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CONTENTS/INHALT

PREFACE	III
 <i>ANTHECOLOGY</i>	
NOTES ON THE PHENOLOGY AND POLLINATION OF THE DIOECIOUS PALMS <i>MAURITIA FLEXUOSA</i> (CALAMOIDEAE) AND <i>APHANDRA NATALIA</i> (PHYTELE- PHANTOIDEAE) IN ECUADOR. F. Ervik	7
THE POLLINATION OF <i>SIPARUNA</i> (MONIMIACEAE) BY GALL MIDGES (CECIDO- MYIIDAE) IN ECUADOR. J. P. Feil	13
AN EVOLUTIONARY FOOD WEB AND ITS RELATIONSHIP TO NEOTROPICAL BIODIVERSITY. L. E. Gilbert	17
BESTÄUBUNG DER FABACEAE <i>MUCUNA FLAGELLIPES</i> DURCH FLUGHUNDE IN KAMERUN. R. Grünmeier	29
ADAPTATIONS OF FLOWERS TO THE POLLINATION BY GLOSSOPHAGINE BATS. O. v. Helversen	41
NOTES ON THE ORGANIZATION OF A NEOTROPICAL HIGH-ALTITUDE HUM- MINGBIRD-FLOWER COMMUNITY. M. Kraemer, U. Schmitt & K.-L. Schuchmann	61
POLLINATION BIOLOGY OF <i>ORBIGNYA SPECTABILIS</i> , A "MONOECIOUS" AMA- ZONIAN PALM. H. Küchmeister, G. Gottsberger & I. Silberbauer-Gottsberger	67
SWING-HOVERING COMBINED WITH LONG TONGUE IN HAWKMOTHS, AN ANTIPREDATOR ADAPTATION DURING FLOWER VISITS. L. T. Wasserthal	77
 <i>FRUGIVORY AND SEED DISPERSAL</i>	
INTERAKTIONEN ZWISCHEN TUKANEN (RAMPHASTIDAE, AVES) UND FRUCHTENDEN PALMEN (<i>OENOCARPUS BACABA</i> , ARECOIDEAE). P. Bühler ...	89
THE ROLE OF PRIMATES IN TROPICAL ECOSYSTEMS. E. W. Heymann	103
CONSEQUENCES OF A FRUIT DIET. D. Levey	109
 <i>TROPICAL BOTANY</i>	
ECOPHYSIOLOGICAL ADAPTATIONS AS A BASIS FOR HIGH DIVERSITY IN THE GENUS <i>CLUSIA</i> . A. Haag-Kerwer & U. Lüttge	115
MELASTOMATAACEEN ALS MYRMECOPHYTEN: EINE MÖGLICHKEIT DER AN- PASSUNG AN DEN LEBENSRAUM. M. Nickol	125
FOREST INVENTORY IN AN ISLAND OF LAKE GURI, VENEZUELA. P. Parolin	139
ÖKOGEOGRAPHISCHE DIFFERENZIERUNG UND DIVERSITÄT DER VEGETA- TION VON INSELBERGEN IN DER ELFENBEINKÜSTE. S. Porembski & W. Barthlott	149

AN EVOLUTIONARY FOOD WEB AND ITS RELATIONSHIP TO NEOTROPICAL BIODIVERSITY

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Abstract. A fundamental concern of biology is the question of why so many species live on the earth and why some habitats, such as rainforests, have so many more species living together than others. Over three decades after G. E. Hutchinson crystallized this problem, there are no simple answers to questions about species diversity. Meanwhile, *biodiversity* has replaced *species diversity* in the rhetoric of community biology. This change represents progress because biodiversity is not simply a list of species, it is a concept which indicates the overall richness of pattern in the interactions among species in a system. *Biodiversity* has captured the imagination and attention of a new generation of biologists concerned with conserving this quality of nature. What it is, how it is measured, and how it is to be studied remains vague. In this paper, I provide an overview of some of what my colleagues and I have learned about one small subset of the Neotropical rainforest system, *Heliconius* butterflies and associated species, whose interactions define a unit of biodiversity. My principal aim is to review and interpret this work, obscured by time and scattered in the literature, for the large audience of young European biologists now planning to initiate research programs in tropical ecology.

Key words: *Biodiversity, food web, Heliconius, Passiflora, Neotropics, Psiguria, pollen feeding, population biology.*

INTRODUCTION

All biologists study some facet of biodiversity, but most today are preoccupied with questions pertaining to the diversity of gene function within a few species. Ultimately, biodiversity must somehow arise from diversification of DNA. However, even if we understood all the functional connections between patterns in DNA and the diversity of morphology and behavior exhibited by organisms in nature, we would fall far short of explaining the arrangements of species in communities and ecosystems. One encouraging recent trend is the broad application of phylogenetic systematics in understanding how evolutionary history contributes to contemporary community patterns (Brooks & McLennan 1991). On the discouraging side is the realization that the chaotic dynamics (May 1979; Murdoch 1979) and indirect interactions of even simple population systems makes community and ecosystem-level patterns difficult to predict from first principles (Yodzis 1988). For individual investigators as well as research foundations concerned with funding research in tropical ecology, the greatest challenge is how limited human and financial resources can most effectively be used to define and understand biodiversity.

One important aspect of biodiversity is structure created by trophic networks called food webs. The formal study of food webs (e.g., Cohen 1978) attempts to develop generalities and predictions about the emergent property of these

species networks. Unfortunately, there are numerous reasons to doubt that this is a meaningful direction for biodiversity studies (see Paine 1988). First, models of even the simplest sets of interacting populations have proven to have such intrinsic complexity that empirically testable predictions about system dynamics are difficult in natural communities (Yodzis 1988). Second, most food web theory has been biased toward vertebrates and other top predators (Pimm 1991). These organisms are also convenient for field studies (Winemiller 1990). Insect-plant interactions, while constituting the majority of interactions in most terrestrial ecosystems, are often over-simplified. Focusing on principle trophic interactions (e.g., herbivory, seed predation) ignores such integral mutualisms as pollination. Such interactions are of minimal importance in energy flow but of major importance in understanding the evolution of food web relationships as I will discuss below. Third, different life stages or sexes of many organisms consume different resources, Werner's (1984) "ontogenetic niche shifts". Splitting these life stages into nodes of a food web ignores the population dynamics consequences of life cycles, a fact of life for organisms such as homometabolous insects. In the real world, genetic connections between larval and adult or between male and female insects constitute an important linkage between ecologically distinct food webs, the study of which ultimately may explain the evolution, as well as the maintenance, of biodiversity.

HOW TO FIND A PROJECT

When I initiated my research in the late 1960s, I had already developed an interest in the problem of tropical species diversity and planned to study the ithomiine butterflies, a prominent group of Neotropical rainforest insects important as models in mimicry complexes. My first goal was to identify a species-rich group of related species which could be studied as individuals and populations, both in the field and in the laboratory. Unfortunately, ithomiines failed on both counts. Fewer than 1% of adults marked in my preliminary studies in Trinidad were ever recaptured. Greenhouse cultures of these insects proved impossible to maintain. On the other hand, I was successful in initiating greenhouse cultures of *Heliconius* at Stanford University. Moreover, the frequent recapture of marked *Heliconius* in preliminary field studies along with similar evidence from Turner (1971) on other *Heliconius* species indicated that studies of population biology and behavioral ecology were extremely promising with these insects. But as a "scientific tourist" with limited time in the field, success at culturing the animals at home in the United States was one of the most compelling reasons for choosing to focus on *Heliconius*.

Although the work of Robert Mac Arthur had helped stimulate my interest in species diversity, it did not long sustain my optimism for theoretical and experimental approaches to community biology which most of my cohort experienced in the late 1960s and early 1970s. I was unable to meaningfully relate theory based upon organisms such as birds and lizards, whose diets could be defined as arrays of prey size, to phytophagous insects, whose diet breadths were based in large part upon host chemistry and whose niche descriptions often involve distinct larval and adult feeding habits. Consequently, I chose to focus on a basic population study of a single *Heliconius* species, *H. ethilla*, which was initiated with P. R. Ehrlich in December 1969. There was no grand question or hypothesis. Rather, we decided to find out something about the structure and dynamics of a rainforest insect population.

HELICONIUS POPULATION BIOLOGY AND POLLEN FEEDING

The mark-release-recapture studies of *H. ethilla* at Arima Pass, Trinidad revealed striking constancy in population size through a dry-wet seasonal cy-

cle which appeared to affect many other conspicuous insects (Ehrlich & Gilbert 1973). The predominant concern of insect population dynamics, then as now, was how to predict damaging outbreaks in crops and commercial forests. The question of how a low-density insect population remains constant in a fluctuating environment had not been posed.

Because the problem of species diversity is reduced to the problem of persistence of rare species, I was drawn to learning more about the community interactions which might explain these population level observations. The dynamics of a population arise from the birth or death and arrival or departure of individuals. Therefore the behavior of individuals resulting from interactions with resources, competitors, predators, and habitat patchiness in time and space is a critical determinant of the size and structure of the population composed of those individuals. My study therefore increasingly became focused on behavioral ecology and natural history of individual *H. ethilla*. By employing the methods used by Ehrlich and his group on *Euphydryas* butterfly population biology (Ehrlich *et al.* 1975), bookkeeping on individuals was part of the population estimation procedure.

Several traits of individual *H. ethilla* appeared to be relevant to explaining population constancy. First, adults were faithful to small parts of the study area as had been described for other *Heliconius* (Turner 1971). Second, adult life span was found to exceed five months, the longest documented for non-diapausing lepidopterans. Third, reproductive activity apparently did not diminish over time for males or females. Marked females housed briefly in outdoor cages for egg production and then released were found to be equally fecund up to four months later (Gilbert 1972). It was this departure from typical lepidopteran egg production and senescence pattern (the general consensus at the time, represented by Engelmann (1970), was that adult Lepidoptera do not assimilate nitrogenous compounds for reproduction) that stimulated a search for other potential inputs of nutrients for maintenance and reproduction in *Heliconius*. It did not take long to guess that the conspicuous pollen loads carried by *H. ethilla* might provide the answer to this problem. Pollen feeding, a characteristic unique to the genera *Laparus* and *Heliconius*, accounts for about 80% of the lifetime reproduction of *Heliconius* females (Dunlap-Pianka *et al.* 1977; Gilbert 1972).

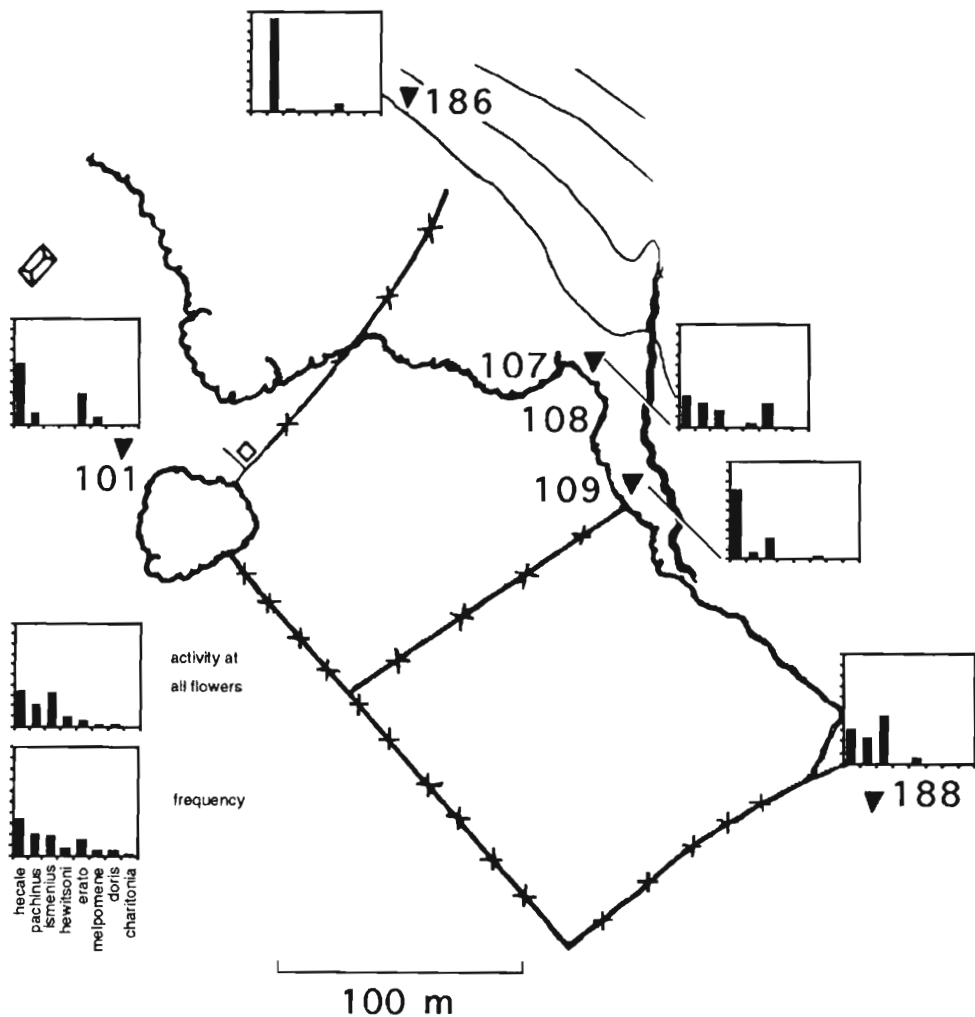


FIG. 1. Spatial variation in visitation to adult floral resource patches by the *Heliconius* community at Sirena, Parque Nacional Corcovado, Costa Rica. Super 8 mm Nizo movie cameras recorded visits at ca. 3 second intervals and typically from 05.30 hrs to 15.00 hrs over three days, 17–19 July 1980. Cameras were focused on single male flowers within five isolated clumps of *Psiguria warscewiczii*. Flower visitors were easily identified from the film. The figure shows histograms of visitation rates by each of the eight pollen feeding butterfly species present, the names and relative abundances of which are shown in the lower left panel. By all three MANOVA tests for significance, all five clumps are different from the others at $p < .01$.

MANOVA test	Value	Approx.	DF	Error DF
Pillais	3.08	11.17	24	80.00
Hotellings	23.48	15.16	24	62.00
Wilks	.00127	14.52	24	60.52

The upper left panel shows distribution of visits by all species over all of many flower patches in the sample area over a 20 day period centered on the camera days. All five patches are potentially within the home range of individual heliconiines (see Murawski & Gilbert 1986) and none fall outside the population boundaries of the component visitors. The individual (numbered) butterflies at each site were regular visitors over many days. These are previously unpublished data.

With respect to population level phenomena, pollen feeding and correlated traits appeared to promote the observed constancy of number. First, because pollen was available throughout the year, egg production was continuous in the area. Microhymenopteran parasitoids of eggs, a major mortality factor could therefore be continuously present. Second, because less than 20% of egg production by *Heliconius* can be attributed to stored larval reserves (Dunlap-Pianka *et al.* 1977), and because pollen sources are limited (Murawski 1987), the slope of increase in eggs laid in the population as a function of adult numbers will be less than 80% of the slope realized under unlimited pollen supply. Third, foraging for pollen and nectar defines resident adult home range (Murawski & Gilbert 1986). Even without suitable oviposition sites on larval hosts (new shoots of *Passiflora*) female *Heliconius* remain in home ranges visiting pollen plants and searching patches of larval host for new shoots. Fourth, recent findings strongly indicate that pollen feeding contributes to adult unpalatability and thus reduces mortality risk discussed by Gilbert (1991).

In summary, pollen-feeding with constant pollen availability promotes constancy in *Heliconius* populations first by indirectly maintaining biological control agents which act on eggs (or larvae) and second, by reducing the probability of prolonged crashes or outbreaks in adult numbers resulting from brief episodes of losses (dispersal out or mortality) or gains (dispersal in or increased birth rates) respectively. The second phenomenon depends upon behavioral rules for establishing residency, namely that a) individual *Heliconius* learn to return to locations based on past success in finding and exploiting pollen plants, and b) failure to establish a foraging network of pollen sources leads ultimately to increased probability of mortality or dispersal for individuals.

Evidence that adult foraging patterns arise from individuals learning the positions of unexploited pollen and nectar sources is indirect. If one records individual visitors to pollen sources, visitors at each source are a consistent subset of the overall population over time, and particular individuals are routinely recaptured only on a subset of available sources. In a system of eight coexisting *Heliconius* populations in Costa Rica, time-lapse recording of visits to flower patches within the study area reveal between-patch dif-

ferences in visitation by different species. Moreover, the set of visits at each patch differs from a random sample of the community (Fig. 1). *Heliconius ismenius* (histogram column 3, Fig. 1), a frequent visitor at many *Psiguria* patches (e.g., stations 107, 109, 188), was not observed over many days at a similar patch at station 101, in spite of its presence at *Psiguria* flowers clearly visible, only a few meters away. Likewise, *H. hecale* (histogram column 1, Fig. 1), although common throughout the site, was absent at the station 186 *Psiguria*. Such observations suggest learned response to reward structure rather than random visitation.

Appropriate experimental study of learning in *Heliconius* as it relates to establishment of residency and foraging networks is difficult and will require large controlled environmental facilities. In any case, the original hypothesis that the behavioral capacity of *Heliconius* (which sets the rules for ecological interaction with pollen plants) is itself an evolutionary result of the pollen feeding habit (Gilbert 1975) still seems viable (Gilbert 1991) and will be discussed in another context below.

CUCURBIT VINES AND POLLEN AVAILABILITY

The assumption of constant pollen availability is useful only in simplifying the discussion of the influence of pollen feeding on population dynamics for a *Heliconius* species. In real situations pollen availability will vary according to flower production and competition. Relative to many flowering plants, however, the key pollen sources of most rainforest *Heliconius*, butterfly specialized species of the cucurbit genera *Psiguria* (= *Anguria*) and *Gurania* are relatively non-seasonal. Everywhere I have studied *Heliconius* in rainforest habitats, some *Psiguria* individuals are producing male flowers at any given time of the year. At Sirena, in Parque Nacional Corcovado, Costa Rica, Murawski (1987) found that the minimum percentage of *P. warszewiczii* in flower on any weekly census from October 1980 to December 1981 was 38% while the high was 80%. Variation in availability of male flowers is somewhat more extreme than variation of plants in flower since some periods with low flowering rates coincide with a bias in female flower production. Nevertheless, this high quality pollen source was always available. Murawski (1987) fur-

ther documented changes in foraging behavior as per-capita flower availability changed. At low levels experienced butterflies simply perch on, and defend, flowers for much of the day. New adults have little opportunity to exploit pollen and nectar during such times and the local population therefore would not increase even with new adults hatching. Mallet (1986) found an increase in dispersal rate among new adults of *H. erato* which may reflect the difficulty that naive adults face in establishing profitable foraging routes in saturated habitat.

Although *Heliconius* adults may be found exploiting wide variety of plant species for nectar and pollen, few of these are reliable sources in primary rainforest, and few species contribute to pollen diet of *Heliconius* at any given locale (Boggs *et al.* 1981). In Corcovado Park, Murawski (1986) recorded visits by at least some *Heliconius* to 27 plant species, including occasional visits to hummingbird species such as *Malva viscus* (Malvaceae), *Heliconius* sp., and *Gurania makoyana*. However, the mean percent of *Psiguria* pollen in the loads of female *Heliconius* varied from 60 to 97% for *H. bewitsoni*, *H. melpomene*, *H. ismenius*, *H. becale*, *H. pacheus*, and *L. doris*. Only *H. erato*, a specialist on small pollen (Boggs *et al.* 1981; Crane 1955), had a low percentage of *Psiguria* pollen (33%).

At Corcovado Park, Murawski (1986) found that as male *Psiguria* flowers declined, all *Heliconius* species increased diversity of pollen types gathered. Most frequent of these types are *Lantana*, a general butterfly flower of disturbed sites visited by dozens of butterfly species, and *Cissus*, a flower that attracts an even wider assortment of Hymenoptera and Lepidoptera. Only *Tournefortia hirsutissima* (Boraginaceae) appears to be predominately visited by *Heliconius* during its seasonal blooming period (personal observation).

Thus, in spite of the large list of flowers that *Heliconius* will visit, few of these appear to have relevance for understanding population or community dynamics of these species. Rather, such visits reflect occasional shortages in favored food sources and the actions of individuals which are not likely to persist as residents. The availability of cucurbit pollen is the only consistent predictor of maximally diverse *Heliconius* communities in rainforest areas; the pollen tetrads characteristic of *Psiguria* and *Gurania* can be found on museum specimens collected through-

out the range of these genera from Brazil to Mexico (Gilbert 1972). Thus, like figs for frugivores, these vines are keystone resources for *Heliconius* (Gilbert 1980). Beyond the core *Heliconius* habitat defined by presence of certain species of *Psiguria* and/or *Gurania*, we generally find persisting only species such as *H. erato*, which can effectively exploit species with small pollen grains (Boggs *et al.* 1981). Such species represent the genus *Heliconius* in tropical deciduous, subtropical, and high elevation habitats. It is interesting to note that these are all members of the pupal mating lineage (Gilbert 1991; Lee *et al.* 1992) and considered to have arisen relatively recently (Brown 1981).

DO CUCURBITS SPECIALIZE ON *HELICONIUS*?

If forest *Heliconius* are specialized on *Psiguria* (and some *Gurania*) is the reciprocal true? At an early stage of study on this system, I proposed that coevolution between these cucurbits and *Heliconius* have shaped traits in both (Gilbert 1975). It seems likely that this interaction evolved from a hummingbird system. Proto-*Heliconius*, having evolved pollen feeding in relation to more typical butterfly flowers soon developed two correlated traits: 1) increased unpalatability made possible by cyanogenic glycosides built from pollen-derived amino acids (Nahrstedt & Davis 1983) and 2) the ability to fly at cooler temperatures, a trait correlated with unpalatability (Srygley & Chai 1990). The ability to fly at cooler temperatures made possible the exploitation of floral resources, such as ancestral *Guraniinae* cucurbits previously exploited by hummingbirds exclusively.

The impact of an efficient pollen thief such as proto-*Heliconius* appeared to have driven floral evolution in these cucurbits along two pathways. First, traits promoting resistance to *Heliconius* evolved and now characterize several *Gurania* species (see Condon & Gilbert 1990). Second, traits promoting specialization on the butterflies can be identified in many *Psiguria* and some *Gurania* species. These include anthesis and nectar flow at later morning hours more favorable to butterfly foraging, and smaller flowers and nectar flow reduced to levels marginally rewarding to birds but adequate for butterflies. For example, *Psiguria umbrosa*, principally a hummingbird visited species in some areas (Feinsinger

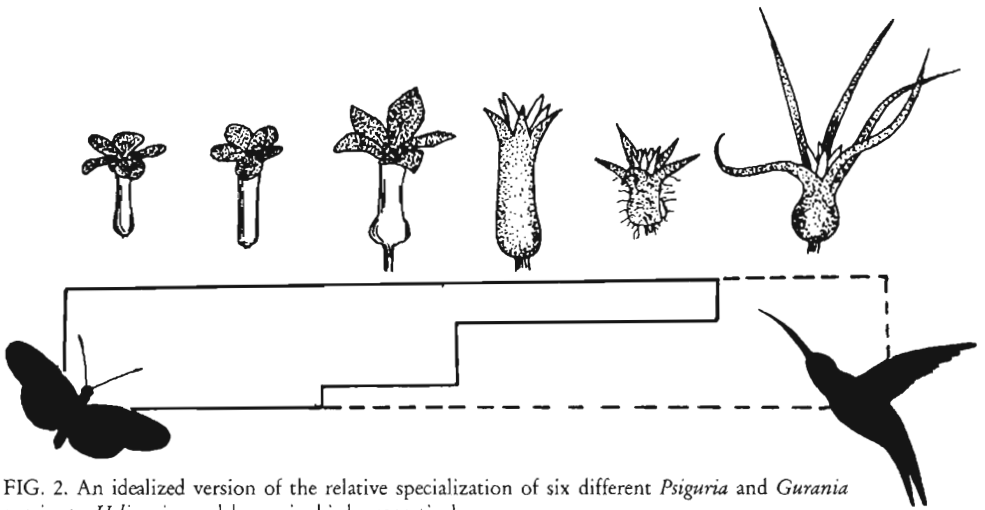


FIG. 2. An idealized version of the relative specialization of six different *Psiguria* and *Gurania* species to *Heliconius* and hummingbirds respectively.

et al. 1982) and by both birds and butterflies in others (Condon 1984), when compared under greenhouse conditions with the butterfly specialized *P. triphylla*, produces pollen and nectar earlier (06.00–11.00 hrs vs 11.00–18.00 hrs) and produces six times the amount of nectar (8 mg/flower to 48 mg/flower) (Gilbert 1975). This interpretation complements that originally given (Gilbert 1975).

Condon (1984) has studied this system extensively in Central and South America and correctly questions some of my initial coevolutionary scenarios (Condon 1984; Condon & Gilbert 1990; Condon, in prep.). Ultimately Condon's on-going studies on the geographical ecology of the system, combined with phylogenetic analysis of the plants, will help resolve the degree to which coevolution with the various bird and butterfly visitors has taken place.

Viewing the system from the perspective of *Heliconius* population biology in Mexico, Costa Rica, and Trinidad, at least some *Psiguria* or *Gurania* are specialized on *Heliconius* in each site while others, if present, are specialized on hummingbirds (Fig. 2). Others are visited by both. In Corcovado Park, Costa Rica visits by *Heliconius* to *Gurania makoyana* are discouraged by calyx spikes and hummingbirds dominate. In contrast, *Heliconius* are the predominant visitors to *Psiguria warszewiczii* (Murawski & Gilbert 1986). Of 1052 visits to 5 flowers at 5 clumps of *Psiguria* recorded by time lapse camera for 3 days (July 1980) in Corcovado Park, Costa Rica, 1042 were

by *Heliconius*, 9 were by other butterflies, and 1 was by a hummingbird. The relative absence of other butterflies indicates the effect of *Heliconius* in exploitative competition for the nectar resources of this plant since these are used readily by a variety of nectar feeders when *Heliconius* is excluded (personal observation).

It was asserted above that the contribution of pollen feeding to the numerical constancy of *Heliconius* populations is due in part to the year-around availability of *Psiguria* pollen. The phenology of male *Psiguria* and *Gurania* inflorescences is such that male flowers may be available for many months at one patch (Gilbert 1975). Are butterfly specialist cucurbit vines less seasonal in flowering than hummingbird specialists? This would be predicted based on the limited number of pollen sources locally available to *Heliconius* (Boggs *et al.* 1981; Murawski 1986) in contrast to the large number of available nectar plants pollinated by hummingbirds (e.g., Feinsinger *et al.* 1982; Snow & Snow 1972; Stiles 1978) over the course of the year. Feinsinger (1978) suggests that selection for flowering season displacement among Neotropical hummingbird plants is driven by pollen loss due to indiscriminate visits to heterospecific flowers rather than direct competition for pollinator attention. The same selective pressure may drive some *Psiguria* or *Gurania* to specialize on attracting the less heterogeneous pollen loads of *Heliconius* as an alternative to seasonal displacement as hummingbird specialists.

THE CUCURBIT FOOD WEB

Aside from hummingbirds and *Heliconius*, there are many other groups of organisms which consistently associate with *Psiguria* and *Gurania* over their ranges (Condon & Gilbert 1990). Of direct importance to *Heliconius* are coreid bugs (e.g., *Paryphes*), pickleworm moth larvae (*Dia-phania*), and tephritid flies (*Blepheneura*) all of which may reduce pollen availability and affect *Heliconius* population dynamics in short ecological timeframes (Gilbert 1977). Recently, Murawski (1987) has attributed decline in *Psiguria* flower production in Costa Rica to the loss of storage roots to pocket gophers *Orthogeomys*. By contrast, other mammal species such as bats which disperse the seed of *Psiguria* and *Gurania* (Condon & Gilbert 1990) are important in maintaining the metapopulations of these vines on a longer timeframe.

A line of questions and observations focused on *Heliconius* population dynamics has opened a pathway into a previously unexplored part of Neotropical biodiversity centered on *Psiguria* and *Gurania*. The resulting scrutiny has corrected a major misconception about sex expression in these plants (Condon & Gilbert 1988) and has led to the discovery by Condon of a remarkable adaptive radiation of the tephritid genus *Blepheneura*, different species of which may specialize on male flowers, female flowers, fruits, and stems of *Psiguria* and/or *Gurania* (Condon in prep., Condon and Steck in prep.).

Many elements of the *Psiguria/Gurania*-based network, including hummingbird pollinated species of these genera, have little direct relevance to understanding the ecological dynamics of *Heliconius* communities, and their ecology is reciprocally unaffected by *Heliconius*. Likewise a subset of *Heliconius* species tends to be more facultative in relation to use of *Psiguria/Gurania* and utilize an array of generalist plants with small pollen. However some of these, such as *H. charitonia* in rainforests of Corcovado Park, may be negatively affected by *Psiguria* since the *Heliconius* species supported by *Psiguria* also compete for the floral resources, such as *Lantana*, to which *H. charitonia* is restricted (Gilbert 1984).

In spite of the fact that many potential links between the cucurbit network and the *Heliconius* community are probably indirect, weak, or non-existent, there remain core pathways of di-

rect and, as noted below, strong indirect interactions between these two units of biodiversity involving species of *Heliconius* and *Psiguria* or *Gurania* which I interpret to be a coevolutionary vortex emerging from a complex network of diffuse interactions.

CUCURBIT POLLEN AND PASSIFLORA BIODIVERSITY

With or without pollen plants, *Heliconius* would not live as breeding populations in an area without larval host of the genus *Passiflora* present and numbers of *Passiflora* species correlate with numbers of *Heliconius* present in rainforest habitats (Gilbert & Smiley 1978). *Heliconius* larvae can be characterized as specialists on new shoots. By comparison, non-pollen feeding genera of the heliconiine tribe typically utilize older leaves of Passifloraceae (Benson 1978).

Comparisons of pollen feeding and non-pollen heliconiine feeding species which utilize the same larval host group have provided some clues as to the impact of that trait on interactions with larval host plants. Several pathways should be considered. From a strictly ecological point of view, the impact of *Heliconius* on host *Passiflora* is more uniform through time because egg laying adults are maintained by pollen plants, and *Psiguria*, through its support of *Heliconius*, has an indirect negative impact on *Passiflora* which share the same habitat (Gilbert 1977).

Other ways that the evolution of pollen feeding affects the *Heliconius-Passiflora* interaction are directly or indirectly related to correlated evolution in the behavior, physiology, and reproductive biology of *Heliconius*. Since nutrients in pollen account for 80% of the lifetime reproduction of a female, inter- and intraspecific competition for this resource has given rise to sophisticated foraging ability (Gilbert 1975). The capacity for spatial and visual memory evolved principally under selection for improved pollen gathering would simultaneously improve efficiency of search for oviposition site by female *Heliconius*. Such capacity for visually locating hosts (found initially by an inefficient process of olfactory orientation and tarsal tasting of leaves) has become one component of natural selection on the foliage morphology of *Passiflora*, and one important cause of leaf shape diversity of this genus (Gilbert 1975; Gilbert 1982; Gilbert 1991).

Shape discrimination and learning are necessary, but not sufficient, attributes which these herbivores must possess in order to impose such selection. How, for example, would pollen feeding enhance the impact of *Heliconius* on differential survival and reproduction of *Passiflora* in relation to leaf shape (Gilbert 1975; Gilbert 1982)? Since the oviposition choices of females are most likely to have a selective impact on small plants and seedlings, it is also important to consider ways that pollen feeding promoted specialization on small parcels of host. First, because of amino acids derived by adults from pollen and resulting life history evolution (Dunlap-Pianka *et al.* 1977), the feeding activity of *Heliconius* larvae contributes little to the resources stored and passed along for adult reproduction. Consequently, it is safe to assume that these insects require less host leaf matter and less time to pupation than non-pollen feeding heliconiines of equal adult body size. Second, the combination of foraging ability and ability to develop on small parcels of host makes seedlings and new shoots of *Passiflora* a viable larval feeding niche for *Heliconius*.

Small, scattered *Passiflora* seedlings in forest light gaps which would escape heliconiines orienting to larger mature plants, are effectively found by species of *Heliconius* which forage for larval hosts in primary rainforest understory. While individual leaf shapes are lost in the gestalt of larger plants, leaf shapes are the dominant visible characteristics of smaller juveniles. Moreover, single *Heliconius* larvae can severely damage, if not kill, small plants (Longino 1984) so that the relationship of forest *Heliconius* to these hosts is closer to predator-prey rather than parasite-host interaction.

Selection for local divergence in leaf shape among *Passiflora* species requires that individual female butterflies of a *host generalist species* learn to search for particular leaf shape of suitable *Passiflora* based on frequency of encountering of *shape*, not *species* (Fig. 3). Only *Passiflora* seedlings with novel leaf shapes would be able to invade the system (Gilbert 1975; Gilbert 1982). It is interesting to note that some of the most common *Heliconius* species which dwell in rainforest understory, *H. cydno*, *H. pacheus* (Central America, northern South America) and *H. numata* (Amazonian forests) are all highly generalized within populations in use of *Passiflora*. They lay eggs singly and avoid host plants bear-

ing previously laid eggs (Williams & Gilbert 1981). Consequently females of these more oligophagous species continually search for new plants, a behavior which contrasts sharply with the behavior of monophagous species, such as *H. hewitsoni*, which place egg clusters on larger plants to which they may return repeatedly over several months (Gilbert 1982; Longino 1984).

Across all environments where heliconiines interact with *Passiflora*, morphological convergence on common non-passifloraceous plants can also be found (Gilbert 1975). This constitutes a form of crypsis, reducing the apparency of the *Passiflora* to searching butterflies and to biologists. My technique for finding the 9–12 *Passiflora* species expected in an unfamiliar rainforest site is to constantly examine the most common vines. For example, this technique worked in the discovery of *P. multiflora* on Key Largo, Florida and *P. mucronata* on Isla do Cardoso, Brazil. Each is virtually identical to local *Smilax* species!

If *Heliconius* diversity is correlated with *Passiflora* diversity, to what extent is the interaction of herbivore and plant generating the biodiversity of the system? Spencer (1988) has suggested that the cyanogenic glycoside system of *Heliconius* functions to defeat that of the plant. He showed that cyanide release by crushed *Passiflora* leaves is inhibited by larval gut juices of *Heliconius* which feed on the plant, and suggested that glycosidase enzymes of the butterfly competitively inhibit those of the plant. It is possible that chemical as well as morphological diversification of the plants has accelerated recently in response to the explosive radiation of pollen feeding heliconiines. The amino acids available from this diet allow much higher levels of cyanogenesis in *Heliconius* and thus greater capacity to coevolve chemically with *Passiflora*. Greater niche diversity for *Heliconius* may result.

The phenomenon of egg mimicry (Gilbert 1982) is an important model for what might be discovered at the level of chemical coevolution. Just as local populations of *Passiflora* have responded by evolving fake eggs at least 7 independent times (based upon the morphological origin of mimetic eggs) (Gilbert, unpublished observation), so too might novel chemical defenses, evolved in response to *Heliconius*, map across the evolutionary landscape of *Passiflora* in a way that would show how and why tropical biodiversity evolves. Because *Heliconius* undoubtedly encoun-

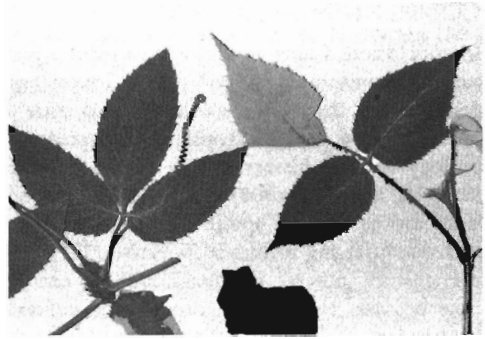
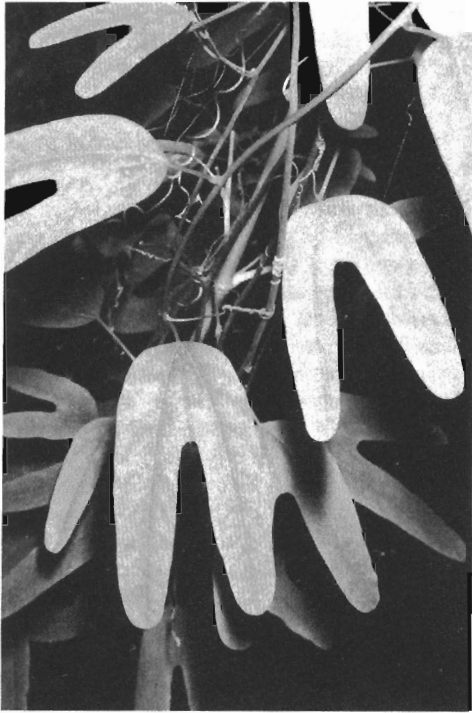


FIG. 3. Leaf shape in *Passiflora*
 a (left). The leaf shape of this *Passiflora* species is best interpreted with respect to its departure from leaf shapes of sympatric species in the same clade.
 b (right). This *Passiflora* leaf shape is best explained as converging on non-*Passiflora* species and would be cryptic to visual search. This montane *Passiflora trisecta* (left) grows with a visually identical *Rubus* (right) in the Andes near Cusco, Peru. (Linda Escobar Collection 1312, University of Texas Herbarium.).

tered the Passifloraceae after its major lineages had differentiated (Benson *et al.* 1976; Mitter & Brooks 1983), coevolution to date is not co-radiation or co-speciation (yet) but co-microevolution or co-adaptation (Benson *et al.* 1976).

THE PASSIFLORA FOOD WEB

To complete the picture of the biodiversity network defined by attempting to understand *Heliconius* population biology, it is useful to describe a local *Passiflora* system, such as that in Corcovado Park, Costa Rica. The nine sympatric *Passiflora* species support 19 heliconiines (6 genera) of which 9 are *Heliconius*. Other specialists in the network are 18 species of flea beetle, two coreid bugs, and two dioptid moths. Except for leaf cutter ants (*Atta*) there are virtually no generalist herbivores of importance. Parallel studies of *Passiflora* flea beetles (Duckett 1987; Duckett 1989; Smiley 1982; Thomas 1987) provide an interesting comparison to the heliconiine perspective.

Relatively little is known of comparative pollination biology, seed dispersal, and demo-

graphy of *Passiflora* other than the fact that hummingbirds, bats, and bees are pollinators, and birds and mammals disperse the seeds. Other than *Atta* and hummingbirds which might visit both *Passiflora vitifolia* and *Psiguria warscewiczii*, there are few connections between the faunal networks on these plants — except of course for the very important connection through *Heliconius*.

A network of predaceous ants, wasps, and parasitic microhymenoptera visit the extrafloral nectaries of *Passiflora*, which they defend against herbivores. Longino (1984) found 75 species of ants visiting the extrafloral nectaries of *Passiflora pittieri* at Sirena in Corcovado Park, Costa Rica. This diffuse mutualism is another part of the population constancy puzzle discussed at the outset. Nectary patrolling ants provide a constant mortality unaffected by changes in butterfly density. Assuming that they take parasitized and unparasitized eggs and larvae indiscriminately, they would tend to damp potential population oscillations of specialist parasitoids and host *Heliconius* (Gilbert 1977).

CONCLUDING REMARKS

In conclusion, I have endeavored to paint a picture of one example of biodiversity. I have suggested, using the example of *Heliconius*, that a foundation of phytophagous insect population biology and life history is an effective tool for mapping an evolutionary food web. Such food webs are defined by specificity of interactions and potential for reciprocal selective effects by participants, not by the magnitude of energy flow between them. They provide the context for studies of both the evolution and maintenance of biodiversity. In the past I have discussed this system from the point of view of how a single *Heliconius* population is regulated (Gilbert 1977) with respect to the diversification of insect faunas (Gilbert & Smiley 1978), with respect to butterfly community biology (Gilbert 1982), with respect to coevolution and mimicry (Gilbert 1982; Gilbert 1983), and in respect to the organization of rainforest diversity and conservation biology (Gilbert 1980). The ideas and concepts developed in these papers are as much a product of natural history and intuition as of data and experiment. A balance of imagination (theory) and data seems the only viable tactic for understanding the structure of tropical biodiversity.

In spite of the complexity of the network of species and relationships I have described, this system is but a small part of the total biodiversity of a Neotropical rainforest. *Passiflora* and *Psiguria* constitute less than 1% of plant species in most rainforests and their contribution to biomass would be substantially less. Nevertheless, I am confident that the type of evolutionary food web I have described here provides the pathway to defining, understanding, and managing biodiversity. I am also convinced that research on the demography and behavioral ecology of component species of locally diverse genera is an effective way to begin to understand patterns at the community and food web levels. For those at the stage of contemplating field studies for thesis work, this approach assures a manageable project with the power of comparative biology and the promise of expansion to studies of more complex levels from a solid base of natural history and population biology.

Whether to study communities from the top down (Pianka 1992) or from the bottom up as I am suggesting, is particularity critical for those initiating studies in the evolution of community

and food web interactions and patterns. For the beginning researcher with constraints of time and finances, the choice may be as much practical as philosophical.

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