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Author(s): Richard P. Seifert and Florence Hammett Seifert

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A COMMUNITY MATRIX ANALYSIS OF *HELICONIA* INSECT COMMUNITIES

RICHARD P. SEIFERT* AND FLORENCE HAMMETT SEIFERT†

Department of Ecology and Evolution, State University of New York at Stony Brook,
Stony Brook, New York 11790

The degree to which species interactions (particularly competition) are important in community structure has given rise to controversy (Hairston et al. 1960; Ehrlich and Birch 1967; Slobodkin et al. 1967). Quantitative laboratory experiments have measured directly the numerical effects of competitive interactions (Vandermeer 1969; Culver 1973), but field experiments either have been qualitative (Bovbjerg 1970; Jaeger 1971; Gill and Hairston 1972) or have used indirect nonmanipulative data (observational rather than experimental data) to quantify the intensity and relative numerical effects of competition (Levins 1968; MacArthur 1968; Culver 1970; Levins et al. 1973).

Competitive relationships are often expressed by the Lotka-Volterra equations expanded to include m species. At equilibrium these equations can be expressed as the single-matrix equation $K = AN^*$, where K is the column vector of carrying capacities, N^* is the column vector of equilibrium densities of species, and A is the square matrix of interaction coefficients (α 's) known as the community matrix (Levins 1968).

While the α 's themselves give us valuable information about species interactions, this "community matrix" can be used to determine community stability and to predict the maximum number of species in a stable community (Vandermeer 1972). Its stability properties have been further examined by May (1973a, 1973b) to describe predator-prey, symbiotic, and competitive relationships.

This theoretical formulation has seldom been applied to data. Vandermeer (1969) estimated α 's among four species of protozoans but did not evaluate properties of stability or the maximum number of species which could exist in his laboratory community. Levins (1968) attempted to predict the number of coexisting *Drosophila* species using an estimate of α based on the joint occurrence of species in the community. His measure assumes that all species are competitors and are all interacting similarly, and that the proportion of joint occurrence is directly related to the amount of competition. The latter assump-

* Present address: Escuela de Biología, Universidad Central de Venezuela, Caracas, Venezuela.

† Present address: Graduate School of Public Health, University of Pittsburgh, Pittsburgh, Pennsylvania 15261.

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tion is often unrealistic (Miller 1964; Bovbjerg 1970; Jaeger 1971). In spite of the assumptions, this measure has been used to estimate coexistence of omnivorous ants (Levins et al. 1973; Culver 1974). MacArthur (1968) used nonmanipulatory data to construct the community matrix for warblers and to determine the conditions under which an additional species can invade. The community matrix also has been used to study coexisting crustacean species in cave communities (Culver 1970, 1973).

An appropriate method for determining α is one which would directly measure (dN_i/dt) as a function of another species, j . Both the qualitative (competitive or symbiotic) and quantitative interspecies effects can be determined by multiple linear regression analysis in which the effect of species i on itself and the effect of each species j on species i are measured by the appropriate partial regression coefficients of $(1/N_i)(dN_i/dt)$ on all N_j . Evaluation of the multiple linear regression equations of the form

$$(1/N_i)(dN_i/dt) = a_i + a_{ii}N_i + \sum_{j=1}^m a_{ij}N_j, \quad j \neq i, \quad (1)$$

yields the partial regression coefficients (a_{ii} and all a_{ij}), which we interpret as interaction effects. Negative signs of the partial regression coefficients indicate competition, and positive signs indicate symbiotic (or predator-prey) relationships. The ratio of the partial regression coefficient for a species j on species i , a_{ij} , divided by the partial regression coefficient of species i on itself, a_{ii} , is the estimate of α_{ij} .

The values and limitations of regression techniques for examining single-species dynamics have been studied by Eberhardt (1970). A regression method comparing differences in local species densities has been used by Schoener (1975) to examine competitive interactions. The method used here for estimating α has several advantages over methods which depend on distinct and constant relationships between proportion of common occurrence and amount of competition. It accommodates all types of species interactions, statistical tests can be applied to each regression equation and each partial regression coefficient and their significance can be determined, and it is based on manipulation experiments. Hence, species interactions can be documented, not just assumed or implied, even among organisms seldom found together.

MATERIAL AND METHODS

Plants holding water in floral parts, leaf axils, and nutrient-gathering organs commonly support a fauna of invertebrates and are ideal habitats for studies of communities. These types of reservoir plants contain well-defined aquatic insect communities and are most common in the tropics (Scott 1914). Maguire (1971) calls these "phytotelmata" and describes their value for studying the dynamics of migration, colonization, and species interactions. Extinction within an individual phytotelmata occurs fairly frequently. This coupled with high colonization rates leads to high species turnover. Maguire also points out that dispersal and colonization proceed rapidly in the wet tropics and that

species interactions are more important in determining species composition in tropical phytotelmata than in temperate phytotelmata. Laessle (1961) examined the limnological properties of the aquatic habitat in Jamaican bromeliads, listed the common inhabitants, and recorded both physiological and interactive properties of some of the inquiline invertebrates. Maguire et al. (1968) show that protozoan communities may be regulated by mosquitoes in *Heliconia bihai* (Musaceae) bracts in Puerto Rico, and Addicott (1974) evaluated the effect of predation by mosquitoes in protozoan communities living in pitcher plants. Communities living in one type of phytotelmata are not necessarily found in taxonomically related or physiognomically similar phytotelmata (Vandermeer et al. 1972).

This community matrix analysis focuses on the most common insects inhabiting the water-filled bracts of two common neotropical wet-forest monocots in the family Musaceae, *Heliconia wagneriana* Peters, which blooms in the dry season, and its wet-season blooming congener, *Heliconia imbricata* (Kuntze), on the Peninsula de Osa, Costa Rica. Information on the ecology of these and other *Heliconia* species is given by Stiles (1975). The insects under study include: *Cephaloleia puncticollis* Baly (Coleoptera: Chrysomelidae), *Gillisia* sp. (Coleoptera: Hydrophilidae), *Quichuana picadoi* Knab (Diptera: Syrphidae), *Copestylum* cf. *obscurior* Curran (Diptera: Syrphidae), *Merosargus* sp. (Diptera: Stratiomyidae), and *Beebeomyia* sp. (Diptera: Richardiidae). Mosquito larvae were excluded from this study because, unlike the above species, they feed on protozoans (Maguire et al. 1968) and therefore compete only slightly, or not at all, with insects whose main food sources are parts of the inflorescence. Some protozoans may be consumed, as the insects under study feed on inflorescence parts. Detailed descriptions of life histories are presented by Seifert (1974), but a description of their salient features is necessary here.

Field Site and Heliconia Species

The research was carried out within a 12-km radius of the Tropical Science Center Field Station near Rincón de Osa, on the Peninsula de Osa on the Pacific coast of Costa Rica in a large area of tropical wet forest (Holdridge 1967). A definite dry season exists here from January through April. The results discussed are based on research from late June through August of 1970 and from November 1971 through September 1972. This second period encompassed an entire blooming season for each species of *Heliconia*.

On the Peninsula de Osa flower buds of *H. wagneriana* begin emerging at the onset of the dry season in late December and continue until late April, shortly before the wet season. A mature inflorescence has between four and eight pairs of bracts. Flowering plants produce a new bract pair about every 9 days (personal observation). Each inflorescence remains on the plant for about 11–13 wk and shows little evidence of rotting until senescence. *Heliconia wagneriana* grows in relatively sunny areas in forest edges, along road cuts, and along stream beds.

Heliconia imbricata flowers during the rainy season from June through September. However, in contrast to *H. wagneriana*, most plants flower synchronously at the beginning of June and only a few inflorescences begin after that time. Thus, at a given time, most of the inflorescences in a locality are of the same age. Each inflorescence lasts on the plant for about 11 wk; however, by the eighth week nearly half of the inflorescence has rotted. Flowering *H. imbricata* plants produce a new bract pair about each 7 days. Mature inflorescences carry between eight and 14 pairs of imbricate bracts, each smaller than those of *H. wagneriana*. *Heliconia imbricata* is found along streams or near treefalls in the forest and was more common in the study area than was *H. wagneriana*. Because these two species of *Heliconia* have essentially non-overlapping flowering seasons, we anticipated that community relationships in one species of inflorescence might be maintained in the second species of inflorescence because the insects living in *Heliconia* inflorescences are exposed to two separate resources which are found at different but predictable times.

During the flowering season of each species of *Heliconia*, inflorescences are found at varying distances from one another, and clumps of inflorescences may be separated by distances greater than 45 m (Seifert 1975). Location of inflorescences by insects is largely dependent on the mobility of adult forms. Moreover, flowering of these plants shows distinct temporal discontinuities. There are at least 3 mo at the end of the wet season and 1 mo at the end of the dry season when few or no inflorescences of *H. wagneriana* and *H. imbricata* are available for insect oviposition and feeding. In addition, larval development times are close to the length of time an inflorescence survives on a plant. Insects emerging as adults from one inflorescence will oviposit on other young inflorescences (Seifert 1974). Location of oviposition sites and survival during nonflowering times must be important for organisms living in these habitats. If community stability based on species interactions can be documented for insects living in *Heliconia* inflorescences, it is likely that community stability will exist in more temporally long-lived communities. Inability to show community stability for insects living in *Heliconia* inflorescences implies that stability based only on species interactions does not occur in ephemeral but predictable habitats.

Insect Species

Cephaloleia puncticollis is one of a number of hispine beetles that feed exclusively on *Heliconia*. Larvae of this species feed on *H. imbricata* inflorescences, and adults feed on young leaves. The larvae rasp the inside of the bract for food and spend about 60 days in larval form in the bracts. The pupae attach directly to the bract and enclose after about 15 days.

An undescribed species of *Gillisius* is the most common beetle found in *Heliconia* inflorescences. *Gillisius* is abundant as an adult in both *H. wagneriana* and *H. imbricata*, although larval forms are not associated with *Heliconia*. Neither dissection of other species of *Heliconia* nor dissection of roots and stems

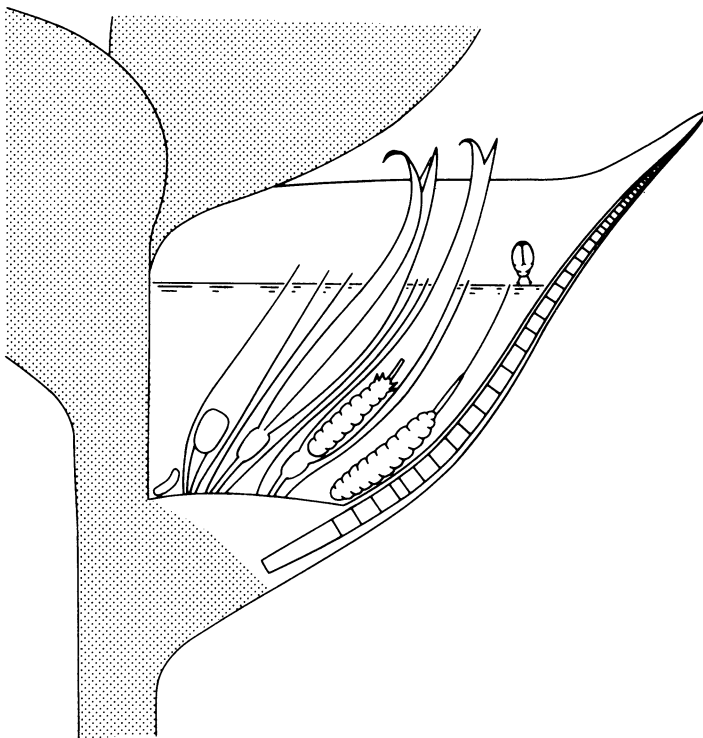


FIG. 1.—Stylized view of *Heliconia wagneriana* showing dissected bract with common inquiline insects. The species shown include *Gillisius* (located on the dissected bract just above the water), *Quichuana* (located at the base of the flower below *Gillisius*), *Copestylum* (located inside the flower), and *Beebeomyia* (located at the base of a seed).

yielded larval forms. Adults feed on floral parts by crawling down the outside of the flower into the water.

The fly *Q. picadoi* is found as a larva in both *H. wagneriana* and *H. imbricata*. Larvae hatch 2 days after oviposition and feed for about 45 days on floral parts, nectar, and detritus. Pupal life lasts about 8 days. While oviposition of *Quichuana* occurs throughout the flowering season of *H. wagneriana*, it occurs in only the first few weeks of the *H. imbricata* flowering season.

The fly *C. cf. obscurior* breeds almost entirely in *H. wagneriana*. Maturation requires 50–60 days. Larvae of this species feed on nectar and detritus.

An undescribed species of the fly *Merosargus* is abundant as a larva in *H. imbricata* but absent from *H. wagneriana*. Maturation from egg to adult takes from 60 to 70 days, and larvae feed on rotting floral parts and detritus.

An undescribed species of the fly *Beebeomyia* is found as a larva in *H. wagneriana* and rarely in *H. imbricata*. Maturation time is not known. Flower parts, particularly the petals, and nectar appear to be the main food sources.

A stylized view of these insects in the two species of *Heliconia* is shown in figures 1 and 2.

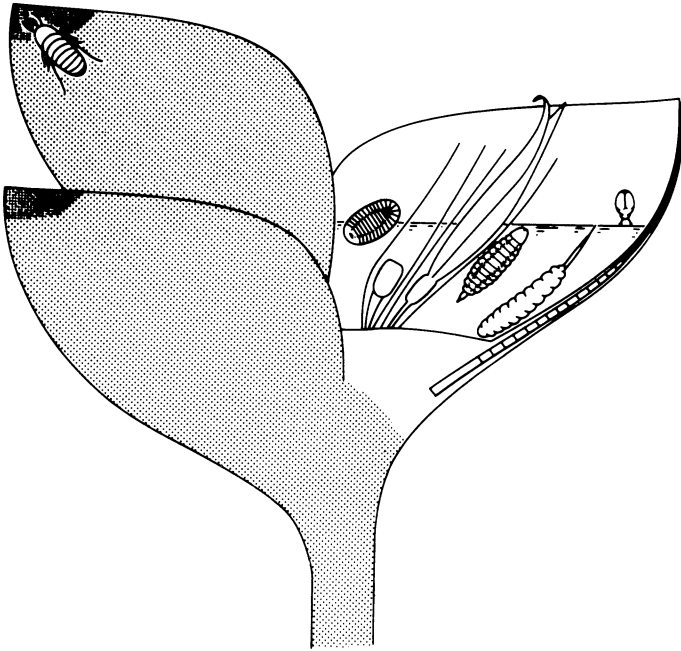


FIG. 2.—Stylized view of *Heliconia imbricata* showing dissected bract with common inquiline insects. The species shown include *Gillisia* (located on the dissected bract just above the water), *Quichuana* (located below *Gillisia*), *Merosargus* (located next to a flower sheath), and *Cephaloleia* (on the edge of the bract entering the water). The cockroach *Litopeltis* is shown on the outside of a bract.

Experiments and Method of Analysis

At the onset of each flowering season, small emergent buds were enclosed in plastic bags securely tied at the rachis to restrict immigration and oviposition. The enclosed buds were allowed to grow in the bags until they had between three and four and one-half bract pairs in *H. wagneriana* and between five and one-half and six and one-half bract pairs in *H. imbricata*. At these sizes, the bags were removed, water was added to the bracts if needed, and varying densities of the four most abundant insect species were introduced. For each treatment, three to 21 inflorescences were initially established. Bags were not replaced on the inflorescences after introduction of the insects. Inflorescences were removed from the plant and dissected to determine insect densities after 2, 4, 6, and 8 days. Preliminary experiments in 1970 were run for 1, 2, 3, 5, and 15 days. These preliminary experiments indicated that most changes in insect densities occurred before the fifteenth day.

For each manipulated plant, the per capita change in number with respect to time for each introduced species was computed (this estimates the dependent variable of eq. [1], $[1/N_i][dN_i/dt]$). A Friedman two-way analysis of variance indicated that only *Quichuana* and *Copestylum* showed a significant amount of

TABLE 1

NUMBER OF INFLORESCENCES, INITIAL DENSITIES, AND RESULTING MEAN DENSITIES (AND STANDARD DEVIATIONS) OF INSECTS USED IN MULTIPLE LINEAR REGRESSIONS FOR *Heliconia wagneriana*

MAXIMUM NO. OF INFLORESCENCES USED PER TREATMENT	INITIAL DENSITIES OF:				FINAL MEAN DENSITIES OF AND STANDARD DEVIATIONS OF:			
	Q.	G.	C.	B.	Q.	G.	C.	B.
9	25	10	0	0	20.11 (± 6.99)	6.11 (± 3.62)	0.56 (± 1.01)	0.33 (± 0.71)
12	40	0	3	0	32.18 (± 4.09)	4.18 (± 3.19)	2.81 (± 1.78)	1.18 (± 3.60)
8	40	20	3	0	28.83 (± 4.49)	10.33 (± 8.52)	3.33 (± 1.03)	0.50 (± 0.55)
9	80	0	3	0	55.28 (± 6.45)	1.43 (± 2.99)	3.43 (± 1.62)	2.28 (± 3.09)
5	80	40	3	0	44.00 (± 7.84)	8.80 (± 8.22)	1.80 (± 0.43)	0.00 (± 0.00)
12	80	40	20	12	58.83 (± 8.25)	4.06 (± 2.97)	10.75 (± 2.45)	2.25 (± 1.42)
9	0	40	3	0	2.22 (± 4.41)	11.44 (± 5.72)	2.88 (± 1.27)	0.00 (± 0.00)
2	0	0	30	0	0.00 (± 0.00)	0.00 (± 0.00)	16.50 (± 2.12)	5.00 (± 7.07)
3	10	0	0	0	10.00 (± 0.00)	1.33 (± 2.31)	3.33 (± 5.77)	2.00 (± 2.64)

NOTE.—The letters Q., G., C., and B. stand for *Quichuana*, *Gillisia*, *Copestylum*, and *Beebeomyia*, respectively.

variation in the change in numbers attributable to the length of time that the organisms were in the inflorescences. Hence, the amount of time spent in the inflorescences for these two species was 1, 2, 3, 4, 5, 6, and 8 days. For the remaining species, the amount of time in the inflorescences was approximated by the number of days after which the first inflorescence in the treatment was harvested (2 or 4 days). The dependent variables are the changes from initial densities divided by the approximate number of days over which the changes took place. These replace the instantaneous change expressed by (dN_i/dt) . In many of these treatments, the initial densities are not close to any "equilibrium" densities. Thus, the expression $(1/N_i)$ uses the initial value of species *i*.

The initial densities of each species placed in the inflorescence were used as the matrix of independent variables of equation (1). Before each multiple linear regression was performed, the gap test (Bliss 1970) was applied to the data to locate and remove points which were outliers. With these outliers removed, the data more closely met the assumptions of multinormal distribution and homogeneity of variances. Tables 1 and 2 list the number of inflorescences and treatments used in the multiple linear regression analyses as well as resulting mean densities with their standard deviations.

Sixty manipulated inflorescences were used to construct the *Beebeomyia* multiple linear regression equation, although *Beebeomyia* was inoculated in only

TABLE 2

NUMBER OF INFLORESCENCES, INITIAL DENSITIES, AND RESULTING MEAN DENSITIES (AND STANDARD DEVIATIONS) OF INSECTS USED IN MULTIPLE LINEAR REGRESSIONS FOR *Heliconia imbricata*

MAXIMUM NO. OF INFLORESCENCES USED PER TREATMENT	INITIAL DENSITIES OF:				FINAL MEAN DENSITIES AND STANDARD DEVIATIONS OF:			
	Q.	G.	M.	C.	Q.	G.	M.	C.
3	50	16	0	0	34.00	9.00	6.00	0.00
					(± 1.00)	(± 3.00)	(± 4.58)	(± 0.00)
21	50	16	30	20	23.53	9.28	23.94	10.39
					(± 9.00)	(± 4.36)	(± 3.67)	(± 3.16)
6*	12	0	0	0	3.50	5.67	0.67	1.00
					(± 3.56)	(± 5.72)	(± 1.21)	(± 1.67)
6*	6	0	0	0	4.33	5.33	0.67	0.00
					(± 5.35)	(± 3.39)	(± 1.63)	(± 0.00)
19	0	16	30	20	0.00	9.85	22.00	6.77
					(± 0.00)	(± 5.06)	(± 5.16)	(± 2.38)
2	0	30	60	0	0.00	11.00	22.00	0.00
					(± 0.00)	(± 8.48)	(± 5.66)	(± 0.00)
1	0	30	60	20	0.00	25.00	32.00	8.00
					(± 0.00)	(± 0.00)	(± 0.00)	(± 0.00)
3*	0	10	0	0	0.00	7.00	1.25	2.25
					(± 0.00)	(± 2.83)	(± 2.50)	(± 0.96)
6*	0	5	0	0	0.20	3.40	1.28	1.00
					(± 0.45)	(± 2.61)	(± 2.05)	(± 1.00)
6	0	0	30	20	3.33	5.00	18.33	10.33
					(± 3.05)	(± 4.36)	(± 6.03)	(± 4.51)
13*	0	0	25	0	0.50	4.17	13.75	1.67
					(± 1.45)	(± 4.39)	(± 5.99)	(± 2.87)
5	0	0	12	0	2.25	1.00	5.50	2.75
					(± 2.63)	(± 0.82)	(± 4.04)	(± 2.50)
20*	0	0	0	8	1.50	7.83	2.39	2.72
					(± 2.55)	(± 7.99)	(± 4.47)	(± 2.37)
11*	0	0	0	4	1.54	2.64	1.27	1.45
					(± 2.77)	(± 2.69)	(± 2.28)	(± 1.29)

NOTE.—The letters Q., G., M., and C. stand for *Quichuana*, *Gillisia*, *Merosargus*, and *Cephaloleia*, respectively.

* Experiments carried out in 1971; all others carried out in 1972.

12 of these. Thus, for this species, the interaction effects are based on both inflorescences which were initially infected with *Beebeomyia* and inflorescences which were not. Immigration from other inflorescences seemed to occur for all species examined (tables 1 and 2). This was most noticeable when manipulated densities were initially low. While the partial regression coefficients are primarily dependent on insect deaths, it seems likely that immigration countered at least some of these deaths. At high insect densities immigration could not be recognized. Oviposition was unimportant in these experiments, because the experiments were run using larger inflorescences which are typically rejected by ovipositing insects (Seifert 1974). When oviposition occurred during the course of the experiments, the small size of the recently emerged larvae made them easily recognizable, so their numbers were not included in construction of regression equations.

Partial regression coefficients generated from the regression equations can be placed in what will be called the unnormalized interaction matrix, U , for the four-species case as

$$\begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{bmatrix}.$$

Dividing each row i by the appropriate element a_{ii} yields the community matrix, A :

$$\begin{bmatrix} 1 & \alpha_{12} & \alpha_{13} & \alpha_{14} \\ \alpha_{21} & 1 & \alpha_{23} & \alpha_{24} \\ \alpha_{31} & \alpha_{32} & 1 & \alpha_{34} \\ \alpha_{41} & \alpha_{42} & \alpha_{43} & 1 \end{bmatrix}.$$

The α 's computed in this manner were influenced by changes in death rates, immigration rates, and emigration rates. These α 's estimate at least a component of the α 's incorporated in the Lotka-Volterra equations. The α 's measured in this research reflect the interactions of the insects inside the inflorescence but cannot give information as to effects outside the inflorescences, such as changes in fecundity or adult survival.

The a priori decision to examine only first-order interactions was made at the beginning of the field research. This decision was based on the then recent inability of Vandermeer (1969) to show the existence of higher-order interactions in a protozoan community. More recent investigations have shown the existence of higher-order interactions in some communities (Wilbur 1972; Neill 1974). Even when such a situation occurs, May (1973*b*) indicates that a community matrix analysis will predict correctly whether or not first-order community stability exists. An a posteriori examination of higher-order interactions using multiple linear regression techniques was undertaken subsequent to construction of the first-order equations. This a posteriori examination is a conservative estimate of the importance of higher-order effects in these communities.

Habitats for *Heliconia* insects are spatially and temporally varied in a manner similar to those studied by Hutchinson (1951), Levins and Culver (1971), and Horn and MacArthur (1972). When such habitats are discrete, migration rates can be important in maintaining competitively inferior species. Thus, it is possible that species interaction effects in a natural community of insects living in *Heliconia* inflorescences may be of secondary importance to effects associated with migration and oviposition rates. Here again, our estimations of α 's, which are based on experiments, express the species interaction effects within the inflorescences and the extent to which these interactions lead to stability. Our α 's cannot express directly the importance or relationship of oviposition and migration. However, Slatkin (1974) forcefully points out that Lotka-Volterra equations describe species interactions within such varied habitats. Moreover, he shows that Lotka-Volterra parameters can be related to those of a colonization extinction model.

TABLE 3

MEAN DENSITIES (AND STANDARD DEVIATIONS) OF INSECTS FOUND IN NONMANIPULATED WILD INFLORESCENCES IN WHICH ONLY THE EXPERIMENTAL SPECIES EXISTED

<i>Heliconia wagneriana</i>			
<i>Quichuana</i>	<i>Gillisius</i>	<i>Copestylum</i>	<i>Beebeomyia</i>
51.00 (± 45.33)	7.56 (± 4.95)	8.78 (± 8.71)	6.67 (± 5.87)
<i>Heliconia imbricata</i>			
<i>Quichuana</i>	<i>Gillisius</i>	<i>Merosargus</i>	<i>Cephaloleia</i>
17.80 (± 11.17)	2.80 (± 1.30)	4.60 (± 4.28)	14.80 (± 5.63)

RESULTS

Interactions

Final mean densities from species interaction treatments are shown in tables 1 and 2. These treatments include situations in which initial densities of each species were greater than those generally found in the field. The results of these interactions can be compared with the mean densities found in nonmanipulated wild inflorescences which contained only all four species of insects under study (table 3).

For each insect species, the total regression equation (1) is significant, thus indicating some species effects. However, 16 of the total 32 partial regression coefficients are not statistically significant at the $P \leq .05$ level. Table 4 shows the unnormalized interaction matrix for the *H. wagneriana* insect community in which nonsignificant elements have been set equal to zero and a final regression equation including only statistically significant elements has been constructed. Note that the effect of *Quichuana* on itself is positive rather than negative, as is the case for the remaining three members of the community. Nine of the 12 interspecific interaction coefficients are not significant. These nonsignificant coefficients indicate a low level of interspecific interactions. In constructing the community matrix for *H. wagneriana* (table 4), we made the signs on the *Quichuana* row to conform with the appropriate signs in the original formulation of the community matrix. This aids in examining the matrix but does not influence stability analysis, which, in this work, is based on the unnormalized interaction matrix and the equilibrium densities. Thus, in the community matrix for *H. wagneriana*, the negative sign for *Beebeomyia* on *Quichuana* indicates that increased densities of *Beebeomyia* reduce the per capita death rate of *Quichuana* (a symbiotic effect). (The alternative a priori explanation that *Quichuana* feeds on *Beebeomyia* must be rejected based on our knowledge of the feeding habits of these insects as described earlier.) *Gillisius* has a small competitive effect on *Beebeomyia*. The absolute value of the effects

TABLE 4
UNNORMALIZED INTERACTION AND COMMUNITY MATRICES: STATISTICALLY SIGNIFICANT COEFFICIENTS ONLY

<i>Heliconia wagneriana</i>											
Unnormalized Interaction Matrix						Community Matrix					
Q.	G.	C.	B.	Q.	G.	C.	B.	Q.	G.	C.	B.
<i>Quichuana</i>	0.00102	0	-0.01754	0.02736	1	0	17.1960	1	0	-26.8235	0
<i>Gillissius</i>	0	-0.00316	0	0	0	1	0	0	1	0	0
<i>Copestylum</i>	0	0	-0.00481	0	0	0	1	0	0	0	0
<i>Bebeomyia</i>	0	-0.00456	0	-0.03310	0	0.1378	0	0	0.1378	0	1
<i>Heliconia imbricata</i>											
Unnormalized Interaction Matrix						Community Matrix					
Q.	G.	M.	C.	Q.	G.	M.	C.	Q.	G.	M.	C.
<i>Quichuana</i>	0	0.00124	0	0	1	-2.5920	0	1	-2.5920	0	0
<i>Gillissius</i>	-0.00096	0.00959	-0.00340	0	0.1001	1	0.3545	0	1	0.3545	0
<i>Merosargus</i>	0	0	-0.00123	0.00416	0	0	1	0	0	1	-3.3821
<i>Cephaloleia</i>	0.00078	-0.00429	0.00260	0	-0.1732	0.8872	-0.9838	0	0.8872	-0.9838	1

on *Quichuana* is much greater than 1, with one α having a positive sign and one having a negative sign.

In the unnormalized interaction matrix for *H. imbricata* (table 4), two of the species, *Quichuana* and *Cephaloleia*, do not show significant intraspecific effects ($.20 > P > .10$ for each species). One intraspecific effect, that of *Gillisia* on itself, is positive. Five of the 12 interspecies effects were not significant. Setting nonsignificant intraspecific effects equal to zero and dividing significant interspecies effects by this term gives the uncomfortable result that the competition coefficient is undefined. To rectify this situation, an estimate of the intraspecific effect was made based on the final multiple linear regression analysis, including data from the initial (nonsignificant) species and from all remaining significant species. Thus, in these cases, α 's were estimated as if the intraspecific effects were significant (table 4). Four of the seven significant α 's show symbiotic effects, and only three α 's show competitive effects. This construction of this community matrix for *H. imbricata* is for heuristic purposes. Later stability analysis is based on the unnormalized interaction matrix and equilibrium densities.

Computation of the average α 's for the original *Heliconia* community matrices shows that both mean α 's are negative (*H. wagneriana* = $-.7908$, *H. imbricata* = $-.4783$), indicating the symbiotic nature of these communities. Each community matrix is dominated by two large (absolute value) α 's. Hence, community dynamics are structured by two of the 12 α 's in each matrix.

A posteriori multiple regression equations including higher-order interactions were examined. Accurate methods for testing significance of the a posteriori regression coefficients are not readily available (Gabriel 1969). For these a posteriori tests, statistical significance was evaluated using a conservative probability level, $P \leq .01$. In all cases, either the regression equation itself or the higher-order partial regression coefficients were not statistically significant. Thus, we have no evidence that higher-order effects are important in these communities.

We may also wish to examine the matrices in which all the partial regression coefficients are entered irrespective of their statistical significance and compare these with the matrices based on statistically significant coefficients. These matrices, based on all partial regression coefficients, are called best estimates and are shown in table 5. The computed values of best estimates of α include both positive and negative values among those that are set equal to zero in the original community matrices.

The community matrices generated from these field manipulations can be compared with matrices constructed by data collected from the periodic harvesting and dissection of inflorescences not previously bagged for the manipulation experiments. This can be done using Levins's (1968) original estimator of α :

$$\alpha_{ij} = \frac{\sum_{h=1}^m p_{ih} p_{jh}}{\sum_{h=1}^m p_{ih}^2},$$

where p_{ih} is the proportion of species i in habitat h (in this case, inflorescence

TABLE 5
UNNORMALIZED INTERACTION AND COMMUNITY MATRICES FOR BEST ESTIMATES: ALL COEFFICIENTS

<i>Heliconia wagneriana</i>											
Unnormalized Interaction Matrix						Community Matrix					
<i>Q.</i>	<i>G.</i>	<i>C.</i>	<i>B.</i>	<i>Q.</i>	<i>G.</i>	<i>C.</i>	<i>B.</i>	<i>Q.</i>	<i>G.</i>	<i>C.</i>	<i>B.</i>
<i>Quichuana</i>	0.00116	-0.00084	-0.01884	0.03100	1	0.7241	16.2412	-0.0140	1	16.2412	-26.7241
<i>Gillissius</i>	0.00004	-0.00286	0.00738	-0.01502	-0.0140	1	-2.5804	0.0632	0.1930	1	5.2517
<i>Copestylum</i>	-0.00036	-0.00110	-0.00570	0.00404	0.0632	0.1930	1	-0.0100	0.1261	-0.0046	-0.7088
<i>Beebeomyia</i>	0.00035	-0.00439	0.00016	-0.03482	-0.0100	0.1261	-0.0046	1			1
<i>Heliconia imbricata</i>											
Unnormalized Interaction Matrix						Community Matrix					
<i>Q.</i>	<i>G.</i>	<i>M.</i>	<i>C.</i>	<i>Q.</i>	<i>G.</i>	<i>M.</i>	<i>C.</i>	<i>Q.</i>	<i>G.</i>	<i>M.</i>	<i>C.</i>
<i>Quichuana</i>	-0.00201	0.00712	-0.00117	-0.00175	1	-3.5423	0.5821	0.1010	1	0.3940	0.8706
<i>Gillissius</i>	-0.00102	0.01010	-0.00398	0.00099	-0.1549	-0.7371	0.0980	-0.1549	-0.7371	1	-1.4319
<i>Merosargus</i>	0.00033	0.00157	-0.00213	0.00305	-0.1732	0.8872	-0.9338	-0.1732	0.8872	-0.9338	1
<i>Cephaloleia</i>	0.00089	-0.00456	0.00480	-0.00514							

TABLE 6
ESTIMATE OF THE COMMUNITY MATRICES BY THE LEVINS TECHNIQUE

<i>Heliconia wagneriana</i>				
	<i>Q.</i>	<i>G.</i>	<i>C.</i>	<i>B.</i>
<i>Quichuana</i>	1	.2177	.2033	.3796
<i>Gillissius</i>1045	1	.0853	.0499
<i>Copestylum</i>3247	.2838	1	.5095
<i>Beebeomyia</i>6329	.1733	.5319	1
<i>Heliconia imbricata</i>				
	<i>Q.</i>	<i>G.</i>	<i>M.</i>	<i>C.</i>
<i>Quichuana</i>	1	.7174	.9095	.5136
<i>Gillissius</i>4592	1	.6853	.3325
<i>Merosargus</i>4847	.5705	1	.3663
<i>Cephaloleia</i>3189	.3225	.4267	1

h), and p_{jh} is the proportion of species *j* in habitat *h*. Thus, α_{ij} is computed from the joint occurrence of species *i* and species *j*. This use of the Levins's estimate treats separate inflorescences as different microhabitats. Although this and similar measures have been frequently used (see Schoener [1974] for examples), Colwell and Futuyma (1971) have shown that this type of measure does not account for varying degrees of distinctness among microhabitats. Matrices constructed using the Levins estimator for *H. wagneriana* and *H. imbricata* (table 6) are considerably different from either the original community matrices or their best-estimate community matrices. Negative α 's do not exist in the Levins matrix simply because this formulation cannot yield negative values. Also, the Levins matrix has only a few values near zero. Moreover, the Levins estimates of α are not greater than 1, although both the original and the best-estimate matrices have α 's whose absolute values exceed 1. To estimate further any correlations between the best-estimate matrices and the Levins matrices, a Spearman rank correlation coefficient was computed for each pair of matrices. Neither coefficient was significant ($r_s = -.308$, $P > .05$, for *H. wagneriana*; $r_s = .006$, $P > .05$, for *H. imbricata*). These different measurements of α are evidently not compatible.

Stability

The conditions under which stability exists for a community matrix have been given by Levins (1968). Both the original and best-estimate community matrices were generated from unnormalized interaction matrices with some positive a_{ii} 's. Division by these positive a_{ii} 's results in competitors having negative signs and symbionts having positive signs in the community matrix. This is contrary to the original construction of the community matrix and would mean that in certain rows positive α 's signify competition while in other rows positive α 's signify symbiotic relationships. To avoid this problem, an

TABLE 7

STANDARD ERRORS FOR THE PARTIAL REGRESSION COEFFICIENTS OF THE UNNORMALIZED INTERACTION MATRICES GIVEN IN TABLE 4 (STATISTICALLY SIGNIFICANT COEFFICIENTS ONLY)

<i>Heliconia wagneriana</i>				
	<i>Q.</i>	<i>G.</i>	<i>C.</i>	<i>B.</i>
<i>Quichuana</i>	±.00033	0	±.00612	±.00859
<i>Gillisius</i>	0	±.00070	0	0
<i>Copestylum</i>	0	0	±.00148	0
<i>Beebeomyia</i>	0	±.00174	0	±.00671
<i>Heliconia imbricata</i>				
	<i>Q.</i>	<i>G.</i>	<i>M.</i>	<i>C.</i>
<i>Quichuana</i>	0	±.00071	0	0
<i>Gillisius</i>	±.00042	±.00267	±.00093	0
<i>Merosargus</i>	0	0	±.00063	±.00059
<i>Cephaloleia</i>	±.00050	±.00235	±.00120	0

TABLE 8

STANDARD ERRORS FOR THE PARTIAL REGRESSION COEFFICIENTS OF THE UNNORMALIZED INTERACTION MATRICES GIVEN IN TABLE 5 (ALL COEFFICIENTS)

<i>Heliconia wagneriana</i>				
	<i>Q.</i>	<i>G.</i>	<i>C.</i>	<i>B.</i>
<i>Quichuana</i>	±.00033	±.00044	±.00600	±.00858
<i>Gillisius</i>	±.00039	±.00132	±.01285	±.01778
<i>Copestylum</i>	±.00274	±.00055	±.00090	±.00610
<i>Beebeomyia</i>	±.00113	±.00188	±.00597	±.01294
<i>Heliconia imbricata</i>				
	<i>Q.</i>	<i>G.</i>	<i>M.</i>	<i>C.</i>
<i>Quichuana</i>	±.00138	±.00299	±.00064	±.00096
<i>Gillisius</i>	±.00044	±.00291	±.00156	±.00213
<i>Merosargus</i>	±.00028	±.00130	±.00102	±.00082
<i>Cephaloleia</i>	±.00039	±.00179	±.00187	±.00381

alternative method of determining stability, depending on the unnormalized interaction matrices and their associated equilibrium densities, was used. For stability to exist, each equilibrium density must be positive (condition 4 of Strobeck [1973]) and the Jacobian matrix must exhibit eigenvalues (λ) which all have negative real parts (Strobeck 1973; Vandermeer 1973). (Here, the Jacobian matrix is constructed by the multiplication of each row in the unnormalized interaction matrix times the equilibrium value of the species represented by that row.) Using the intercepts of the regression equations as estimates of the intrinsic rates of growth (table 9) and evaluating equation (1)

TABLE 9
COLUMN VECTORS OF INTRINSIC RATES OF GROWTH WITH THEIR STANDARD ERRORS

	Original Matrix	Best Estimate
<i>Heliconia wagneriana</i>		
<i>Quichuana</i>	$\begin{bmatrix} -.10438 & (\pm .01566) \end{bmatrix}$	$\begin{bmatrix} -.09941 & (\pm .01547) \end{bmatrix}$
<i>Gillissius</i>	$\begin{bmatrix} -.07340 & (\pm .02318) \end{bmatrix}$	$\begin{bmatrix} -.08643 & (\pm .02578) \end{bmatrix}$
<i>Copestylum</i>	$\begin{bmatrix} .01967 & (\pm .01728) \end{bmatrix}$	$\begin{bmatrix} .05837 & (\pm .04210) \end{bmatrix}$
<i>Beebeomyia</i>	$\begin{bmatrix} .24550 & (\pm .03400) \end{bmatrix}$	$\begin{bmatrix} .22810 & (\pm .07861) \end{bmatrix}$
<i>Heliconia imbricata</i>		
<i>Quichuana</i>	$\begin{bmatrix} -.10892 & (\pm .00941) \end{bmatrix}$	$\begin{bmatrix} -.07167 & (\pm .02747) \end{bmatrix}$
<i>Gillissius</i>	$\begin{bmatrix} -.12533 & (\pm .03252) \end{bmatrix}$	$\begin{bmatrix} -.13266 & (\pm .03640) \end{bmatrix}$
<i>Merosargus</i>	$\begin{bmatrix} -.10588 & (\pm .01828) \end{bmatrix}$	$\begin{bmatrix} -.08797 & (\pm .02442) \end{bmatrix}$
<i>Cephaloleia</i>	$\begin{bmatrix} -.16200 & (\pm .01098) \end{bmatrix}$	$\begin{bmatrix} -.12632 & (\pm .02862) \end{bmatrix}$

TABLE 10
COLUMN VECTORS OF SPECIES EQUILIBRIUM DENSITIES ESTIMATED FROM THE MATRIX EQUATION $N^* = -U^{-1}R^*$

	Original Matrix	Best Estimate
<i>Heliconia wagneriana</i>		
<i>Quichuana</i>	$\begin{bmatrix} -112.1182 \end{bmatrix}$	$\begin{bmatrix} -206.7054 \end{bmatrix}$
<i>Gillissius</i>	$\begin{bmatrix} -23.2294 \end{bmatrix}$	$\begin{bmatrix} 87.8347 \end{bmatrix}$
<i>Copestylum</i>	$\begin{bmatrix} 4.0898 \end{bmatrix}$	$\begin{bmatrix} 269.2484 \end{bmatrix}$
<i>Beebeomyia</i>	$\begin{bmatrix} 10.6170 \end{bmatrix}$	$\begin{bmatrix} 105.0605 \end{bmatrix}$
<i>Heliconia imbricata</i>		
<i>Quichuana</i>	$\begin{bmatrix} 77.8998 \end{bmatrix}$	$\begin{bmatrix} 93.4894 \end{bmatrix}$
<i>Gillissius</i>	$\begin{bmatrix} -38.2944 \end{bmatrix}$	$\begin{bmatrix} 133.9859 \end{bmatrix}$
<i>Merosargus</i>	$\begin{bmatrix} 21.4010 \end{bmatrix}$	$\begin{bmatrix} 327.0370 \end{bmatrix}$
<i>Cephaloleia</i>	$\begin{bmatrix} 12.2604 \end{bmatrix}$	$\begin{bmatrix} 178.1483 \end{bmatrix}$

NOTE— R^* = column vector of intrinsic rates of growth, U = unnormalized interaction matrix, and N^* = column vector of equilibrium densities.

when (dN_i/dt) equals zero, we can estimate equilibrium densities using the matrix equation

$$N^* = -U^{-1}R, \tag{2}$$

where N^* is the column vector of the equilibrium abundances, U is the unnormalized interaction matrix, and R is the column vector of the intrinsic rates of growth. Solution of equation (2) indicates that negative equilibrium densities are associated with each original matrix and with the *H. wagneriana* best-estimate matrix (table 10). For these three matrices there exists no equilibrium where all four species will have densities greater than zero. Equilibrium densities greater than zero for all four insect species exist for only

TABLE 11

EIGENVALUES FOR JACOBIAN MATRICES
CONSTRUCTED BY MULTIPLYING THE UNNOR-
MALIZED INTERACTION MATRICES TIMES THE
APPROPRIATE MEAN SPECIES DENSITIES
FOUND IN NONMANIPULATED WILD
INFLORESCENCES

Original Matrix	Best Estimate
<i>Heliconia wagneriana</i>	
-.2207	-.2069
.0520	.0917
-.0422	-.0442
-.0239	-.0311
<i>Heliconia imbricata</i>	
.0372	-.0801
-.0003	.0177
.0094	-.0329
-.0252	.0020

the *H. imbricata* best-estimate matrix. Both positive and negative real eigenvalues (λ 's = 1.1641, -0.1199, -1.5801, 0.08941) exist for the Jacobian matrix associated with the *H. imbricata* best estimate. Thus, none of these matrices is stable, and only one has an unstable solution where all four species exist.

The equilibrium values generated from equation (2) are strikingly different from the mean species density values found in nonmanipulated inflorescences (table 3). This suggests that insect densities found in the nonmanipulated inflorescences are not equilibrium densities but, rather, are the results of processes not dependent on species interactions. Even so, positive real eigenvalues exist for each Jacobian matrix (both original and best estimates) constructed using insect densities from nonmanipulated inflorescences as an alternative estimate of equilibrium densities (table 11). Thus, the conditions for stability are not satisfied: *Heliconia* insect communities are not stable by any of these measures.

The statistical distribution of the unnormalized interaction (or community) matrix is unknown. For this reason, standard errors of the partial regression coefficients are given (tables 7 and 8). A sample estimate of the unnormalized interaction matrix might predict instability, while the true, parametric value of the matrix would predict stability. Simulation of a statistical distribution for one such matrix would require the construction of 3^{16} matrices. Thus, the solution of this problem is outside the scope of this work.

DISCUSSION

Estimation of competition coefficients (α 's) and evaluation of the community matrix for *Heliconia* insect communities have shown results quite different from

other, similar studies (Levins 1968; MacArthur 1968; Culver 1970, 1974). This may be due to the experimental rather than observational procedures used in this estimation of α . Both symbiotic and competitive relationships are shown to exist in *Heliconia* insect communities. Nonsignificant α 's, which are found in both *Heliconia* communities, imply that each species is interacting with only a portion of the community. May (1973b) independently suggested that such a situation should arise in a community in which the species which interact with other species do so strongly. The presence of some α 's with absolute value greater than 1 and other α 's which are nonsignificant supports May's contention that species in a community either should interact strongly with a few other species (such as is the case for *Heliconia* communities) or should interact weakly with many other species.

Positive density (Allee 1938, 1951) and nonsignificant as well as competitive intraspecific effects occur in these insect communities. Previous studies on less ephemeral systems have indicated that positive density effects may be common (Rosenzweig 1969; Maly 1969). Insect species showing positive density effects do so in one species of *Heliconia* but show competitive intraspecific effects in the other. Thus, survival is facilitated by increased densities in one host but is reduced by increased densities in the other host.

That nonsignificant intraspecific effects occur in spite of the high densities used in the manipulations may indicate that populations are regulated to low levels in life stages outside *Heliconia* inflorescences. An alternative interpretation is that stochastic processes in previous years reduced populations to levels so low that large ovipositions on inflorescences could not occur. It has been pointed out (D. H. Janzen, personal communication) that in certain years at one wet forest on the Atlantic slope of Costa Rica almost all *H. wagneriana* plants failed to bloom in spite of the presence of considerable vegetative growth. This reduction of flowering by *Heliconia* would severely reduce the population densities of the inquiline insect species. In such a situation, when *Heliconia* resumes flowering, populations will increase, greater larval densities will be found in inflorescences, and maximum densities of the inflorescences will be reached. If a similar situation occurred on the Peninsula de Osa, the high densities which should have been used in the manipulations could not have been predicted from the densities encountered in wild, nonbagged *Heliconia* inflorescences. However, census data from a 2-yr period are comparable and do not indicate drastic changes of species densities in wild *Heliconia* inflorescences (Seifert 1974). Thus, there is no evidence to support a reduction in flowering of *Heliconia*.

The two methods studied of estimating α give strikingly different results. The Levins (1968) technique equates spatial overlap with a current state of competition, but spatial overlap often measures postcompetitive situations. These may include situations where inferior competitors are excluded from habitats or where resources are discretely partitioned. Equating spatial overlap to competitive intensity also rejects the possibility of the occurrence of symbionts (negative α) in a community. Thus, the Levins technique does not indicate the highly symbiotic nature of *Heliconia* insect communities. The

estimation of α based on manipulation experiments indicates the inadequacy of the Levins technique. Other overlap measures have been devised (MacArthur 1968; Culver 1970; Schoener 1974) and cannot be considered satisfactory in light of this research. Culver (1973) comments on the inappropriateness of his earlier measurement. The adequacy of any nonmanipulatory measure of α must be verified with suitable manipulation experiments.

Neither community is stable as estimated by the species equilibrium densities and by the Jacobian (and thus community) matrix. This lack of stability means that species interactions taken as a whole are destabilizing. May (1973b) shows that positive density effects and symbiotic effects, both of which are found in *Heliconia* insect communities, are actively destabilizing. Moreover, our analyses do not give evidence to support the existence of stabilizing higher-order effects in *Heliconia* insect communities.

The term "community" has been given a variety of meanings (Wilbur 1972), some of which seem to imply stability as a property of communities. Here, insects in *Heliconia* inflorescences are considered a community because of their potential for species interactions and their restriction within a single habitat. We use knowledge of species interactions to determine whether stability exists in *Heliconia* insect communities. The extent to which one might expect to find stability in this type of larval, evanescent community is difficult to assess. If stability were a universal condition, it would then be found for insects living in *Heliconia* inflorescences. Since stability for these communities cannot be postulated on the basis of the community matrix analysis, it can be inferred that stability is not universal in occurrence. If deterministic, interspecies interactions are of sole importance in community structure, stability would be implied. As nondeterministic factors become important in structuring the community, stability will be less common (May 1973b). These results imply that *Heliconia* insect communities are not structured strictly by interspecies interactions.

If, as suggested above, stability is not universal in occurrence, the probability of observing stability in the *Heliconia* insect community would be less than for communities which are longer-lived. In *Heliconia* communities, events associated with migration and oviposition are probably important in structuring the community. Each bract of *H. wagneriana* and each inflorescence of *H. imbricata* are effectively available for oviposition for a period of only a few days. Species failing to find an inflorescence in a short time will be excluded from that inflorescence. Thus, the a priori probability of finding stability in these communities is lower than for longer-lived communities. If stability had been found in these communities, a powerful statement about the occurrence of stability in tropical communities would have been implied. Because stability was not found, a less powerful statement about the lack of stability in evanescent communities is made.

Knowledge of first-order species interactions is not sufficient to account for the maintenance of these communities. Indeed, equilibrium densities estimated from the field experiments are quite different from the mean insect densities found in nonmanipulated inflorescences. This indicates that such insect densities

found in nonmanipulated inflorescences are not strictly the result of deterministic species interactions. It is likely that processes of migration, oviposition, and extinction (here including the death of a clutch of eggs), which were not studied, may be important in structuring these communities, the habitats of which are both spatially and temporally separated. Hutchinson (1951) postulated that high migration rates may maintain certain competitively inferior copepod species. Mathematical examination of this case (Horn and MacArthur 1972; Levins and Culver 1971; Slatkin 1974; Levin 1974) shows that competitively inferior species can exist in communities if they invade uninhabited patches more quickly than do competitively superior species. Maguire (1959, 1970, 1971) indicates that processes of extinction and migration are important for true and artificial phytotelmata in temperate and tropical regions. Maguire's work included systems which were available for colonization for an entire year and yet were continually influenced by migration and extinction. Culver (1973) found that incorporating extinction rates in a competition model leads to an accurate analysis of simple invertebrate communities living in spatially heterogeneous cave streams. The processes of migration, location of oviposition sites, and local extinction and survival of oviposited eggs may be as important in *Heliconia* communities which are available for only two 4-month periods each year.

SUMMARY

Field manipulations were designed to determine interspecific interaction coefficients (α 's) for insect species living in the water-holding bracts of *Heliconia wagneriana* and *H. imbricata*. Community stability was investigated by the analysis of species equilibrium densities and the matrix of regression coefficients of mortality rate on the density of each species.

1. Both positive and negative coefficients of interspecific interaction (α 's) exist, meaning that both competitive and symbiotic effects occur. Some α 's are not statistically significant, indicating no interspecies effects.

2. Occasional positive and nonsignificant intraspecific coefficients were found, meaning that over the densities studied intraspecific competition was not occurring for some species in one or the other *Heliconia* community. In the two cases of positive intraspecific coefficients, negative intraspecific coefficients occurred in the other *Heliconia* community.

3. Each community matrix is dominated by two α 's which have high absolute values. The mean α for each community is negative, indicating the symbiotic nature of these communities.

4. The Levins (1968) estimate of α gave results which were not comparable with those α 's generated from the field experiments. The Levins measure is deemed inadequate because it cannot estimate symbiotic relationships.

5. Neither the *H. wagneriana* community nor the *H. imbricata* community is stable as estimated by the equilibrium densities and by the eigenvalues of the Jacobian matrix (the unnormalized interaction matrix of partial regression coefficients times their equilibrium densities).

6. Migration, oviposition, and local extinction processes, which were not measured, may be important in structuring these communities.

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ERRATUM

In W. Y. Brockelman, "Competition, the Fitness of Offspring, and Optimal Clutch Size," 109 (1975): 677–699, on page 682, figure 3, curves *A* should read *B*, and curves *B* should read *A*.