

ECOLOGICAL CHARACTERISTICS OF AN ARBOREAL COMMUNITY OF CHRYSOMELIDAE IN PAPUA NEW GUINEA

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1. Introduction

The species richness and the abundance of chrysomelids foraging within the crowns of rainforest trees, particularly in the tropics, is considerable (e.g., Erwin and Scott, 1980; Farrell and Erwin, 1988; Stork, 1991; Basset, 1991; Allison *et al.*, 1993). Despite this, only 2 of the 78 contributions in the series "Biology of the Chrysomelidae" (Jolivet *et al.*, 1988; Jolivet *et al.*, 1994) dealt with the ecology of chrysomelids associated with tropical trees. One paper presented some general aspects of community structure of chrysomelids and staphylinids collected with pyrethrum knockdown in an Amazonian rain forest (Farrell and Erwin, 1988); the other described the biology of Eumolpinae associated with cacao trees in Brazil (Ferronato, 1988). Surely, this does not reflect lack of scientific interest in the ecology of chrysomelids associated with tropical trees, but, rather, logistical problems in collecting and identifying these beetles, as well as in estimating their host range.

Since chrysomelids are abundant in canopy samples, they may also fill important roles in the countless food-webs existing in tropical rain forests. A better understanding of rainforest ecology will clearly depend on our future inclination to invest more research efforts into studying the taxonomy and ecology of numerically or ecologically important arthropod groups foraging in the rainforest canopy, such as chrysomelids. For the ecologist, one particular challenge is to assess the host-range of both juvenile and adult stages by appropriate techniques, and, with other information in hand, to estimate the number of species associated with a particular tree species. In this regard, data obtained on chrysomelids foraging in temperate woodlands may not be readily applicable to their tropical rainforests counterparts, because selection pressures acting on insect herbivores in these two environments appear different (Basset, 1992). Jolivet (1988), in reviewing food selection in Chrysomelidae, indeed identified the major gap in knowledge as being the lack of information about species foraging within tropical forest canopies.

A local study of the fauna of chewing insects associated with ten species of forest trees in Papua New Guinea (Basset, in review) provided us sufficient material to undertake a relatively detailed analysis of the ecological characteristics of the community of adult chrysomelids collected on the foliage of these tree species. In this contribution, we examine broad patterns in taxonomic composition, species-richness, density, host specificity, species abundance and body size, synecology and seasonal activity for

, pp. 1-7.

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these beetles. Our field methods and analyses aimed particularly at assessing whether species feed on the foliage of the study trees and, if not, at finding alternative explanations for their presence on these trees.

2. Material and methods

Study site and insect collecting

The study was performed on the slopes of Mt 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 1,100-2,362 m (summit), but was mostly confined around 1,200-1,400 m. Mt Kaindi has been locally cleared, 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 detailed further by Gressitt and Nadkarni (1978) and Van Valkenburg and Ketner (1994). Chrysomelids were collected from ten plant species, representing native forest trees and shrubs of different successional status and patterns of leaf production (Table 1). Hereafter, the tree species are designated by their generic names.

Chrysomelids were collected by Y. B. from the foliage of the study trees by hand collecting, foliage beating, branch clipping, intercept flight traps and pyrethrum knock-down. The four first of these methods were used both during day- and night-time, whereas pyrethrum knockdown was only performed during day-time, in early morning. Live specimens from the first three methods were used in feeding trials (see next section). Hand collecting and foliage beating represented, for each tree species, about 50 hours of hand-collecting activity and 300 beating samples distributed among different individual trees. Branch clipping (as in Basset *et al.*, 1992) represented, for each tree species 55 samples of about 33 m² of leaf surface, obtained from different individuals. One intercept flight trap (as described in Springate and Basset, *in press*) was set up in the middle of the crown of one individual of each tree species. The trap collected insects continuously during the course of one year and was surveyed approximately every eleven days. One individual of each tree species was sampled using pyrethrum knockdown (solution of 5% Pyranone® and kerosene), using from 12 to 20 trays of 1 m² of surface, depending on tree size (total 159 trays used for all tree species). The protocol of Allison *et al.* (1993) was followed with the only difference being that trees were fogged by climbing directly into them, not from an adjacent tree.

Active sampling was performed from February to July 1992 and from November 1992 to April 1993, while the traps were run from April 1992 to April 1993. Field data have thus been gathered over more than a year and account for the seasonal variation in insect diversity and abundance at the Wau site. When the foliage 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 and all material thus derived has been considered for subsequent analyses.

Table 1. Study trees, their successional status (Pi = pioneer, Pe = persistent), average height when mature (S < 15 m, T > 15 m), their phenology of leaf production and their type of flowers in relation to attractiveness to beetles

Hosts	Plant family	Status, H	Phenology	Flowers (1)
<i>Elmerrillia tsiampacca</i> (L.) Dandy	Magnoliaceae	Pe, T	Continuous	4
<i>Cinnamomum cf. culilaban</i> (L.) Presl	Lauraceae	Pe, S	Intermittent (2)	5
<i>Piper plagiophyllum</i> K. Sch. and Laut.	Piperaceae	Pi, S	Continuous	1
<i>Ficus nodosa</i> Teys. and Binn.	Moraceae	Pi, T	Deciduous (2)	1
<i>Pipturus argenteus</i> Wedd.	Urticaceae	Pi, S	Continuous	1
<i>Castanopsis acuminatissima</i> A. DC.	Fagaceae	Pe, T	Intermittent (2)	5
<i>Calcdluvia brassii</i> Hoogl.	Cunioniaceae	Pi, S	Continuous	3
<i>Aleurites moluccana</i> Willd.	Euphorbiaceae	Pe, T	Continuous	2
<i>Melicope denhamii</i> (Seem.) T. Hartley	Rutaceae	Pe, S	Intermittent (2)	5
<i>Cordia dichotoma</i> Forst.	Boraginaceae	Pi, T	Deciduous (2)	3

(1) Type of flowers: 1 = concealed flowers or difficult to forage on; 2 = large, unattractive flowers for beetles; 3 = small, unattractive flowers; 4 = large, attractive flowers; 5 = small, attractive flowers.

(2) Apparently 2-3 leaf flushes a year, as a synchronous event

Chrysomelids were first assigned to morphospecies, on the basis of external characters, by Y.B. in Papua New Guinea. Since knowledge of the ecology of most Papuan beetles is fragmentary, insect specialization had to be assessed from feeding trials in the laboratory. Live 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, they were then tested in random order for 24 h periods on the foliage of the 9 other study species. Feeding damage was scored visually, relative to insect body size, 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. Insects were assigned to four leaf-feeding categories according to the results of these tests: (a) "specialists", *i.e.*, insects tested on three or more plant species but which only fed on the plant they were collected from (sum of feeding scores < 100); (b) "generalists", *i.e.*, insects tested on three or more plant species and which fed on two or more plants belonging to different plant families (sum of feeding scores \geq 100); (c) "unknown specialization", *i.e.*, insects which fed, but because of death, could not be tested on more than two plant species; and (d) "incidentals", *i.e.*, insects which did not feed in the trials. Categories (a), (b) and (c) were further termed "proven feeders". Further, species collected dead (*i.e.*, by intercept flight traps or pyrethrum knockdown) and not otherwise tested in feeding trials were assigned to the category "additional".

As far as possible, mean body size of each morphospecies was determined from a series of ten measurements, taken, in most cases, in alcohol, and to the nearest 0.1 mm. The relation between body size (mm) and body weight (mg of dry weight) was obtained using the equations provided by Schoener (1980) for tropical Coleoptera.

The chrysomelid material was later dry mounted at the Bishop Museum, Honolulu. Morphospecies assignment, hereafter "species" for sake of simplicity, was checked and updated by G.A.S. The material has been deposited in the collections of the Bishop Museum.

Statistical methods

Using the program ADE 3.6 (Chessel and Dolédec, 1993), we performed a canonical correspondence analysis (CCA; Ter Braak, 1986; Lebreton *et al.*, 1988; Palmer, 1993) using the abundance (no. of individuals) of the most common species of chrysomelids collected on the tree species studied (= "sites"). CCA is a powerful multivariate analysis, particularly appropriate when species show nonlinear relationships with environmental variables, and which relates known variation in the environment to community composition. Ordination axes are chosen in the light of known environmental variables by imposing the extra restriction that the axes be linear combinations of environmental variables. Therefore, it is a direct gradient analysis (Ter Braak, 1986). CCA allowed us to infer the relative contribution of several host-related variables to the variance in the distribution of chrysomelid species among the study trees. These variables included: average leaf water content (coded as "water" in the ordination diagram); taxonomic isolation (*i.e.*, no. of congeneric plant-species in New Guinea, "tax. is."); average leaf area in cm² ("leaf area"); area of young foliage collected throughout the year in branch clipping samples ("young l."); maximum altitude at which the tree species grows locally ("altitude"); and flower attractiveness to beetles (Y. Basset, pers. obs.; nominal variable "flowers"). Exception made of the variable "flowers" (see Table 1), the measurement and the values of all variables have been reported elsewhere (Basset, *in review*).

3. Results

Taxonomic considerations

In terms of species richness, Chrysomelidae were the most prominent leaf-feeding insect family on the foliage of the study trees, followed by Curculionidae (leaf-feeding species only), Geometridae, Tortricidae, Noctuidae and Lymantriidae. Overall, 2183 individuals of Chrysomelidae representing 134 species were collected from the foliage of the study trees. Although Galerucinae dominated the samples when the total number of species collected was considered, Eumolpinae were more prominent in terms of individuals and biomass, and of species which fed on the tree species studied (Table 2). Thus, in our system, chrysomelid samples were dominated by (in decreasing order): Eumolpinae, Galerucinae, Alticinae and Cryptocephalinae. None of the Cassidinae and Chrysomelinae collected appeared to feed on the study trees. The Appendix details the identity (when known) of species which fed on the foliage or which were relatively common (see below).

Densities of adults on foliage

Mean adult chrysomelid densities as recorded year-long by branch clipping for all tree species amounted to 0.324 ± 0.055 individuals (s.e.) per sample, which, on average consisted of 5998.6 ± 108.8 cm² of leaf area ($n = 550$, double-sided area). This translates roughly as estimates of 0.5 individuals per m² of foliage. This appears to be in the range of densities found for chrysomelids in Australia, on eucalypt foliage (0.4–0.8 individuals per m²: Ohmart *et al.*, 1983), and on a subtropical species of rainforest tree (1.9 individuals: Basset and Arthington, 1992). Adult densities were significantly dif-

Table 2. Total number of species, of individuals and of biomass (no. of individuals x average body weight) of Chrysomelidae collected from the foliage of study trees, detailed by subfamily and by insect category (F = proven feeders, T = all species)

Subfamily	Species →		Individuals →		← Biomass (mg DW)	
	F	T	F	T	F	T
Cryptocephalinae	1	9	4	34	4.9	24.1
Eumolpinae	22	42	1312	1437	2120.0	2375.6
Chrysomelinae	0	2	0	2	0	15.4
Galerucinae	9	52	105	293	781.8	1214.9
Alticinae	3	26	272	411	220.8	389.6
Cassidinae	0	3	0	6	0	27.8

ferent among tree species (Kruskall-Wallis $W = 125.4$, $p < 0.001$; Table 3). Higher densities occurred on *Pipturus*, *Piper*, *Ficus* and *Caldcluvia*. Interestingly, densities were significantly higher on pioneer trees than on persistent trees (Mann-Whitney $U = 47904.0$, $p < 0.001$). The low densities recorded on the foliage precluded confident reporting of density estimates for particular species.

Adult host specificity and circulation among tree species

Of the 134 species collected, proven feeders represented 36 species (24 specialists, 9 generalists and 3 species of unknown status), incidentals 42 species and additional 56 species. In other terms, 58% of the species collected could be used in feeding trials, and, out of these, 54% rejected food. Further, out of the species which could be assigned either to specialists or generalists, specialists represented 73% of the species. Although proven feeders represented only 27% of the total number of species collected, they represented 78% of the number of individuals collected (Table 2). Hence, the high number of incidental and additional species present on the foliage of the study trees must be of concern and our subsequent analyses were in part directed towards exploring this problem.

When each tree species was considered as a separate habitat (Table 3), there was no correlation between the number of species feeding on that tree and the number of incidental plus additional species ($r = -0.07$, $p = 0.86$). Densities were correlated with the number of specialist species feeding on each tree, ($r = 0.92$, $p < 0.001$), not with the total number of species collected on each tree ($r = 0.38$, $p = 0.28$). Interestingly, trees with the highest proportion of incidental plus additional species (*Melicope* and *Cinnamomum*, > 96% of the total no. of species collected, Table 3) have small flowers which attract high numbers of beetles (Y. Basset, pers. obs.).

The different beetle categories (proven feeders, incidentals, additional) were not uniformly distributed among subfamilies (Cryptocephalinae, Eumolpinae, Galerucinae, Alticinae; G-test, $G = 33.02$, $p < 0.001$). Eumolpinae dominated the proven feeders category, whereas Galerucinae dominated the incidental and additional categories.

The appendix details the number of individuals collected from each tree species and the results of feeding trials with the foliage of these tree species. We list data for the 36 proven feeders plus 10 common species (i.e., when 10 or more individuals were collected) in the incidental and additional categories. Within Eumolpinae, *Stethotes* spp. were often specialists, whereas *Rhyparida* spp. and *Rhyparidella?* spp. included both specialists and generalists. In Galerucinae, the *Neolepta?* spp. tested were specialists

Table 3. Abundance and species richness of chrysomelids on their hosts: densities (mean no. of individuals (s.e.) collected per branch clipping sample); no. of species collected (specialists, generalists, proven feeders, incidentals and additionals); and no. of individuals collected (proven feeders and total)

Host	Density	Spec.	Gen.	Feed.	Inc.	Add.	Ind.F.	Ind.Tot.
<i>Elmerrillia</i>	0.0	1	1	2	4	8	5	22
<i>Cinnamomum</i>	0.02 (0.02)	1	0	1	6	21	2	133
<i>Piper</i>	0.69 (0.13)	4	0	4	8	9	235	299
<i>Ficus</i>	0.60 (0.37)	3	7	10	2	15	274	300
<i>Pipturus</i>	1.35 (0.33)	9	3	14	10	8	325	391
<i>Castanopsis</i>	0.04 (0.03)	3	0	4	10	12	18	143
<i>Caldcluvia</i>	0.33 (0.11)	4	0	5	18	16	147	378
<i>Aleurites</i>	0.11 (0.06)	1	2	3	2	10	35	54
<i>Melicope</i>	0.02 (0.02)	0	1	1	10	17	204	362
<i>Cordia</i>	0.09 (0.04)	2	0	2	2	8	47	101

or did not feed. The few Alticinae listed were specialists.

Scanning the data of the Appendix allows us to check whether the results of feeding trials reflected accurately the distribution of chrysomelid species in the field. Out of 33 cases at hand (all specialists and generalists), there was a perfect match (*i.e.*, beetles were prominent only on the host-trees from which they fed) in 25 cases (76% of cases). Thus, in general, there was a good correspondence between the food preferences as assessed in feeding trials and insect presence in particular tree species. In 4 cases (all generalists), beetles fed on hosts from which they were not collected. As long as the emphasis is on assessing whether a particular species is a specialist or a generalist, as in the present paper, and not on recording host-records, these discrepancies are not particularly important and may reflect either sampling inadequacies or the idiosyncrasies of particular species. The other 4 cases (all specialists), where beetles were collected on a particular host but systematically refused to feed upon it, are more interesting. They suggest that either feeding trials were inadequate in these cases, or that beetles may sometimes be attracted to particular trees for other reasons than for leaf-feeding.

Looking at the specialist data, we noted a trend for species sustaining high populations to have been collected in a high number of habitats (*i.e.*, host-trees; Spearman's rank correlation coefficient between the no. of individuals collected and the no. of habitats in which the species was collected, $r_s = 0.57$, $p < 0.01$, $n = 24$). This suggests that for specialist species sustaining high populations, the probability of finding individuals of that particular species in marginal habitats, presumably dispersing, increases.

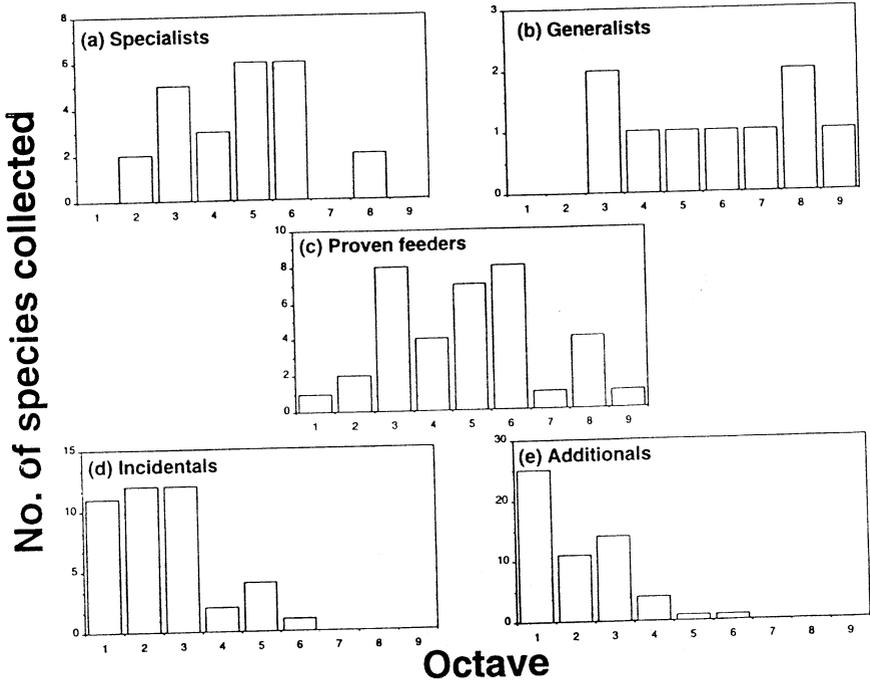


Fig. 1. Species-abundance distribution (no. of individuals) plots for (a) specialists; (b) generalists; (c) proven feeders; (d) incidentals; and (e) additional. Octaves represent abundance classes in base 2 (i.e., octave 1 = 1 individual; oct. 2 = 2-3 ind., oct. 3 = 4-7 ind., oct. 4 = 8-15 ind., etc.).

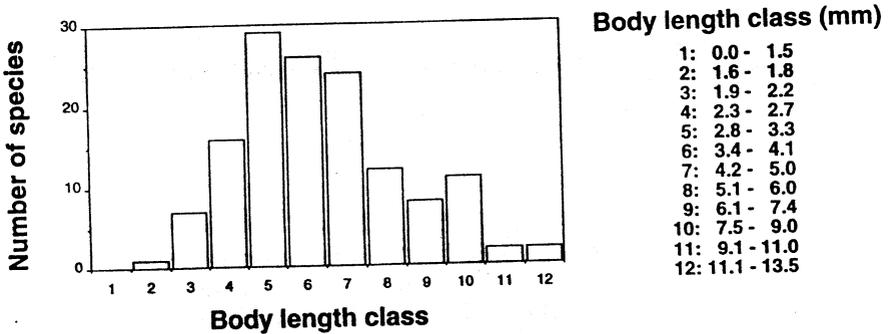


Fig. 2. Distribution of body length for all chrysomelid species collected.

Species abundance and body size

Fig. 1 summarizes the distribution of the number of individuals per species, according to the different feeding categories. These distributions showed striking differences. In particular that of the proven feeders was significantly different from both that of incidentals (G -test with four first classes and the remaining pooled in a fifth class, $G = 29.3$, $p < 0.001$) and that of additional ($G = 50.0$, $p < 0.001$). However, the distributions of incidentals and additional were not significantly different from each other (G

Table 4. Canonical coefficients and intraset correlations for the different environmental variables included in the CCA (see text)

Variable	Canonical coefficients				Correlation coefficients			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Leaf water	0.388	0.498	-1.489	-1.344	-0.313	0.594	-0.042	-0.276
Tax. isolation	-0.652	0.853	0.032	0.760	-0.240	0.553	0.130	-0.413
Leaf area	0.827	-0.770	-0.642	-2.187	0.034	-0.048	0.414	-0.869
Area of young l.	-0.063	-0.018	-0.508	-0.614	-0.053	-0.179	-0.102	0.477
Altitude	1.062	0.438	-0.440	-0.409	0.763	0.205	-0.004	0.386
Flowers	0.307	-0.377	-1.624	-0.957	0.078	-0.566	-0.648	0.356

= 5.79, $p = 0.22$). In general, proven feeders sustained much higher populations and a much lower proportion of singleton species than incidentals and additional did (proportion of singleton species: proven feeders = 3%; incidentals = 26%; additional = 45%). The proportion of couplet (*i.e.*, 2 individuals) species in different categories followed a similar trend (proven feeders = 3%; incidentals = 9%; additional = 13%).

The distribution of species body size is summarized in Fig. 2. We retained the body size classes of Morse *et al.* (1988), for ease of comparison. Most species fell into the fifth class, between 2.8 and 3.3 mm. Surprisingly, there was a non-significant trend for generalist chrysomelids to be more abundant than specialists (Mann-Whitney $U = 150.5$, $p = 0.086$). Body weight was not significantly different between specialist and generalist species ($U = 132.0$, $p = 0.33$). Although these analyses may be obscured by the low sample size (no. of species) and phylogenetic considerations, we found little evidence for specialist chrysomelids to be smaller and more abundant than their generalist counterparts. Further, our data showed no evidence that either larger or smaller species have, on average, greater dispersal abilities (Spearman's rank correlation between the average body weight of specialist species and the number of tree species in which they were collected, $r_s = -0.072$, $p > 0.50$).

Synecological aspects

The canonical correspondence analysis was performed using the number of individuals collected on each tree species (the results of all sampling methods being pooled) for the 46 chrysomelid species which are listed in the Appendix. The ordination diagram (Fig. 3) describes the strength of the relations among the chrysomelid species, between the chrysomelid species and their hosts, and between the chrysomelid species and the environmental variables measured. Most of the variance in the system was explained by four axes (Fig. 3a). The eigenvalues of axes 1, 2, 3 and 4 were 0.910, 0.790, 0.686 and 0.4138, respectively, for a total eigenvalue of 3.349. Fig. 3b accounts for 50.5% of the variance in the system, as constrained by the environmental variables; Fig. 3c for 32.8%. We also performed a correspondence analysis (CA) and compared the results with those of the CCA, as advised by Ter Braak (1986). The CA grouped the species in a similar way to the CCA and most of the correlations between the species scores of the two ordinations were high (0.971, 0.766, 0.983 and 0.261 for axes 1, 2, 3 and 4, respectively), suggesting that the constraints (our environmental variables) that we imposed on the system did not greatly distort the real matrix of observations (see Ter Braak, 1986). Indeed, the environmental variables measured represented about 87% of the total variance in the unconstrained system (sum of eigenvalues for the CCA di-

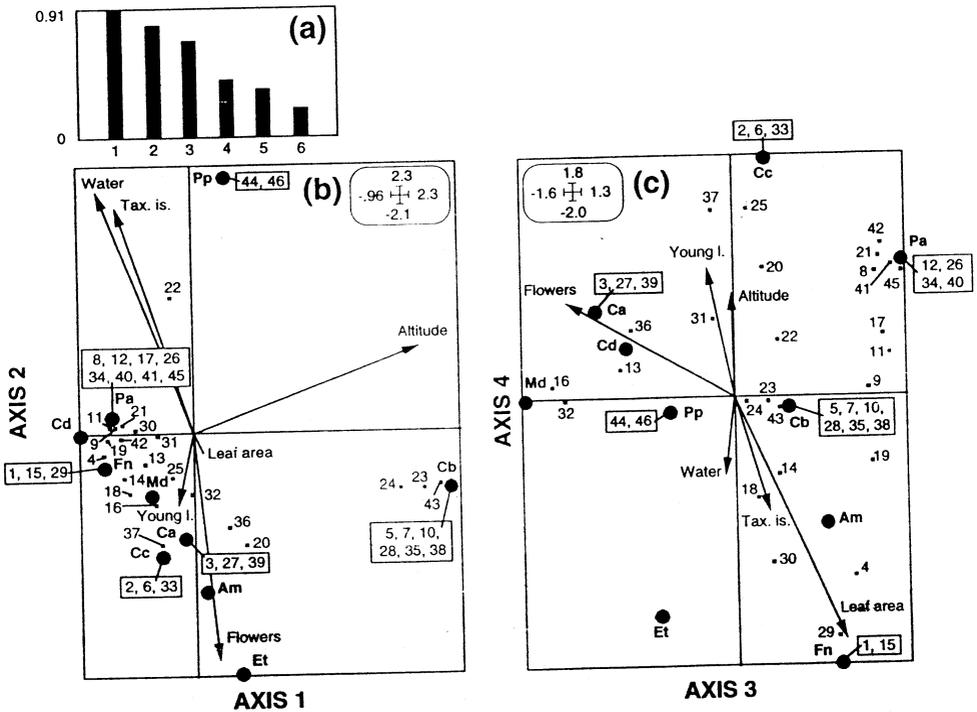


Fig. 3. CCA diagram for the 46 chrysomelid species listed in the Appendix: (a) graph of eigenvalues for the 6 axes extracted; (b) plot of canonical axes 1 and 2; and (c) plot of canonical axes 3 and 4. Species are identified by their code numbers (see Appendix), sites (tree species) by their initials (see Table 1) and environmental variables by their code (see text). For the sake of clarity, arrows of environmental variables were scaled up by a factor of x 8.56 and x 4.20 in (b) and (c), respectively.

vided by the sum of eigenvalues for the CA, = 3.859, see Borcard *et al.*, 1992).

Table 4 presents the canonical coefficients and the intraset correlations of the CCA (see Ter Braak, 1986). These results suggest that the best explanatory variables for the formation of axes 1, 2, 3 and 4 were altitude, leaf water, flowers and leaf area, respectively (and see the directions and relative lengths of the arrows in the ordination diagram). However, the relative contribution of each variable often differed when appraised from the canonical coefficients or the intraset correlations. This can result when the variables are highly inter-correlated (Ter Braak, 1986) or, most likely in our case, when the number of variables (6) approaches the number of sites (tree species, 10), thus weakening the robustness of the CCA (Lebreton *et al.*, 1988).

Ter Braak (1986) explains concisely how to interpret ordination diagrams of CCA. Let us just recall that the closer particular species or sites are plotted on a particular plane, the more affinities they have in this plane; and that the scores of the species on a particular variable axis can be appraised by extending the arrow of that variable in both directions and dropping a perpendicular from the species point to the axis variable: high scores denote high affinities with the variable. From the first plane of the ordination (Fig. 3b), we can infer that chrysomelid species foraging on *Caldcluvia* and *Piper* were quite isolated spatially from the others. The first axis is presumably an altitudinal gradient: *Caldcluvia* grow at higher altitudes than the rest of the host-trees. This axis

probably segregated the chrysomelid species according to their altitudinal occurrences on Mt Kaindi. The second axis is perhaps the most difficult of all to interpret. Leaf water content and taxonomic isolation explained best the formation of this axis. It could be related to a complex set of factors (e.g., host biochemistry, past history of insect-plant interactions, etc.) and may reflect to some extent the strength of the affinity of chrysomelids with their hosts. In the first plane, specialists tended to be grouped next to their hosts, whereas generalists and actively dispersing species did not. Interestingly, the few Alticinae included in the CCA seemed to be located in the upper part of the plane (nos. 43, 44, 45 and 46 in the ordination diagram).

The second plane of the ordination (Fig. 3c) seems more straightforward to interpret. Axis 3 was related to the attractiveness of flowers to beetles and may have segregated species which are actively visiting flowers (e.g., on *Melicope*) from these which are not (*Ficus*, with its concealed flowers scores poorly on this axis). Axis 4 appeared to be related to the leaf size of the host. It may have segregated species which forage into a dense, small-leaved foliage (e.g., *Cinnamomum*) from these foraging in a sparse, large-leaved foliage (e.g., *Ficus*).

The CCA also allowed us to infer the likelihood of species' interactions. Species plotted in "boxes" in the first plane of the ordination (i.e., they have the same coordinates, see Fig. 3b) were more likely to interact with each other. There appeared to be little consistent taxonomic grouping in these "boxes". It was also possible to examine the similarities in chrysomelid fauna among host-trees with the first plane of the ordination: the closer the trees plotted, the more similar they were. In this regard, as already emphasized, *Caldcluvia* and *Piper* stood out. As for the rest of the tree species studied, there was little obvious clustering, suggesting for example that the taxonomic identity of the tree had little bearing overall on the fauna that it shared with other tree species. For example, *Ficus* and *Pipturus*, presumably amongst the taxonomically closest trees in the system (families Moraceae and Urticaceae), were relatively distant from each other (Fig 3b and 3c).

We also checked whether the distribution of potential enemies, particularly ants, had any effect on the distribution of chrysomelid species on the different tree species. There was no obvious correlation between ant abundance on foliage (data in Basset, in review) and the number of species of proven feeders, the total number of species collected and the density of chrysomelids on their hosts ($r = 0.10$, $p = 0.77$; $r = 0.25$, $p = 0.48$; $r = -0.03$, $p = 0.92$, respectively). These trends were similar when we considered the abundance of spiders, with the exception of a non-significant trend for the number of specialist species to be correlated with the abundance of spiders. Thus, from a community viewpoint, the abundance of ants, and perhaps also that of spiders, appeared to have little impact on the distribution of adult chrysomelid species on the study trees (but see discussion).

Seasonal activity of adults

At Wau, chrysomelids tended to be equally active during day- and night-time, as judged by their abundance in intercept flight traps surveyed during a one-month period (Springate and Basset, *in press*). Seasonal patterns of adult activity during the study year as recorded by these traps are summarized in Fig. 4. It is difficult to comment on putative differences in flight activity of chrysomelids at the base and near the summit of Mt Kaindi, since there was no replicate in the latter case.

At the base of Mt Kaindi, chrysomelids did not show strong peaks of activity overall (Fig. 4b). At most, there may have been a slight decrease in activity during the driest

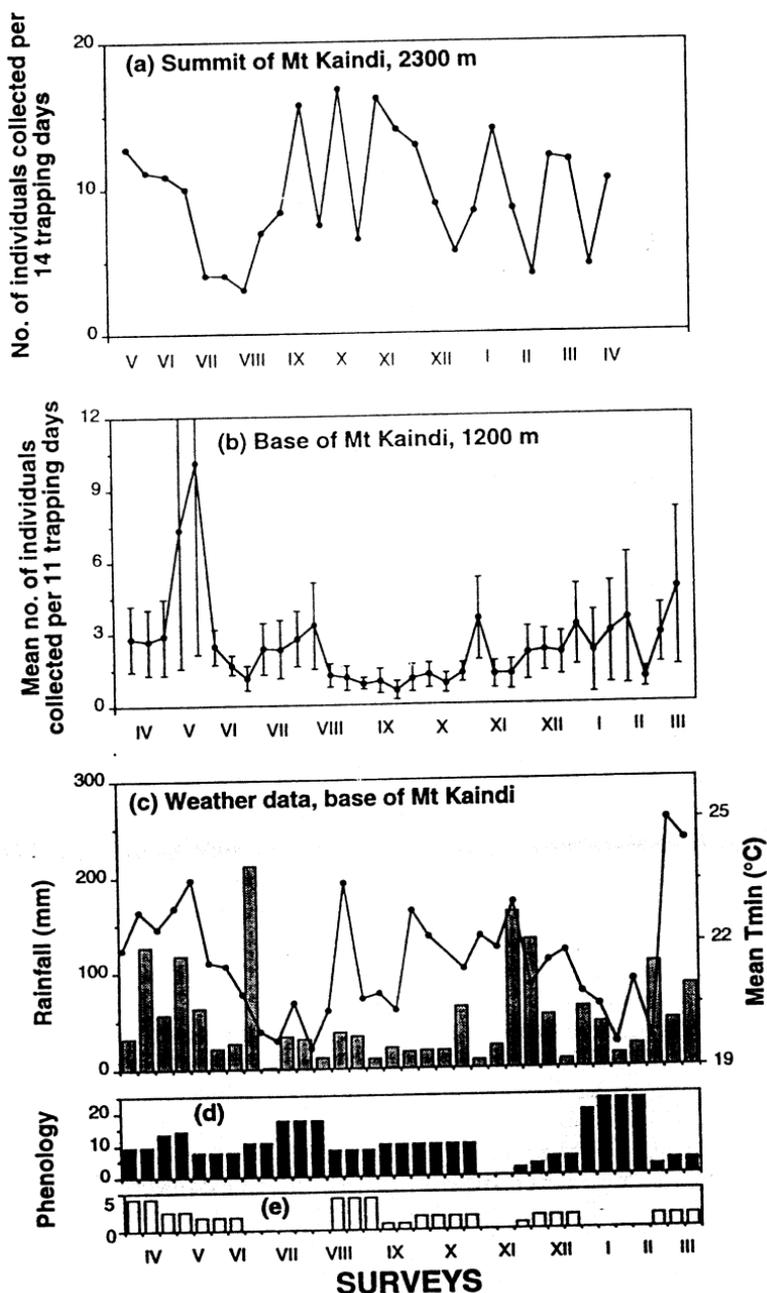


Fig. 4. Seasonal patterns of activity in adult chrysomelids as collected by intercept flight traps: (a) data from a single trap located on *Caldcluvia* near the summit of Mt Kaindi at 2300 m, from May 1992 to April 1993; (b) data from nine traps located at the base of Mt Kaindi, 1200 m (vertical bars = standard errors), from April 1992 to March 1993; (c) average daily minimum temperature (line) and sum of rainfall (bars) during the corresponding trapping periods at the base of Mt Kaindi; (d) index of leaf production (%) and (e) number of tree species flowering at the base of Mt Kaindi (data for study trees only; see text).

period, in September-October 1992. The weather data available at the study site (data courtesy Wau Ecology Institute) consisted of daily temperature, minimum and maximum temperatures, and daily rainfall. None of these variables could be related to overall chrysomelid activity (correlations were all well below statistical significance and compare Figs 4b and 4c). From our field observations, we further derived an index of leaf production (% of young leaves present in study trees at the study site, averaged for all tree species) and recorded the number of tree species studied flowering during corresponding trapping periods. Again, none of these variables was obviously correlated with overall chrysomelid activity (compare Figs 4b and 4d,e). Rainfall and temperature usually vary little during the course of the year at Wau (Gressitt and Nadkarni, 1978) and therefore did not greatly affect overall chrysomelid activity during our study year. The different tree species were often in fairly different phenological states during a particular survey and this might have obscured the overall influence of leaf and flower productions.

Although seasonal plots for each trap revealed that distinct peaks in activity, not necessarily congruent, existed in several host-trees (*Pipturus*, *Ficus*, *Castanopsis* and *Melicope*, notably), it was difficult to relate these peaks to the phenology of the study trees. Confounding factors may include the absence of replicates, the incidental and additional species collected, as well as the idiosyncrasies of numerically dominant species.

Dissection of presumed pollen-feeders

From our various results, we deduced that the foraging of at least some chrysomelid species in our study trees may have more to do with the presence of flowers than with leaf-feeding on these trees. To test whether some species fed upon pollen, a few species were dissected by G. A. S. Our choice was guided by the diagram of the CCA (see Fig. 3c) and we selected Eumolpinae and Galerucinae which scored highly on the flower axis of these diagrams (nos. 3, 13, 16, 27, 31, 32, 33, 36, 37, 39). One to six individuals each of these species were dissected and examined for alimentary pollen. Correlatable feeding observations were not made.

Only two Eumolpinae turned out to positively contain pollen grains; these were two *Rhyparidella?* spp. (nos. 13, 16). Both were collected with intercept flight trap on *Melicope*, and numerous specimens were available in these collections. Up to 50% of the specimens examined were positive for pollen. In these dissections the oesophagus and crop contents were examined first, and then in positive samples the remainder of the gut was examined, which also showed pollen. Pollen grains were mixed with other food material. In some dissections, pollen was absent to infrequent, being < 10% of the alimentary contents; however in other specimens pollen made up about 50% of the material in the gut. We could not identify the non-pollen material, although some of it may be flower parts.

The other eumolpines dissected (nos. 3, 27) were not positive, but were taken in low numbers, and were obviously not massing at flowers at the time of collection. The Galerucinae dissected (nos. 31, 32, 33, 36, 37, 39) were negative for pollen, and none of these were particularly numerous in our samples.

4. Discussion

Feeding trials and chrysomelid host-specificity

Since the general interpretation of community characteristics in the system studied relies heavily on the results of the feeding trials, it is appropriate to discuss these first. We generally found a good correspondence between the food preferences as assessed in the feeding trials and insect presence in particular tree species. This occurred because the emphasis of the experimental protocol was on recording possible feeding on hosts belonging to different plant families, rather than recording feeding on related hosts and the number of such hosts accepted. For example, Begossi and Benson (1988; see Table 1) came, in substance, to a similar conclusion with feeding trials using flea beetles from the tribe *Oedionychina* collected from different herbaceous plants in southeastern Brazil.

Our objective was to classify chrysomelids into two broad categories, "specialists" and "generalists". Thus, in our experimental context, "specialist" does not mean that this species feeds only on a particular tree; it just appears not to be able to feed on the other plant families tested. As for the species feeding on hosts from which they were not collected (records "0/100" in the Appendix), the point is that they are able to feed on other plants and, therefore (but see discussion about local specialization in Fox and Morrow, 1981), it is possible that they sustain populations on other tree species than the study trees. Thus, we conclude that a broad dichotomy such as the one adopted here is relevant to our aims and may help to shed some light on ecological patterns structuring the chrysomelid communities studied. However, it is obvious that these results should be interpreted with caution when discussing the ecology of particular species. For example, *Rhyparidella wauensis* was assigned to the generalist category since it both fed upon and occurred on *Ficus* and *Pipturus*. Other workers may interpret this as being relatively host-specific, feeding only on related plant families (Moraceae and Urticaceae). Further discussion of the results obtained with feeding trials is provided elsewhere (Basset, 1994).

There were striking differences between our study and that of Farrell and Erwin (1988), who fogged tropical forest canopies in Peru. Their list of 126 "common" species was dominated by Alticinae (70 spp.), Eumolpinae (29 spp.) and Galerucinae (16 spp.), whereas our samples were dominated by Eumopinae, Galerucinae and Alticinae (in decreasing order of importance). These differences may be due to the choice of our tree species, but, more likely, to larger-scale differences between the Peruvian and Papua New Guinean sites. Our samples appear to reflect the importance of the above subfamilies in the New Guinean fauna (Gressitt, 1982). Farrell and Erwin (1988) noted that many genera in their samples included temperate counterparts associated with herbs in families that were well represented as canopy-trees on their site. Although three (Euphorbiaceae, Urticaceae and Boraginaceae) out of the eight plant families cited as examples in this regard by Farrell and Erwin (1988) were represented in our study trees, we found no such trend. Since the review provided by Jolivet (1988) suggests that Alticinae may be often more specific than Eumolpinae and that the few species of Alticinae that feed on our study trees were all specialists, it is possible that the chrysomelids collected at the Peruvian site may be on average more specific than at the Papua New Guinean site. This illustrates the point that ecological data obtained at a particular rainforest site may not automatically be relevant elsewhere and that caution must be exercised when attempting to make generalizations. Clearly, we need to

invest more effort in contrasting taxonomic and ecological patterns between different types of rain forests (Basset, 1992).

The most generalist chrysomelids in our feeding trials, accepted 3 out of the 10 tree species provided. For comparison, some generalist Lymantriidae and Noctuidae collected from the study trees accepted nearly all tree species provided. However, most chrysomelid species (about 70%) collected in the present study behaved as specialists when adults. This represents a high proportion, perhaps higher than in temperate woodlands (see Basset, 1994), but it also emphasizes that it would be misleading to assume that every chrysomelid species collected on tropical foliage is likely to be a specialist. Insect host-specificity may depend, in part, on forest type and characteristics of the host tree (Basset, *in review*). Although generalists were not particularly speciose, they nevertheless built up large populations and together represented 50.5% of individuals which could be assigned to either specialist or generalist categories.

Life histories and foraging patterns

Life histories of our tree-associated chrysomelids are virtually unknown. In Eumolpinae, larvae are root feeders (e.g., Jolivet, 1988) but we have little data on their occurrence and host affinities. Adults of some species are quite abundant on certain hosts, and these trees may also be larval food plants. The same is true for many Galerucinae and Alticinae, speciose subfamilies whose larval feeding habits include roots. These two subfamilies also include surface feeders, and some Alticinae additionally have larval leaf miners (see Jolivet, 1988). The Cryptocephalinae are surface feeders, as are the Cassidinae. The latter, in our material, mostly have affinities with the vines *Ipomoea* spp. (Convolvulaceae). Hispinae comprise a large and diverse group in New Guinea, where species are associated with a wide array of monocot hosts, including *Pandanus* and palms. Adults and larvae are often found together deep in leaf axils in the folded surfaces of developing leaf bundles. However, no hispines turned up as incidentals or additional in our samples.

Despite the many hours that Y. B. spent within the foliage of study trees, the only larvae found belonged to a single (presumably) species in the Alticinae-Galerucinae complex, surface-feeding on *Ficus*. However, roots of study trees were not sampled. In the absence of information about larval ecology, it is impossible to discuss whether larval development constrains adult foraging and feeding. Indirect measurements of larval constraints, such as intraspecific variation in body size, suggest that it could be the case and that specialist root-feeding larvae may remain specialists as adults, and generalist root-feeding larvae may remain generalists as adults, for example (Basset *et al.* *in press*).

Our CCA emphasized patterns in adult foraging and circulation among tree species, not feeding upon tree species. The latter could be analyzed by the same procedure, by ascribing weights to the species, for example the scores of feeding trials. A further interest of the CCA procedure is that it performs well and describes accurately species and site associations even in cases with potentially serious problems, such as when important variables are not measured (Palmer, 1993). In our system, foraging patterns in chrysomelid beetles were attributed foremost to altitude, strength of affinity with host-tree, attractiveness to flowers and leaf size (and presumably denseness) of foliage. Gressitt and Nadkarni (1978) noted that turnover of phytophagous beetles with altitude on the slopes of Mt Kaindi was high, a pattern also found by A. Allison (*pers. comm.*) when fogging *Castanopsis* trees in the Wau Valley. The second axis was the most enigmatic and may perhaps be also related to some aspects of larval ecology which could

influence adult foraging. Surprisingly, the availability of young foliage was not particularly important to adult foraging patterns. Two factors may explain this. First, young foliage is not directly related to larval food resource for most species considered here. Second, a certain proportion of species may feed as adults on other food resources than young foliage, such as pollen, nectar or flower parts (Samuelson, 1994; and see below).

Ants and spiders did not greatly influence chrysomelid distributions on the study trees (at least from a community viewpoint), presumably because adults have different defense strategies at their disposal, such as thanatosis, regurgitation, jumping or simply flying off, when harassed by ants (see Selman, 1988). However, other measures of enemy-free space (*e.g.*, abundance of dominant ants and of parasitoids, foraging of vertebrate predators, etc.) may be more relevant to adult chrysomelids, and soil-dwelling ants may be important regulators of root-feeding larvae (*e.g.*, Ferronato, 1988). Further, some species are likely to be more sensitive to the enemy factor than others.

Overall chrysomelid seasonality was not well-marked in Wau but the low number of replicates and specimens collected precluded the analysis of apparent peaks of abundance in relation to the phenology of the host trees.

Chrysomelid species richness in samples

We collected a relatively high number of chrysomelid species (134) from the foliage of 10 tree species, using various techniques. To put this into perspective, Farrell and Erwin (1988) collected over 650 chrysomelid species in fogging an estimated 11075 m³ of foliage dominated by 38 tree families in five forest types in Peru. Stork (1991) collected 107 chrysomelid species in fogging 10 Bornean lowland rainforest trees (representing five tree species). Allison *et al.* (1993) found 55 chrysomelid species in fogging 8 individuals of two fagaceous tree species in the Wau area (a further 26 species were discovered in processing samples from 6 additional individual trees; Allison *et al.*, unpubl. data). For a temperate comparison, the total number of chrysomelid species in the whole of Switzerland does not exceed 515 (Besuchet, 1992; and pers. comm.) and that in the United Kingdom 255 species (Ward and Spalding, 1993). Thus, the species richness of chrysomelids foraging within the foliage of tropical trees is remarkable.

However, only 27% of species collected actually fed on the study trees, the others rejected food (31%) or could not be tested (42%). Why are these "incidental" and "additional" species present on the foliage of study trees? Let us examine the case of incidentals first. The results of our feeding trials could be wrong and a substantial proportion of species could actually be feeding on the study trees. This is not supported by our field records (see Appendix). Second, these species may be true "incidentals", dispersing to other habitats (tree species) and being collected from the foliage of study tree by chance. In this case, they are more likely to be represented in the collections by a few individuals only. We indeed found that proven feeders are much less likely to be found in small numbers than were other categories, and that the proportion of "rare" species are high in the incidental and additional categories (see Fig. 1). Within our study system, we further found that the more numerous specialist species were, the more likely they could be found on other tree species than their host. There is no reason to doubt that this can also happen to specialist species associated with host-trees not considered as our study trees. Thus, the number of incidental species present on a particular species may be a function of the species-richness of the surrounding vegeta-

tion. Note also that some of the incidentals which were collected as couplets may have been copulating and resting on the foliage of study trees.

Third, some "incidental" species may be associated with the study trees but not feeding on their foliage. The results of the CCA suggested that a certain proportion of species may be associated with flowers. We know that some eumolpines do feed on flowers. For example, Hawkeswood and Jolivet (1988) reported that *Cleptor inermis* Lefèvre (Eumolpinae) feeds on flowers in Queensland, from which pollen was presumably ingested with flower parts. Since we found both pollen and vegetal debris in the guts of two eumolpine species, and unidentified food material in the gut but no pollen in other species, this suggests that some species may be either facultative nectar/pollen-feeders and/or flower-eaters. Species facultatively associated with flowers are more likely to occur in higher numbers than the "true incidentals". In turn, this could explain the relatively high species frequency for the third octave in the distribution of species abundance in the incidental category.

As for "additional" species, we observed that the number of rare species was extremely high and that only 14 species were distributed in the third octave (Fig. 1). These species are more likely to feed on the foliage of study trees or to be associated with flowers. These considerations suggest that the actual number of chrysomelid species feeding as adults on the foliage of our study trees at the study site may not be considerably higher than that presented here.

5. Summary and conclusions

We can summarize the major ecological characteristics of this community of arboreal chrysomelids as follows.

1. Eumolpinae, followed by Galerucinae and Alticinae, dominated our samples, which overall represented 134 species and 2,183 individuals. Only 0.7% of species were larval surface-feeders and most species were probably larval root-feeders. As adults, they often measured 2.8-3.3 mm and were relatively host-specific when feeding on foliage, although some species may have been facultative nectar feeders.

2. Generalists, despite not being species-rich, were nevertheless able to sustain high population levels and overall represented half of the leaf-feeding individuals. We found little evidence that specialist species were smaller and more abundant than generalist species. Population densities on foliage were not particularly high (average 0.5 individuals per m² of foliage), although they differed considerably among tree species, being often higher on pioneer than on persistent trees.

3. One out of two chrysomelid species collected from a particular tree species did not feed on its foliage (if additional species are included, this proportion could be as high as two species out of three). The most likely explanations for the presence of these non-feeding species on the foliage of study trees are: (a) they may be "rare" specialists, dispersing from other tree-species; and (b) they may be facultative nectar/pollen feeders or flower-eaters. Therefore, collections made from the rainforest canopy to estimate the number of beetle species associated with a particular tree species are likely to greatly inflate the actual species richness of leaf-feeders, unless some information about beetle host-range is known.

4. The foraging of adult chrysomelids in our system appeared to be influenced mostly by altitude, strength of affinity with the host, attractiveness to flowers and denseness of foliage, and less by the availability of young foliage and the abundance of ants or spiders. Adults closely associated with particular hosts clustered on these in a

predictable way but faunal similarities among tree species had little to do with tree phylogenetic considerations.

5. Overall seasonal activity of adults at our study site, which showed little climatic fluctuation through the year, appeared to have been relatively even during the study year. The effects of host-tree phenology were not evident at the community level.

6. Additional information about the larval ecology of the species collected may further improve our understanding of adult foraging patterns. However, we doubt that generalizations about the characteristics of tropical arboreal communities of chrysomelids can be fruitful before a certain number of communities have been studied and compared in different habitats and continents.

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Appendix. Number of individuals collected on each tree species (first entry) and results of feeding trials for all chrysomelids which fed (second entry; 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding; ?: not tested) plus common incidental and additional species (> 10 individuals collected; see text). Tree species are identified by their initials (see Table 1)

Taxa	Status	Et	Cc	Pp	Fn	Pa	Ca	Cb	Am	Md	Cd
Cryptocephalinae											
1. <i>Coenobius kleinhoviae</i> Gressitt	specialist	0/0	0/0	0/0	4/100	0/0	0/0	0/0	0/0	0/0	0/1
2. <i>Coenobius</i> sp.	additional	0	11	0	0	0	0	0	0	0	0
Eumolpinae											
3. <i>Micromolpus</i> sp.	specialist	0/?	0/0	0/?	0/0	0/?	3/100	0/0	0/?	0/?	0/10
4. <i>Rhyparida coriacea</i> Jacoby	generalist	0/10	0/10	0/0	11/100	3/10	0/10	0/100	0/100	0/1	0/0
5. <i>Rhyparida</i> sp. (bryanti group)	unknown	0/?	0/?	0/?	0/?	0/?	0/0	53/100	0/?	0/?	0/?
6. <i>Rhyparida</i> sp.	specialist	0/?	2/100	0/?	0/?	0/0	0/1	0/0	0/0	0/?	0/0
7. <i>Rhyparida</i> sp.	specialist	0/0	0/0	0/0	0/0	0/0	0/10	34/100	0/0	0/0	0/1
8. <i>Rhyparida</i> sp.	specialist	0/0	0/0	0/0	0/1	24/100	0/0	0/0	0/0	2/0	0/0
9. <i>Rhyparidella wauensis</i> Gressitt	generalist	1/0	3/1	6/0	53/100	113/100	0/10	0/0	1/0	2/0	0/1
10. <i>Rhyparidella</i> ? sp.	specialist	0/0	0/0	0/0	0/0	0/0	0/0	41/100	0/0	0/0	0/0
11. <i>Rhyparidella</i> ? sp.	specialist	0/0	0/0	0/0	3/10	10/100	0/0	0/0	0/0	0/0	0/0
12. <i>Rhyparidella</i> ? sp.	specialist	0/0	0/0	0/0	0/0	16/100	0/0	0/0	0/0	0/0	0/0
13. <i>Rhyparidella</i> ? sp.	specialist	7/0	5/7	14/0	6/0	23/?	16/?	0/?	2/100	9/7	36/0
14. <i>Rhyparidella</i> ? sp.	generalist	1/100	9/0	1/0	39/100	9/10	8/0	0/10	5/0	1/0	12/100
15. <i>Rhyparidella</i> sp.	generalist	0/100	0/0	0/0	46/100	0/10	0/0	0/10	0/0	0/0	0/100
16. <i>Rhyparidella</i> ? sp.	generalist	4/100	5/0	1/0	0/1	1/0	35/10	0/0	4/100	203/100	4/0
17. <i>Rhyparidella</i> ? sp.	generalist	0/0	0/0	1/0	4/100	19/100	0/0	0/100	0/0	0/0	0/0

Appendix. Cont.

Taxa	Status	Et	Cc	Pp	Fn	Pa	Ca	Cb	Am	Md	Cd
Eumolpinae (cont.)											
18. <i>Rhyparidella?</i> sp.	generalist	0/0	2/0	0/0	0/100	0/0	5/10	2/0	29/100	17/0	34/100
19. <i>Rhyparidella?</i> sp.	unknown	0/?	0/?	0/?	2/?	2/100	0/?	0/?	0/?	0/?	0/?
20. <i>Rhyparidella?</i> sp.	additional	1	7	0	0	0	0	3	0	0	0
21. <i>Stethotes integra</i> Baly	specialist	0/0	4/0	1/0	0/10	38/100	1/0	0/0	0/0	0/0	0/10
22. <i>Stethotes n. lateralis</i> Baly	specialist	0/0	0/0	20/0	0/10	19/100	0/0	0/0	0/0	1/0	0/10
23. <i>Stethotes ?nigritula</i> Baly	incidental	0	0	0	0	0	2	28	0	1	0
24. <i>Stethotes suturalis</i> Bryant	specialist	0/?	0/0	0/0	0/0	0/0	1/0	14/100	0/0	2/?	0/?
25. <i>Stethotes</i> sp.	specialist	0/0	4/0	1/100	0/0	0/0	0/0	0/0	0/0	0/0	0/0
26. <i>Stethotes</i> sp.	specialist	0/0	0/0	0/0	0/1	9/100	0/0	0/1	0/0	0/0	0/1
27. <i>Thyrasia?</i> sp.	specialist	0/0	0/0	0/?	0/?	0/?	4/100	0/0	0/0	0/0	0/?
28. <i>Thyrasia?</i> sp.	additional	0	0	0	0	0	0	36	0	0	0
Galerucinae											
29. <i>Aypsa</i> sp.	specialist	0/1	1/0	0/0	18/100	0/0	0/0	0/0	0/0	0/0	0/10
30. <i>Aulacophora</i> sp.	generalist	0/0	0/0	1/100	4/100	0/?	1/?	0/?	0/?	0/0	0/?
31. <i>Cassena</i> sp.	incidental	0	0	4	0	11	10	0	0	4	0
32. <i>Momæa?</i> sp.	specialist	0/0	0/0	0/0	0/0	0/0	0/0	2/0	0/0	12/100	0/0
33. <i>Monolepta?</i> sp.	additional	0	15	0	0	0	0	0	0	0	0
34. <i>Neolepta?</i> sp.	specialist	0/0	0/?	0/?	0/?	4/100	0/0	0/0	0/0	0/0	0/0
35. <i>Neolepta?</i> sp.	specialist	0/?	0/?	0/?	0/?	0/0	0/0	6/100	0/10	0/?	0/0
36. <i>Neolepta?</i> sp.	specialist	0/0	0/0	0/?	0/?	0/0	14/100	3/0	0/?	0/?	0/0
37. <i>Neolepta?</i> sp.	additional	0	13	0	0	0	3	0	0	2	0

