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A COMMUNITY MATRIX ANALYSIS OF *HELICONIA* INSECT COMMUNITIES

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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 (1973*a*, 1973*b*) 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-

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