species of insect-pollinated plants (e.g., *Phytolacca*, *Heliocarpus*, several Solanaceae, *Eupatorium angulare*, *Urera*, and *Bocconia*) that dominate large portions of cutovers and cast considerable shade in such areas. These results suggest that for understory vegetation, and for both the pollinators and seed dispersers dependent on such species for food, treefalls are foci of crucial reproductive and feeding activity, respectively.

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APPENDIX

Flower diversity of plots. \bar{X} is the mean value of Simpson's diversity index D ; cv is the coefficient of variation expressed as a percentage. $D = 1 - \sum \frac{n_i(n_i - 1)}{N(N - 1)}$, where n_i = number of individuals of species i , and N = total number of species. Years 1 and 2 are combined.

Species set	Cutovers				Treefalls						Forest			
	A	B	C	D	I	J	K	L	M	N	E	F	G	H
LSI \bar{X}	0.47	0.47	0.64	0.39	0.46	0.57	0.57	0.61	0.50	0.54	0.56	0.64	0.52	0.58
cv	63.1	48.6	34.1	70.1	46.0	37.6	36.7	29.0	56.1	46.9	34.5	23.8	36.5	31.8
LS \bar{X}	0.63	0.52	0.62	0.39	0.52	0.57	0.57	0.60	0.50	0.54	0.56	0.63	0.52	0.58
cv	32.8	38.7	36.5	70.1	48.4	37.6	37.4	29.3	56.1	46.9	34.5	24.0	36.5	31.8
L \bar{X}	0.56	0.50	0.56	0.38	0.42	0.54	0.55	0.59	0.42	0.39	0.42	0.61	0.33	0.55
cv	37.1	38.4	41.0	73.7	79.5	53.9	40.7	37.1	63.5	63.2	69.1	35.6	89.3	33.3
S \bar{X}	0.33	0.07	0.32	0.02	0.31	0.27	0.30	0.37	0.19	0.32	0.21	0.37	0.27	0.33
cv	83.6	310.3	81.1	489.9	101.4	99.9	98.8	48.2	147.7	100.5	117.0	64.4	91.6	65.0