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Insect herbivores foraging on seedlings in an unlogged rain forest in Guyana: spatial and temporal considerations

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Abstract

About 9,000 individuals of sap-sucking and leaf-chewing insects, representing 345 species, were collected from 10,000 seedlings belonging to 5 rainforest tree species in an unlogged forest in Guyana. For the 40 most common species, it was possible to estimate their host specificity, diurnal activity, seasonal distribution, spatial aggregation, abundance and body weight. Most species were generalists but more specialised species tended to show a higher spatial aggregation, a more restricted diurnal activity and a higher seasonality. Although insect abundance was highest at the onset of the long wet season in May, seasonal amplitude was not pronounced. The combined effects of host and rainfall explained 14.5% of the total variance in insect seasonality, which was poorly explained by the leaf production of seedlings. The spatial distribution of insects was often aggregated and, overall, explained by host effect, production of young foliage, number of conspecific trees within a radius of 50m, and number of dead seedlings at each collecting station. However, these variables explained only 7% of the variance in spatial distribution. The lack of notable influence of leaf production and other important variables recorded at the collecting stations suggests that the seedlings represent a marginal food resource for most of the insect species collected.

Keywords: Insect herbivores, seedlings, host specificity, spatial distribution, rain forest, seasonality, Guyana.

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INTRODUCTION

In temperate latitudes, forest entomologists are familiar with such concepts as, among others, delayed bud-breaks as a defense against insect herbivores (Hunter, 1992); the effect of intraspecific leaf size on insect success (Dixon & Logan, 1973; Bultman & Faeth, 1986; Faeth, 1991); or that of sunlight regime (Claridge et al., 1981); spatial decisions facing ovipositing females (Moore et al., 1988). These concepts lead to predictable patterns of temporal and spatial distribution of insects in temperate forests. Arguably, these patterns result from the phenology of the host-plants and the interactions with abiotic factors to provide suitable oviposition, feeding and mating sites to insects. At least from a tropical perspective, temperate forests appear to provide rather uniform, predictable food resources for insect herbivores, where distinct herbivore guilds may succeed each other from bud break in spring to leaf senescence in autumn (Feeny, 1970; Dixon, 1976; Larsson, 1985).

Tropical rain forests may differ from temperate forests in many aspects for insect herbivores. For example, more species of both unrelated and related hosts may co-exist locally in tropical rain forests, host foliage may be better protected, host leaf-flushing may be more difficult to locate due to frequent asynchronous or opportunistic leaf production, or the effects of abiotic factors may be more contrasted both on horizontal (i.e., closed forest versus gaps) and vertical (i.e., understorey versus canopy) gradients, resulting in a more heterogeneous (and often hostile) environment (Basset, 1991a; Coley & Aide, 1991; Basset et al., 1992; van Schaik et al., 1993). Entomologists working in the tropics must also cope with the apparent low insect densities in tropical rain forests (Elton, 1975; Basset et al., 1992) and the lack of taxonomic expertise to identify tropical specimens reliably (Erwin, 1995). Given all of the above, it is not surprising that spatio-temporal distribution patterns of insect herbivores in tropical rain forests are known poorly. At present, the lack of baseline data, particularly relevant to insect spatial distribution, prevents the development of testable hypotheses which could lead to useful concepts applicable in the tropics and similar to those listed above for temperate insect herbivores.

Insect seasonality in the tropics is perhaps best known from the pioneering studies of Henk Wolda in Panama (Wolda, 1978, 1980, 1983, 1992). With the help of various trapping devices, many subsequent studies focused on predicting fluctuations in the abundance of insects, and particularly correlations with rainfall, or leaf production, which appear to represent the major sources of variation in insect abundance over time (Smythe, 1982; Janzen, 1992; Wolda, 1992; Murali & Sukumar, 1993; Gombauld & Rankin-de-Mérona, 1998). In contrast, diel activity of tropical insects has been poorly documented (e.g., Springate & Basset, 1996).

The spatial distribution of tropical insect herbivores is often inferred from their damage on vegetation, or herbivory. In addition to being limited to leaf-chewing insects, this practice may result in serious biases and has severe limitations (Marquis, 1991; Basset & Höft, 1994). Data on the spatial distribution of tropical insect herbivores, particularly in rain forests, are surprisingly scarce when studies related to leaf damage are excluded. Usually, these are concerned with vertical gradients (Sutton, 1983; Wolda, 1983; Basset et al., 1992) or rainfall, edaphic and altitudinal gradients (Janzen & Schoener, 1968; Wolda, 1983, 1987; Orr & Haeuser, 1996). Rarely, data are presented about the distribution of insect herbivores between or within their host-plants in natural conditions (Basset, 1991a, 1991b; Novotny, 1993; Novotny & Lepš, 1997; Novotny & Basset, 1998).

In tropical rain forests, seedlings are much easier to access and survey for insects than canopy foliage. As such, seedlings may represent an interesting system for studying spatial and temporal patterns of distribution of insect herbivores. However, insect density on seedlings is rather low (Becker, 1983) and this calls for greater sample size and number of spatial and temporal replicates. This situation is particularly well-suited for parataxonomist work (Novotny et al., 1997). At Mabura Hill, central Guyana, the insect fauna foraging on close to 10,000 seedlings belonging to five rainforest tree species was studied in an unlogged plot with monthly surveys during one year (Basset, 1999). Selective logging was then simulated in the plot and the insect surveys resumed for an other year. The present contribution analyses the diurnal, seasonal and spatial distribution of insect herbivores in the pre-logging treatment, providing baseline data for comparing the situation in the post-logging treatment. Beside possible relationships with rainfall, production of young foliage and the spatial distribution of the sampling units themselves, particular attention is paid to possible correlations between insect distribution and life histories, particularly host specificity, and the proportion of the variance in insect distribution that could be explained by such attributes.

MATERIALS AND METHODS

Study site and study plants

Insect sampling was performed in a squared plot of 0.92 km^2 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 = *ca.* 30 m). The main forest types in Block 17 include well- and poorly-drained mixed forests (ter Steege et al., 1996). Annual rainfall at Mabura Hill is high and variable, between 2500 to 3400 mm, while annual air temperature is about 25.9°C. A long wet season usually occurs between May and August and a short one between December and February (ter Steege et al., 1996).

This study focused on the seedlings of the following species, which are either important timber species in Guyana or relatively common in Block 17: *Chlorocardium rodiei* (Scomb.) (Lauraceae, Greenheart); *Mora gonggrijpii* (Kleinh.) Sandw. (Caesalpiniaceae, Morabukea); *Eperua rubiginosa* Miq. (Caesalpiniaceae, Water Wallaba); *Pentaclethra macroloba* (Willd.) Kuntze (Leguminosae, Trysil); *Catostemma fragrans* Benth. (Bombacaceae, Sand Baromalli). Hereafter, they are designated by their generic names. All species can be classified as shade-tolerant seedlings and canopy tree as adults. A collecting station was defined as a fixed number of tagged seedlings (40 for *Chlorocardium* and *Catostemma*, 50 for *Mora* and *Eperua* and 15 for *Pentaclethra*) growing below the parent tree or in its vicinity. Fifty such collecting stations were chosen for each species in Block 17 (total 250 stations and 9,750 seedlings). As far as possible, stations were spread in the study site and experienced different light regimes. Most seedlings had less than 5 leaves and were often 30–40 cm tall. Those which died during the course of the study were replaced by other non-tagged seedlings growing below the parent tree. On average,

seedlings increased their leaf area by 4.7% at the end of the sampling program. Other characteristics of the study site, stations and plants are detailed elsewhere (Basset, 1999).

Insect collecting and processing

The sampling protocol targeted free-living insect herbivores foraging during day-time on the tagged seedlings (leaf-chewing insects: Chrysomelidae, some Curculionidae, juvenile Lepidoptera, some Orthoptera; sap-sucking insects: many Hemiptera). Most of the insect collecting was performed by field assistants who had been trained beforehand for this purpose. From October 1996 to September 1997, 11 monthly insect surveys were organized (none was performed in August 1997). During each survey, all the tagged seedlings were inspected once, during daytime. Live insects were collected by hand-collecting and the use of small aspirators, for further rearing and assessment of host specificity (see below). As far as possible, insects which flew away were recorded to the insect family. On average, one assistant spent at least 30 minutes at each collecting station, inspecting carefully each tagged seedling. The sampling protocol involved 4-5 field assistants. During each survey, groups of closely situated stations were assigned to assistants in a random fashion, in order to reduce the collector's effect. Juveniles of leaf-chewing insects (all caterpillars) were collected and reared with young foliage from seedlings grown for this purpose. Juveniles of sap-sucking insects were not collected, but recorded to the family level.

The assistants recorded the number of mature and young leaves present on each tagged seedling. An estimate of the leaf area sampled at each station during each survey was computed by multiplying the number of young and mature leaves recorded by the average specific leaf area (Basset, 1999). The average total leaf area monitored at each station varied from about 0.5 m^2 of leaf area (*Chlorocardium*) to 3.0 m^2 (*Mora*). However, given the extremely low insect densities recorded, these differences in sample size could be neglected and unadjusted densities were considered in the analyses (Basset, 1999). The assistants also recorded time of sampling at the nearest hour and whether the weather could be described as sunny, cloudy or rainy (sampling was not performed during heavy rainfall).

Live insects were brought to a laboratory in Mabura Hill, killed by storage in a freezer, mounted on points, dried and identified by a personal accession number. Insects were then sorted by morphospecies (hereafter species for sake of simplicity) and assigned an insect code. Checking of genitalia on male material was performed in doubtful cases. Further, the insect material was checked by various taxonomists (see acknowledgments).

Environmental and plant variables

These variables were recorded to assist in the interpretation of the insect data. Daily rainfall was measured at the study site, to avoid possible bias due to spatial variability of rainfall parameters which, in the Amazon region, may be significant, even in the case of adjacent study sites (Ribeiro & Adis, 1984). Further, the following variables were recorded at each sampling station:

- diameter at breast height (DBH) of the parent tree;
- average area of young foliage (cm^2) recorded on seedlings during each insect survey;
- illumination of seedlings, estimated with the index of Clark and Clark (1992) (varies from 1 to 5), recorded and averaged over the 4 main cardinal points of each station in September 1997;
- leaf water content of mature leaves (LWC), measured and averaged from 5 seedling leaves at each station in September 1997;
- number of conspecific trees (DBH > 16 cm) with seedlings within a radius of 50m of the parent tree;
- total number of seedlings which died at each station during the 11 insect surveys; this did not account for seedlings destroyed by peccaries (*Tayassu tajacu* L.) and represents a surrogate for the physiological stress experienced by seedlings.

Insect parameters

Firstly, analyses considered the total number of insect herbivores, sap-sucking and leaf chewing insects collected, either on particular hosts or on all hosts, and how these various figures varied between time of day and sampling stations (Kruskal-Wallis tests). Circular statistics (Zar, 1984) were used to test whether or not the seasonal distribution of insects was uniform on a particular host (Rayleigh's tests), or whether the seasonal distributions of insects were significantly different between their hosts (Watson-Williams tests). In addition, the distribution of the following insect species, which were abundant and amenable to statistical analyses, was also examined:

- *Isogonoceraia* sp., the most common specialist

species, a psyllid, whose nymphs feed on *Eperua*;
- *Soosiulus fabricii* Metcalf, the most common generalist species, a cicadellid (Cicadellinae) sucking the xylem of all hosts studied;
- *Cryptocephalus esuriens* Suffrian, a specialist chrysomelid (Cryptocephalinae) preferring *Mora*;
- an unidentified species of chrysomelid (CHRY007; Galerucinae), specialist and feeding on *Catostemma*.

Secondly, data were filtered as to retain species common enough to estimate their host specificity, diurnal distribution, seasonality, spatial aggregation, abundance and body weight. For both sap-sucking and leaf-chewing insects, only species collected with a minimum of 15 individuals in total were considered for these analyses, as this represented a threshold critical to the reliable estimation of seasonality (see below). Hereafter, these are termed common species. The total number of individuals collected at all stations for each common insect species was used as an abundance parameter. Insect specific body weight (in mg dry weight) was estimated from measurement of body size using the equations of Schoener (1980). Other insect parameters were estimated by Lloyd's index of patchiness (Lloyd, 1967), which is relatively insensitive to sample size, performs well in a variety of situations (Lepš, 1993; Wolda & Marek, 1994) and is calculated as:

$$L = \frac{S_X{}^2 - \overline{X}}{\overline{X}^2} + 1,$$

where $S_X{}^2$ and $\overline{X}$ are the variance and mean of the sample. The index increases for insects that are more concentrated within particular sample units. The insect parameters were estimated as follows:

1. Host specificity

Definitive feeding records are difficult to obtain, particularly for sap-sucking insects (Basset, 1999). Apparent host-specificity for sap-sucking insects refers mainly to patterns of distribution on their putative hosts, not to actual feeding records, with very few exceptions. A species was considered to be a specialist (rather than generalist) on a particular host if its Lloyd's index was ≥ 3.0. This approximately corresponds to a situation where at least 80% of the individuals were collected on a single host, for sample sizes typically encountered in this study. For leaf-chewing insects, it was possible to take the analysis one stage further. Caterpillars were, as far as possible, reared to adults. Others, such as beetles and grasshoppers, were kept in plastic vials with young leaves of the host-plant species they were collected from. The vials were kept for 3-4 days in Block 17 and records of leaf damage and frass were checked subsequently. Insect species responsible for obvious damage were later assigned in the feeding category, others, including dead insects, in the non-feeding category. Only the former were later assigned to morphospecies. These simple tests allowed to remove transients, as well as species feeding infrequently on the seedlings, for the analyses. The validity of using feeding tests in captivity, how they compared with the actual distribution of the insects in the field and the advantages of such an approach, are discussed elsewhere (Cullen, 1989; Basset & Samuelson, 1996). In the present context, specialist should be interpreted as a species which showed a clear preference for one of the five host species studied, but without implication of monophagy, as no information is available on the use of other possible hosts within the study area.

2. Diurnal distribution (diel activity)

The number of individuals of common species collected during hourly periods from 8h00 to 16h00 (all stations pooled) was weighted by the number of stations surveyed during the hourly periods. Lloyd's index was then calculated using these average values.

3. Seasonal distribution (seasonality)

Lloyd's index was calculated for the common species across the 11 surveys performed from September 1996 to September 1997. Since the assumption of independence of the variability measure to the mean is crucial for analyses of seasonality (Lepš, 1993), common species were selected as to satisfy this assumption. The pragmatic approach recommended by Lepš (1993) was followed, in which the data set is reduced until the mean annual catch becomes independent from the coefficient of variation. In the present study, the assumption was fulfilled when considering a total catch of 15 specimens or more per species during the collecting year.

4. Spatial aggregation

Two problems may occur when measuring insect aggregation, namely (a) when the sample size of the sampling unit varies (Connor et al., 1997); and (b)

when the sample size of insect specimens greatly varies in community studies (Novotny et al., 1997). Item (a) is particularly relevant to outbreak pests (Connor et al., 1997). Since insect densities are rather low in tropical forests (Basset et al., 1992), the greatest statistical challenge with the present data is likely to be (b). Although Lloyd' s index performs very well with regard to (b) and was used to describe the aggregation of the common insect species among the 250 sampling stations, it still represents a biased estimator (Lepš, 1993; Wolda & Marek, 1994).

Community analyses

These analyses attempted to extract overall patterns in insect distribution from the assemblage consisting of common species foraging on the seedlings. Since the variance due to diurnal activity was rather low (see results), these analyses emphasized the seasonal and spatial variance of insect distribution, accounting for possible interactions due to insect host specificity. The seasonal variance of insect species was studied by computing a correspondence analysis (CA) and a canonical correspondence analysis (CCA) on a matrix of species x insect surveys grouped by host species (40 lines × 55 columns). The CCA was constrained by the monthly rainfall during the surveys, the production of young foliage during the surveys for each host, and a categorical variable coding for the effect of host species. Similarly, the spatial variance of insect species was studied by computing CA and CCA on a matrix of species x sampling stations (40 lines × 250 columns). Here, the CCA was constrained by the variables recorded at each station (see above) and a categorical variable coding for the effect of host species. A Mantel test (Legendre & Fortin, 1989) was computed to check the independence between the spatial location of the stations and their similarity in insect fauna. The first matrix included Euclidean distances between the cartesian coordinates of the stations, whilst the second included Euclidean distances between the occurrence of the 40 common insect species at the 250 sampling stations.

Eventually, a principal component analysis (PCA) was performed on the 6 insect parameters (host specificity, diel activity, seasonality, spatial aggregation, abundance and body weight) estimated for each of the 40 common species, to extract most of the uncorrelated variance likely to account for insect distribution patterns. CA, CCA and PCA were computed using the software ADE 3.4 Chessel & Dolédec, 1992), whereas the Mantel test was computed with the Progiciel R (Legendre & Vaudor, 1991).

RESULTS

Host specificity, abundance and body weight of insects

Overall, 9,056 insect specimens were collected, representing 345 species. Host specificity and abundance data are discussed elsewhere (Basset, 1999). Most of the insect species were generalists, as the distribution of Lloyd' index suggested (mode between 1.00 and 1.50 for 111 species; see also Fig. 1A for common species). The common species included 40 species (6 leaf-chewing and 34 sap-sucking species; 6 specialist and 34 generalist species). Their modes in abundance and body weight were between 20 and 40 individuals and between 0.50 and 0.75 mg dry weight, respectively (Fig. 1E and 1F).

Diurnal activity of insects

The distribution of the mean number of insect herbivores collected per station was rather even during day-time, with small peaks at 9h00 and 16h00 (Fig. 2). However, no significant differences were detected during collecting hours (Kruskal-Wallis $W = 14.88$, $p = 0.09$). This trend was also similar for leaf-chewing ($W = 12.33$, $p = 0.20$) and sap-sucking insects ($W = 12.00$, $p = 0.22$). However, the effect of weather, as described earlier, was significant, for all herbivores ($W = 34.76$, $p < 0.001$), and particularly for sap-sucking insects ($W = 39.68$, $p < 0.001$). More insects were collected during rainy periods (244 cases out of 2750). Interestingly, this trend was not significant for leaf-chewing insects (confirmed feeders; $W = 0.48$, $p = 0.78$), but it was for non-feeding leaf-chewing insects ($W = 13.68$, $p < 0.05$), which represented about 53% of the total number of leaf-chewing insects collected and can be classified as transients. This suggests that during rainy periods, insects seek shelter within the foliage of seedlings and this involved many transient species.

Variance in diurnal activity was also low when considering particular insect species. Most of Lloyd's indices were between 0.50 and 1.50 (Fig. 1B), suggesting no real peak time during 8h00 and 16h00. There was no significant difference in the diurnal distribution of sap-sucking versus leaf-chewing insects (Mann-Whitney $U = 67.0$, $p = 0.19$). However,

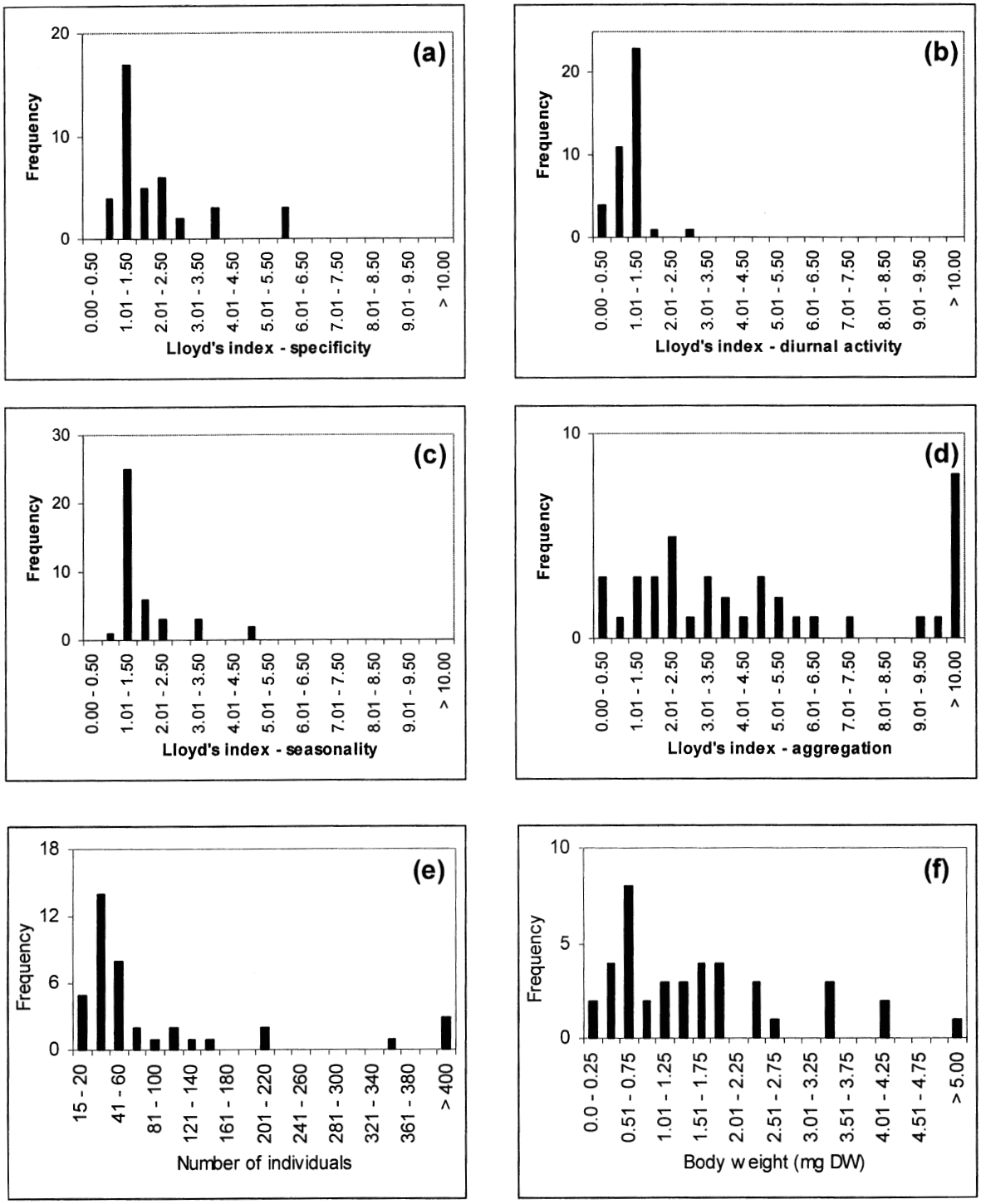

Fig. 1. Distribution of insect parameters for the 40 common insect species: Lloyd's index calculated (a) across the 5 study hosts (host specificity); (b) across hourly periods from 8h00 to 16h00 (diel activity); (c) across the 11 monthly insect surveys (seasonality); and (d) across the 250 sampling stations (spatial aggregation); (e) insect abundance; and (f) insect body weight.

specialist species tended to have a more aggregated daily distribution than those generalist (higher L; U = 169.0, $p < 0.05$). The former tended to be more active late in the day, between 15h00 and 16h00 (average of 0.76 insect specialist collected per station at that time).

Insect seasonality

Overall, the seasonal distribution of insect herbivores showed a marked peak in March 1997, which was due, almost solely, to nymphs of the psyllid *Isogonoceraia* sp., feeding on *Eperua*. Similar plots for leaf-chewing insects and for sap-sucking insects, excluding psyllid nymphs, revealed a less distinct seasonality (Fig. 3). The ratio seasonal minimum to maximum (Wolda, 1980), here calculated with monthly data, was 0.227, 0.303 and 0.533 for all herbivores, leaf-chewing insects and sap-sucking insects without psyllid nymphs, respectively. The seasonal distribution of all herbivores, leaf-chewing and sap-sucking insects was overall non-uniform (Rayleigh's z = 18.5, 12.6 and 16.7, respectively; all with $p < 0.001$), and differed significantly among host-plants (Watson-Williams tests, F = 5.45, 16.55 and 5.32, respectively; all with $p < 0.05$).

Annual rainfall during the study was 2535 mm, with the wetter months from May to August (Fig. 4), not an exceptional situation for Mabura Hill (ter Steege et al., 1996). Leaf production was not distributed uniformly across the surveys (Rayleigh's z = 45.2, $p < 0.001$) and its peak occurred in April 1997 (Survey 7; Fig. 4). Similarly, on all host-plants studied, the seasonal distribution of leaf production was non-uniform, often with a peak in April 1997 (Rayleigh's tests, all with $p < 0.001$). The seasonal distribution of leaf production also differed significantly between host-plants (Watson-Williams test, F = 527.6, $p < 0.001$). There was a significant positive correlation between monthly rainfall and leaf production, with a time lag of two months (i.e., leaf production increased two months after an increase of rainfall; r = 0.778, $p < 0.05$).

Maxima of herbivore abundance coincided approximately with the onset of the long wet season of May to August, and significantly more herbivores and leaf-chewing, but not sap-sucking, insects were collected during the wetter period (3 surveys, May to June 1997) than during the drier period (3 surveys, September 1997 and October-November 1996) (Mann-Whitney U = 3.08E05, 3.02E05 and 2.89E05, $p < 0.01$, $p < 0.001$ and $p = 0.31$, respectively).

However, no significant relationship existed between the abundance of leaf-chewing insects, sap-sucking insects, all herbivores and leaf production and rainfall, even when considering different time lags (all correlation with $p > 0.05$). There was a correlation between the abundance of *S. fabricii* and rainfall with a time lag of two months (r = 0.803, $p < 0.05$), but no such relationships existed with leaf production. Despite the adults of the Galerucinae

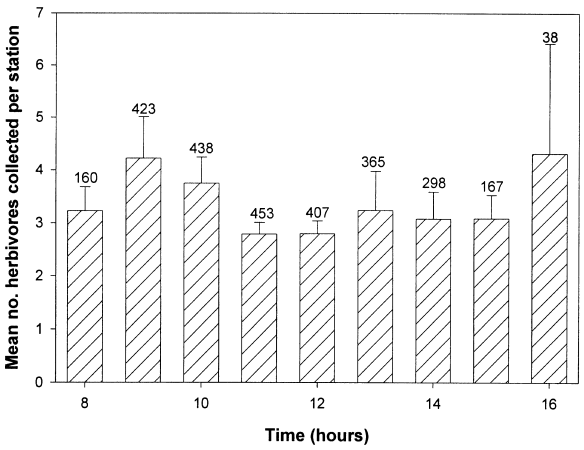

Fig. 2. Distribution of the mean number of herbivores collected per station during the day (8:00 to 16:00), all stations pooled. Error bars represent s.e.m. and values above the error bar indicate the number of stations surveyed at a particular time of the day.

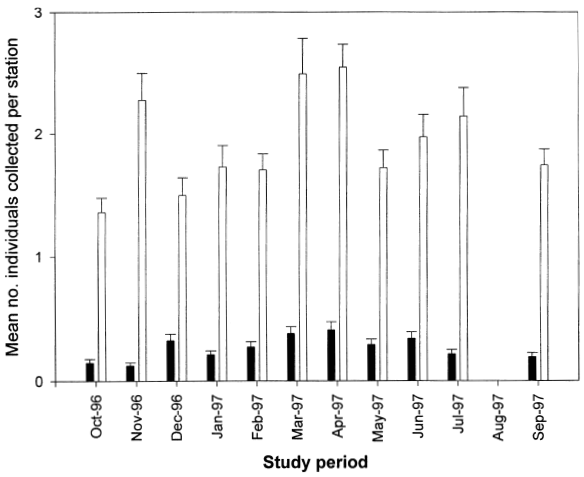

Fig. 3. Seasonal distribution of leaf-chewing insects (closed bars) and sap-sucking insects without accounting the nymphs of *Isogonoceraia* sp. (open bars). Error bars represent s.e.m. No insect survey was performed in August 1997.

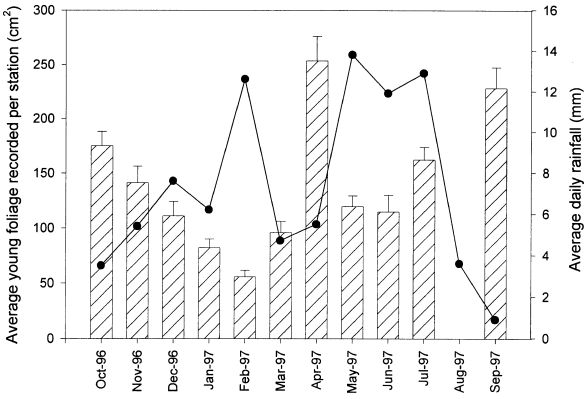

Fig. 4. Seasonal distribution of rainfall (curve) and leaf production (bar graph with s.e.) during the monthly insect surveys. Leaf production data unavailable for August 1997.

CHRY007 and the psyllid nymphs of *Isogonoceraia* sp. feeding only on young foliage of *Catostemma* and *Eperua*, respectively, no relationship existed between the seasonal occurrence of such specialists and leaf production, even when considering different time lags (all correlations with $p > 0.05$).

The mode of the seasonal Lloyd's index was between L = 1.00 and 1.25, which corresponded to a fairly even distribution across the whole period of sampling (Fig. 1C). The seasonality of CHRY007 and *Isogonoceraia* sp. were more pronounced with L = 1.411 and L = 1.298, respectively (note that the later refers to adult psyllid, not their nymphs). There was no significant difference between the seasonality of leaf-chewing insects and that of sap-sucking insects (Mann-Whitney U = 68.00, $p = 0.20$). However, when sap-sucking insects were considered, specialists were significantly more seasonal (higher L) than generalists were (U = 81.00, $p < 0.05$).

The appearance of the two seasonal ordinations were different, as judged by the plot of axes 1 versus 2 (Fig. 5A and 5B). The total inertia of the CA was 2.491 and the plot of axes 1 versus 2 in Figure 5A explained 34% of the total variance, whereas Figure 5B explained 87% of the variance explained by the CCA, but only 14.5% of the total variance (see graphs of eigenvalues in Fig. 5). The correlations between the scores of the species in the CA and CCA were significant for axes 1, 2 and 3 (r = 0.818, 0.606 and 0.443, respectively). The best explanatory variables for the formation of the canonical axes were host identity for axis 1 and monthly rainfall for axis 2 (Table 1, Fig. 5B).

Spatial aggregation

Chlorocardium, *Mora* and, to a lesser degree, *Pentaclethra* grow in a clumped fashion, whereas the distribution of *Eperua* and *Catostemma* is more random (ter Steege et al., 1996). The location of the sampling stations, and hence insect densities, partly reflected the aggregation of the host plants (Fig. 6). For example, the spatial distribution of *S. fabricii* appeared to be related to its preference for *Chlorocardium* (Fig. 6). Overall, there were significant differences in insect abundance between the stations only when insect densities were relatively high, such as in the case of sap-sucking insects on *Chlorocardium* and *Eperua*, and leaf-chewing insects on *Mora* and *Catostemma* (Kruskal-Wallis tests, all with at least $p < 0.05$).

Few significant correlations existed between insect densities and the variables recorded at each station (Tables 2 and 3). The strongest correlations, particularly after applying Bonferroni's correction, involved young foliage produced at each station, and this for hosts such as *Eperua* and *Catostemma* and their specific herbivores (Table 3). On these same hosts, weak negative correlations existed between densities of sap-sucking insects and the number of dead seedlings recorded. The number of conspecifics within a 50m radius only exerted a weak negative influence on sap-sucking insects foraging on *Mora*. Illumination and leaf water varied relatively weakly between stations and did not appear to influence insect populations, as did the size (DBH) of the parent tree.

The distribution of the spatial Lloyd' s index reflected two modes (Fig. 1D). The spatial distribution of species with L = 2.00-2.50 was relatively uniform, whereas that of those with L > 10.00 was highly aggregated. There was no significant difference in spatial aggregation between sap-sucking and leaf-chewing insects (Mann-Whitney U = 58.0, $p = 0.09$) but specialists were significantly more aggregated than generalists (U = 192.0, $p < 0.001$).

The appearance of the spatial CCA was rather different from the spatial CA (Fig. 7A and 7B), suggesting that the variables recorded at each station explained only a small fraction of the total variance. The total inertia of the CA was 5.631 and the plot of axes 1 versus 2 in Fig. 7A explained 18% of the total variance, whereas Fig. 7B explained 72% of the CCA variance, but only 7.4% of the total variance (graphs of eigenvalues in Fig. 7). The correlations between

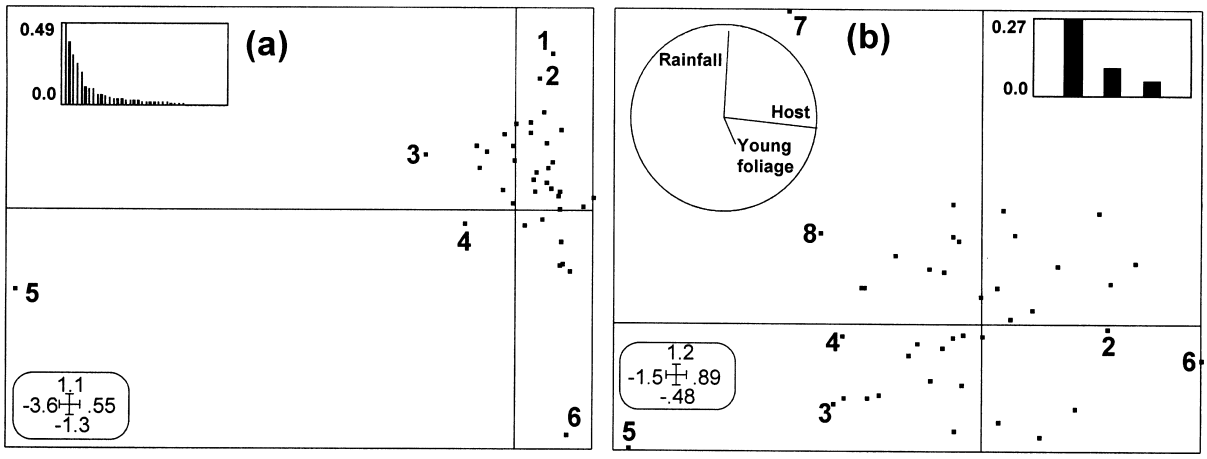

Fig. 5. Ordinations of the 40 common insect species across the 11 surveys and 5 hosts. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Notable insect species (plotted far away from the barycentre of the ordination) as follows: 1 = ALEY001 (Aleyrodidae); 2 = TORT001 (Gelechiidae); 3 = *Southia* sp. (Kinnaridae); 4 = *Herpis* sp. (Derbidae); 5 = COCC002 (Pseudococcidae); 6 = *Isogonoceraia* sp. (Psyllidae); 7 = *Macugonalia moesta* (F.) (Cicadellidae); 8 = DERB009 (Derbidae).

the scores of the species in the CA and CCA were significant for axes 1, 2 and 3 (r = 0.773, 0.704 and 0.509, respectively) but not for axis 4 (r = 0.390). The best explanatory variables for the formation of the canonical axes were host identity for axis 1 and the number of conspecifics for axis 2 (Table 1, Fig. 7B). Further, the two matrices of distances between the cartesian coordinates of the stations and their insect fauna were independent from each other (Mantel test, r = 19.56, t = 0.307, p = 0.38).

Relationships between insect parameters

There were several weak correlations among insect parameters but a strong correlation between host specificity and spatial aggregation persisted after applying Bonferroni's correction (Table 4). Insect species that were more host specific were more likely to show a higher spatial aggregation, a more restricted diurnal activity and a higher seasonality, in order of decreasing robustness of correlation. This appeared to be independent of insect abundance. However, there was a weak positive relationship between abundance and diel activity. This suggested that it was easier to collect some species when they were aggregating in large numbers at a particular time of the day. Insect body weight showed no significant correlation with other insect parameters.

When the respective values of the Lloyd indices describing the host specificity, diurnal activity, seasonality and spatial aggregation were considered for

TABLE 1. Canonical coefficients and intraset correlations for the different variables included in the seasonally and spatially constrained CCAs. Variables not included in the ordinations are indicated by dashed lines (see methods).

Variables	CCA – seasonal				CCA – spatial			
	Coefficients		Correlations		Coefficients		Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Monthly rainfall	0.058	0.920	0.040	**0.967*** **	—	—	—	—
Host	1.028	–0.108	**0.992*** **	–0.001	0.867	–0.590	**0.836*** **	**–0.563*** **
Young foliage	0.127	–0.280	–0.254	**–0.394*** **	0.310	0.155	–0.008	**0.413*** **
DBH	—	—	—	—	0.176	0.316	0.031	**0.707*** **
Light	—	—	—	—	–0.072	–0.317	–0.107	–0.165
Leaf water	—	—	—	—	–0.099	–0.271	**–0.555*** **	0.089
No. conspecifics	—	—	—	—	0.163	0.595	**0.282*** **	**0.727*** **
No. dead seedlings	—	—	—	—	0.135	–0.064	**–0.463*** **	0.018

* p < 0.05, ** p < 0.01, *** p < 0.001

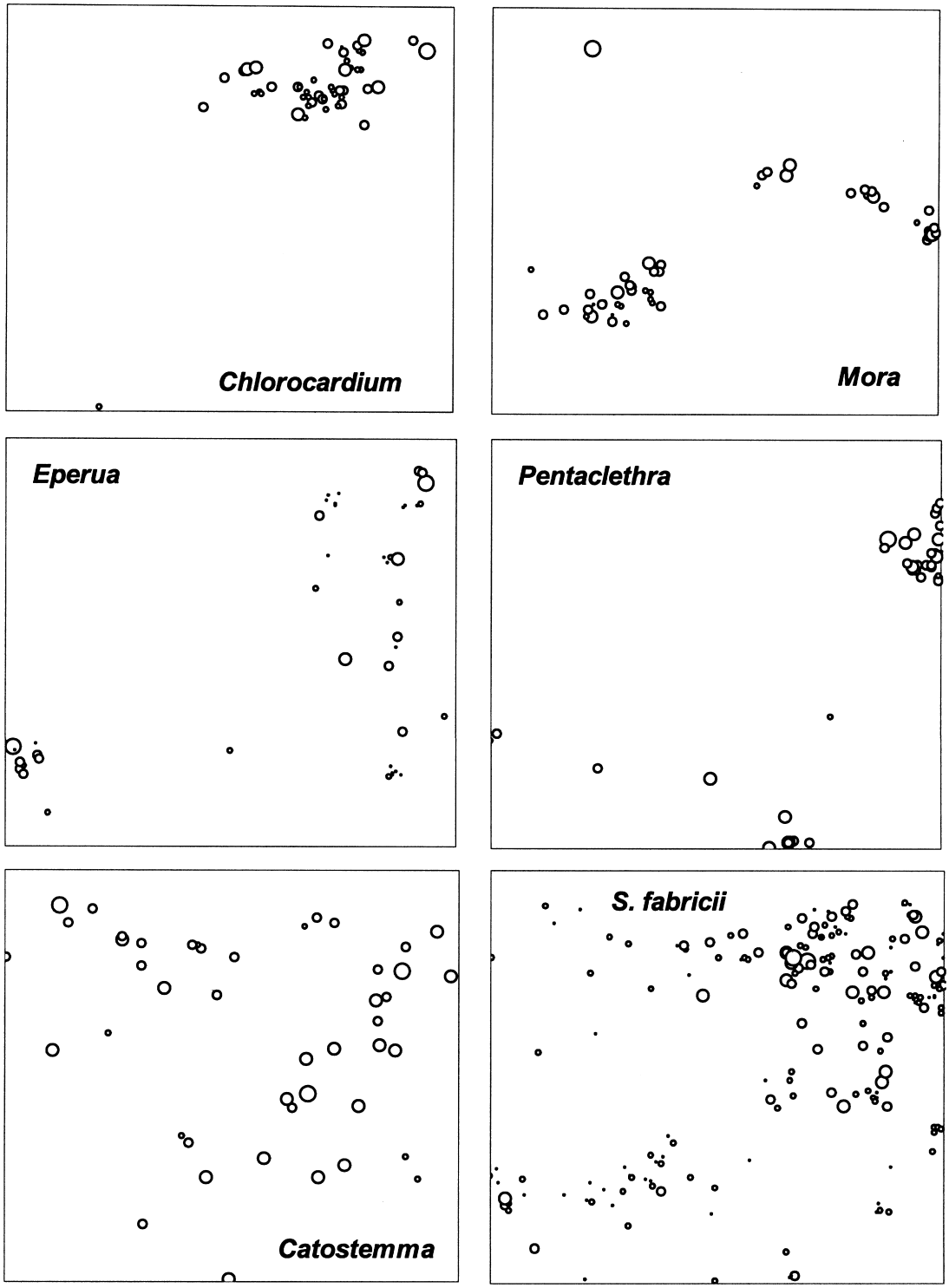

Fig. 6. Density plots (mean number of insect herbivores collected at each station) detailed for each host plant and for the generalist *Soosiulus fabricii* at all stations (total number of specimens collected at each station; most of stations plotted in this case). The boxes represent most of the study area (800 m along the X-axis, 1200 m along the Y-axis; North up) and the size of the bubbles is proportional to insect density. Largest bubbles are 6.9 herbivores per station for *Chlorocardium*; 4.4 for *Mora*; 26.2 for *Eperua*; 3.3 for *Pentaclethra*, 5.2 for *Catostemma* and 11 individuals per station for *S. fabricii*.

TABLE 2. Average values of variables of 50 stations, grouped per plant species.

Host	DBH of parent trees (cm) Mean (s.e.)	Young foliage of seedlings (cm^2) Mean (s.e.)	Light (index) Median	Leaf water content (%) Mean (s.e)	No. conspecifics (No.) Median	No. dead seedlings (No.) Median
Chlorocardium	68.1 (3.4)	2441 (110)	1.75	62.7 (0.46)	39.5	19.5
Mora	99.0 (6.7)	2042 (173)	1.63	59.8 (0.34)	28.5	6.0
Eperua	51.5 (1.8)	1476 (187)	1.63	57.5 (0.31)	38.5	9.5
Pentaclethra	35.9 (6.4)	736 (61)	1.75	58.1 (0.36)	11.5	3.0
Catostemma	39.8 (1.5)	996 (86)	1.63	60.7 (0.48)	4.0	15.5
All hosts	58.2 (2.5)	1538 (31)	1.63	59.8 (0.21)	21.0	9.0

TABLE 3. Significant Spearman rank correlation coefficients calculated between insect variables (22 altogether) and variables measured at each sampling station (DBH, Young foliage, Light, LWC, No. conspecifics and No. dead seedlings). Only significant coefficients are reported and those underlined are significant after applying Bonferroni's correction with p = 0.05/132 = 0.0004.

Insect variables	DBH	Young foliage	No. conspecifics	No. dead seedlings
All herbivores on *Mora*	—	0.345*	–0.372*	–0.329*
Sap-sucking insects on *Mora*	—	—	–0.330*	–0.303*
All herbivores on *Eperua*	—	0.600***	—	–0.333*
Sap-sucking insects on *Eperua*	—	0.586***	—	–0.327*
Leaf-chewing insects on *Eperua*	—	0.382**	—	—
Isogonoceraia sp. on *Eperua*	—	0.334*	—	–0.326*
All herbivores on *Catostemma*	—	0.302*	—	—
Leaf-chewing insects on *Catostemma*	—	0.497***	—	—
CHRY007 on *Catostemma*	—	0.436**	—	—
All herbivores on all hosts	—	0.220***	—	0.184**
Sap-sucking insects on all hosts	—	0.224***	0.192**	0.210***
Leaf-chewing insects on all hosts	–0.210***	—	–0.371***	—
Soosiulus fabricii on all hosts	—	—	—	0.213***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

each species, aggregation appeared to be the prime factor of variance. Of the 40 common species, aggregation was the highest of the four parameters for 33 species, host specificity was the highest for 4 other species and seasonality was the highest for a further 3 species. Finally, the PCA performed with the different insect parameters suggested that the first axis of the ordination was related to spatial aggregation, while the second was related to insect abundance (Fig. 8). The plot of axis 1 versus 2 represented 59% of the total variance (graph of eigenvalues in Fig. 8). Although spatial aggregation scored highly on axis 1 (0.889), host specificity represented a large part of this variance (72%), as estimated by its score on axis 1 (0.643). The possible influence of insect taxonomy was difficult to determine from the analysis.

DISCUSSION

Some of the correlations among insect parameters may have been inflated, because they could not be estimated independently from each other. For example, specialists always appeared highly aggregated when all sampling stations and study hosts were considered, less so when only sampling units relevant to their true hosts were considered. The PCA suggested that about 70% of variance in spatial aggregation may be due to host specificity alone. Although it may be argued that these measurements all depend on the sampling universe (when comparing data across different study systems; e.g., number of study hosts, resolution of the sampling units at the spatial and seasonal scales, etc.), one of the key problems when

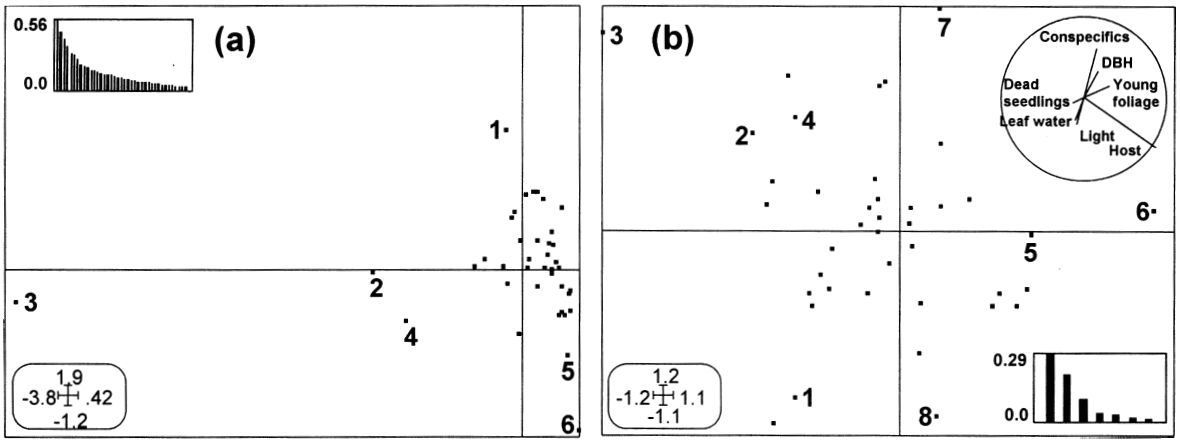

Fig. 7. Ordinations of the 40 common insect species across the 250 sampling stations. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Notable insect species as follows: 1 = ALEY001 (Aleyrodidae); 2 = DERB009 (Derbidae); 3 = COCC002 (Pseudococcidae); 4 = *Herpis* sp. (Derbidae); 5 = DERB012 (Derbidae); 6 = *Isogonoceraia* sp. (Psyllidae); 7 = *Cryptocephalus esuriens* (Chrysomelidae); 8 = TORT001 (Gelechiidae).

comparing different insect species within the same study system is the estimation of their true host range. Typically, in tropical rain forests, this parameter is unknown and difficult to measure (Novotny et al., 1997).

Diurnal distribution

In the rather dense and dark forest of Block 17, it might have been expected that collectors would have been more efficient at collecting insects during the brighter hours of the day, around 12 o'clock, but the data do not reflect this possible bias. Rather, insect foraging on the seedlings appeared to be fairly even between 8h00 and 16h00, although catches were increased during periods of light rainfall, as many insects sought shelter in the foliage of the seedlings. Variance in diel activity was much lower than the variance in spatial aggregation, host specificity and seasonality. Thus, assuming that the present results may also be relevant to other tropical systems, sampling protocols in tropical rain forests may not need to account much for insect activity within day-time, although accounting for the activity of nocturnal insects is another matter (Springate & Basset, 1996). Still, specialist species tended to concentrate their activity more at certain times than did generalists. Whether and why the behaviour of the former may be finely tuned to be active only during certain time periods, remain open questions.

Seasonal aspects of insect distribution

Although insect abundance was highest at the onset of the long wet season in May, seasonal amplitude was not pronounced (compare seasonal maxima in

TABLE 4. Upper matrix of correlation (Spearman coefficients) between the different insect parameters for the common insect species (coefficients in bold are significant, coefficients underlined are significant after applying Bonferroni's correction with p = 0.05/15 = 0.003; n = 40).

Parameter	Diel activity	Seasonality	Aggregation	Abundance	Weight
Host specificity	**0.450****	**0.407****	**<u>0.607</u>*****	0.123	0.011
Diel activity	—	0.274	0.255	**0.341***	–0.152
Seasonality	—	—	**0.351***	–0.076	–0.122
Aggregation	—	—	—	0.110	–0.102
Abundance	—	—	—	—	0.031

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

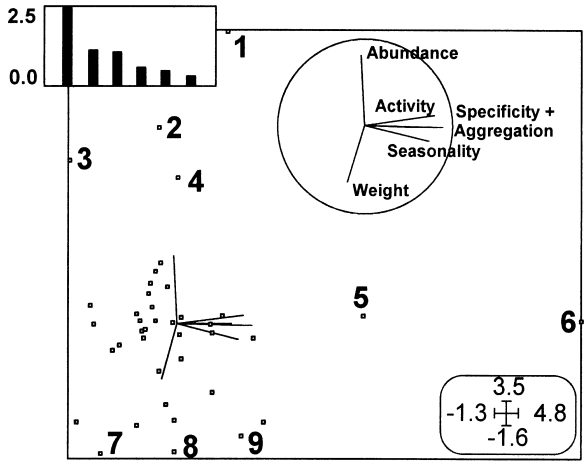

Fig. 8. Plot of axes 1 and 2 of the PCA on insect parameters. The inset box details the graph of eigenvalues and the circle the vectors representing the variables. Notable insect species as follows: 1 = *Isogonoceraia* sp. (Psyllidae); 2 = *Pintalia* sp. (Cixiidae); 3 = *Soosiulus fabricii* (Cicadellidae); 4 = *Pintalia* sp. (Cixiidae); 5 = COCC002 (Pseudococcidae); 6 = ALEY001 (Aleyrodidae); 7 = *Amblyscarta invenusta* (Cicadellidae); 8 = *Dasmeusa* sp. (Cicadellidae); 9 = CHRY007 (Chrysomelidae).

Wolda, 1980; Basset, 1991b). This was confirmed by the rather low seasonal Lloyd's indices calculated for the 40 common insect species. Although a relationship between rainfall and leaf production existed with a time lag of two months, no such relationship existed between rainfall or leaf production and overall insect abundance. However, particular insect species were sensitive to rainfall, since the combined effects of host and rainfall explained 14.5% of the total variance in insect seasonality. In contrast, the influence of seedling leaf production was weak, even for specialist insects. Many insect species were generalists and, as *S. fabricii,* fed both on young and mature foliage (Basset, 1999). The abundance of these species may be related to overall patterns of leaf production in the forest or to those of their preferred host-plants, which, in both cases, could not be monitored. For specialist species, leaf production may be significant when considering overall seedling populations at the study site (in contrast to specific collecting stations), or the leaf production of conspecific and/or related mature trees. Further, specialist species appeared to be more seasonal than generalist species, particularly for sap-sucking insects, as found in another study in Papua New Guinea (Novotny & Basset, 1998). This suggests that food resources are more seasonal for specialists than generalists and that the latter thrive on a large resource base which could support high population densities (Novotny & Basset, 1998).

The tagged seedlings produced young foliage throughout the year, in small quantities but with significant amplitudes among species. However, specialists did not track the seasonal variance of leaf production, but, rather, its spatial variance. Two hypotheses may account for this: (1) young foliage is consistently more suitable or abundant at certain locations, than during certain periods of the year; and (2) specialists also feed on the foliage of parent or related trees near the collecting stations. With regard to (1), at least the leaf water and specific leaf weight (unpublished data) of the mature foliage of seedlings did not vary much among the stations and did not influence insect abundance. Rather, hypothesis (2) seems more plausible, although direct support for it is lacking. Leaf production in parent and/or related trees may be more important for specialists than the small amounts of young foliage produced by seedlings. The weak influence of leaf production of seedlings also suggests that they represent a marginal food resource for most of the insect species collected. The stronger influence of rainfall over leaf production, for generalist species such as *S. fabricii* as well as for most insect species, is consistent with this interpretation.

Spatial aspects of insect distribution

Many insect species showed some preferences for specific stations and their distributions were relatively aggregated as indicated by Lloyd's indices. In part, these preferences resulted from the host identity and from several variables that could be measured at each sampling station, such as the production of young foliage, number of conspecific trees within a radius of 50m, and the number of dead seedlings. However, these variables explained only 7% of the variance in insect spatial distribution. The number of conspecific trees was significant for *Mora* insects. Since *Mora* stations were larger in leaf area than other stations (Basset, 1999), this suggests that this variable may be important only above a certain threshold, and that the resource represented by seedlings may often be below this threshold.

The Mantel test confirmed the independence between the spatial location of the stations and their similarity in insect fauna. This suggests that some variables not measured in the present study may in-

fluence insect distribution beyond the scale of the sampling stations. Since host preferences accounted for the major part of the explained variance in insect distribution, it is well possible that the spatial distribution of optimal host-plants not considered in the present study may be one such variable.

Insect parameters and life histories

Few data sets for tropical insects are comprehensive enough to examine the relationships between host specificity, spatial aggregation, seasonality and diel activity and other parameters likely to explain variance in insect abundance (Novotny & Basset, 1998). The present data could be improved by measuring nocturnal activity, annual variability, and improved estimation of host range and insect abundance. Nevertheless, they suggest that specialised species tend to show a high spatial aggregation, a restricted diurnal activity and a high seasonality. This appears to be relatively independent of abundance and body weight, which may be more related to insect phylogeny and availability of food resources.

Spatial aggregation was the prime factor of variance, with a strong component of host specificity (about 70%). It may represent the strongest source of idiosyncrasy at the specific level and may also prove to be the most difficult parameter to study for tropical insects. For example, a definitive study of the distribution of *S. fabricii* in Block 17 would require first studying host preference among all plant species present, then the application of massive sampling.

Conclusion

The data suggest that the presence of optimal host plants nearby the stations, as well as their seasonal phenology, are more likely to explain the spatial and temporal distribution of the insect collected than the variables measured at the seedling stations. It is probable that many insect species foraging on seedlings in Block 17 obtain their food from other sources than the seedlings, and these may represent a marginal food resource. For example, generalist insects are not devoid of host preferences and the hosts studied may not represent optimal hosts for many of them. Alternative food resources for specialists may not only include parent trees, but also congeneric and other related hosts present in Block 17. Arguably, tropical rain forests may be depicted as systems where many alternative food resources may be available to insect herbivores, as opposed to their counterparts in temperate forests. As such, tropical herbivores are unlikely to respond to changes affecting their (optimal) hosts in a similar way than temperate herbivores might. In addition to the problems presented in the introduction, the diversity of potential food resources in tropical rain forests may also complicate the study of tropical insect herbivores.

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