

Diversity and abundance of insect herbivores foraging on seedlings in a rainforest in Guyana

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Abstract. 1. Free-living insect herbivores foraging on 10 000 tagged seedlings representing five species of common rainforest trees were surveyed monthly for more than 1 year in an unlogged forest plot of 1 km² in Guyana.

2. Overall, 9056 insect specimens were collected. Most were sap-sucking insects, which represented at least 244 species belonging to 25 families. Leaf-chewing insects included at least 101 species belonging to 16 families. Herbivore densities were among the lowest densities reported in tropical rainforests to date: 2.4 individuals per square metre of foliage.

3. Insect host specificity was assessed by calculating Lloyd's index of patchiness from distributional records and considering feeding records in captivity and *in situ*. Generalists represented 84 and 78% of sap-sucking species and individuals, and 75 and 42% of leaf-chewing species and individuals. In particular, several species of polyphagous xylem-feeding Cicadellinae were strikingly abundant on all hosts.

4. The high incidence of generalist insects suggests that the Janzen–Connell model, explaining rates of attack on seedlings as a density-dependent process resulting from contagion of specialist insects from parent trees, is unlikely to be valid in this study system.

5. Given the rarity of flushing events for the seedlings during the study period, the low insect densities, and the high proportion of generalists, the data also suggest that seedlings may represent a poor resource for free-living insect herbivores in rainforests.

Key words. *Catostemma*, *Chlorocardium*, *Eperua*, Guyana, host specificity, *Mora*, *Pentaclethra*, seedling, species richness.

Introduction

Some of the insects that feed on seeds and seedlings have the potential to kill their hosts, i.e. to devour most of the seeds or damage seedlings beyond recovery (e.g. Clark & Clark, 1985), thus their importance for tree regeneration and local diversity in tropical rainforests has attracted much scientific attention (e.g. Janzen, 1970). Most studies have focused on the actual damage and mortality sustained (e.g. Becker, 1983; Clark & Clark, 1985; de la Cruz & Dirzo, 1987; Aide, 1991), rather than on the identity and occurrence of the insect species responsible for the damage (e.g. New, 1983; Folgarait *et al.*, 1995; Gombauld, 1996). One problem with the latter is related to sample size. Surveying adequate numbers of seedlings for prolonged periods of time may represent a task of Herculean

proportions for a single researcher, particularly if seedling patches are scattered in the forest. Some workers have overcome this problem by surveying seedlings in tree plantations (e.g. New, 1983; Folgarait *et al.*, 1995). As a consequence, pioneering works such as those of Fowler (1985) and Godfray (1985), comparing the communities of insect herbivores feeding on birch seedlings and parent trees in Britain, have, to date, not been followed in natural habitats in the tropics. These data are needed because they may help botanists to comprehend patterns of attack on seedlings, perhaps as a result of insect dispersal or contagion from parent trees.

Furthermore, many studies addressing herbivory on seedlings have focused on testing whether the Janzen–Connell model could be substantiated (e.g. Wilson & Janzen, 1972; Augspurger, 1984; Condit *et al.*, 1992). In brief, the model states that patterns of herbivore attack below the parent tree are density-dependent and decrease with increasing distance from the parent tree (Janzen, 1970; Connell, 1971). This process

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could promote botanical diversity by prohibiting the establishment of young trees near conspecific parents (e.g. Janzen, 1970; Connell, 1971; Coley, 1993). One of the implicit assumptions in the Janzen–Connell model is that most insect herbivores that feed on seedlings are specialists that may also feed on the parent tree (Leigh, 1994). This assumption has rarely been tested in a synecological context (e.g. Thomas, 1990).

The present contribution is part of a larger study monitoring the influence of selective logging on the insect herbivores foraging on rainforest seedlings at Mabura Hill, central Guyana. Large numbers of insects were collected on seedlings in an unlogged plot, providing the opportunity to detail broad patterns in the composition, abundance, and species richness of the insect fauna. The faunal differences among host species are of particular interest, because acceptance of a null hypothesis of no difference among hosts will invalidate the implicit assumption of insect host-specificity in the Janzen–Connell model.

Materials and methods

Study site and characteristics of study plants

The insect survey was performed in a plot of 0.92 km² of unlogged forest (block 17), in the Camoudi compartment of the logging concession of Demerara Timbers Limited, some 40 km south of Mabura Hill, Central Guyana (5°13'N, 58°48'W, altitude ≈ 30 m). Annual rainfall at Mabura Hill is high and variable, between 2500 and 3400 mm, and the mean annual air temperature is approximately 25.9 °C (ter Steege *et al.*, 1996). The main forest types in block 17 included well-drained and poorly drained mixed forests (see ter Steege *et al.*, 1996). A field camp was established at the study site, to deal with all aspects of insect collection and field observations.

The main characteristics of the five shade-tolerant tree species studied are summarised in Table 1. Hereafter, they are designated by their generic names. *Chlorocardium*, *Mora*, *Catostemma*, and *Eperua* are important timber species in Guyana (ter Steege, 1990) and *Pentaclethra* was relatively common in block 17. All study trees with a diameter at breast height of > 32 cm were mapped in the study site. The dominant species in block 17 was *Eperua*, which, together with *Mora* and, to a lesser extent, *Chlorocardium*, is known to grow as

mono- or co-dominant stands in Guyana (e.g. ter Steege, 1990).

Seedling appearance may be rather distinct when comparing different tree species. Here, number of leaves and estimated leaf area (see below) were used to quantify seedling size. A first pilot study examined the distribution of the number of leaves per seedling of each study species. The first mode of the distribution was chosen as the maximum number of leaves to qualify as a seedling for each study species (Table 2). Next, the average specific leaf area was measured from 200 seedlings for each species (Table 2) and this value was used to estimate the total leaf area sampled at each collecting station (see below). A collecting station was defined as a fixed number of seedlings (Table 2) growing below the parent tree or in its vicinity. Fifty such collecting stations were chosen for each species (total 250 stations and 9750 seedlings). As far as possible, stations were spread out in the study site and experienced different light regimes. Seedlings were tagged at each station; those that died during the course of the study were replaced by others growing below the parent tree.

Insect collecting and assessment of the leaf area monitored at each station

The sampling protocol targeted free-living insect herbivores foraging during the daytime on the tagged seedlings. This included leaf-chewing (e.g. Chrysomelidae, some Curculionidae, mostly Lepidoptera, some Orthoptera) and sap-sucking (many Hemiptera) insects. Most of the sampling was performed by field assistants who had been trained for this purpose. From October 1996 to September 1997, 11 monthly insect surveys were performed (no survey was performed in August 1997). During each survey, all the tagged seedlings were inspected once by the field assistants, who collected insects alive by hand or with small aspirators. Insects that flew off were recorded to family level. On average, one assistant spent at least 30 min at each collecting station. During each survey, groups of closely situated stations were assigned to assistants randomly, in order to reduce collector effects. In short, the problem of low abundance of insects on seedlings was overcome by training *insect parataxonomists* (see Janzen, 1992; Novotny *et al.*, 1997) to survey a high number of seedlings for a relatively long period of time.

Table 1. Main characteristics of the tree species studied.

Species	Family	Common name ^a	No. in block 17 ^b	Reference ^c
<i>Chlorocardium rodiei</i> (Scomb.)	Lauraceae	Greenheart	465	ter Steege, 1990
<i>Mora gonggrijpii</i> (Kleinh.) Sandw.	Caesalpiniaceae	Morabukea	368	ter Steege, 1990
<i>Eperua rubiginosa</i> Miq.	Caesalpiniaceae	Water wallaba, Watapa	3370	ter Steege, 1990
<i>Pentaclethra macroloba</i> (Willd.) Kuntze	Mimosaceae	Trysil	88	Hartshorn, 1983
<i>Catostemma fragrans</i> Benth.	Bombacaceae	Sand baromalli	239	Polak, 1992

^aIn Guyana.

^bNumber of adult trees with a diameter at breast height of > 32 cm in the 0.92 km² study plot.

^cMain ecological reference relevant to Guyana, if available.

The assistants recorded the number of mature and young leaves present on each seedling. An approximate estimate of the leaf area sampled at each station during each survey was calculated by multiplying the number of young and mature leaves recorded by the average specific leaf area (all measurements were single-sided, Table 2). For these calculations, the leaf area of young leaves was assumed to be half that of mature leaves. Production of new leaves on the seedlings was relatively rare (percentage growth, Table 2). Thus, sample size during the study period was assumed to be relatively constant within a particular host species and to have little effect on insect abundance and species richness.

Assessment of host-specificity and processing of insect material

Only insect species represented by a minimum of five individuals were considered for analyses of host specificity, because insects could only be collected from five possible host plants. Hereafter, these are termed *common* species. A species was considered to be a *specialist* (as opposed to a *generalist*) on a particular host if its Lloyd index of patchiness (Lloyd, 1967) was ≥ 3.0 . This corresponds roughly to a situation where at least 80% of the individuals were collected on a single host, for sample sizes typically encountered in this study (mode of the distribution of the index = 1.0). Lloyd's index is relatively insensitive to sample size, performs well in a variety of situations (e.g. Lepš, 1993; Wolda & Marek, 1994), and is calculated as:

$$L = \frac{S_x^2 - \bar{X}}{\bar{X}^2} + 1$$

where S_x^2 and \bar{X} are the variance and mean of the sample. In the present case, the total number of individuals collected per

species on each host was considered ($n=5$). The index increases for more specialised insects. In the present context, one should consider a *specialist* as a species that showed a clear preference for one of the five host species studied, but without implication of monophagy.

Host-specificity for sap-sucking insects refers to patterns of distribution on their putative hosts, not to actual feeding records (with some rare exceptions). For leaf-chewing insects, it was possible to take the analysis one stage further. Caterpillars were, as far as possible, reared to adults. Beetles and grasshoppers were kept in plastic vials with young leaves of the host plant species from which they were collected and leaf damage and frass were recorded. Insects responsible for obvious damage were later assigned to the *feeding* category; others, including dead insects, were assigned to the *nonfeeding* category. Only the former were later assigned to morpho-species. These simple tests allowed the removal of transient species, as well as those feeding infrequently on the seedlings, from the analyses. The validity of using feeding tests in captivity is discussed elsewhere (e.g. Cullen, 1989; Basset, 1994).

Live insects were brought from the field camp to the insect laboratory in Mabura Hill every 2–3 days. They were killed by storage in a freezer for a few hours, mounted on points, dried, and identified by a personal accession number. Insects were then sorted by morphospecies (hereafter *species* for the sake of simplicity). Checking of genitalia was only performed in doubtful cases and when male material was available.

Insect variables and statistical analyses

Sap-sucking insects were classified according to their feeding mode: xylem-, phloem-, and mesophyll-feeders (e.g. Novotny & Wilson, 1997). Leaf-chewing insects were

Table 2. Characteristics of seedlings and collecting station for each study species. Values in brackets represent SE.

Species	No. of leaves per seedling ^a	Height (cm) ^b	Leaf area (cm ²) ^c	No. of seedlings per station	Average leaf area per station (m ²) ^d	Average area of young leaves (m ²) ^e	Growth (%) ^f
<i>Chlorocardium</i>	1–5	0–40	25.3 (1.8)	40	0.4916 (0.008)	0.0222 (0.0008)	5.6
<i>Mora</i>	1–5	0–80	109.6 (3.6)	50	2.9721 (0.024)	0.0186 (0.0013)	1.7
<i>Eperua</i>	1–4	0–55	120.3 (7.1)	50	2.3075 (0.024)	0.0135 (0.0012)	7.4
<i>Pentaclethra</i>	1–4	0–35	87.1 (8.0)	15 ^g	0.5420 (0.008)	0.0067 (0.0005)	3.6
<i>Catostemma</i>	1–5	0–35	56.5 (3.4)	40	1.0506 (0.017)	0.0091 (0.0005)	5.2

^aThis value is used as the definition of a seedling at the onset of the monitoring period.

^bThis represents rough equivalents to the previous value, for comparison with other studies.

^cAverage area of one leaf, for seedlings as defined in this study.

^dAverage total leaf area of each station during surveys 1–11 (young and mature leaves).

^eAverage leaf area of young leaves at each station during surveys 1–11.

^fPercentage growth of leaf area during surveys 1–11, expressed as:

[(mean station area during survey 11) – (mean station area during survey 1)]/(mean station area during survey 1).

^gIncluding four stations set up with 10 seedlings and two stations set up with 13 seedlings.

classified as adult feeders, larval feeders, or nonfeeders. Estimates of insect biomass were calculated using the regression equations between length of body (mm) and dry weight (mg) provided by Schoener (1980) for arthropods collected in a tropical rainforest in Costa Rica.

Because the leaf area sampled at each station varied greatly among hosts (Table 2), both insect densities (expressed either in terms of abundance or biomass) and species richness were adjusted to a common sample size with regressions between insect variables and total leaf area sampled. This was achieved with a common sample size of 1 m² of leaf area for half of the samples, obtained by adding together the results of two stations for *Chlorocardium* and *Pentaclethra*, considering only the first 17 and 22 seedlings at each station for *Mora* and *Eperua*, respectively, and with no change for *Catostemma*. Regressions (leaf area = X, insect numbers = Y) were computed between double log-transformed data, and forced through the origin (no insects when leaf area = 0). Insect variables are presented both as raw and adjusted data.

Adjustment of species richness was first assessed by plotting accumulation curves of the number of species against the number of individuals for each host species. Second, the *Chao1* statistic was calculated to estimate the total number of species present, as it is relatively insensitive to sample size and performs well in the presence of large numbers of singletons

(e.g. Colwell & Coddington, 1994). Third, rarefaction (Hurlbert, 1971) was used to estimate the number of species present within a sample size of 500 individuals for sap-sucking insects and 20 individuals for leaf-chewing insects (i.e. the largest sample size common to all hosts).

Results

Overall faunistic composition: sap-sucking insects

Sap-sucking insects represented 7435 individuals and at least 244 species from 25 families (Table 3). Juveniles represented 35% of the individuals recorded and most included psyllids feeding on the young leaves of *Eperua*. Although Acari were sometimes collected, no Thysanoptera were found on the seedlings. Out of the 4508 specimens recognised as adults, phloem feeders dominated, with 3225 individuals and 194 species (72 and 80% of the totals, respectively), followed by xylem-feeders with 1100 individuals and 25 species (24 and 10%, respectively), and mesophyll-feeders with 183 individuals and 25 species (4 and 10%, respectively). In particular, xylem-feeding Cicadellinae represented 1082 individuals and 19 species (81 and 27%, respectively) of the adult Cicadellidae collected on seedlings.

Table 3. Families of sap-sucking insects collected on seedlings, listed in order of decreasing diversity and abundance, with corresponding values for common species (see Methods).

Taxa	No. of sp.	No. of individuals	No. of common sp.	No. of individuals – common sp.
Cicadellidae	71	1484	25	1253
Derbidae	48	628	23	570
Membracidae	35	161	9	111
Achiliidae	18	160	7	140
Cixiidae	15	1100	11	1075
Pentatomidae	8	21	1	11
Coreidae	7	19	1	9
Issidae	7	14	1	5
Cercopidae	6	18	1	7
Aleyrodidae	4	21	1	16
Dictyopharidae	4	13	1	8
Psyllidae	3	2837	1	698
Flatidae	3	9	1	6
Acanaloniidae	2	3	–	–
Scutellaridae	2	3	–	–
Fulgoridae	2	2	–	–
Pseudococcidae	1?	481	1	147
Plataspidae	1	153	1	122
Kinnaridae	1	47	1	47
Nogodinidae	1	6	1	6
Cydnidae	1	5	1	5
Delphacidae	1	5	1	5
Achilixiidae	1	4	–	–
Tropiduchidae	1	1	–	–
Lygaeidae	1	1	–	–
Fulgoroidea – juveniles	? ^a	51	?	?

^aJuveniles difficult to assign to species.

Table 4. Families of leaf-chewing insects collected on seedlings, listed in order of decreasing diversity and abundance, with corresponding values for common species (see Methods).

Taxa	No. of sp.	No. of individuals	No. of common sp.	No. of individuals – common sp.
Chrysomelidae – feeding	54	582	20	485
Eumolpinae	21	154	10	136
Alticinae	21	94	4	62
Galerucinae	11	253	5	235
Cryptocephalinae	1	52	1	52
Chrysomelidae – not feeding ^a	?	659	–	–
Curculionidae – feeding	22	51	3	23
Entiminae	6	23	2	14
Zygopinae	7	16	1	9
Cryptorhynchinae	6	7	–	–
Curculionidae – not feeding ^a	?	184	–	–
Acrididae – feeding ^b	?	8	–	–
Acrididae – not feeding ^a	?	11	–	–
Pyrallidae	4	4	–	–
Noctuidae	3	3	–	–
Geometridae	2	6	–	–
Lycanidae	2	3	–	–
Scarabaeidae – feeding ^c	2	2	–	–
Scarabaeidae – not feeding ^{a,c}	?	13	–	–
Limacodidae	2	2	–	–
Oecophoridae	2	2	–	–
Hesperiidae	2	2	–	–
Gelechiidae	1	25	1	25
Saturniidae	1	4	–	–
Tortricidae	1	1	–	–
Apionidae	1	1	–	–
Arctiidae	1	1	–	–
Cerambycidae – not feeding ^a	?	2	–	–
Lepidoptera – caterpillars ^d	?	53	?	?

^aIndividuals not feeding were not assigned to species; see Methods.

^bAll juveniles, difficult to assign to species.

^cAll Melolonthinae.

^dRearing to adults failed, difficult to assign to species, see Methods.

Table 5. Unadjusted and adjusted insect densities (number of individuals collected per station; see Methods). Unadjusted densities refer to a specific mean leaf area per station as detailed in Table 2 and are presented with their standard errors. Coefficients of regression are presented with their standard errors (all regressions highly significant). Adjusted densities refer to 1.0 m² of leaf area and are presented untransformed with 95% confidence limits. Data for leaf-chewing insects refer to feeding individuals only.

Variable	<i>Chlorocardium</i>	<i>Mora</i>	<i>Eperua</i>	<i>Pentaclethra</i>	<i>Catostemma</i>	All
Unadjusted densities						
Total herbivores	2.778 (0.186)	1.902 (0.088)	7.274 (0.926)	1.618 (0.078)	3.035 (0.126)	3.321 (0.196)
Sap-sucking	2.289 (0.178)	1.325 (0.072)	6.675 (0.926)	1.027 (0.058)	1.969 (0.100)	2.657 (0.194)
Leaf-chewing	0.065 (0.013)	0.264 (0.028)	0.182 (0.021)	0.195 (0.041)	0.616 (0.049)	0.264 (0.013)
Regression coefficients						
Total herbivores	0.129 (0.011)	0.027 (0.009)	0.143 (0.012)	0.076 (0.008)	–	0.096 (0.005)
Sap-sucking	0.010 (0.013)	–0.011 (0.010)	0.125 (0.013)	0.020 (0.010)	–	0.059 (0.006)
Leaf-chewing	–0.215 (0.014)	–0.166 (0.012)	–0.188 (0.009)	–0.168 (0.012)	–	–0.153 (0.006)
Adjusted densities						
Total herbivores	3.276	1.281	3.718	2.015	3.035	2.414
95% CL	(4.014–2.674)	(1.502–1.093)	(4.604–3.003)	(2.346–1.731)	(3.282–2.788)	(2.650–2.199)
Sap-sucking	2.553	0.901	3.173	1.202	1.969	1.722
95% CL	(3.222–2.022)	(1.079–0.752)	(4.040–2.491)	(1.450–0.996)	(2.165–1.773)	(1.919–1.546)
Leaf-chewing	0.138	0.218	0.177	0.212	0.616	0.244
95% CL	(0.179–0.121)	(0.269–0.176)	(0.209–0.151)	(0.263–0.171)	(0.712–0.520)	(0.273–0.218)

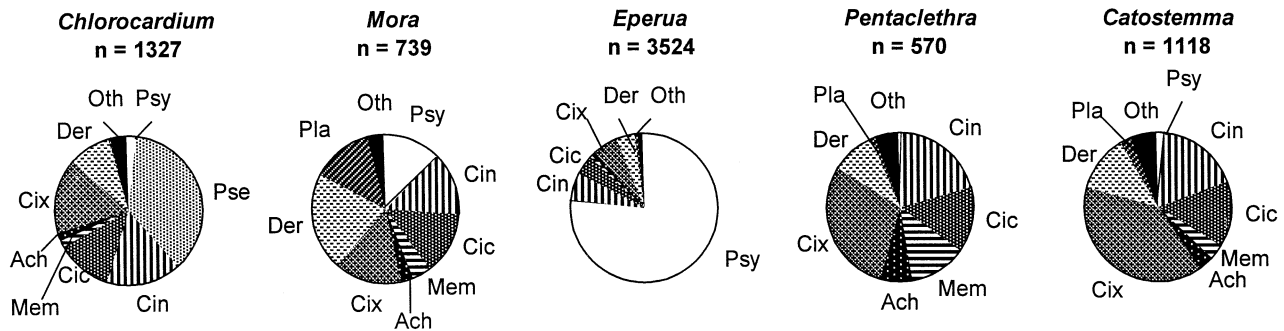
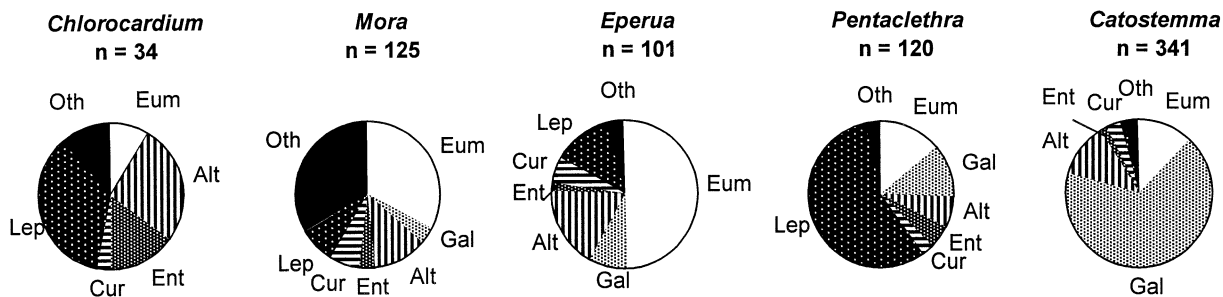
(a) Sap-sucking insects**(b) Leaf-chewing insects**

Fig. 1. Distribution of individuals among the major insect taxa on each host species, for (a) sap-sucking insects (Psy=Psyllidae, Pse=Pseudococcidae, Cin=Cicadellinae, Cic=other Cicadellidae, Mem=Membracidae, Achi=Achilidae, Cix=Cixiidae, Der=Derbidae, Pla=Plataspididae, Oth=others), and (b) leaf-chewing insects (Eum=Eumolpinae, Gal=Galerucinae, Alt=Alticinae, Ent=Entiminae, Cur=other Curculionidae, Lep=Lepidoptera, Oth=others).

Eighty-seven sap-sucking species were represented by singletons (36% of the total number of species collected). Common species represented 89 species and 88% of the adult individuals collected (Table 3). The five most abundant species were an undescribed species of *Isogonoceraia* (Psyllidae), whose nymphs fed on the young leaves of *Eperua*, a xylem-feeding Cicadellinae, *Soosius fabricii* Metcalf, two unidentified species of *Pintalia* (Cixiidae), and ?*Oragua* sp. (Cicadellinae). The last four species were found in large numbers on the five host species.

In terms of biomass, the five most abundant species were *Soosius fabricii*, the very large but rather uncommon *Pachylis* cf. *laticornis* F. (Coreidae), *Pintalia* sp., ?*Oragua* sp., and *Canopus* sp. (Plataspididae), abundant on *Mora*. Other salient features of the sap-sucking fauna included large-bodied Cicadellinae (e.g. *Amblyscarta* spp., *Dasmeusa* spp.), some Coelidiinae (e.g. *Docalidia* spp., *Baluba* spp.), some Derbidae (*Mysidia* spp. and *Herpis* spp.), and some Achilidae (*Sevia* spp. and *Plectoderes* spp.).

Overall faunistic composition: leaf-chewing insects

The leaf-chewing collections represented 1621 individuals and at least 101 species from 16 families, but many caterpillars

could not be reared to adults (Table 4). In total, 868 individuals did not feed in trials (53%). Many nonfeeding Chrysomelidae included generalist species, with some individuals feeding occasionally, e.g. *Wanderbiltiana* sp. (22% of nonfeeding individuals). Others included Cassidinae, probably feeding on convolvulaceous vines (*Charidotella* spp., *Charidotis* spp., etc.), Hispinidae, probably feeding on palms or on Monocotyledones, and some Galerucinae feeding on *Cecropia* spp. (*Coelomera* spp.). Nonfeeding Curculionidae included some generalist Entiminae feeding occasionally (13% of nonfeeding weevils), but most were Cryptorhynchinae that probably did not feed on leaves at all (64% of the nonfeeding weevils).

Feeding individuals were dominated by adult feeders (80% of species and 40% of individuals). Singletons represented 31 species and 31% of the total number of species. Common species included 24 species (mostly of Chrysomelidae) that represented 71% of the insects that fed on the seedlings. The five most abundant species included an unidentified Galerucinae feeding on the young leaves of *Catostemma*, an unidentified Eumolpinae feeding on all hosts but preferring *Eperua* and *Catostemma*, *Cryptocephalus esuriens* Suffrian (Cryptocephalinae), which preferred *Mora*, an unidentified Alticinae feeding on all hosts with preference for *Catostemma* and *Mora*, and an unidentified Eumolpinae feeding on all hosts but preferring

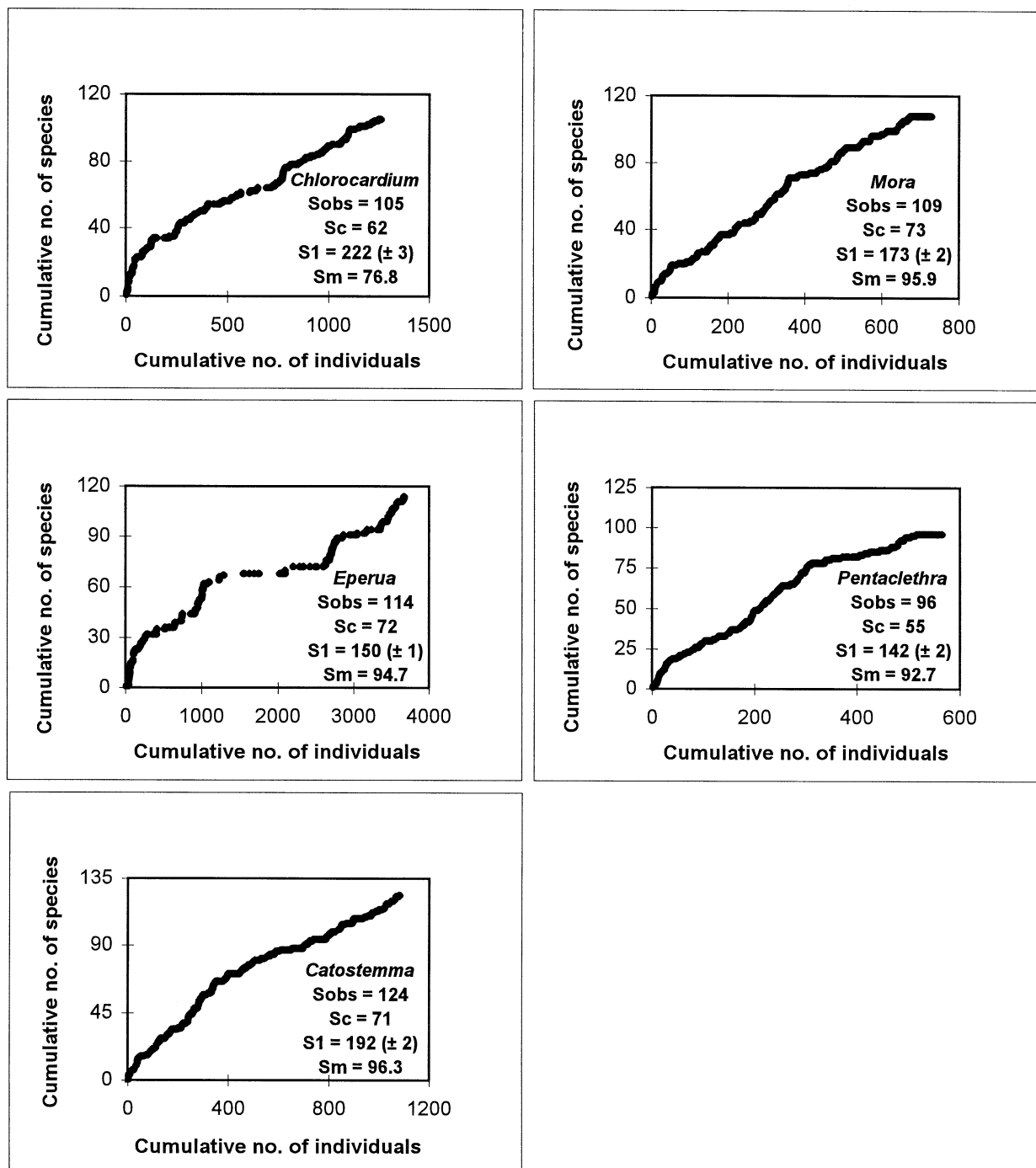


Fig. 2. Cumulative number of individuals against the number of species collected for sap-sucking insects on each study host. Sobs=the actual number of species observed, Sc=the number of common species, S1=the estimated total number of species (± 95% CL) in the set calculated with the Chao1 index, Sm=the estimated number of species within a sample of 500 individuals. Note that the number of individuals includes juveniles.

Mora. The same five species also contributed much in terms of biomass, particularly the Galerucinae. Other conspicuous

features of the leaf-chewing fauna included several species of *Pseudopinarus* (Zygopinae) and *Compsus* (Entiminae).

Insect densities and biomass on the foliage of seedlings

In total, the leaf area monitored on seedlings during the 11 surveys represented 4050 m², but this included only 39 m² of young foliage. Overall herbivore densities amounted to 2.4 individuals per m² of foliage (Table 5). Densities of leaf-chewers were low and difficult to estimate precisely. As indicated by the 95% confidence limits for adjusted values, herbivore densities on *Eperua*, *Chlorocardium*, and *Catostemma* were significantly higher than on *Pentaclethra* and *Mora*; densities of sap-sucking insects followed a similar trend; densities of leaf-chewing insects were significantly higher on *Catostemma* than on other study plants (Table 5).

Similarly, unadjusted biomass densities were 4.1 mg dry weight (± 0.20 SE) for all herbivores on all study plants, including 2.7 mg (± 0.19) and 0.6 mg (± 0.03) of sap-sucking and leaf-chewing insects, respectively. Adjusted biomass to 1 m² of foliage was 3.3 mg dry weight (95% CL = 3.6 and 3.0) for all herbivores, including 1.7 mg (CL = 1.9 and 1.5) and 0.6 mg (CL = 0.6 and 0.5) of sap-sucking and leaf-chewing insects, respectively. Considering that 1 kg of dry weight of foliage from the study plants represented 18.8 m² of foliage, this was likely to support about 46 insect herbivores, or a biomass of 6.2 mg dry weight of insects per 100 g dry weight of consumable plant material.

Differences in fauna and species richness among plant species

Major insect taxa were not distributed uniformly across host species, either for sap-sucking ($G = 6553.1$, $P < 0.001$) or leaf-chewing ($G = 539.4$, $P < 0.001$) individuals (Fig. 1). This was evident even for closely related hosts, such as *Mora* and *Eperua*. Cumulative numbers of sap-sucking and leaf-chewing species collected on each host did not asymptote (Figs 2 and 3), suggesting that many other insect species occur on the seedlings. The Chao indices suggested that, on average, 1.5 to two times as many insect species may be present. The collections from *Catostemma* were the most diverse in sap-sucking insects and remained so when the data were scaled down to 500 individuals. The number of common species was not very different among the study hosts, however, scaling at about 70 species (Fig. 2). The distribution of feeding guilds among the host plants was uniform when considering the number of species ($G = 3.16$, $P = \text{NS}$), but not when considering the number of individuals ($G = 536.9$, $P < 0.001$): high numbers of phloem-feeders and mesophyll-feeders occurred on *Eperua* and *Mora*, respectively.

Collections from *Catostemma* were also the richest in leaf-chewing insects, but the rarefaction and Chao index showed that collections from *Pentaclethra* were more diverse (Fig. 3). The distribution of feeding guilds among hosts was non-uniform both when considering the number of species ($G = 11.83$, $P < 0.05$) and the number of individuals ($G = 371.9$, $P < 0.001$): high numbers of species and individuals of adult and larval feeders occurred on *Catostemma* and

Pentaclethra, respectively, whereas high numbers of nonfeeding individuals occurred on *Chlorocardium*.

Feeding records and insect host-specificity

Overall, generalists dominated sap-sucking collections, representing 84% of the common species (74 species out of 88) and 78% of their individuals (3304 adult individuals out of 4241). Many species were collected in large numbers on all five hosts (32 out of the 88 common species, 36%). Species-abundance plots on each host also reflected this pattern (Fig. 4). The distribution of specialist and generalist sap-sucking insects among the study hosts was uniform when considering the number of species ($G = 0.159$, $P = \text{NS}$), but not when considering the number of individuals ($G = 675.6$, $P < 0.001$). High numbers of specialists occurred on *Eperua*, *Chlorocardium*, and *Mora*, however the proportion of generalist species within Cixiidae and Cicadellinae was high (Fig. 5a). As illustrated by the distribution of xylem-feeding Cicadellinae (Table 6), many common species probably feed on seedlings and may be generalists.

Patterns were different for leaf-chewing species. Whereas generalists dominated in terms of species richness (75%, 18 species out of 24), they were not dominant in terms of individuals (42%, 224 individuals out of 533). Only 8% of the common species were able to feed on all five hosts (two species out of 24). The distribution of specialist and generalist leaf-chewing insects among the study hosts was uniform when considering the number of species ($G = 2.13$, $P = \text{NS}$), but not when considering the number of individuals ($G = 84.16$, $P < 0.001$). The most abundant species on *Pentaclethra*, *Mora*, and particularly *Catostemma* were specialists (Fig. 6), however the proportion of generalist species in the Entiminae, Eumolpinae, and Galerucinae was high (Fig. 5b).

Some of the common species, particularly in the Chrysomelidae, were observed feeding *in situ* on young foliage, and many species of Eumolpinae, for example, fed on several hosts (Table 7).

Discussion*Limitations of the present work*

Some limitations of the study are obvious. First, the data refer to diurnal insects only. Many Chrysomelidae and Cicadellidae may be as active, or more active, during the day than at night (e.g. Springate & Basset, 1996). The occurrence of nocturnal Orthoptera, Phasmatodea and perhaps of some Lepidoptera, however, is likely to have been underestimated. Second, the monitoring of the fixed stations underestimated the actual number of insect species foraging on the seedlings in block 17, as cumulative plots suggest. The data relevant to common species appear robust, however, and the subsequent discussion focuses on them. Third, the data are relevant to free-living insects only, because surveying leaf-

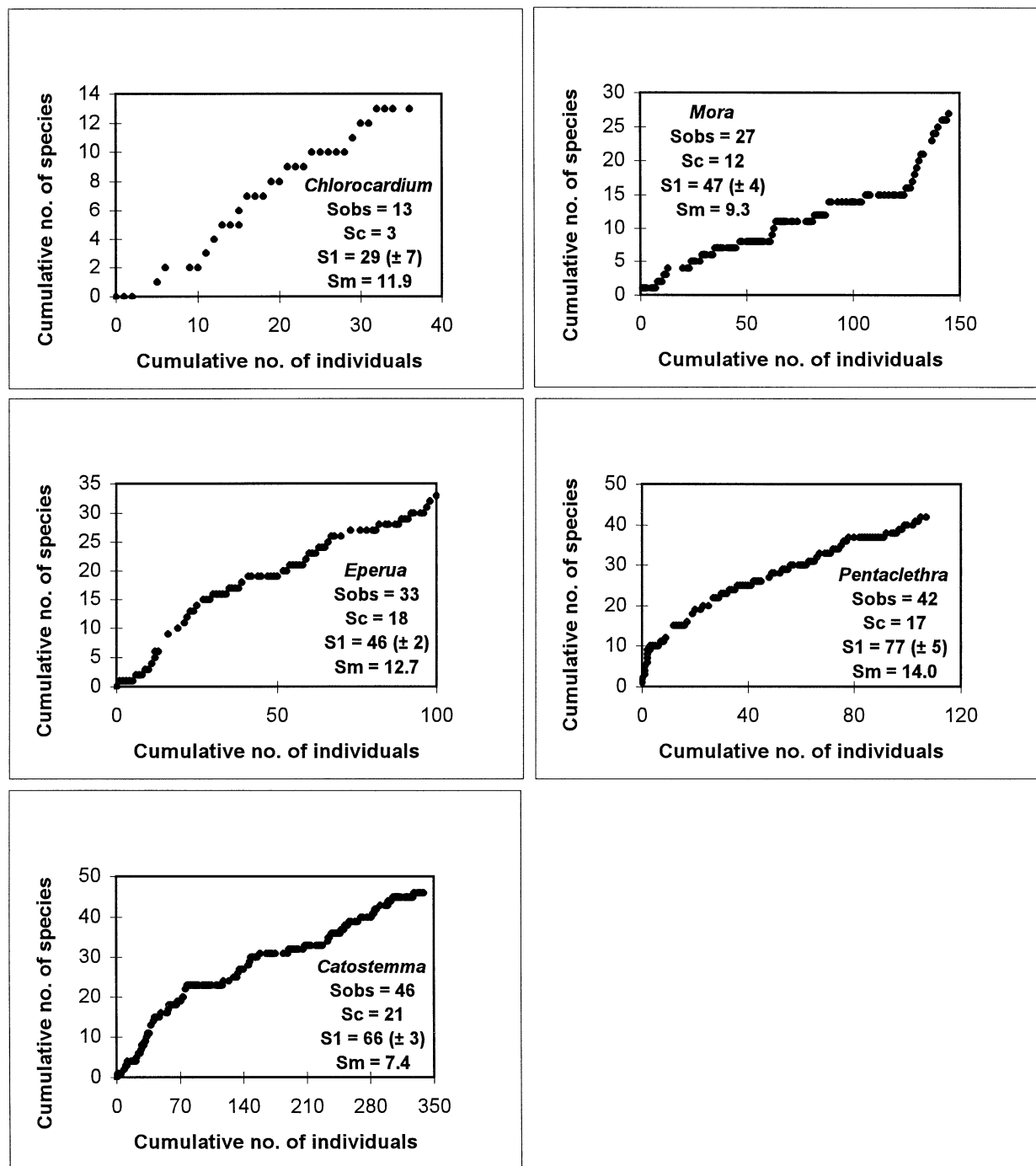


Fig. 3. Cumulative number of individuals against the number of species collected for leaf-chewing insects on each study host. Sobs=the actual number of species observed, Sc=the number of common species, S1=the estimated total number of species ($\pm 95\%$ CL) in the set calculated with the Chao1 index, Sm=the estimated number of species within a sample of 500 individuals. Note that the number of individuals includes juveniles.

miners and stem-borers efficiently would have required a different sampling strategy. Fourth, feeding records could not be verified for most sap-sucking insects and those for leaf-chewing insects related to field collections and feeding records

in captivity. This procedure has proved useful, however, even for vagile taxa such as Chrysomelidae (e.g. Basset & Samuelson, 1996). There may be many reasons why various beetles do not feed in captivity: (1) the taxa collected are not

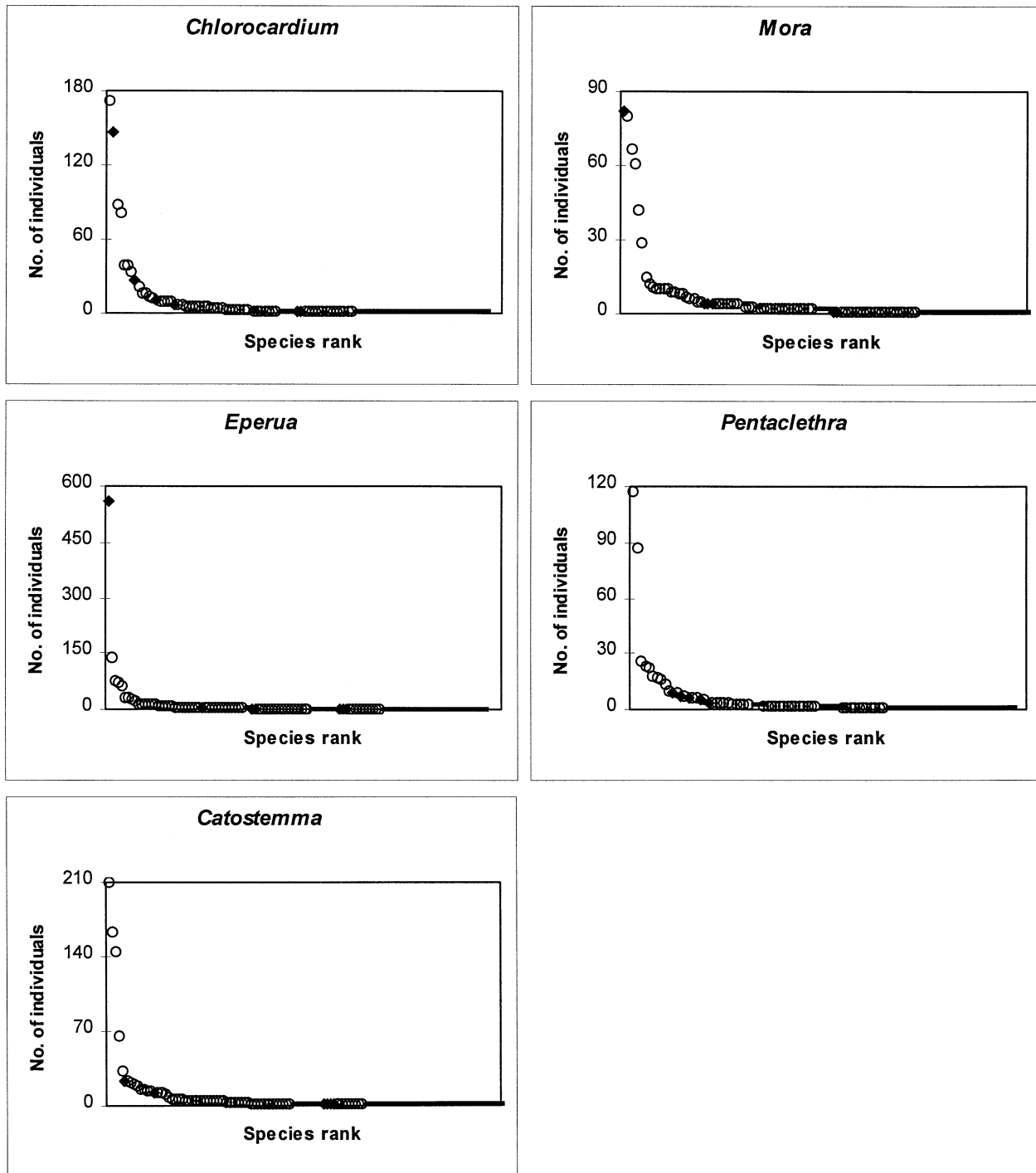


Fig. 4. Distribution of the number of individuals of sap-sucking insects on each host. ◆=specialists, ○=generalists, --=not known (total number of individuals collected <5).

actually leaf-feeders; this may be difficult to evaluate beforehand for certain Cryptorhynchinae, for example; (2) specimens in poor condition or diapausing; (3) generalists feeding sporadically, such as the alticine *Wanderbiltiana* sp. (note

that occasional use of secondary hosts is well documented within Alticinae—Jolivet & Hawkeswood, 1995); (4) transient species, dispersing from other habitats. Available data suggest that categories 3 and 4 are relatively common on tropical

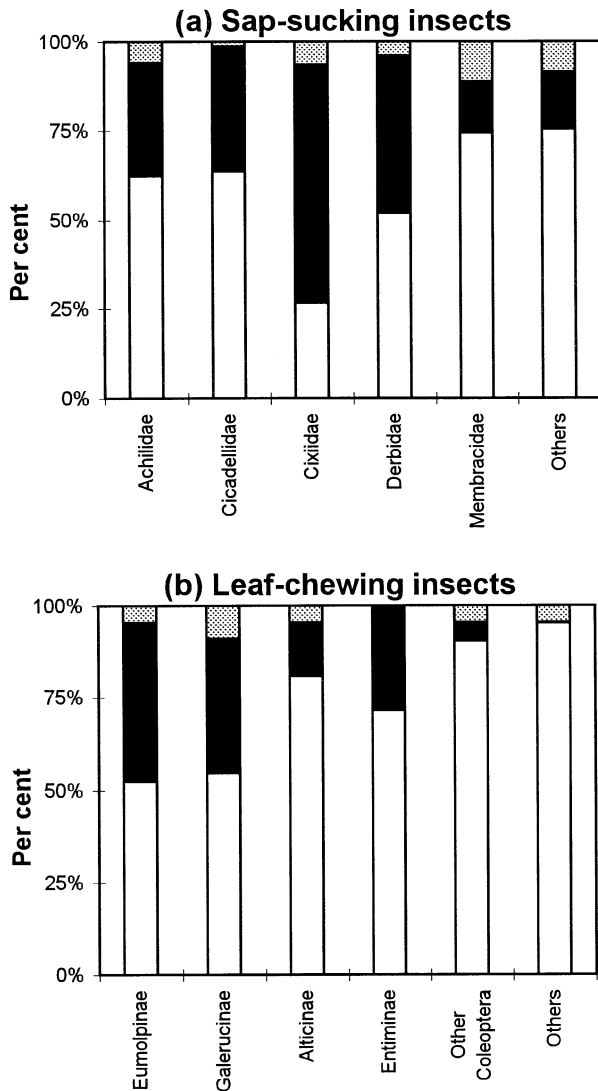


Fig. 5. Distribution (percentage occurrence) of the Lloyd's index within the main insect taxa for (a) sap-sucking insects and (b) leaf-chewing insects. ■ = generalist species ($L < 3.0$), □ = specialists ($L = 3.0$), ▨ = not known (total number of individuals collected < 5).

foliage (e.g. Moran *et al.*, 1994; Basset, 1997; V. Novotny and Y. Basset, unpublished). In the present system, category 1 was also well represented, including weevil species presumably feeding on seeds rather than foliage (e.g. *Conotrachelus* spp.).

Faunal composition and abundance of insects feeding on seedlings

Community studies of the insect fauna feeding on the seedlings of tropical plants are infrequent (e.g. Gombauld, 1996). In Australia, New (1983) recorded about 4000 phytophagous insects representing 78 species on seedlings of 21 species of acacia. The present study, with a sample size of

about 9000 specimens and 342 species, appears to be one of the very first quantitative assessments of the free-living insect herbivores foraging on seedlings in a tropical rainforest.

Despite the bark (and probably leaves) of *Chlorocardium* containing a suite of alkaloids related to curare (Hearst, 1963; ter Steege, 1990), it does not support a particularly scarce insect fauna. Although its leaf-chewing fauna is rather infrequent and a high proportion of beetles collected on its foliage were nonfeeding transients, sap-sucking insects were abundant, and many (e.g. *Soosiulus fabricii*) may feed on this host. The ability to feed on xylem and thus circumvent chemical defences in the phloem or in the mesophyll tissues of the plant may explain the abundance of such generalist species. Hollis and Martin (1997) suggested that the phytochemistry of Lauraceae is a more efficient barrier for leaf-chewing insects than for sap-suckers and the present data for *Chlorocardium* support this hypothesis.

Insect densities on seedlings appeared to be very low, as also noted by Becker (1983) and Folgarait *et al.* (1995). To date, they are the lowest reported from tropical rainforests. This interpretation remains true whether the data are expressed in terms of individuals per square metre of foliage (present study: 2.4 individuals/m², temperate vegetation: 19–78 individuals/m², Basset & Burckhardt, 1992; subtropical vegetation: 11 individuals/m², Basset & Arthington, 1992; tropical vegetation: 6 individuals/m², Basset *et al.*, 1992), of individuals per kg of dry weight of foliage (present study: 46 individuals/kg; subtropical foliage: 163 individuals/kg, Basset & Arthington, 1992), or of insect biomass (dry weight) per 100 g dry weight of consumable plant material (present study: 6 mg/100 g; temperate vegetation: 12–51 mg/100 g, Schowalter *et al.*, 1981; subtropical vegetation: 27 mg/100 g; Basset & Arthington, 1992). Densities appeared particularly low on the foliage of *Mora* and *Pentaclethra*. These two hosts produced few young leaves during the study period (Table 2). This suggests that the abundance of many herbivores may depend on the presence of young foliage. Some xylem feeders, such as *Soosiulus* spp., however, are able to feed on both mature and young foliage.

Host specificity of insects feeding on seedlings and implications for the Janzen–Connell model

Although leaf-chewers were often more specialised than sap-sucking insects, they included a non-negligible proportion of generalist species. Furthermore, despite a rather conservative definition of specialisation (meaning that species show a clear preference for one of the five study hosts), the proportion of generalist species (84 and 75% of sap-suckers and leaf-chewers, respectively), and particularly of individuals that they represented (78 and 42% of sap-suckers and leaf-chewers, respectively), appeared higher than in other studies of tropical herbivores (review in Basset, 1996; Novotny *et al.*, 1999). For example, the high proportion of xylem-feeding Cicadellinae, which are often highly polyphagous (e.g. Novotny & Wilson, 1997), was striking. Although formal comparisons with other tropical studies of seedling insects are currently unavailable,

Table 6. Distributional records (number of individuals) available and Lloyd's index of patchiness for common Cicadellinae. Numbers in bold indicate that males were available for genitalia extraction and study. *Indicates that the species was observed feeding *in situ* on that particular host (exudation of droplets).

Species code	Identification	Lloyd's index	No. of individuals				
			<i>Chlorocardium</i>	<i>Mora</i>	<i>Eperua</i>	<i>Pentaclethra</i>	<i>Catostemma</i>
CICA005	<i>Acrocampsia pallipes</i> F.	2.48	5	1	0	0	1
CICA006	<i>Amblyscarta invenusta</i> Young	0.98	3	8	5	3	6
CICA025	<i>Cardioscarta quadrifasciata</i> L.	1.31	2	5	1	0	3
CICA001	<i>Dasmeusa pauperata</i> Young	1.14	9	5	11	2	11
CICA076	<i>Dasmeusa</i> sp.	2.13	1	2	25	4	14
CICA058	<i>Ladoffa aguilarii</i> Lozada	1.72	0	1	6	3	1
CICA054	<i>Ladoffa comitis</i> Young	1.00	0	0	2	1	*2
CICA003	<i>Ladoffa ignota</i> Walker	1.50	3	0	6	*2	1
CICA077	<i>Ladoffa</i> sp.	1.00	2	0	1	2	0
CICA033	<i>Poeciloscarta cardinalis</i> F.	1.35	1	2	0	0	3
CICA004	<i>Soosiulus fabricii</i> Metcalf	1.13	*172	61	*138	87	*145
CICA081	<i>Soosiulus interpolis</i> Young	0.96	16	15	*12	10	12
CICA010	? <i>Oragua</i> sp.	1.30	39	11	61	26	66
CICA080	? <i>Oragua</i> sp.	1.48	5	2	14	3	14

Gombauld (1996) suggested that many leaf-chewing species feeding on the foliage of *Eperua* spp. in French Guyana were generalists. New (1983) also indicated that the insect fauna colonising acacia seedlings in Australia included many generalist species.

Studies supporting the Janzen–Connell model refer to particular host-specific insects and do not address the whole suite of herbivores feeding on seedlings (e.g. Janzen, 1971; Lemen, 1981; Maeto & Fukuyama, 1997). In the present study, abundant specialist species included the psyllid *Isogonoceraia* sp. on *Eperua*, and the Galerucinae *CHRY007* on *Catostemma*. Psyllids are rarely considered as pests (e.g. Burckhardt, 1989), and the chrysomelid only occurred at 66% of the *Catostemma* stations and rarely defoliated them heavily. Thus, most of the present data indicate that the Janzen–Connell model, explaining specifically seedling attack with regard to specialist insects originating from parent trees, is unlikely to be valid for the study system. Similarly, Thomas (1990), studying *Passiflora* ssp. and their herbivores in Costa Rica, also found the Janzen–Connell model of limited value, because the majority of insect species were not monophagous.

Furthermore, attacks of generalists on seedlings may not be as severe as those of endophagous herbivores, which in the present case included leaf-mining Gracillariidae, Agromyziidae, and an unidentified taxa on *Chlorocardium*, *Catostemma*, and *Eperua*, respectively, bud-galling Cecidomyiidae on *Eperua*, and a stem-boring Stenominae on *Catostemma*. Their damage on seedlings during the study period, however, was rather low. The Janzen–Connell model may be applicable when there are high loads of insect specialists on parent trees and when contagion on the seedlings occurs (Maeto & Fukuyama, 1997), or when meristem-feeders are abundant in the study system. Clearly the model needs to be re-formulated to account for the action of generalist herbivores and

meristem-feeders, but adequate tests of causal mechanisms will need more data on seedling survival.

Conclusion – are rainforest seedlings a poor resource for insect herbivores?

Leaf-flushing events for the seedlings were rare during the study period, as in many studies monitoring seedlings in rainforests. For example, Clark and Clark (1985) indicated that many seedlings of shade-tolerant rainforest trees do not produce any new leaves during the first 7 months of their lives, whereas adult trees can experience several leaf-flushes a year or produce leaves continuously. Because tropical insect herbivores often depend on young foliage (e.g. Aide, 1991), rainforest seedlings may not attract many insect herbivores, unless their leaves are particularly palatable when mature. Indeed, the tagged seedlings supported very low densities of insects, which included many generalist species. This suggests that seedlings, particularly those with mature leaves that wait for an opportunity to develop further as saplings, may represent a poor nutritive resource for insect herbivores (Gombauld, 1996).

An alternative explanation may account for the high incidence of generalists on the seedlings in block 17. In Guyana, monodominant forests growing on nutrient-poor soils prone to flooding are common (e.g. ter Steege *et al.*, 1996). Many parts of block 17 appear characteristic of monodominant stands. Because monodominant species often grow slowly (e.g. Hart, 1990), they may be well-defended chemically and relatively unpalatable to insects. This may promote the abundance of generalist insect herbivores locally. Thus, it would be profitable to study the communities of insects attacking seedlings in nutrient-rich rainforests.

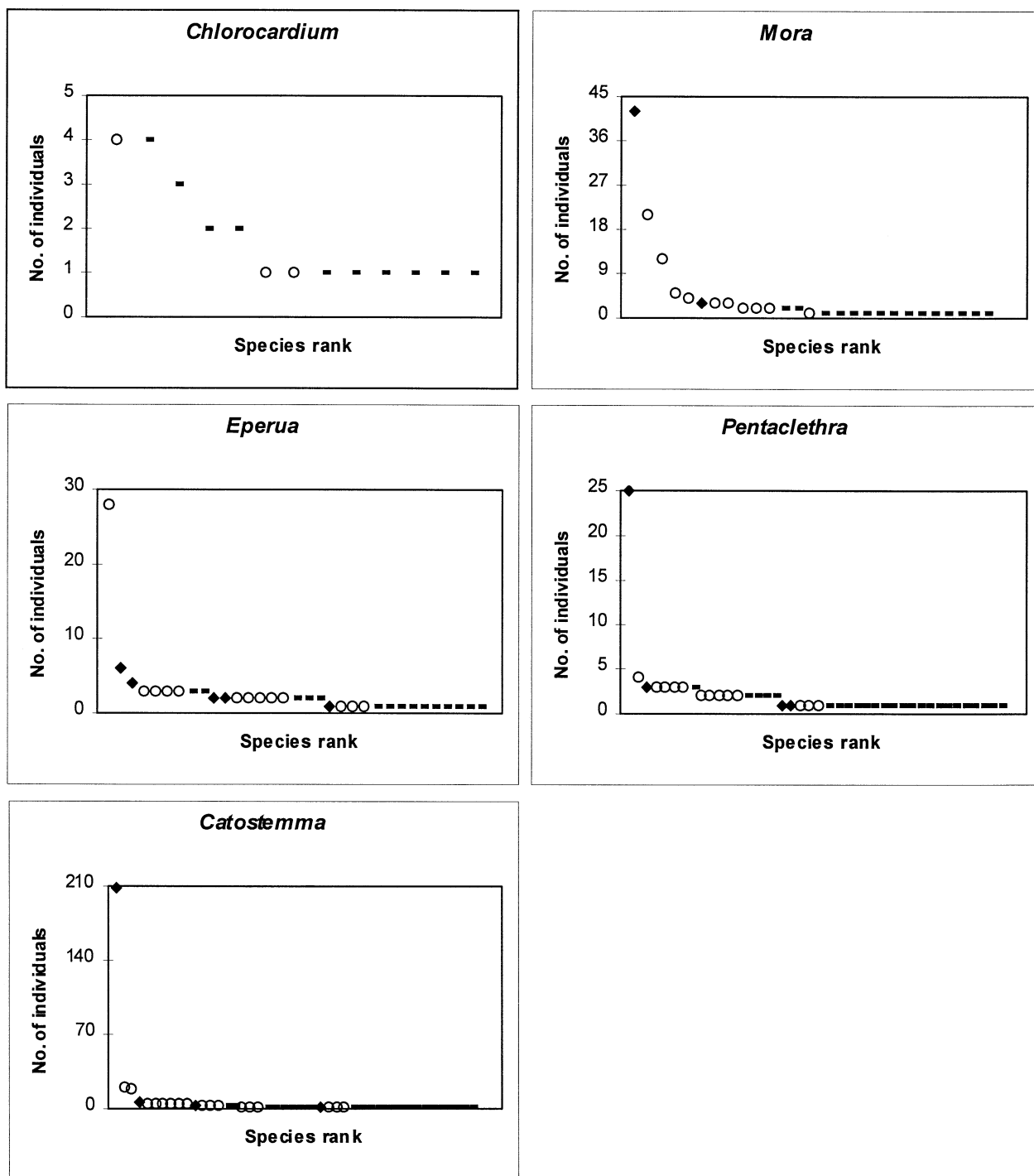


Fig. 6. Distribution of the number of individuals of leaf-chewing insects on each host. ◆=specialists, ○=generalists, --=not known (total number of individuals collected <5).

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Table 7. Distributional records and Lloyd's index of patchiness for common Eumolpinae (all feeding in captivity). Numbers in bold indicate that males were available for genitalia extraction and study. *Indicates that the species was observed feeding *in situ* on that particular host.

Species code	Identification	Lloyd's index	No. of individuals				
			<i>Chlorocardium</i>	<i>Mora</i>	<i>Eperua</i>	<i>Pentaclethra</i>	<i>Catostemma</i>
CHRY019	<i>Otilea</i> sp.	1.00	0	3	1	1	1
CHRY001	?	1.16	0	* 3	1	* 4	4
CHRY006	?	1.35	0	3	1	0	2
CHRY008	?	2.10	1	*5	* 28	2	18
CHRY010	?	2.85	0	21	3	2	4
CHRY025	?	2.00	0	*2	0	3	0
CHRY026	?	1.50	0	1	0	1	3
CHRY033	?	2.22	0	0	3	0	4
CHRY049	?	1.50	0	0	1	3	1
CHRY051	?	5.17	0	0	6	0	0

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