



## Species richness of insect herbivore communities on *Ficus* in Papua New Guinea

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Received 5 May 1998; accepted for publication 20 December 1998

Insect herbivores were sampled from the foliage of 15 species of *Ficus* (Moraceae) in rainforest and coastal habitats in the Madang area, Papua New Guinea. The collection included 13 193 individuals representing 349 species of leaf-chewing insects and 44 900 individuals representing 430 species of sap-sucking insects. Despite a high sampling intensity, the species accumulation curve did not reach an asymptote. This pattern was attributed to the highly aggregated distribution of insects on individual host trees. The number of insect species collected on a particular *Ficus* species ranged from 34 to 129 for leaf-chewing and from 51 to 219 for sap-sucking insects. Two *Ficus* species growing on the seashore sustained less speciose insect communities than their counterparts growing in forest. For the forest figs, significant predictors of insect species richness included leaf palatability and leaf production for leaf-chewing insects (40% of the variance explained), and tree density and leaf expansion for sap-sucking insects (75%). The high faunal overlap among *Ficus* communities and the importance of local resources for insect herbivores suggest that highly specialized interactions between insect herbivores and *Ficus* in Papua New Guinea have not been conserved in evolutionary time. This is at variance with the dogma of old, extremely specialized and conservative interactions between insect herbivores and their hosts, providing numerous ecological niches in the floristically rich tropics.

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ADDITIONAL KEY WORDS:—Auchenorrhyncha – host plant – leaf-chewing insects – Lepidoptera – Moraceae – sap-sucking insects – rain forest.

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## INTRODUCTION

Typically, the number of species of insect herbivores supported by a species of tropical tree is large and unknown (but see Marquis, 1991 and Basset, 1996). Counting insects on a wide variety of trees is essential for any progress in the study of the global magnitude and distribution of insect diversity (see Basset *et al.*, 1996 for recent summary of discussion sparked by Erwin, 1982). The identification of plant traits correlated with the number of herbivores feeding on various tree species is important in understanding factors generating and maintaining this diversity.

Since historical chance events often play an important role in shaping contemporary pattern of insect-plant associations, a comprehensive explanation of variance in the diversity of herbivore communities feeding on various plants cannot be envisaged. For example, feeding on xylem fluid is a specialised trait, and it is probable that this has arisen only twice in the evolution of arthropods (Novotny & Wilson, 1997). As a rare evolutionary event, this key character might have not evolved at all, with significant consequences for the distribution of sap-sucking insects among tree species. Since xylem fluid is an extremely poor food source, the absence of xylem feeders might not be interpreted as a vacant niche in herbivore communities (see Lawton, 1984 for more on unsaturated communities).

Insect-plant associations often exhibit considerable evolutionary conservatism (e.g. Ackery, 1991; Farrell & Mitter, 1993). As a consequence, phylogenetic relationships among host plants might account for a significant part of similarities in their contemporary species pool of associated herbivores. Specific plant traits, that promote or constrain species richness of herbivore faunas in evolutionary time, have been identified (e.g. Dixon *et al.*, 1987; Berenbaum, 1990; Farrell & Mitter, 1993). The importance of such plant traits varies among and within plant lineages, requiring broadly-based research on herbivore diversity involving plant species from a variety of taxa. For example, the presence of latex is an important factor in plant anti-herbivore defence systems (Farrell, Dussourd & Mitter, 1991). However, some herbivores, such as some noctuid caterpillars, are able to circumvent this defence by trenching, i.e. cutting lactifers and then feeding on the distal part of the leaf (e.g. Dussourd & Eisner, 1987; Compton, 1989).

Historical changes in the geographical distribution of plant and insect species is another important factor shaping contemporary ecosystems. Analyses of temperate

tree species indicate that the size of geographical range, altitudinal range, and the age of establishment are, together with taxonomic isolation, often important explanatory variables for the regional species richness of herbivorous insects (e.g. Strong, 1979; Claridge, 1987; Cornell & Lawton, 1992). Local processes of competition, predation, colonization, extinction and stochastic variation operate on the herbivore species which are present regionally as a result of evolution and geographic dispersal (Ricklefs, 1987). The few studies available in the tropics suggest that local factors, such as host plant abundance, leaf production and abundance of predators, might be particularly important there (e.g. Strong, 1977; Gilbert & Smiley, 1978; Lewinsohn, 1991; Marquis, 1991; Basset, 1996).

There is no theoretical framework for predicting whether species richness of insects feeding on rainforest tree species may be attributed largely to short-term local processes, long-term regional processes or to idiosyncrasies of the evolutionary history of plant-herbivore interactions. It should also be noted that some factors may influence both evolutionary and ecosystem processes. For example, a synchronous production of a large amount of young foliage by a tree species can promote evolution of specialist herbivores with synchronized life histories, as well as attract generalist feeders present in surrounding habitats.

The taxonomic composition and size of regional species pools from which local communities of herbivorous insects recruit are largely unknown in the tropical, in comparison with temperate, ecosystems (Southwood, Moran & Kennedy, 1982; Ward, Hackshaw & Clarke, 1995). Thus the relative importance of local, regional and historical processes can only be inferred by contrasting various plant variables as predictors of the local species richness of insect herbivores. As noted by Cornell and Kahn (1989), this approach is particularly promising when the plant traits are qualitatively similar but quantitatively varying, as is often the case in closely related species.

Among the numerous genera of plants that are particularly speciose in the tropics, and therefore, highly amenable for a study of herbivore diversity on closely related hosts, *Ficus* (Moraceae) is of particular interest. Fig pollination by agaonid wasps has attracted considerable scientific interest worldwide and generated substantial literature (e.g. reviews in Janzen, 1979; Wiebes, 1979; McKey, 1989; Bronstein, 1992; Compton, Wiebes & Berg, 1996). The interest in *Ficus* for conservation studies is equally considerable, as the genus is known to attract a wide range of frugivorous animals (e.g. Terborgh, 1986). Yet, the insect fauna feeding on *Ficus* leaves is not well known and most records involve species of agricultural or ornamental interest (Basset, Novotny & Weiblen, 1997).

An attempt was made to predict the numbers of species in insect herbivores (leaf-chewing and sap-sucking), using an array of historical, physiological and local host plant traits. Analyses of species composition and host specificity of these herbivore communities, to be presented elsewhere, will complement this study.

## MATERIAL AND METHODS

### *Study sites and plants*

The study area was situated in the Madang province of Papua New Guinea and was delimited as part of the lowlands (0–400 m asl), stretching from the coast to the

TABLE 1. Species of *Ficus* studied in the Madang area: their taxonomic placement, architecture, preferred habitats (Hab), leaf texture (Leaf), and number of tree inspections for leaf-chewing and sap-sucking insects, respectively (No. inspec.)

<i>Ficus</i> species	<i>Ficus</i> section	Habitus	Hab <sup>1</sup>	Leaf <sup>2</sup>	No. inspec. Chw	No. inspec. Sap
<i>F. bernaysii</i> King	Sycocarpus	Small evergreen	P	Sc	513	168
<i>F. botryocarpa</i> Miq.	Sycocarpus	Medium evergreen	S	Sc	489	276
<i>F. conocephalifolia</i> Ridley	Sycidium	Small evergreen	P	Sc	574	265
<i>F. copiosa</i> Steud.	Sycidium	Medium evergreen	S	Sc	451	229
<i>F. dammaropsis</i> Diels	Sycocarpus	Small evergreen	S	Sm	428	95
<i>F. hispidioides</i> S. Moore	Sycocarpus	Medium evergreen	R, S	Sc	478	272
<i>F. microcarpa</i> L.	Conosycea	Large evergreen	Ss	Sm	103	93
<i>F. nodosa</i> Teysm. & Binn.	Neomorphe	Large deciduous	S, P, R	Sm	388	167
<i>F. phaeosyce</i> Laut. & K. Schum.	Sycidium	Small evergreen	P	Sc	735	415
<i>F. pungens</i> Reinw. ex Bl.	Sycidium	Medium evergreen	S	Sc	328	137
<i>F. septica</i> Burm.	Sycocarpus	Small evergreen	R, S	Sm	510	228
<i>F. tinctoria</i> Forst.	Sycidium	Medium evergreen	Ss	Sm	376	290
<i>F. trachypison</i> K. Schum.	Sycidium	Medium evergreen	S	Sc	470	307
<i>F. variegata</i> Bl.	Neomorphe	Large deciduous	P, S	Sm	438	243
<i>F. wassa</i> Roxb.	Sycidium	Small evergreen	P, S	Sc	550	355

<sup>1</sup>P = primary forest; S = secondary forest; R = ruderal; Ss = seashore. <sup>2</sup>Sc = scabrid; Sm = smooth.

slopes of the Adelbert Mts, which lie between Gogol and Sempri Rivers. This approximate rectangular area of  $17 \times 31$  km encompasses about 434 km<sup>2</sup> of primary and secondary forests, 21 km<sup>2</sup> of coastal habitats (including seashore and ruderal vegetation in coconut plantations) and the town of Madang. Field work focused in primary and secondary lowland forests near Baitabag ( $145^{\circ}47'$  E,  $5^{\circ}08'$  S, *c.* 100 m), Ohu ( $145^{\circ}41'$  E,  $5^{\circ}14'$  S, *c.* 200 m) and Mis ( $145^{\circ}47'$  E,  $5^{\circ}11'$  S, *c.* 50 m) Villages, as well as in secondary locations (Baiteta, Erima, Nainai, Ninfon, and Reinduk). Coastal fig species (see below) were sampled near Riwo Village ( $145^{\circ}48'$  E,  $5^{\circ}09'$  S, 0 m) and on islands nearby, in all cases less than 3 km from the mainland.

Annual rainfall in the Madang area is 3558 mm, usually with a distinct dry season from July to September, while air temperature varies very little during the year, with mean monthly temperature ranging from 26.2 to 26.7°C (long-term averages for Madang; see McAlpine, Keig & Falls, 1983). General descriptions of a forest site (Baiteta) similar to the primary sites and of the Madang Lagoon and coastal areas are found in Bowman *et al.* (1990) and Jebb and Lowry (1995), respectively.

Fifteen species of *Ficus* trees were selected (Table 1), which represented a substantial proportion of local *Ficus* flora in terms of abundance and biomass. These species were also easy to recognize in the field. They differ in growth habit, architecture and regeneration niche, but all are essentially sympatric in our study area. All species are gynodioecious, with the exception of *Ficus microcarpa*, which is monoecious.

#### *Insect collecting*

Leaf-chewing insects (Orthoptera, Phasmatodea, Coleoptera and Lepidoptera) and sap-sucking insects (Auchenorrhyncha) were collected by hand or by the use of an aspirator. Since most tree species are small (<10 m), trees were climbed or sampled from the ground. Larger trees were accessed with the single rope technique

(Perry, 1978). Insects were collected during day by five collecting teams: three local collectors in each of the four main study sites and three technical assistants ('parataxonomists') plus the authors in all locations.

Collecting effort was recorded as the time spent looking at the foliage of each of the *Ficus* species studied, which was approximately proportional to the leaf area examined. Since numerous trees were sampled at different times of the year and day, it was not practical to keep record of the number of individual trees sampled. Instead, the number of 'tree inspections' (i.e. a particular tree sampled at a particular time) was recorded. It is estimated that the actual number of individual trees sampled is over 1000, representing approximately 500 person-days of field work. Overall, the sampling programme, which surveyed individual trees in a variety of age classes and growing in various habitats, was optimized towards the estimation of the total number of insect species feeding on each of the *Ficus* species studied.

Since leaf-chewing and sap-sucking insects differ in various aspects of their biology, data collecting and analyses were slightly different for each of these groups. For example, the density of leaf-chewing insects is generally lower than that of sap-sucking insects, but their feeding preferences can be assessed more reliably because their feeding can be easily recorded (see next section).

Leaf-chewing insects were collected from July 1994 to March 1996 and sap-sucking insects from July 1995 to June 1996. For the leaf-chewing insects, collecting effort was similar for each tree species and amounted, on average and for each *Ficus* species, to 24.7 hours and 455 tree-inspections (Table 1; total 370 hours and 6831 tree-inspections for all species). Leaf-chewing data were not correlated with sampling effort (see results). For sap-sucking insects, the sampling effort was 15.7–21.3 hours spent searching the foliage of each *Ficus* species. This corresponded to approximately 227 tree-inspections per *Ficus* species (3408 tree-inspections in total; Table 1). In order to achieve identical sampling effort for each *Ficus* species, randomly selected samples were removed from final data set, adjusting thus sampling effort to exactly 15.7 hours per *Ficus* species.

In order to quantify distribution of herbivores among individual trees, an exhaustive collection was made of all sap-sucking insects on 191 individuals of *Ficus phaeosyce*, and the size of each plant recorded (in m<sup>3</sup> of compact foliage), at a single sampling site (Baitabag). Census of insects was feasible since *F. phaeosyce* is a small understorey shrub.

#### *Processing of insect material*

Live leaf-chewing insects collected in the field were stored in plastic vials at room temperature, provided with fresh *Ficus* foliage, and kept until they died or fed. Only the specimens which fed were considered in the analyses, to exclude transient species from the samples. Caterpillars were reared to adults whenever possible. No simple feeding tests on excised leaves in laboratory conditions could be devised for sap-sucking insects so that all individuals found on the foliage of a particular *Ficus* species were included the analysis.

Rearing, mounting and subsequent sorting to morphospecies involved the three technical assistants and the authors. For sap-sucking insects, the morphology of male genitalia was routinely used for the assignment of the species, but the status of all herbivore morphospecies was verified later by various taxonomists. Taxonomic

information on leaf-chewing insects was published by Miller *et al.* (in press). Voucher specimens of insects and plants are deposited at Bishop Museum, Honolulu, with duplicates in the collections of specialists and Lae Herbarium.

Insect data were grouped into the following categories for analyses of species richness within the communities feeding on each *Ficus* species: number of leaf chewing species, lepidopteran species, sap-sucking species, phloem-, mesophyll-, and xylem-sucking species. Insects whose fitness may be directly shaped by selection pressures related to foliage characteristics may be of particular interest when seeking correlations between foliage-chewing insects and foliage characteristics. Lepidoptera are appropriate for such community analyses because (a) their larvae feed on foliage, (b) the fitness of their larvae depends, in part, on choices by the ovipositing adults; and (c) some species of micro-Lepidoptera do not move far away from their hosts as adults.

Sap-sucking insects represent an ecologically heterogeneous group, encompassing three guilds, feeding on phloem sap, xylem sap and the mesophyll cells of leaf parenchyma, respectively. Species were assigned to their respective guilds following evidence on feeding modes for higher auchenorrhynchan taxa (see Novotny & Wilson, 1997). Note that these guilds are in fact taxon-guilds (*sensu* Simberloff & Dayan, 1991), as only species from the Auchenorrhyncha were studied. The present study does not concern Stenorrhyncha, which represent another major part of the phloem-feeding guild.

#### *Assessment of possible bias in feeding trials and measurement of leaf palatability*

One particular concern with using *Ficus* as a study plant is that latex outflow, a reputed major defence against insect herbivores (e.g. Farrell *et al.*, 1991; Dussourd & Denno, 1991), does not occur on excised leaves. Therefore, it is possible that some insect generalists may be able to feed on excised leaves in the laboratory, but not in the wild. This is less likely for microlepidopteran caterpillars, which usually do not leave their host, but it could potentially be a serious bias for larger caterpillars and, particularly, for beetles. Further, such biases may be more severe for certain *Ficus* species, depending on their latex outflow and leaf palatability. The converse situation, a generalist or specialist able to feed in the wild but not in laboratory conditions, was never observed.

To investigate the above concern an experiment was devised, which compared the leaf palatability of leaves *in situ* and of excised leaves. Highly generalist weevils (*Oribius* sp., species 'CURC012') were starved for 24 h and then set up on potted saplings. Each weevil was introduced inside a plastic vial which contained one leaf *in situ*. Feeding damage was scored visually after 24 h 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. The leaf on which the weevil was allowed to feed was marked and the insect was then starved again for 24 h. The marked leaf was cut, placed into a plastic vial with its corresponding weevil, and stored next to the saplings. Eventually, feeding damage was recorded after 24 h. During these experiments, two to five saplings were used for each *Ficus* species. To increase intraspecific variability in leaf palatability for each *Ficus* species, weevils were set up on both young and mature leaves. On

average, the feeding damage of 22 different weevils was measured for each *Ficus* species (total observations = 330).

An index of palatability, either for leaves *in situ* or for excised leaves, varying from 0 to 1 and nearly continuous, was derived for each *Ficus* species by recording the number of cases in which a score of 100 was attributed, divided by the number of cases tested.

#### *Host plant characteristics*

The selection of plant traits was guided by hypotheses on the key factors determining species richness and abundance of herbivores (e.g. Lawton & Schröder, 1977; Kennedy & Southwood, 1984; Aide & Londoño, 1989; Jones & Lawton, 1991; Basset, 1996). These variables included:

(1) *Taxonomic isolation*. This is the number of species present in New Guinea and belonging to the same taxonomic series as designated by Corner (1965). A robust phylogeny of *Ficus* is not yet available, so we relied on Corner's classification (1965). Despite the arbitrary nature of taxonomic rank, the number of species per series was chosen as an estimate of taxonomic isolation because Corner's series appear to reflect groups of closely related species in geographical proximity.

(2) *Geographical distribution*. This was calculated as the sum of areas (km<sup>2</sup>) of countries where the *Ficus* species has been reported (*vide* Corner, 1965).

(3) *Altitudinal range*. This was determined as the highest altitude recorded from herbarium specimens in the collections of the Forestry Research Institute (Lae, Papua New Guinea) and Bishop Museum (Honolulu, U.S.A.).

(4) *Patterns of leaf production*. Following our observations in the field, *Ficus* species were assigned to three groups, depending on the presence and extent of leaf flush: (i) deciduous trees (when mature; variable with a dummy value of 3); (ii) trees which produce distinct and rather extended leaf flushes, involving a large proportion of vegetative buds (value = 2); and (iii) trees which do not produce distinct, extended leaf flushes (value = 1).

(5) *Leaf expansion*. This was measured on potted saplings (two to five per *Ficus* species); leaves were tagged at bud break and the number of days required for them to become mature (i.e., fully expanded and pigmented) was recorded. An average of 48 leaves were measured for each *Ficus* species (range 24–71; total 714 leaves).

(6) *Leaf palatability in situ*, as determined in the previous section.

(7) *Latex outflow in mature leaves*. An undamaged leaf was cut transversally and latex outflow was measured at the midrib on the twig side. Outflow was measured in mm (33 mm = 3 µL) using glass capillaries of 3 µL (see Dussourd & Denno, 1991). One measurement was performed per individual tree and 20 trees were measured at different periods of the year for each *Ficus* species.

(8) *Leaf pubescence*. The number and length of hairs on a 10 × 0.15 mm area of abaxial and adaxial lamina were estimated for 25 leaves per *Ficus* species (five leaves per tree and five trees per species). A leaf pubescence index was calculated as median hair density × median hair length, averaged for abaxial and adaxial leaf surfaces.

(9) *Tree density*. This was estimated from 189 surveys, each representing a 20 minute walk surveying an approximate area of  $380 \times 4$  m, during which all trees belonging to the 15 *Ficus* species taller than 1.5 m were counted. Density was estimated separately for the four main sampling sites and their average, weighted by sampling effort at each site, was calculated to characterize the whole study area. The area surveyed was about 29 ha, in which 9409 trees were recorded.

(10) *Predation rates on the foliage of the host*. This was estimated by recording the disappearance of live baits from the foliage during day-time (adapted from Olson, 1992). Baits consisted of workers of *Microcerotermes biroi* (Desneux 1905), a common termite in the study area. Each bait was secured on the leaf surface by an insect pin. Thirty such baits were set up on one individual tree. After 30 minutes, the disappearance of the baits or the attendance of ants to the baits was recorded. Twenty measurements were performed throughout the year for each *Ficus* species. All experiments were carried out during day time since additional experiments on *F. wassa* indicated that predation rates during night were negligible in our study area (pers. obs.).

Variables 1–3 are clearly historical, whereas variables 4–10 are rather related to local ecological processes. However, variables 5–8 are also related to plant physiology and it can be debated as to whether they account for regional or local processes.

#### *Statistical methods*

The analysis of the relationships between the species richness of different insect assemblages as defined above and host characteristics followed a three-step strategy. First, since insect species richness between hosts varied considerably (see results), the variance of host characteristics was considered. Host characteristics which did not vary significantly between *Ficus* hosts were not retained in further analyses. Second, correlations between insect data and host characteristics were calculated. For these and later analyses, all continuous variables which did not pass the Kolmogorov–Smirnov–Liliefors test of normality were transformed using either log, square-root, reciprocal square-root or exponential to satisfy the assumption of normality. Since 60 simultaneous correlations were computed, approximately three spurious correlations could be expected, using  $P=0.05$ . Our approach to this problem follows the view of Stewart-Oaten (1995) advising against the use of rigid significance levels for multiple comparisons. For example, test results obtained with the Bonferonni correction depend not only on data relevant to the question, but also on irrelevant information such as the number of other questions studied. Note also that the degree of freedom of the present analyses may have been inflated (i.e. the plant data are not independent from each other but constrained by phylogeny, see e.g. Jones & Lawton, 1991). This problem is considered in the discussion, in light of the results.

Third, stepwise multiple regressions (with  $\alpha$ -to-enter and  $\alpha$ -to-remove = 0.05) were computed to predict insect variables, using host characteristics achieving the highest correlations with the dependent variables. However, not all data points in the multiple regression models were used. The two ‘banyan’ species (strangling or hemiepiphytic figs, also sometimes free-standing) typically growing on the seashore, *F. microcarpa* and *F. tinctoria*, appeared to support a very different insect fauna from

that feeding on fig species growing in forests. This was confirmed in a correspondence analysis of the insect variables across the 15 *Ficus* species (unpubl. data). The first axis of the ordination represented 89.5% of the variance and segregated the two seashore species from the rest of the *Ficus* species. This is of concern for the present analyses because the predictive power of certain plant variables may be very different in seashore and forest habitats. As many coastal tree species from other genera (e.g. Tomlinson, 1986), these two *Ficus* have glossy thick leaves, a large geographic range and linear distribution along the shore which result in low tree density and narrow altitudinal range. In other words, there was collinearity between several plant variables which made it difficult to attribute any traits of insect communities on *F. microcarpa* and *F. tinctoria* to effects of a particular plant variable. From a statistical viewpoint, two variables in particular may complicate the analysis. First, these species are proportionally much scarcer than other *Ficus* species, so that spurious correlations may arise from tree density, interacting with sampling effort. Second, the geographical distribution of seashore species, as estimated here, is certainly much less correlated with actual area occupied than for other *Ficus* species. Therefore, we tested whether habitat type (seashore or forest) had a significant effect on each insect variable, as measured by a Mann–Whitney test. If the test was significant, the two seashore species were excluded from the data points used in the regression models.

## RESULTS

### *Sampling effort and representativeness of sampling*

A total of 13 193 individuals representing 349 species of leaf-chewing insects were collected from the 15 *Ficus* species. The effect of sampling effort was not significant, whether we considered all *Ficus* species, or only *Ficus* species growing in forests (i.e. excluding the seashore species). For example, correlations with all *Ficus* species for the total number of insect species collected (see Table 2) were  $r=0.323$  and  $P=0.240$  with time spent collecting;  $r=0.444$  and  $P=0.097$  with no. of tree-inspections. The higher correlation with the number of tree-inspections appeared to be related to the relative scarcity of seashore *Ficus* species, as the relation was clearly not significant when accounting only for *Ficus* species growing in forest ( $r=-0.115$ ,  $P=0.707$ ).

As leaf-chewing insects feeding on *Ficus* are poorly known in New Guinea, species accumulation curves provided an additional measure of sampling effort. After more than 6800 tree-inspections, the rate of species accumulation approached but never reached zero (Fig. 1). In brief, due to the rather large sampling effort, sampling was representative. However, it may have been less so for the seashore *Ficus* species, due to their relative scarcity.

Altogether 52 079 individuals and 444 species of sap-sucking insects were collected, but the data set was reduced to 44 900 individuals from 430 species by adjustment for identical sampling effort (see Methods). As for leaf-chewing insects, the species accumulation curve was examined to assess the representativeness of sampling. After about 3400 tree-inspections, the species accumulation curve did not reach an asymptote and the number of species grew steadily, although at a diminishing rate (Fig. 2). The steeper slopes of species accumulation curves for individual *Ficus* trees,

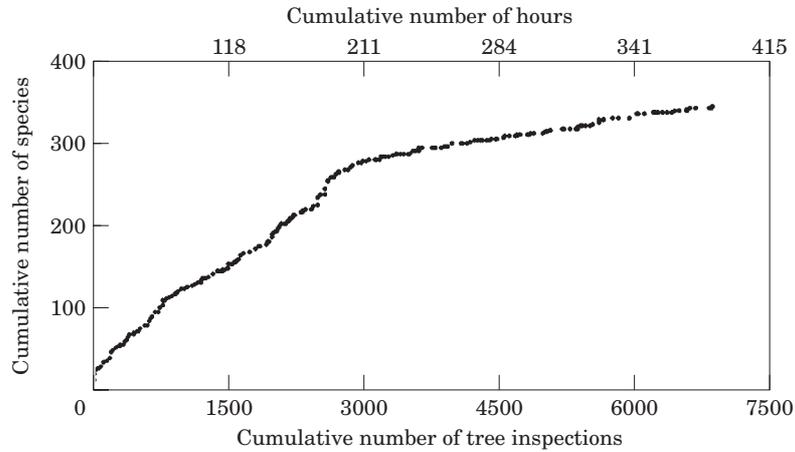


Figure 1. Cumulative number of leaf-chewing species collected on 15 *Ficus* species plotted against the number of tree inspections and the number of hours spent examining foliage.

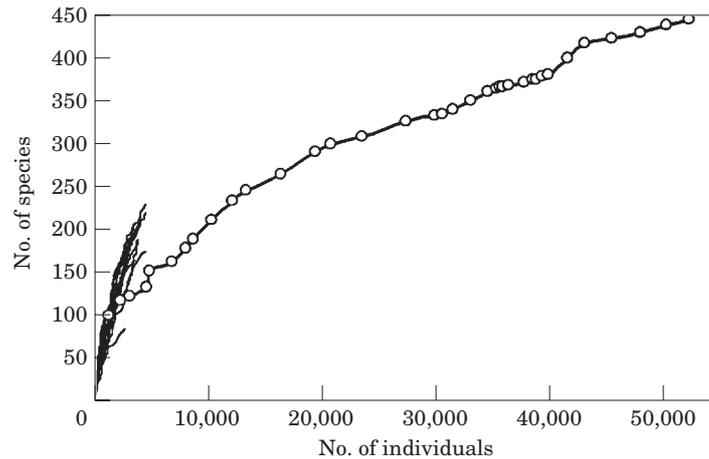


Figure 2. Cumulative number of sap-sucking species plotted against the cumulative number of individuals. (○) Total number of species found on 15 *Ficus* species (data points correspond to increments after 10 days of sampling); (—) Species accumulation curves for individual *Ficus* species.

in comparison with that for a composite data set, indicated considerable faunal overlap between component *Ficus* communities. It is unlikely that the total local species richness of insect herbivores was sampled, but, most likely, common species were.

Since faunal overlap was considerable among *Ficus* species (see below), data for species accumulation curves were pooled for all host species. Patterns of species accumulation were similar for both sampling effort (tree inspections) and sample size (number of individuals) as an independent variable. Therefore, only the former is reported for leaf-chewing and the latter for sap-sucking insects.

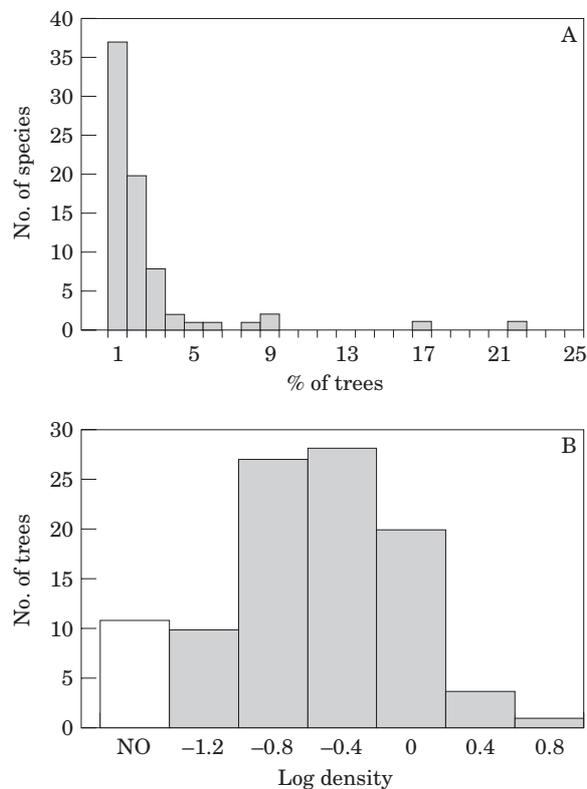


Figure 3. Sap-sucking insects on *Ficus phaeosyce* trees. A, colonization of individual trees. Insect species are classified according to the percentage of individual trees they occupy ( $N = 191$  trees). B, density of sap-sucking insects on individual trees (individuals per  $m^3$  of foliage). Non-zero values are scaled into  $\log_{10}$  density classes  $[-1.4; -1.0]$ ,  $[-1.0; -0.6]$ , ...,  $[0.6; 1.0]$ ; the number of trees with no sap-sucking insects is depicted separately (empty column).

Census of sap-sucking insects on 191 individuals of *F. phaeosyce* yielded 427 individuals from 73 species. Most insect species were found only on a single shrub (Fig. 3A). The distribution of total density of sap-sucking insects on *F. phaeosyce* was skewed positively, with only a fraction of shrubs supporting high density of herbivores (Fig. 3B).

#### *Species richness of herbivore communities*

The number of species of both leaf-chewing and sap-sucking insects was distinctly lower for the coastal species *F. microcarpa* and *tinctoria* in comparison with forest species (Table 2). Further, mesophyll-feeders were virtually absent from coastal *Ficus* communities. The richest communities of leaf-chewing insects were found on *F. wassa*, *F. variegata* and *F. nodosa*, whereas *F. phaeosyce*, *F. conocephalifolia* and *F. wassa* supported the highest number of sap-sucking species. There was no correlation between the number of leaf-chewing and sap-sucking species collected on each *Ficus* (Spearman rank correlation  $r_s = 0.315$ ,  $P = 0.253$ ). However, there was a significant

TABLE 2. Species richness of insect herbivore communities on *Ficus* trees

<i>Ficus</i> species	No. of leaf-chewing species		No. of sap-sucking species			
	All	Lepidoptera	All	phloem	xylem	mesophyll
<i>F. bernaysii</i>	83	23	175	129	28	18
<i>F. botryocarpa</i>	86	35	172	123	29	20
<i>F. conocephalifolia</i>	107	30	204	147	27	30
<i>F. copiosa</i>	97	31	172	126	29	17
<i>F. dammaropsis</i>	104	33	175	129	31	15
<i>F. hispidooides</i>	73	23	198	138	31	29
<i>F. microcarpa</i>	34	21	51	40	11	0
<i>F. nodosa</i>	119	44	156	109	29	18
<i>F. phaeosyce</i>	94	35	219	159	31	29
<i>F. pungens</i>	99	22	173	121	25	27
<i>F. septica</i>	58	21	164	118	28	18
<i>F. tinctoria</i>	40	15	79	61	16	2
<i>F. trachypison</i>	84	22	183	128	32	23
<i>F. variegata</i>	120	41	157	108	28	21
<i>F. wassa</i>	129	40	203	150	26	27
All <i>Ficus</i> species	349	138	430	304	48	78

correlation between the number of Lepidoptera and non-Lepidoptera species collected on each *Ficus* species ( $r_s = 0.643$ ,  $P < 0.01$ ). Similarly, all three pair-wise correlations between sap-sucking guilds were positive and significant ( $r_s = 0.752$ – $0.909$ ,  $P < 0.01$ ).

For forest-growing *Ficus* species, there was a wider difference between the poorest and richest communities of leaf-chewing insects (min. 58, max 129 species) than of sap-sucking communities (min. 156, max. 219 species). This may partly reflect the exclusion of transient species in the leaf-chewing data.

Overlap of insect communities among the *Ficus* species was considerable. For leaf-chewing insects the combined number of species collected from all hosts was 349, instead of an expected tally of 1327 species for totally non-overlapping faunas, whereas respective data for sap-sucking insects were 430 collected and 2481 expected species (Table 2).

#### *Measurement of leaf palatability in situ and on excised leaves*

Leaf palatability measured on excised leaves was significantly higher than leaf palatability measured *in situ* (Wilcoxon signed ranks test,  $Z = 14.6$ ,  $P < 0.001$ ). Measures of leaf palatability were similar (close to a ratio of 1.0) only for *F. trachypison* and *F. variegata* (Fig. 4). Differences in palatability were particularly high for *F. septica*, *F. microcarpa*, *F. hispidooides* and *F. botryocarpa*. However, none of these hosts had an unusually high proportion of Lamiinae, Eumolpinae or non-Aganainae Noctuidae, which represent the insect groups most likely to include some generalist species able to feed on *Ficus* in the laboratory but not in the wild.

There was also a correlation between the palatability *in situ* and on excised leaves ( $r_s = 0.573$ ,  $P < 0.05$ ; Fig. 4). *Ficus dammaropsis* and *F. variegata* were the most palatable of *Ficus* hosts *in situ*, whereas *F. microcarpa* and *F. septica* were the least. Leaf palatability *in situ* varied significantly among *Ficus* hosts (Kruskal–Wallis test with raw data,  $W = 51.4$ ,  $P < 0.001$ ) but could not be explained readily by any other host characteristics

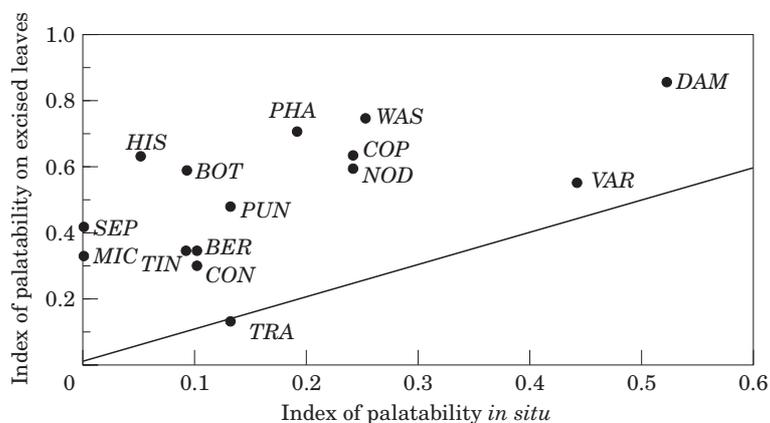


Figure 4. Plot of the index of palatability for leaves measured *in situ* against leaves excised for the 15 species of *Ficus* studied. These are identified by the first three letters of their specific name. The line denotes a slope of 1.

and, in particular, by latex outflow ( $r_s=0.034$ ,  $P>0.50$ ). This suggests that leaf palatability represents a complex array of biochemical and physical factors and that it should be considered distinct from other host characteristics.

The total number of insect species collected on each *Ficus* host was correlated with leaf palatability *in situ* ( $r_s=0.84$ ,  $P<0.001$ ), not with the palatability of excised leaves ( $r_s=0.46$ ,  $P=0.09$ ). In addition, there was no significant correlation between latex outflow and the palatability of excised leaves ( $r=0.002$ ,  $P>0.50$ ), suggesting that palatability was not influenced strongly by the deactivation of latex outflow. All of the above suggest that insect species feeding on *Ficus* in the laboratory but not in the wild are unlikely to be significant source of error in the data.

#### *Measurement of other plant variables*

Most plant variables exhibited considerable variation among the 15 *Ficus* species (Tables 3 and 4). Geographic distribution ranged from species endemic to New Guinea (*F. conocephalifolia*, *dammaropsis* and *phaeosyce*) to those distributed throughout most of the tropical Asia (*F. tinctoria*). *Ficus* assemblages are generally more diverse at lower elevations, but four species from the present lowland study area (*F. copiosa*, *dammaropsis*, *wassa* and *trachypison*) were recorded at or above 2500 m and the first three of these are common in montane forests.

Leaf characteristics displayed large interspecific variability. Latex outflow varied by a factor of 45 between the *Ficus* species producing the least (*F. trachypison*) and the most (*F. dammaropsis*) latex. Seven *Ficus* species had glossy leaves, whilst density of leaf hairs varied greatly in the others; *F. pungens* and *hispidoides* had especially pubescent leaves. Leaf expansion averaged 24 days when all *Ficus* species were considered and it was slower in shade tolerant species (*F. phaeosyce* and *F. bernaysii*) than in light gap colonists (e.g. *F. septica*).

Tree density varied ten-fold among forest species, with *F. wassa*, *phaeosyce* and *conocephalifolia* ranking among the most abundant species in the forest understorey.

TABLE 3. Historical plant variables used in the analyses (see text for further details).

<i>Ficus</i> species	Taxonomic isolation (no. species)	Geographical distribution (10 <sup>6</sup> km <sup>2</sup> )	Altitudinal range (m)
<i>F. bernaysii</i>	18	0.87	1220
<i>F. botryocarpa</i>	1	1.44	1660
<i>F. conocephalifolia</i>	7	0.83	1900
<i>F. copiosa</i>	5	2.91	2500
<i>F. dammaropsis</i>	1	0.83	2600
<i>F. hispidioides</i>	18	3.96	1260
<i>F. microcarpa</i>	4	10.12	1330
<i>F. nodosa</i>	4	0.99	1460
<i>F. phaeosyce</i>	7	0.83	2000
<i>F. pungens</i>	2	1.19	1800
<i>F. septica</i>	18	18.69	1560
<i>F. tinctoria</i>	2	20.02	1150
<i>F. trachypison</i>	8	0.92	2530
<i>F. variegata</i>	4	17.55	1660
<i>F. wassa</i>	5	1.06	2750

Predation rates by ants on *Ficus* species averaged about 7 baits removed per experiment and it was the only variable which did not vary significantly among *Ficus* species (Table 4) and was, therefore, not considered further in the analyses.

#### *Relationships between insect species richness and host characteristics*

The relationships between insect variables and host characteristics were relatively weak (Table 5). For leaf-chewing insects, the strongest correlations involved tree density and leaf palatability. Leaf production and leaf palatability were the best predictors of the number of species of Lepidoptera. For sap-sucking insects, the strongest correlations with host characteristics involved tree density and geographic range. Tree density was the best predictor of species richness for each of the sap-sucking guilds.

The species richness of both leaf-chewing and sap-sucking communities on coastal figs (*F. microcarpa* and *F. tinctoria*) was significantly lower than that on forest figs. This was also the case when considering Lepidoptera and the three sap-sucking guilds separately (Mann–Whitney tests, in all cases  $P < 0.05$ ).

The results of regression models computed while excluding the two species of *Ficus* growing on the seashore are summarized in Table 6. For leaf-chewing species, a single variable was the best predictor of either the total number of species or the number of species of Lepidoptera. Leaf palatability explained 40% of the variance in the total number of leaf-chewing species collected and leaf production explained 50% of the variance in species richness of Lepidoptera.

For sap-sucking insects, leaf expansion and tree density proved to be the most important plant variables. Together they explained 75%, 78% and 30% of the variance in the number of sap-sucking, of phloem-feeding and mesophyll-feeding species, respectively. It was not possible to correlate species richness of xylem feeders with any plant variable.

TABLE 4. Local and physiological plant variables used in the analyses (see text for details). When applicable, means and s.e. (in brackets) of measurements are reported, followed by overall estimates for all *Ficus* species and a Kruskal–Wallis test for the analysis of variance

<i>Ficus</i> species	Leaf production (category)	Leaf pubescence (mm/mm <sup>2</sup> )	Latex outflow (mm)	Leaf expansion (no. days)	Tree density (no. per km <sup>2</sup> )	Predation rates (no. baits)
<i>F. bernaysii</i>	1	2.3	12.1 (2.2)	31.4 (1.2)	2036	7.4 (1.6)
<i>F. botryocarpa</i>	2	4.5	12.3 (2.1)	21.2 (0.9)	1689	4.2 (1.1)
<i>F. conocephalifolia</i>	1	0	21.6 (2.0)	27.9 (1.0)	4780	7.3 (1.7)
<i>F. copiosa</i>	2	0	15.5 (3.1)	21.1 (0.8)	1714	10.5 (2.2)
<i>F. dammaropsis</i>	1	0.1	108.7 (12.3)	17.0 (0.9)	1475	7.8 (1.8)
<i>F. hispidioides</i>	1	10.3	3.3 (0.8)	29.6 (1.0)	1181	5.9 (1.2)
<i>F. microcarpa</i>	2	0	16.4 (2.2)	26.8 (0.9)	4	9.7 (1.9)
<i>F. nodosa</i>	3	0.2	24.4 (6.3)	20.0 (1.2)	635	5.2 (1.5)
<i>F. phaeosyce</i>	2	0.1	2.3 (0.3)	33.1 (1.2)	4552	5.3 (1.7)
<i>F. pungens</i>	1	6.1	43.9 (6.7)	21.0 (1.2)	1159	5.2 (1.0)
<i>F. septica</i>	1	0	19.5 (3.2)	20.4 (1.0)	1280	4.4 (1.4)
<i>F. tinctoria</i>	1	0	48.0 (5.8)	22.4 (0.8)	184	8.6 (1.6)
<i>F. trachypison</i>	2	4.7	1.8 (0.5)	28.5 (1.0)	1041	7.4 (1.7)
<i>F. variegata</i>	3	0	5.0 (0.7)	18.1 (0.6)	1746	7.1 (1.3)
<i>F. wassa</i>	2	0	4.7 (1.2)	25.0 (0.5)	6723	6.8 (1.5)
All <i>Ficus</i> species	–	–	22.6 (1.9)	24.3 (0.3)	–	6.9 (0.4)
W	–	–	200.7	271.6	–	20.0
P	–	–	<0.001	<0.001	–	0.13

These results also confirm that the strong correlations between insect species richness and geographical distribution and altitudinal ranges result from the inclusion of the two *Ficus* species growing on the seashore.

## DISCUSSION

### *Limitations of the study*

One potential problem with comparisons of insect communities among *Ficus* species is the non-independence of host-species (i.e. phylogenetic constraints, Harvey & Pagel 1991). Three lines of evidence suggest that this problem is unlikely to be very serious in the present system. First, a cluster analysis of *Ficus* species with insect data showed that the grouping of the tree species had little correspondence with

TABLE 5. Pearson's correlation of the number of species of insect herbivores with host tree characteristics. Only correlations with  $P < 0.05$  are reported.  $N = 15$  *Ficus* species

Dependent variable	Independent variable	$r$	$P$
All leaf-chewing	Tree density	0.682	>0.01
All leaf-chewing	Leaf palatability	0.675	>0.01
All leaf-chewing	Geographical distribution	0.575	0.03
All leaf-chewing	Altitudinal range	0.559	0.03
Lepidoptera	Leaf production	0.667	>0.01
Lepidoptera	Leaf palatability	0.637	0.01
Lepidoptera	Tree density	0.546	0.03
All sap-sucking	Tree density	0.851	>0.001
All sap-sucking	Geographical distribution	-0.648	>0.01
Phloem-feeders	Tree density	0.851	>0.001
Phloem-feeders	Geographical distribution	-0.655	>0.01
Mesophyll-feeders	Tree density	0.764	0.001
Mesophyll-feeders	Geographical distribution	-0.539	0.04
Xylem-feeders	Tree density	0.529	0.04
Xylem-feeders	Geographical distribution	-0.522	0.046

TABLE 6. Multiple regressions of the number of herbivore species with host tree characteristics.  $N = 13$  forest species of *Ficus* analysed. Tree density square-root transformed. Parameters with standard errors (SE), significance level ( $P$ ), and adjusted  $r^2$  are given for each regression model

Dependent var.	Independent var.	Par. (SE)	$r^2$	$P$	$F$	$r^2$ adj.
All leaf-chewing	Constant	79.8 (7.2)				
	Leaf palatability	89.8 (30.0)	0.447	0.012	8.9	0.397
Lepidoptera	Constant	16.8 (3.8)				
	Leaf production	8.3 (2.1)	0.548	0.004	13.4	0.507
All sap-sucking	Constant	106.6 (13.2)				
	Leaf expansion	1.9 (0.6)	0.562			
	Tree density	0.6 (0.2)	0.794	<0.001	19.2	0.752
Phloem-feeders	Constant	72.7 (9.7)				
	Tree density	0.6 (0.1)				
	Leaf expansion	1.3 (0.4)	0.815	<0.001	22.0	0.778
Mesophyll-feeders	Constant	8.1 (5.9)				
	Leaf expansion	0.6 (0.2)	0.357	0.031	6.1	0.299

the classification of Corner (1965) (see Table 1). Second, plant phylogeny and herbivore feeding preferences showed no clear correspondence for both leaf-chewing and sap-sucking insects (G. Weiblen *et al.*, unpubl. data). Last, taxonomic isolation of the host was clearly unrelated to insect species richness (but see the caveats associated with this variable in the methods).

The sampling methods were directed toward maximizing the number of trees examined in a variety of habitats and sampling sites. This strategy was intended to obtain reliable data on the species richness and composition of herbivore communities. The census on *E. phaeosyce* showed that the distribution of insect herbivores among individual trees was highly aggregated. Each herbivore species colonised only a fraction of the host trees present, and only a fraction of trees supported a high density of herbivores. Therefore, a large number of replicate collections is needed in order to collect most of the insect species feeding on a particular host species and even substantial sampling effort may not be sufficient to achieve this

aim. Continuing increase in the number of species may be due, in part, to transient (tourist) species, which accumulate with increasing sample size. However, even leaf-chewing communities did not appear to have been exhaustively sampled. Similar patterns of a low proportion of individual plants colonized and an ever-increasing number of species in the samples were reported also for other herbivore communities, notably for Lepidoptera on *Erythroxylum* (Price *et al.*, 1995).

#### *Overall characteristics of herbivore communities*

Herbivore communities on *Ficus* in the Madang area were diverse but patterns of diversity did not correlate between leaf-chewing and sap-sucking insects. This may result from differences in biology, particularly feeding requirements, and their interaction with host-plant characteristics, which varied considerably between the hosts studied. Further, no compensatory effects, manifested as negative correlations of species numbers, were detected among the species richness of either Lepidoptera and non-lepidopteran leaf-chewing insects, or the different guilds of sap-sucking insects. Therefore, it is not surprising that no single host characteristics emerged as the best predictor of all herbivore groups. Similarly, Cornell and Kahn (1989) did not detect such negative correlations between insect guilds on British trees.

However, habitat type, namely the distinction between coastal and forest habitats, proved to be an important factor determining species richness of both leaf-chewing and sap-sucking insects (although this conclusion is based on the comparison involving only two coastal *Ficus* species). Many plant variables differ between forest and coastal habitats, so it is impossible to pinpoint individual factors responsible for differences in insect communities. However, the results demonstrate convergent effects of coastal habitats on two distantly related *Ficus* species. Specific physiological traits of leaves and low density of these two *Ficus* species, low overall diversity of coastal vegetation, and low abundance and diversity of other *Ficus* species in this habitat may contribute to low diversity of *Ficus* herbivores. Further, saltwater mist and salt deposit on the foliage of coastal *Ficus* species may also affect insect herbivores. Generally, herbivore communities in coastal, mangrove habitats are species-poor (e.g. Robinson & Tuck, 1993).

#### *Herbivore communities and host characteristics*

The species richness of herbivore communities on *Ficus* in the Madang area was best correlated with tree density, leaf palatability, leaf expansion and leaf production. Correlation between local tree abundance and herbivore richness was also found for tropical insect herbivores on various species of *Piper* (Marquis, 1991), on 12 South African trees (Moran *et al.*, 1994), as well as on *Passiflora* (Gilbert & Smiley, 1978). Locally, more abundant plants may support more herbivore species as a result of (1) higher colonisation rates, caused by (a) their wider micro-distribution, or (b) their occurrence in a higher number of habitats; or (2) lower extinction rates as they can sustain large populations of herbivores (reviewed by Price, 1983; Lewinsohn, 1991; Stevens, 1986).

Leaf palatability was the best predictor of the number of leaf-chewing species, but a similar variable could not be easily estimated for sap-sucking insects. With the

data available, leaf palatability may account best for the resource base provided by each *Ficus* species to its leaf-chewing community. The greater the resource base, the richer the community (e.g. Price, 1992; Basset, 1996). However, leaf palatability derived from experimentation with a particular species of generalist weevil may only be partially applicable to other insect taxa. For example, it had no significant effect on Lepidoptera species (see further discussion in Basset, 1994).

Similarly, leaf expansion time, the most important explanatory variable for sap-sucking communities, appears to be directly related to resource abundance and persistence. Young leaves are a high-quality, rare and short-lived resource for herbivores (Aide, 1993; Coley & Aide, 1991; Scriber & Slansky, 1981). Sap-sucking insects often prefer young foliage because growth means increased translocation of nutrients via phloem and, to some extent, xylem (Raven, 1983; Press & Whittaker, 1993). Leaf expansion time corresponds to the length of availability of a high-quality resource unit. The importance of this variable should be highest for host-specific herbivores with low dispersal ability, such as mesophyll-feeders, as the present data suggest. Likewise, Wood, Olmstead and Guttman (1990) showed that availability of young, growing twigs was crucial for phloem feeding membracids. Host plant variables failed to explain species richness of xylem feeders, since this guild is so widely polyphagous that the differences in species richness among individual *Ficus* hosts are small and prone to stochastic effects.

It was marginally easier to predict the number of Lepidoptera species on each *Ficus* than the total number of leaf-chewing species. Caterpillars are likely to be directly influenced by several foliage characteristics, such as leaf production, whereas the fitness of other leaf-chewing species, such as wood-boring Cerambycidae and root-feeding Chrysomelidae, is likely to be independent from these foliage characteristics. However, our leaf production data are too crude to analyse these patterns in detail. Other studies of Lepidoptera larvae in temperate forests reported similar difficulties in predicting species richness from host-plant characteristics (e.g. Futuyma & Gould, 1979; Karban & Ricklefs, 1983).

Several host variables, such as taxonomic isolation, latex outflow, leaf pubescence and predation pressure, were expected to be good predictors of insect species richness, but proved to be of lesser significance in the present system. For example, the number of closely related plants which might serve as a source of potential herbivore colonizers could be an important predictor of herbivore species richness. Taxonomic isolation was important in some temperate herbivore-plant systems (Cornell & Washburn, 1979; Neuvonen & Niemela, 1983; Connor *et al.*, 1980), but not in others (Leather, 1986; Lawton & Schröder, 1976). Lack of a relationship between the taxonomic isolation of a tropical plant and the species richness of its herbivores, as found in the present study and others (e.g. Moran *et al.*, 1994; Basset, 1996), may be expected if important plant traits for herbivores are not phylogenetically conservative. However, the concept of taxonomic isolation is not strictly phylogenetic and it is not possible to make strong inferences about the evolution of host plant traits without a robust phylogeny.

Latex usually acts as a deterrent to many leaf-chewing insects (e.g. Dussourd & Eisner, 1987; Farrell *et al.*, 1991). However, in the present study, considering congeneric host-plants with a wide range of latex outflow, the predictive value of this variable was minimal. This either suggests that latex composition and/or stickiness are far more important than its outflow, or that most of *Ficus*-feeding insects are well-adapted to tolerate latex defences. Leaf pubescence was demonstrated

to be effective as a defence against sap-sucking insects (Tingey, 1985), but, despite the large differences of this variable in the study hosts, it had no detectable effect on the species richness of sap-sucking insects. Similarly, leaf pubescence did not influence the extent of feeding damage by hemipterans in a rain forest community in Sulawesi (Hodkinson & Casson, 1987).

Predation pressure may be another factor preventing the successful exploitation of certain plant resources by insect herbivores (e.g. Bernays & Graham, 1988; Berdegue *et al.*, 1996). Despite predation rates on the foliage of *Ficus* species being highly variable over short periods of time and among individual trees, no consistent differences were found (unpubl. data). Predation rates on *Ficus* were comparable to those measured in the understorey of a primary forest in Cameroon, but much lower than in the canopy (Olson, 1992). Predation might remain an important factor in *Ficus* herbivore communities, but is unlikely to contribute to differences in species richness among *Ficus* hosts.

#### *Regional versus local predictors of insect species richness*

In recent years, there has been much interest in the relative contribution that regional (including historical) and local factors exert on local species richness (review in Cornell & Lawton, 1992). Most analyses of insect herbivores have focused on regional patterns in the temperate zone. They report a correlation between plant regional distribution and regional herbivore richness (reviewed in Lawton, 1978; Strong, 1979; Claridge, 1987). Lewinsohn's (1991) study on herbaceous Asteraceae is exceptional in confirming the effect of plant distribution on herbivore regional richness for tropical herbivores. However, information on regional species richness is practically non-existent for arboreal herbivores in the tropics. It is likely that the differences between local and regional species composition will be larger than those found in temperate zone. For example, Southwood *et al.* (1982) recorded 40% of the regional (British) herbivore species associated with a particular tree species by sampling as few as three individual trees. Note that since the relationship between local and regional species richness may assume several forms (Ricklefs, 1987), the differences between *Ficus* communities reported in the present study cannot be extrapolated to larger areas. As long as knowledge of the New Guinean insect fauna is not comparable to that of the British fauna, regional patterns in insect species richness there cannot be adequately analysed.

In our system, historical factors, such as taxonomic isolation, geographic distribution and altitudinal range failed to explain local species richness, particularly when the two seashore *Ficus* species were removed from the analyses. The substantial overlap in species composition among *Ficus* hosts indicates that many herbivorous species are able to feed on numerous *Ficus* species, so that their host choice may reflect local conditions, such as ambient host plant quality and abundance, rather than phylogenetic constraints. This implies the importance of local and short-term processes of herbivore colonization and extinction and stresses the importance of local factors for plant-herbivore systems in the tropics (see Basset, 1996). Even for taxa closely associated with *Ficus*, such as fig wasps (Agaonidae), species richness is partially constrained by historical factors and phylogeny, but also depends on ecological factors (Compton & Hawkins, 1992).

Further, resource abundance and quality may affect herbivore communities on

*Ficus* world-wide, but these factors act on different regional pools of herbivore and *Ficus* species. For example, the dioecious subgenus *Ficus* prevails in New Guinea (and in the present study), but the monoecious subgenus *Urostigma* prevails in the Neotropical region (Berg, 1989). Similarly, there are large intercontinental differences in the relative species richness of various sap-sucking taxa (e.g. the exceptional diversity of Membracidae in the Neotropical region; Wood & Olmstead, 1984). Such differences are inevitably reflected in the composition of *Ficus* communities (Basset *et al.*, 1997). Clearly, replicates of this study are needed to address the relative importance of local and regional factors properly.

### Conclusion

Since faunal overlap between *Ficus* hosts was high, both for leaf-chewing and sap-sucking insects, this suggests either that many evolutionary interactions between *Ficus* and its herbivores have developed recently, mostly from a pool of generalist insect taxa; or that highly specialized interactions have not been conserved in evolutionary time and that host switching has been/is a common event. The former seems unlikely because (a) of the considerable diversity and endemism of *Ficus* in New Guinea, which suggests that the genus has long been established there; (b) at least leaf-chewing insects feeding on *Ficus* recruit from a relatively small number of higher taxa and are highly predictable (Basset *et al.*, 1997); and (c) many insect species appear to be relatively well-adapted to feeding on *Ficus* spp. and leaf palatability *in situ* was uncorrelated with latex outflow.

The second hypothesis, that specialized interactions have not been conserved, would be consistent with a pattern of accumulation of rather oligophagous species (at least able to feed on several *Ficus* spp.) dependent chiefly on food quality and availability, as suggested by the present data.

To conclude, our data do not appear to support the dogma of old, extremely specialized and conservative interactions between insect herbivores and their hosts, providing numerous ecological niches in the tropics (reviewed in Pianka, 1966). It would be stimulating to compare the present patterns with those involving other species-rich plant genera in the tropics and the insect herbivores feeding on them.

### ACKNOWLEDGEMENTS

We are pleased to acknowledge the help of Chris Dal, Martin Kasbal and Kenneth Sehel-Molem who assisted with most of the technical aspects of the project. Manek Pius Balide, Tatau Wesly Molem, Kellie Dewilog, Nataniel Mataton, Kau Beck, Wamei Nataniel, Loman Kau, John Auga, Mafi Lom, Maros Lom, Baiom Meng, Stean Baiom, Philip Damag, Wiliam Boen, Freddie Dal and Bais Dal collected many of the insect specimens. The landowners Kiatik Batet, Hais Wasel and Sam Guru kindly allowed us to collect in Baitabag, Ohu and Mis, respectively. Larry Orsak, Anne Borey-Kadam and the staff of the Christensen Research Institute provided invaluable assistance with the logistics of the project. Taxonomic help was provided by C. Berg, Arnold de Boer, Thierry Bourgoïn, Daniel Burckhardt, J. P. Duffels, Jeremy Holloway, Jaroslav Holman, Paul Katik, Bill Knight, Pavel Lauterer,

John Medler, Jacqueline Miller, Scott Miller, Olivier Missa, Eugene Munroe, Gaden Robinson, Al Samuelson, Klaus Sattler, Michael Schaffer, Roy Snelling, Kevin Tuck, Richard Vane-Wright and Mick Webb. Various drafts of the MS benefited from discussions with and comments from Scott Miller, Bill Knight, George Weiblen, Neil Springate and Anthony Dixon. The project was funded by the National Science Foundation (DEB-94-07297, DEB-96-28840 and DEB-97-07928), the Christensen Fund (Palo Alto, California), the National Geographic Society (grant no. 5398-94), the Czech Academy of Sciences (grants no. C6007501 and A6007705), the Czech Ministry of Education (grant ES 041), and the Otto Kinne Foundation.

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