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*Ecology*, Volume 77, Issue 6 (Sep., 1996), 1906-1919.

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## LOCAL COMMUNITIES OF ARBOREAL HERBIVORES IN PAPUA NEW GUINEA: PREDICTORS OF INSECT VARIABLES<sup>1</sup>

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**Abstract.** As a contribution to enlarging and widening the array of studies available for examination of insect–plant relations, this study contrasts local and regional predictors of species richness and host specificity of leaf-chewing insects feeding on New Guinea trees. I tested the degree to which the variance in local insect variables (species richness, ratio of specialist to generalist chewers, abundance, and biomass) for leaf chewers associated with different species of tropical trees was accounted for by local and regional host-related variables, and by local abundance of potential enemies. Leaf-chewing insects feeding externally on ten species of forest trees were collected over a 1-yr field study in a submontane area in Papua New Guinea. The tree species were taxonomically distant, and the list included species of different successional status, different patterns of leaf production, and different heights. The affinity of chewing insects with particular tree species was ascertained by feeding trials in the laboratory. Local insect species richness varied greatly among tree species, by more than four-fold between the poorest (18 species) and the richest (94 species) tree species. The proportion of specialist insect species associated with particular tree species was significantly different among tree species and ranged from 16 to 72%. Trees supporting a rich fauna usually also supported a high proportion of specialists. The abundance and biomass of leaf-chewing insects per host species was difficult to predict. However, path analyses showed that most of the causal variance in insect species richness and in the ratio of specialist to generalist chewers was accounted for by five properties of the tree species: numbers of young leaves available throughout the year, ant (i.e., enemy) abundance, leaf palatability, leaf water content, and altitudinal range. Most of the variation in local species richness could be predicted from local processes (i.e., food resources and abundance of enemies), not from regional processes. This study and others suggest that in complex environments, such as tropical rain forests, local processes may be comparatively more important in maintaining the local species richness of insect herbivores than in less complex ones, such as temperate woodlands. The implications of these findings are evident: the effects of moderate habitat fragmentation and ecological stress may be more pronounced in tropical systems than in temperate systems and may result in a greater proportional loss of local biodiversity in the former.

*Key words:* ants; host specificity; insects; insect–plant interactions; leaf production; Papua New Guinea; species richness.

### INTRODUCTION

Models accounting for the differing loads of insect herbivores on their host plants are still few. Determinants of the species richness and host specificity of insect herbivores can be grouped into three categories: (a) history of speciation within insect taxa and of interactions between insects and their hosts (geographical and phylogenetic history, e.g., Farrell et al. 1992), (b) host-related variables and their relations with disturbance and abiotic factors (e.g., Lawton and Schröder 1977, Zwölfer 1987, Maddox and Root 1990), and (c) abundance and foraging efficiency of predators and parasitoids (e.g., Bernays and Graham 1988). The fraction of the variance in insect species richness and host spec-

ificity explained by each of these categories is difficult to quantify (e.g., Farrell et al. 1992).

Research has often focused on predictors of insect species richness at the regional scale on particular hosts (see recent review in Jones and Lawton 1991) and on predictors of insect host-specificity within particular insect taxa (e.g., Futuyma 1991). Regional and local processes (sensu Cornell 1985) have been contrasted recently in studies of herbivore species richness (e.g., Cornell 1985, Compton et al. 1989, Basset and Burckhardt 1992). At the regional scale, species richness is thought to be influenced predominantly by biogeographical processes such as past climatic history, speciation rates, widespread extinction, and geographical position of dispersal barriers and corridors. On the other hand, local species richness depends both on biogeographical and ecological processes, the latter including predation, parasitism, competition, disturbance, and abiotic fluctuation (Ricklefs 1987, Cornell and Lawton 1992). Many natural communities, partic-

<sup>1</sup> Manuscript received 25 May 1995; revised 27 November 1995; accepted 7 December 1995.

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ularly insects on plants, appear to be unsaturated and non-interactive, implying that the size of local assemblages should be strongly dependent on the size of regional pools (Cornell and Lawton 1992). However, most of the data supporting this theoretical idea, and particularly the influence of regional variables at the local scale, have been gathered from temperate environments. Further, few studies have considered regional and local factors simultaneously (review in Cornell and Lawton 1992).

The local importance of certain ecological factors in tropical ecosystems, particularly in rain forests, also demands attention. For example, habitat diversity and disturbance (Connell 1978, Shmida and Wilson 1985), predation and parasitism (e.g., Janzen 1983), temporal heterogeneity of resource availability (Shmida and Wilson 1985, Lewinsohn 1991), and local specialization (Fox and Morrow 1981, Cornell 1985) may number among the local processes that could weaken the relationship between species richness at the regional and the local scales (Cornell 1985) in complex tropical systems. Hence, studies of species richness at the local scale may help us to untangle some of the patterns behind the complexity of tropical ecosystems, and to predict the escalating effects of the fragmentation of natural habitats. However, such studies are few and focus almost exclusively on the Neotropics (e.g., Cytrynowicz 1991, Lewinsohn 1991, Marquis 1991). Furthermore, local studies are almost obligatory in the tropics, for tropical faunas are poorly known, both at the regional and local scales (Cytrynowicz 1991, Lewinsohn 1991).

The present study reports on host-related variables and enemy abundance as predictors of insect species richness and host specificity at a tropical site. Its specific aims were (a) to document the local species richness, host specificity, abundance, and biomass of leaf-chewing insects feeding externally on ten tropical tree species belonging to different plant families in Papua New Guinea; and (b) to test whether a substantial proportion of the variance in these different insect variables could be explained by selected host-related variables (accounting for both regional and local processes) and the local abundance of potential enemies. As far as possible, I tried to contrast biogeographical and local variables. A strict protocol with similar sampling effort on each host plant during a 1-yr field study ensured valid comparisons of species richness among host plants. However, as the reader will appreciate, my conclusions are clearly limited by the number of trees sampled, as the amount of work needed to document each data point is considerable. Other important variables describing these insect communities, such as the identity of the insect species, their diet breadth, and the relationships between species richness, species abundance, and body size, are important and will be detailed elsewhere.

## METHODS

### *Study area and study plants*

Sampling was performed on the slopes of Mount Kaindi, near and within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7°24' S, 146°44' E). Altitude of collecting ranged from 1100 to 2362 m (summit), but was mostly confined around 1200–1400 m. Mt Kaindi has been cleared locally, leaving a mosaic of grasslands and forest patches, dominated by secondary forest (Van Valkenburg and Ketner 1994). The main forest formations encountered on the slopes include lower and mid-montane rain forest (Johns 1982). The climate is "humid to perhumid mesothermal with little or no water deficit" (McAlpine et al. 1983). The study area is further detailed by Gressitt and Nadkarni (1978) and Van Valkenburg and Ketner (1994).

Ten woody plant species (native forest trees and shrubs) were studied (Table 1). Criteria for choosing these species included: (a) they were common within the Mt Kaindi area; (b) they were representatives of ten different plant families; and (c) they included species of different successional stage, different leaf production patterns, and different height. Hereafter, they are designated by their generic names.

### *Insect sampling*

Leaf-chewing insects feeding externally (i.e., most of Lepidoptera larvae; some adults and larvae of Curculionidae, Chrysomelidae, and other beetles; some larvae and adults of Orthoptera and Phasmatodea) were collected from the foliage of the study trees. Sampling was performed almost continuously from February to July 1992 and from November 1992 to April 1993. Insects were collected alive during both day and night by hand-collecting, beating, and branch-clipping. When the foliage of trees could not be sampled from the ground, the single-rope technique provided access to the crowns (Perry 1978). Sampling effort was the same for each tree species (300 beating samples, ≈33 m<sup>2</sup> of foliage clipped, and 50 h of hand-collecting distributed among different individual trees, for each tree species).

### *Assessment of abundance of herbivores and of potential enemies*

Branch clipping was also used to estimate the relative abundance and biomass of leaf-chewing insects, as well as the abundance of potential arthropod enemies (population intensities, sensu Southwood 1978) and new leaf production. For each tree species, 55 branch-clipping samples were obtained from various individual trees, at different times of the year, both during day (40 samples) and night (15 samples). A few branches were enclosed in a 110-L heavy-duty plastic bag, the branches were clipped off, and the contents of the bag examined in the laboratory. Arthropods were counted

TABLE 1. Characteristics of tree species examined in a study of communities of leaf-chewing insects in Papua New Guinea. †

Hosts	Plant family	Status	Expansion (no. days)	Palatability score	Nitrogen (% DM)	Leaf production
<i>Elmerrillia tsiampacca</i> (L.) Dandy	Magnoliaceae	Pe	29.6 ± 1.8	22.13 (n = 247)	1.69	Continuous
<i>Cinnamomum cf. culilaban</i> (L.) Presl	Lauraceae	Pe	35.5 ± 0.3	15.94 (n = 247)	1.31	Intermittent leaf flushes‡
<i>Piper plagiophyllum</i> K. Sch. and Laut.	Piperaceae	Pi	20.7 ± 1.5	6.52 (n = 242)	3.68	Continuous
<i>Ficus nodosa</i> Teys. and Binn.	Moraceae	Pi	24.2 ± 0.4	40.55 (n = 243)	1.78	Deciduous, leaf flushes‡
<i>Pipturus argenteus</i> Wedd.	Urticaceae	Pi	32.5 ± 1.0	12.14 (n = 246)	2.68	Continuous
<i>Castanopsis acuminatissima</i> A. DC.	Fagaceae	Pe	26.5 ± 0.6	19.97 (n = 243)	1.60	Intermittent leaf flushes‡
<i>Caldcluvia brassii</i> Hoogl.	Cunoniaceae	Pi	70.0 ± 3.3	21.77 (n = 247)	1.17	Continuous
<i>Aleurites moluccana</i> Willd.	Euphorbiaceae	Pe	34.9 ± 4.0	31.32 (n = 246)	2.24	Continuous
<i>Melicope denhamii</i> (Seem.) T. Hartley	Rutaceae	Pe	26.2 ± 0.9	15.49 (n = 243)	2.26	Intermittent leaf flushes‡
<i>Cordia dichotoma</i> Forst.	Boraginaceae	Pi	19.8 ± 0.4	26.86 (n = 244)	3.42	Deciduous, leaf flushes‡

† Plant family, successional status (Pi = pioneer; Pe = persistent), leaf expansion time (mean ± 1 SE), leaf palatability score (range 0–100; n = no. morphospecies tested), total N content of mature leaves, and leaf-production phenology.

‡ Apparently 2–3 times a year, as a synchronous event.

and assigned to feeding guilds as in Basset (1991b). Herbivore morphospecies were measured (up to ten individuals measured for each morphospecies) and the biomasses of individuals estimated using the regressions on body length (in millimetres) and insect biomass (in grams of dry mass) computed by Schoener (1980) for tropical rain forest insects. The abundance of potential enemies was estimated by recording the number of ants, other insect predators, insect parasitoids, and spiders found in the samples. The leafy parts of the samples were oven-dried for 24 h at 100°C. Previously established highly significant regressions (Y. Basset, unpublished data) between leaf mass and leaf area for each tree species were used to compute the total leaf area of the sample. Since the sample size of leaf area varied little among individual trees and species, catches were not corrected for sample size.

#### Assessment of insect host-specificity in captivity

Since plant diversity is high in tropical habitats, delineation of the host range for a particular insect species is likely to require years of massive sampling (Marquis 1991). Instead, host range was predicted from feeding trials in laboratory conditions. Live chewing insects were stored in plastic vials, at room temperature and in conditions of near-saturated relative humidity. They were provided with fresh foliage of the tree species from which they were collected, until they died or accepted food. In the latter case, insects were assigned to morphospecies codes. This procedure (a) prevented inclusion of incidental morphospecies in the analyses (i.e., those resting on the foliage but not feeding); and (b) reduced the influence on the results of parasitized

specimens, or other insects with abnormal behavior. As far as possible, each assigned individual was tested once on another plant species over a 24-h period and then moved randomly to another plant species for a similar test, until the 9 other tree species under study had been provided. The number of specimens tested per morphospecies varied greatly, from one (if only one individual was collected) to several tens (if many were collected). Insects molting during trials were provided with the original foliage from which they were collected; these individuals were further tested once they resumed feeding. Both young and mature leaves were used in the trials, as seasonal availability of leaf cohorts permitted. Morphospecies assignment (hereafter termed "species" for sake of simplicity) was checked by taxonomists.

Feeding damage was scored visually on a logarithmic scale, as follows: 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding. This procedure emphasized regular feeding as compared to food-probing. To minimize possible differences among tested individuals of a particular species, and differences due to varying leaf age, the results of the feeding trials were judged as follows: for a particular species, the highest score recorded for any individual of that species, regardless of leaf age, was the score assigned to that species. Insects were assigned to three categories according to the results of these feeding tests: (a) "specialists," i.e., insects tested on three or more plant species but which only fed extensively on the plant from which they were collected (sum of feeding scores <100); (b) "generalists", i.e., insects tested on three or more plant species and which fed extensively on two

or more plants belonging to different plant families (sum of feeding scores  $\geq 100$ ); and (c) "uncertains," i.e., insects that because of death or pupation could not be tested on more than two plant species. The advantages and limitations of this procedure are discussed in Basset (1994).

*Selection and measurement of potential predictors of insect variables*

Insect variables that I attempted to predict included local species richness, local percentage of specialist species (i.e., ratio of specialist species to all leaf-chewing species, excluding "uncertains"), and local abundance and local biomass of leaf-chewing insects. Numerous host-related factors may influence these variables. I selected independent variables on the basis of a priori relationships with insect species richness that have been previously established or that could be expected at a tropical site. These independent variables included:

*A) Regional variables.*—The following represent historical variables that have been found to be important determinants of regional richness of insect species on British plants (e.g., Lawton and Price 1979, Kennedy and Southwood 1984, Leather 1986):

1) *Taxonomic isolation of the host.* This was determined as the number of confamilial plant-species reported in New Guinea (Höft 1992).

2) *Age of plant family.* As time since establishment in New Guinea was not available for any of the tree species studied, I considered the age of each plant family as a surrogate for this variable. This was determined as the first fossil pollen record, in units of  $10^6$  yr before the present (Muller 1981).

3) *Geographical distribution.* This was calculated as the sum of areas of states in Southeast Asia, Australia, and the Pacific where the tree species has been reported. The distribution was inferred from the following floras: Hawaii: Wagner et al. 1990; Malaysia: Burkill 1935; Vietnam, Laos, Cambodia, and Thailand: Lecomte 1907–1951; Japan: Ohwi 1965; Australia: Bodkin 1986; Fiji: Parham 1972; Philippines: Merrill 1926. Since no complete flora was available for Indonesia, I obtained information for this country using the records of the Bishop Museum (Honolulu) herbarium.

4) *Altitudinal range.* This represents a surrogate for the number of habitats in which the host grows, obtained from Streimann (1983).

*B) Local variables.*—

*B1) Variables related to leaf production.*—In recent years, patterns of leaf production have been emphasized as having an important impact on insect herbivores in the tropics (e.g., Aide 1993, Aide and Londoño 1989, Clark and Clark 1991, Basset 1991a). Since patterns of leaf production are particularly diverse in the tropics (e.g., Opler et al. 1980) and may vary locally (e.g., Koriba 1958), they may exert significant pressure

on local communities of tropical herbivores. I considered three variables:

5) *General pattern of leaf production.* This is shown via a dummy variable, which takes a value of 1 for a continuous production throughout the year, and 2 for intermittent leaf flushes.

6) *Number of newly emerged leaves/leaflets.* Total numbers as recorded over a 1-yr period in all branch-clipping samples.

7) *Leaf expansion.* The average number of days required to expand from bud burst to full mature size as measured by tagging leaves in the field (sample sizes ranging from 10 to 100 leaves).

*B2) Variables related to host architecture and abundance.*—I selected the following variables, which have been found to be important for insect herbivores in Europe (e.g., Lawton and Price 1979, Kennedy and Southwood 1984, Leather 1986, Basset and Burckhardt 1992):

8) *Mean tree height* ( $n > 15$  trees).

9) *Specific mass of mature leaves* (leaves oven-dried for 24 h,  $n = 11$  samples).

10) *Local host abundance:* from 1 (least abundant) to 4 (most abundant).

*B3) Variables related to simple aspects of plant chemistry.*—Examples of the importance of plant chemistry in insect-plant interactions are countless (e.g., reviews in Jones and Lawton 1991, Slansky 1992) and I selected the following variables, easily measurable:

11) *Mean water content of mature leaves* (leaves oven-dried,  $n = 11$  samples).

12) *Total foliar nitrogen of mature leaves* (Kjeldahl analysis, 3 samples pooled).

13) *Leaf palatability.* This was estimated by summing all scores obtained during the feeding experiments for a particular tree species and dividing this value by the number of insect species tested on leaves of this tree species. This index ranges from 0 to 100 and allows comparison among plant species. Since insects were tested but not scored on the hosts from which they were collected, palatability scores are independent of the number of insect species collected from the tree species considered. This variable is distantly related to plant chemistry (long-term effects such as those from digestibility reducers are not considered) and also accounts for some physical properties, such as leaf toughness. See further discussion of leaf palatability in Basset (1994).

*C) Other variables.*—

14) *Enemy abundance.* Another factor of particular importance in structuring communities of insect herbivores may be predation and enemy-free space (e.g., Jeffries and Lawton 1984). Generalist predators, particularly ants, may shape herbivore behavior (e.g., Bernays 1989) and this effect may be important in tropical

TABLE 2. Characteristics of chewing insect species found in a study of communities of these animals feeding on trees in Papua New Guinea.†

Hosts	No. species				Specialists		Chewers in clip samples‡	
	Spec.	Gen.	Unc.	Chw.	%	Ind.	No. inds.	Biomass (mg DM)
<i>Elmerrillia</i>	4	7	9	20	36.4	33	0.42 ± 0.12	1.09 ± 0.30
<i>Cinnamomum</i>	16	17	4	37	48.5	183	1.53 ± 0.47	5.74 ± 1.84
<i>Piper</i>	6	10	2	18	37.5	195	1.09 ± 0.16	2.51 ± 0.72
<i>Ficus</i>	36	21	4	61	63.2	209	1.69 ± 0.41	3.96 ± 0.99
<i>Pipturus</i>	24	16	12	52	60.0	490	3.16 ± 0.54	12.85 ± 2.67
<i>Castanopsis</i>	53	20	21	94	72.6	335	3.13 ± 0.60	8.44 ± 1.74
<i>Caldcluvia</i>	11	25	3	39	30.5	283	1.07 ± 0.17	7.96 ± 3.40
<i>Aleurites</i>	3	16	6	25	15.8	77	0.55 ± 0.12	1.39 ± 0.39
<i>Melicope</i>	13	20	3	36	39.4	108	0.47 ± 0.10	7.74 ± 2.16
<i>Cordia</i>	19	23	3	45	45.2	177	2.22 ± 0.32	5.80 ± 1.16
All trees	185	155	59	399	54.4	2090	1.53 ± 0.12	5.75 ± 0.59

† Number of species of specialists, generalists, uncertain, and all chewing insects combined, percentage of specialists in relation to all chewers (excluding uncertain), and number of individuals of specialist species, that were collected from the study trees.

‡ Number of leaf-chewing insects and their biomass (both as mean ± 1 SE) in branch-clipping samples. With all tree species combined, these 550 samples represented 5998.6 ± 108.8 cm<sup>2</sup> of double-sided leaf area.

environments, particularly in rain forests (e.g., Elton 1973, Fiala et al. 1989, Majer 1993). I used enemy abundance as the mean number of potential enemies recorded in branch-clipping samples, but later restricted this variable to ant abundance in these samples (see *Results*).

15) *Sampling effort*. Total no. of individual trees sampled for each tree species.

The most important variables are presented for each study tree in Table 1 and in the Appendix.

#### Statistical analyses

My statistical analyses included a three-step strategy. First, as an exploratory procedure to assess the strength of the a priori relationships considered in the previous section, I calculated Pearson correlation coefficients between all dependent and independent variables. Most of the variables used in the analyses satisfied the assumption of normality (Kolmogorov-Smirnov-Liliefors test,  $P > 0.05$ ) and were left untransformed; ant abundance was log transformed. The interpretation of simple correlations is complicated by the following problems: (a) inflated degrees of freedom because plant data are not independent from each other (Jones and Lawton 1991); (b) multicollinearity between independent variables; (c) the presence of both causal and non-causal correlations; and (d) the number of simultaneous tests being made. Thus, coefficients of determination and probability values reported in simple regression or multiple regression analyses may be greatly biased and thus necessitated further statistical analysis of my data.

As a second step, I selected independent variables on the basis of both strength of correlation and more explicit hypotheses, which are detailed in the results section. In the final step, I developed path analysis models with these selected variables and performed path analysis with the program "Piste" of Vaudor (1991). Path analysis has been routinely used for study-

ing predictors of insect species richness (e.g., Cornell 1986, Zwölfer 1987, Lewinsohn 1991) and abundance (e.g., Basset 1991c). It appeared to be the most informative method for exploring my questions. With my data set, the problem of inflated degrees of freedom [problem (a) above] was not serious, since I compared tree species belonging to different plant families. Although path analysis can better accommodate multicollinearity [problem (b)] than can multiple regression, its power can still be reduced when strongly intercorrelated independent variables are included in the model (Mitchell 1993). However, multicollinearity was relatively low among the set of variables that I chose for the path analysis (see Table 5). Path analysis can disentangle direct from indirect effects [problem (c)] and this represents one of the strengths of this technique (Sokal and Rohlf 1981). Simultaneous testing [(d)] of models and independent variables was more a problem for the testing of variables than for that of models (eventually, only two path models were worth calculating). Because my models included several independent variables and the sample size of my data set was low, I refrained from testing a posteriori the significance of path coefficients, since such significance tests may be suspect (Mitchell 1993). Thus, my approach uses path analysis as a descriptive tool and follows that of Crespi (1990) as considering path modelling as independent of testing for statistical significance. Presentation of path diagrams follows Mitchell (1993). My interpretations and conclusions rely mostly on the results of the path analyses.

## RESULTS

### *Species richness, abundance, and host specificity of leaf-chewing insects*

The species richness of leaf-chewing insects was more than four times greater on the richest (*Castan-*

*opsis*) than on the poorest hosts (*Piper*, *Elmerrillia*; Table 2). In general, the plots of cumulative number of species collected on each host against time began to level off at the end of the study year (Fig. 1). Thus, the sampling program probably detected most of the common species associated with the hosts at the time of sampling. However, herbivore species richness may have been underestimated on trees that had a pattern of intermittent leaf flushing. On these trees (see for example the data points in Fig. 1 forming obvious "steps" in the cases of *Cordia*, *Castanopsis*, *Cinnamomum*, and *Melicope*), new species were more likely to be discovered during leaf-flushing periods.

For all trophic categories and all tree species considered, the mean number of arthropods collected per branch-clipping sample (average 0.6 m<sup>2</sup> of leaf area) amounted to  $14.82 \pm 0.90$  individuals (mean  $\pm$  1 SE, of which  $6.75 \pm 0.48$  individuals were insect herbivores (chewing and sap-sucking insects). Loads of leaf-chewing insects, expressed either as number of individuals or as biomass, were significantly different among tree species (Table 2, Kruskal-Wallis  $W = 96.96$ ,  $df = 9$ ,  $P < 0.001$  and  $W = 72.69$ ,  $df = 9$ ,  $P < 0.001$ , respectively). The number of chewing species collected on a particular tree species was correlated with the number of individuals collected on this tree species ( $r = 0.79$ ,  $df = 8$ ,  $P < 0.01$ ).

In laboratory conditions and for all tree species considered, 54.4% of species of chewing insects behaved as specialists (185 species out of the 340 that could be assigned either to specialist or generalist categories; Table 2). Significant differences in the ratio of specialist to generalist chewers were evident between study trees ( $G$  test,  $G = 39.9$ ,  $df = 9$ ,  $P < 0.001$ ), with the highest proportion of specialists being found on *Castanopsis* (72.6%), and the lowest on *Aleurites* (15.8%). Interestingly, there were strong correlations between the overall number of chewing species and both the number of specialists ( $r = 0.980$ ,  $df = 8$ ,  $P < 0.001$ ) and the ratio of specialists to all chewers ( $r = 0.835$ ,  $df = 8$ ,  $P < 0.01$ ). This suggests that trees with a rich fauna also supported a high proportion of specialist species.

#### *Abundance of arthropod enemies*

Despite the fact that predaceous mites and parasitic Hymenoptera were probably underestimated in branch-clipping samples (see Basset et al. 1992), most enemy categories differed significantly among tree species (Table 3). Ants represented most of the potential invertebrate enemies and  $\approx 25\%$  of all arthropod individuals collected from branch-clipping samples when all tree species were pooled. This figure was similar in samples derived from pyrethrum knockdown (Y. Basset, unpublished data). However, ant loads in branch-clipping samples ranged from 1.4% (*Caldcluvia*) to 57.7% (*Castanopsis*) of all arthropods collected. The abundance of ants was slightly higher on intermittently

flushing trees than on trees producing leaves continuously (Mann-Whitney two-sample test,  $U = 3.00$ ,  $df = 1$ ,  $P < 0.05$ ). Ants were the only category of potential enemies to show this trend. I used ant abundance as the enemy variable in correlations and path models.

#### *Predictors of insect variables*

Pearson correlation coefficients between insect variables and independent variables are presented in Table 4. Most of the a priori relationships were weak, particularly those involving the abundance and biomass of leaf-chewing insects. Predicting these two variables appeared particularly difficult and I did not attempt path analyses with them.

The species richness and ratio of specialist species appeared more clearly influenced by the number of young leaves recorded in clipping samples. In particular, a variable accounting for the resource base provided over the course of a year by each tree species (as defined by [the number of young leaves recorded during that year]  $\times$  [leaf palatability]) represented the best single predictor of the number of chewing species collected ( $r = 0.935$ ,  $df = 8$ ,  $P < 0.0001$ ). The positive relationship with ant abundance further suggested that ants spent more time foraging on tree species with high herbivore loads. Therefore, I based my path analysis model (diagram in Fig. 2) on a chain of logical interactions between the variables accounting for the resource base, leaf production, ant abundance, and two other variables with relatively high correlation coefficients, altitudinal range and leaf water. Multicollinearity among these various variables was relatively low (Table 5) and the variance explained in the regressions involving correlated variables was never  $>90\%$  (Wootton 1994). I assumed that the same general paths could be considered to predict both the number of species and the ratio of specialist to generalist chewers, but that the magnitude of the direct effects (path coefficients) would be different. The following logical assumptions were used to build these models:

a) Since higher leaf turnover rates exist in deciduous than in evergreen trees (e.g., Mooney and Gulmon 1982), patterns of leaf production could influence the number of young leaves produced throughout the year, which in turn, could influence the number of chewing species present; leaf production patterns could also have a direct influence on the number of chewing species.

b) Ant foraging affects the number of chewing species present.

c) Ants may forage preferably where abundant prey are available (on young leaves), therefore leaf production patterns and number of young leaves may influence ant abundance directly.

d) Leaf palatability and water content influence the numbers of chewing species present; subtle interactions (correlations) exist between leaf water and the number

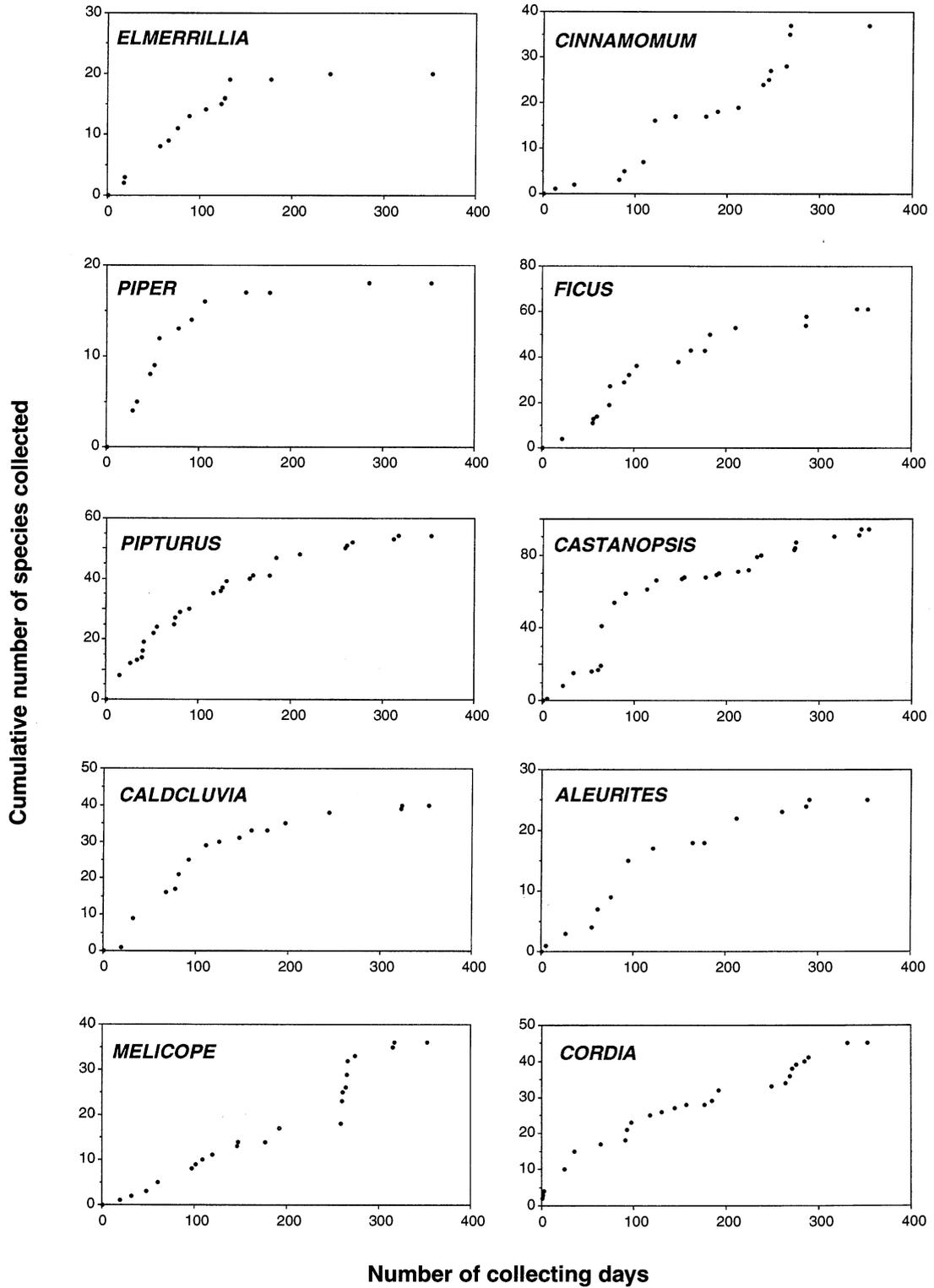


FIG. 1. Cumulative number of leaf-chewing species collected on each tree species over the course of the study.

TABLE 3. Abundances of enemies of leaf-chewing insects foraging on the study trees (given as number of individuals per branch-clipping sample) in Papua New Guinea. Data are means  $\pm$  1 SE.

Host	Ants	Arthropod predators	Insect predators	Insect parasitoids	All enemies
<i>Elmerrillia</i>	0.93 $\pm$ 0.35	1.15 $\pm$ 0.21	0.80 $\pm$ 0.17	0.04 $\pm$ 0.03	2.91 $\pm$ 0.44
<i>Cinnamomum</i>	4.89 $\pm$ 2.19	2.44 $\pm$ 0.39	0.15 $\pm$ 0.06	0.11 $\pm$ 0.04	7.58 $\pm$ 2.25
<i>Piper</i>	2.75 $\pm$ 0.92	1.84 $\pm$ 0.31	0.55 $\pm$ 0.14	0.04 $\pm$ 0.04	5.16 $\pm$ 0.93
<i>Ficus</i>	4.11 $\pm$ 1.19	0.93 $\pm$ 0.13	0.38 $\pm$ 0.08	0.04 $\pm$ 0.03	5.45 $\pm$ 1.22
<i>Pipturus</i>	4.49 $\pm$ 2.37	3.04 $\pm$ 0.34	0.29 $\pm$ 0.07	0.02 $\pm$ 0.02	7.84 $\pm$ 2.38
<i>Castanopsis</i>	12.25 $\pm$ 4.32	1.64 $\pm$ 0.29	0.27 $\pm$ 0.08	0.05 $\pm$ 0.03	14.22 $\pm$ 4.43
<i>Caldcluvia</i>	0.18 $\pm$ 0.07	1.24 $\pm$ 0.17	0.27 $\pm$ 0.09	0.04 $\pm$ 0.04	1.73 $\pm$ 0.18
<i>Aleurites</i>	0.58 $\pm$ 0.33	1.27 $\pm$ 0.21	0.58 $\pm$ 0.15	0.13 $\pm$ 0.06	2.56 $\pm$ 0.50
<i>Melicope</i>	3.07 $\pm$ 1.61	1.60 $\pm$ 0.26	0.78 $\pm$ 0.21	0	5.45 $\pm$ 2.64
<i>Cordia</i>	3.78 $\pm$ 2.64	1.38 $\pm$ 0.15	0.35 $\pm$ 0.08	0.11 $\pm$ 0.05	5.62 $\pm$ 2.66
Kruskal-Wallis W	54.52	45.07	25.48	13.00	36.23
P (df = 9)	<.001	<.001	<.001	= .16	<.001
All trees	3.70 $\pm$ 0.68	1.65 $\pm$ 0.09	0.44 $\pm$ 0.04	0.05 $\pm$ 0.01	5.85 $\pm$ 0.70

of young leaves produced, as well as between leaf water and leaf palatability.

e) Tree species widely distributed altitudinally support more chewing species (increase of the local pool of species available); and young foliage is more readily available on tree species widely distributed altitudinally (possible asynchronous flushing throughout the year).

In the model for the number of species collected (Table 6a), the following direct paths were important (as judged by the magnitude of path coefficients): number of young leaves, leaf water content, and leaf palatability. In the model for the specialist ratio (Table 6b), the important paths included ant abundance, number of young leaves, altitudinal range (negative path), and unexplained factors. A high proportion of variance was explained in both models (96 and 84%, respectively).

## DISCUSSION

### *Sampling insect herbivores on tropical foliage*

One complication in this study was the considerable amount of work needed to document each data point

reliably (i.e., the insect variables associated with each host-tree species). As a result, the sample consisted of only 10 data points (10 tree species) and the interpretation of statistical analyses could not be straightforward. Under these circumstances, my conclusions remain tentative. However, the insect data for each tree species are unprecedented, as far as whole communities of insect herbivores feeding on wild tropical trees are concerned. During the last 20 yr, sampling insects on tropical vegetation has often been associated with the use of canopy-fogging techniques (e.g., Erwin and Scott 1980). Although there is no doubt that these techniques have greatly improved our taxonomic knowledge of canopy insects, they may be less appropriate to study insect host specificity since (a) in most instances specimens cannot be obtained alive; (b) the origin of the specimens is difficult to trace with precision, particularly when sampling the entangled foliage of different trees and vines; and (c) frequent diurnal, seasonal, and spatial replicates of individual trees are time-consuming and costly to obtain (Basset et al., *in press*). The present study overcame these lim-

TABLE 4. Coefficients of correlation (df = 8) between insect variables and independent tree variables in a study of leaf-chewing insects feeding on trees in Papua Guinea.

Independent variables	Insect variables			
	No. chewer species	Specialist ratio	Abundance	Biomass
1) Taxonomic isolation	-0.268	-0.346	-0.183	-0.174
2) Age	0.311	0.317	0.369	-0.198
3) Geographical distribution	0.364	-0.023	0.267	-0.041
4) Altitudinal range	0.697	0.440	0.463	0.531
5) Leaf flush	0.556	0.555	0.283	0.169
6) Young leaves	0.891	0.704	0.678	0.575
7) Leaf expansion	-0.098	-0.355	-0.183	0.230
8) Tree height	0.250	0.121	-0.035	-0.526
9) Leaf mass	0.088	-0.092	-0.251	0.106
10) Abundance	0.524	0.471	0.475	0.745
11) Leaf water	-0.477	-0.290	-0.135	-0.269
12) Leaf nitrogen	-0.279	-0.102	0.112	-0.076
13) Leaf palatability	0.225	-0.003	-0.093	-0.348
14) Log of ant abundance	0.588	0.809	0.645	0.315
15) Sampling effort	-0.211	-0.264	-0.165	0.325

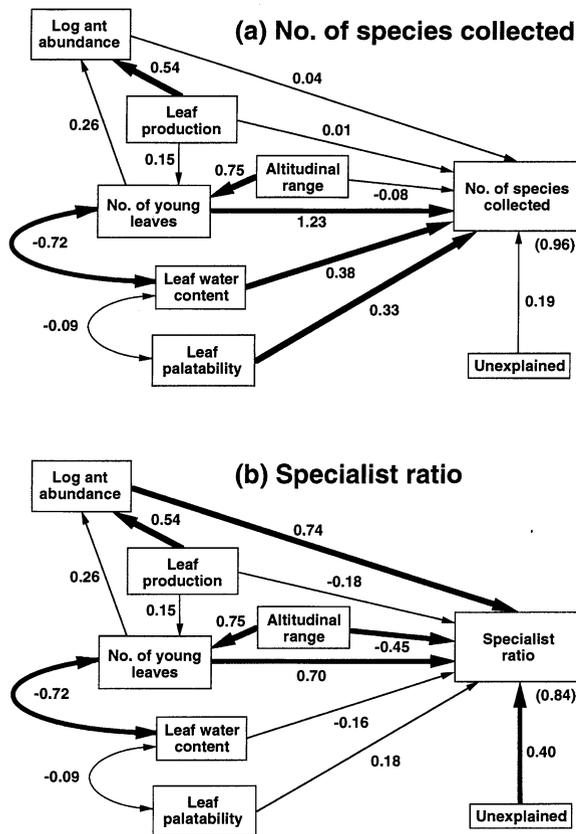


FIG. 2. Path analysis diagrams for (a) the number of leaf-chewing species collected; and (b) the ratio specialist : specialist + generalist chewing species. Path (direct effects) and correlation coefficients are indicated for each interaction, along with the coefficient of determination of the model (in brackets). A one-headed arrow indicates a causal interaction of one variable on another; a double-headed arrow indicates a correlation. Major interactions (coefficients > 0.30) are drawn with a thick line. See also Table 6.

itations and represents one of the very first attempts to predict insect variables on different species of wild tropical trees.

Despite the field study being limited to one year, the combination of hand-collecting, beating, and branch-clipping, which provided live insects for feeding trials, appeared to be particularly efficient for sampling chewing insects, because it ensured high numbers of spatial

and seasonal replicates (i.e., different individual trees sampled at different seasons; Basset et al., *in press*). Compilation of the limited literature available on insect-plant interactions at Wau showed that representativeness of sampling was good (Y. Basset, *personal observation*). However, the curves of cumulative insect species suggest that the number of chewing species and of specialists could have been underestimated in intermittently flushing trees. Path models did not clearly confirm this (the magnitude of the paths from leaf production patterns to independent variables is rather low, see Fig. 2).

It is appropriate to discuss the role of sampling effort in my analyses. The amount of effort expended with the different collecting techniques was the same for all tree species. When I further expressed sampling effort in terms of the number of individual trees sampled, I found no detectable effect. The number of young leaves harvested in branch-clipping samples obtained over 1 yr could be interpreted as being related either to sampling effort, in a fashion similar to what Lewinsohn (1991) termed "random placement," or to a measure of the food resource available to the herbivore community over 1 yr, or both. However, the path-analysis models (Fig. 2) suggested that the causal effect of the number of young leaves was unlikely to be related to an effect of leaf production patterns on sampling effort (compare the respective direct paths, particularly in Fig. 2a). In short, there is evidence to suggest that the causal effect of the number of young leaves is real, important, and distinct from that of sampling effort.

*Assessing the specialization of tropical chewing insects*

It is well known that feeding trials in laboratory conditions tend to produce more positive responses from insect herbivores than trials in natural conditions, particularly when host plants are closely related (e.g., Rowell-Rahier 1984). However, there was a good correspondence between food preferences as assessed in feeding trials and insect presence in particular tree species (Basset and Samuelson, *in press*). This probably resulted from studying rather unrelated plant species. Note also that in my present experimental context, "specialist" does not mean that this species feeds only on a particular tree species, only that it appeared not

TABLE 5. Lower matrix of correlation coefficients (df = 8) computed for the independent variables retained in path analyses.

	Alt. range	Leaf flush	Young leaves	Leaf water	Palatability	Ants
Alt. range	1.0					
Leaf flush	0.392	1.0				
Young leaves	0.876	0.466	1.0			
Leaf water	-0.786	-0.303	-0.721	1.0		
Palatability	-0.054	0.268	-0.062	-0.090	1.0	
Ants	0.310	0.664	0.512	-0.021	-0.170	1.0

TABLE 6. Results of path analyses modelling species richness and host specificity of leaf-chewing insects feeding on trees in Papua New Guinea. For each model, the coefficient of determination is indicated below the dependent variable.

Variables in correlation		Correlation	Direct effect	Indirect effect	Effect coefficient
Dependent	Independent				
a) No of species $R^2 = 0.964$ df = 8	No. of young leaves	0.890	1.231	-0.246	0.985
	Leaf water	-0.476	0.382	-0.135	0.247
	Leaf palatability	0.225	0.334	-0.037	0.296
	Altitudinal range	0.697	-0.080	0.741	0.661
	Ant abundance	0.588	0.039	0	0.039
	Leaf production	0.556	0.013	0.165	0.178
b) Ratio of specialists $R^2 = 0.837$ df = 8	Ant abundance	0.809	0.739	0	0.739
	No. of young leaves	0.704	0.695	0.322	1.016
	Altitudinal range	0.440	-0.446	0.765	0.319
	Leaf production	0.555	-0.182	0.550	0.368
	Leaf palatability	-0.003	0.176	0.032	0.208
	Leaf water	-0.290	-0.164	-0.091	-0.254

to have been able to feed on the other tree species tested.

I found that, overall,  $\approx 54\%$  of species tested behaved as specialists. Basset and Burckhardt (1992), studying the host specificity of chewing insects associated with 10 woodland tree species in Switzerland using a similar protocol, found overall a lower proportion (28 specialists out of 78, or 36%). This suggests that at least some of the tropical communities that I investigated in New Guinea had a much higher proportion of specialists than their counterparts in Switzerland. Of particular interest was the observation that tree species in New Guinea that supported a rich fauna overall also supported a highly specialized fauna and a high proportion of specialists.

#### *Abundance and biomass of insect herbivores on tropical foliage*

There are remarkably few year-long estimates of herbivore densities on the foliage of wild tropical trees. Herbivore densities in the present system appeared similar to those reported for *Argyrodendron actinophyllum*, a tree species of subtropical rain forests in Australia (11 individuals/m<sup>2</sup>; Basset and Arthington 1992), and, as far as we can judge, were lower than similar measurements obtained from temperate woodlands (e.g., 19–78 individuals/m<sup>2</sup>; Basset and Burckhardt 1992).

Nevertheless, my analyses showed that it was more difficult to predict the local abundance and biomass of chewing insects than their species richness. Depending on the prevalence of dominant species within the community, insect abundance and biomass are likely to depend strongly on the population dynamics of a few of these dominant species. Abundance and biomass may be better predicted using specific parameters applicable to the dominant species. Such parameters may be different among tree species and may include, among others, food quality, plant defenses, and microclimatic requirements, such as foliage illumination (e.g., Basset 1991c).

#### *Determinants of local species richness and specialist ratios*

Several variables appeared important for predicting the local species richness and the ratios of specialist to generalist leaf-chewing insects. First, the number of young leaves collected over the course of a year in branch-clipping samples had a direct positive effect on both insect variables. Several studies have shown that plant height, plant architecture, or leaf biomass were important predictors of herbivore species richness (e.g., Lawton and Schröder 1977, Strong 1977a, b, Kennedy and Southwood 1984, Cytrynowicz 1991, Marquis 1991). It is likely that these variables represent crude measurements of the availability and diversity of food resources (Lawton 1983), which are better estimated for insect herbivores in rain forests by the availability and predictability of young leaves, as several authors have discussed (e.g., Aide and Londoño 1989, Clark and Clark 1991, Basset 1992). This result is also consistent with Price (1992), who argued that the resource base on which a community is founded can influence many aspects of trophic structuring, including the number of species in food webs. Further, Cornell (1986) pointed out that specialists are less apt to evolve on small resource bases, a result also mirrored in my model (Fig. 2b).

Why should the number of young leaves be particularly important in this regard? The probability of encounter between ovipositing adults and host plant may be increased when high numbers of vegetative modules are produced. This factor may be of particular importance in a diverse habitat, such as a rain forest. This may be an illustration of what has been termed "plant apparency" (Feeny 1976) or "encounter-frequency hypothesis" (e.g., Strong et al. 1984) in an evolutionary context.

Second, ant abundance had an important direct effect on specialist ratios, but not on species richness. In ecological terms, this suggests that generalists may more

readily be attacked by ants, and, in evolutionary terms, that particular herbivore behaviors may be shaped by enemy presence, and these may often include specialization (e.g., Bernays and Graham 1988). The importance of the ant variable is likely to depend on the particular host plants considered and whether those actively promote ant foraging on their foliage, i.e., with extrafloral nectaries, hollow stems, and other myrmecophytous syndromes (e.g., Fiala et al. 1989). Note that my measurements of enemy abundance were crude: they could be better assessed in terms of biomass, species richness, or aggressive behavior of the dominant species. Ants at any one site usually have a large spectrum of diets (e.g., fungivores, nectar feeders, homopteran tenders, etc.) and all species present on tropical foliage may not function primarily as generalist predators (Tobin 1989). Further, the contribution that parasitoids made to the enemy variable was difficult to assess in the present study.

Third, leaf water content and leaf palatability also had direct positive influences on insect species richness. Although plant biochemistry has often been identified as being a factor of primary importance in particular insect-plant associations (e.g., Zangerl and Berenbaum 1993), its significance at the level of the insect community is difficult to demonstrate (Jones and Lawton 1991). This is a probable consequence of plant chemistry being an important determinant of plant use in certain insect lineages, but not in others (Futuyma 1991, Miller 1992). A palatable foliage with high water content (see Slansky 1992) could promote radiation of insect lineages associated with particular tree species or could suffer from attacks by a wide range of generalists. Other interpretations are also possible.

Last, the altitudinal range of the tree species had a strong negative path to the specialist ratio. This suggests that tree species growing in restricted habitats are more likely to support a high ratio of specialist to generalist chewers.

#### *Effects of local and regional processes on tropical insect herbivores*

My analyses may have been impeded by both a low sample size (i.e., low number of tree species; the high coefficients of determination of the path models result from the inclusion of many independent variables in the models) and the difficulties in obtaining an adequate number of variables likely to act at the regional scale. Although my interpretations remain tentative under these circumstances, they are nevertheless consistent with the results of other studies.

Certain factors operating on an ecological time-scale outside the local community may be important (Cornell and Lawton 1992, Shmida and Wilson 1985), but in the present system it was not possible to identify them, with the exception of the altitudinal range of the host. The influence of these regional variables in my system, and, particularly, of the geographical distribution of the

host tree, was much weaker than in similar temperate systems (review in Cornell and Lawton 1992). The most important predictors in my system are all likely to vary considerably on a local scale: food resources, ant abundance, leaf palatability, and leaf water. In the tropics, even leaf production patterns may vary locally (e.g., Koriba 1958). In particular, plant apparency and predictability are affected by resource availability and environmental stress (Chew and Courtney 1991) and, likewise, may differ greatly from one tropical locality to another.

My results parallel those of several authors who studied tropical insect-plant interactions. For example, Strong (1977a, b) found that local species richness of hispine beetles on their Zingiberales hosts in Costa Rica depended on host size, local abundance and diversity. Gilbert and Smiley (1978) reviewed the determinants of local species richness for three insect-plant systems in Costa Rica: satyrine butterflies on Graminae, ithomiine butterflies on Solanaceae, and heliconiine butterflies plus flea beetles on Passifloraceae. They found no evidence for geographical distribution of the host being important. Rather, in the third system, they found that local abundance, expressed in terms of available productivity, and host size were important. Marquis (1991) reported that local tree abundance and tree height had a significant influence on the species richness of geometrids and weevils associated with *Piper* spp. at La Selva, Costa Rica. In a subtropical Cerrado community in Brazil, Cytrynowicz (1991) found that herbivore richness was correlated with the total number of leaves per plant. Lewinsohn (1991), studying insects in flower heads of Asteraceae in Brazil, concluded that taxonomic isolation had an important effect on local species richness, but not plant geographical range. He believed that many local absences of herbivore species reflected the availability of their food resource. Compton and Hawkins (1992) investigated the species richness of fig wasp assemblages associated with *Ficus* trees in South Africa. They concluded that ecological factors, such as tree height and habitat characteristics, are at least equally influential in determining wasp richness as historical factors, such as tree latitudinal range.

Hence, to date, the evidence suggests that local communities of tropical insect herbivores are weakly controlled by present-day biogeographical variables and taxonomic isolation.

#### CONCLUSIONS

In substance, Cornell and Lawton (1992) argued, on theoretical grounds, that discounting the possible effects of past interactions (historical events) is likely to result in a significant loss of ability to explain the variance of species richness at both regional and local scales. This seems plausible for regional richness, but for local richness, recent history (i.e., recent disturbance, such as fragmentation or loss of habitat; Lewinsohn 1991) could be confounded with local processes

acting in ecological time, and might complicate the picture. This is a difficult subject which is beyond the scope of this paper. However, the present study and others suggest that local processes may be comparatively more important in the tropics than in temperate environments in maintaining local species richness of insect herbivores (in addition see the "intermediate disturbance hypothesis" of Connell 1978). I am not arguing that regional processes are unimportant in tropical systems, nor that the insect communities studied at Wau are interactive and saturated (Cornell and Lawton 1992), but merely that regional processes are more difficult to elucidate, and/or relatively less important in structurally and seasonally complex environments, such as tropical rain forests, than in comparatively less complex environments, such as temperate woodlands. In other terms, local assemblages in the tropics may be much farther from reaching local equilibria set by regional and historical events than those in temperate areas, because of the comparatively greater influence of local processes in the tropics. The implications of my conclusions are obvious: the effects of moderate habitat fragmentation and ecological stress may be more pronounced in tropical systems than in temperate systems and these effects may result in a greater proportional loss of local biodiversity in the former systems.

## ACKNOWLEDGMENTS

It is a pleasure to acknowledge the help in the field of Patrick Basset, Nathan Daniel, Robert Höft, Martin Hutten, Martin Kasbal, Neil Springate, and George Weiblen, as well as the Director and staff of Wau Ecology Institute for everyday support. J. D. Holloway (CAB International, London), M. Horak, E. C. Zimmerman (CSIRO Division of Entomology, Canberra), S. E. Miller, G. A. Samuelson (Bishop Museum, Honolulu), R. T. Thompson, K. Tuck, K. Sattler (Natural History Museum, London), and E. G. Munroe checked my morphospecies assignments. Clyde Imada helped me to retrieve some botanical information. The manuscript benefited from comments by Roland Brandl, Buck Cornell, Robert Cowie, Jonathan Majer, Scott Miller, Tom Philippi, and two anonymous reviewers. The National Agricultural Chemistry Laboratory, Boroko, performed the chemical analyses. The study was funded by the Swiss National Science Foundation and the National Science Foundation (grant DEB-94-07297 to S. E. Miller, A. Allison, and Y. Basset).

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## APPENDIX

Plant-related variables determined for each tree species in a study of communities of leaf-chewing insects feeding on trees in Papua New Guinea.

Tree genus	Tree species variables†								
	Leaf water (% DM)	Specific leaf mass (mg/cm <sup>2</sup> )	Isolation (no. spp.)	Altitudinal range (m)	Distribution (10 <sup>6</sup> km <sup>2</sup> )	Height (m)	Young leaves (no.)	Trees sampled (no.)	Local abundance (classes)
<i>Elmerrillia</i>	61.2	9.84	2	640	1.90	19.4	114	8	2
<i>Cinnamomum</i>	49.0	10.73	21	1010	0.63	7.0	1097	8	3
<i>Piper</i>	74.3	4.12	100	80	0	4.5	132	28	2
<i>Ficus</i>	61.1	8.14	138	430	0	16.5	710	8	2
<i>Pipturus</i>	65.0	6.53	12	840	4.75	4.2	925	21	4
<i>Castanopsis</i>	49.1	8.94	1	1590	14.89	17.2	2382	10	4
<i>Caldcluvia</i>	52.9	13.22	5	820	0	3.4	828	41	3
<i>Aleurites</i>	63.9	7.63	1	670	16.95	16.3	302	9	2
<i>Melicope</i>	61.5	8.54	37	870	0	6.1	647	21	3
<i>Cordia</i>	71.8	4.10	5	610	4.28	12.7	395	3	1

† Leaf water content, specific (dry) leaf mass, taxonomic isolation in New Guinea, altitudinal range, geographical distribution in adjacent countries, tree height, number of young leaves recorded in branch clipping samples, number of trees sampled, and local abundance (higher numbers denote greater tree density).