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Seasonality of sap-sucking insects (Auchenorrhyncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea

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Abstract Sap-sucking insects (Auchenorrhyncha, Hemiptera) were sampled quantitatively from the foliage of 15 species of *Ficus* (Moraceae) in a lowland rain forest in Papua New Guinea. Continuous sampling throughout 12 months produced 61,777 individuals and 491 species. Two seasonality parameters, circular statistics and Lloyd's index, were calculated for 139 species with a sample size of more than 36 individuals. Most of the species were present in the adult stage for at least half of the year, and many of them continuously throughout the year. However, almost all species exhibited marked seasonal changes in abundance. The abundance peaks of species were scattered throughout most of the year, but more species reached their population maximum during the wet, especially early wet, season than during the dry season. Overall species richness and abundance of Auchenorrhyncha were also higher during the wet than the dry season. A significant correlation between seasonality and host specificity was revealed in the auchenorrhynchan community. In particular, species evenly distributed throughout the year had a tendency to feed on a larger number of *Ficus* species than seasonally more restricted species. The seasonality, and the seasonality versus specificity correlation, were independent of species abundance. Among the most abundant species ($n > 300$) there was a marginally significant negative correlation between abundance and host specificity, so that polyphagous species had, on average, larger populations than specialists. There was no similar correlation among rarer species. The Auchenorrhyncha comprises three feeding

guilds, which were also analysed separately. The mesophyll-feeding guild exhibited more pronounced seasonality than the phloem- and xylem-feeders. This difference could be explained as a part of the overall correlation between seasonality and host specificity as mesophyll-feeders were significantly more host specific than the other two guilds.

Key words Herbivores · Host specificity · Insect abundance · Phenology · Species diversity

Introduction

Herbivorous insects in rain forests display almost all conceivable patterns of seasonal change in abundance and activity (Wolda 1988). Various types of seasonality, displayed by species in the same ecosystem, probably result from specific life history traits. Among such traits, host plant range may be a particularly important one since (1) the phenology of host plants, especially their production of new leaves, is an important factor in the population dynamics of herbivorous insects (Scriber and Slansky 1981; Wolda 1982; Coley and Aide 1991; Aide 1993; Coley and Barone 1996), and (2) rainforest trees display a wide variety of seasonal patterns in leaf, flower and seed production (van Schaik et al. 1993; Reich 1995). Thus, a reasonable expectation may be that herbivores able to feed on a wide range of locally available plant species will be facing less constraints on their distribution throughout the year than monophagous species. As a result, species with a wide range of host plants will exhibit low seasonality. Host specificity limits the amount of resources available in any particular ecosystem, while seasonality limits the length of time that available resources can be used. Other things being equal, polyphagous and non-seasonal species are likely to attain the highest population size in herbivore communities since the largest amount of resources is available to them.

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Quantitative descriptions of community-wide patterns of insect seasonality in rain forests are few, probably because they require a continuous, at least year-long, monitoring of many, usually hundreds, of species (e.g. Wolda 1980, 1982; Wolda and Broadhead 1985; Barlow and Woiwod 1990; Basset 1991; Janzen 1992). Sampling devices most suitable to accomplish such task are continuously operated traps which monitor the activity of insects, such as light, pitfall or Malaise traps (Basset et al. 1997a). Indeed, most seasonality studies targeting tropical insect communities are based on samples obtained by such traps, often light traps. Unfortunately, data provided by these methods cannot be used for interspecific comparisons of abundance since various species may respond differently to traps, and they do not provide information on the spatial distribution or host plant preferences of insects. In contrast to studies on temperate insects, these shortcomings cannot be rectified by using additional information because most of the species are not even formally described (e.g. Hodkinson and Casson 1991).

In the present study, the relationships between insect seasonality, host specificity and abundance are explored in the community of sap-sucking insects (Auchenorrhyncha) feeding on 15 species of *Ficus* in a lowland rain forest in Papua New Guinea. This analysis, probably the first to examine the relationships between seasonality and host specificity in a tropical insect community, was made possible by large-scale hand collecting of live insects from the foliage of trees, which simultaneously provided information on insect seasonality, abundance and host specificity.

Materials and methods

Study area and insect collecting

The study area was situated in the lowlands of the Madang Province in Papua New Guinea, extending from the coast to the slopes of the Adelbert Mountains and bounded by the Gogol and Sempri Rivers. This area encompasses about 434 km² of primary and secondary rain forests, 21 km² of coastal habitats and some developed areas. Field work was concentrated in primary and secondary lowland forests near the villages of Baitabag, Ohu and Mis, and in a coastal area near Riwo village (145°41'–8'E, 5°08'–14'S, ca. 0–200 m). These four sampling sites were from 3 to 25 km distant from each other. General descriptions of a forest similar to these sites is given by Bowman et al. (1990).

Climatic data relevant to the study area are available for Madang (1956–1970; McAlpine et al. 1983). Most of the climatic parameters vary little throughout the year. Monthly means range from 26.2 to 26.7°C for temperature, from 85 to 89% for humidity, and from 126 to 168 mm for evaporation. Rainfall is more seasonal, with a relatively dry season from June to September. The average annual rainfall is 3,588 mm. During the study year, the annual rainfall was 3,766 mm, i.e. close to the long-term average (Fig. 1).

Fifteen species of *Ficus* trees (Appendix 1), all locally abundant and easy to recognise in the field, were selected for the study. These species included trees of various architectures and growing in different habitats, i.e. primary and secondary forest, regrowth in abandoned gardens, and coastal vegetation (see Basset et al. 1997b for further details on their ecology).

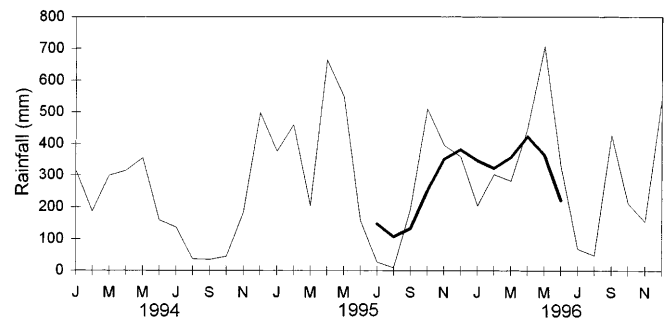


Fig. 1 Rainfall in the study area (Christensen Research Institute, Jais Aben, Madang) from January 1994 to December 1996 (thin line). The long-term monthly average in Madang (20 km south of Jais Aben, thick line) is plotted for comparison with the study period of July 1995–June 1996

All species of Auchenorrhyncha were the subject of this study. This group is one of the four lineages in Hemiptera, although recent analyses indicate that it may be a paraphyletic taxon (Sorensen et al. 1995). All species of Auchenorrhyncha are sap-sucking herbivores, members of one of the following three guilds (see Novotny and Wilson 1997 for details): (1) xylem-feeding: Cercopoidea, Cicadoidea, Cicadellidae: Cicadellini (sensu Hamilton 1983; Cicadellinae sensu Young 1968) and Mileewini (their position is unclear; they were treated as xylem-feeders, based on the present field observations); (2) mesophyll-cell-feeding: Cicadellidae: Typhlocybinae; (3) phloem-feeding: the remaining Auchenorrhyncha (note that the present study does not concern Sternorrhyncha, which form another important part of the phloem-feeding guild).

All species of Auchenorrhyncha were sampled from the foliage, individually by hand or with an aspirator. Only adults were sampled and analysed. Most trees could be sampled from the ground or easily climbed; access to larger trees was gained using the single-rope technique (Perry 1978). Insects were collected by five collecting teams with, usually, three people per team. Collecting effort was recorded as the time spent looking at the foliage of each of the *Ficus* species studied, which was approximately proportional to the leaf area examined. Sampling effort was kept identical for each species of *Ficus*. Samples from all 15 *Ficus* species and all four sampling sites were pooled and analysed together. The total sampling effort amounted to 316 h spent searching foliage for insects and to 4,573 tree inspections (i.e. a particular tree sampled at a particular time). The sampling was semi-continuous, carried out on 182 sampling days scattered throughout 1 year, from 1 July 1995 to 30 June 1996. For the analysis of seasonality, this sampling period was partitioned into 36 10-day sampling units. Monthly sampling effort varied from 17.5 to 37.8 h.

All insects were assigned to morphospecies. Diagnosis of morphospecies was based on external morphology as well as morphology of male genitalia, with few exceptions where only females were available. In critical groups, which included most of the Typhlocybinae as well as several species complexes in other taxa, all specimens were routinely dissected and morphotyped using characters on genitalia. The status of many species was later verified by specialists.

Data analysis

The seasonality of each species was quantified as the variance of its distribution among 36 10-day periods, which were the basic time units in the analysis. Lloyd's index

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

where S_x^2 and \bar{X} are variance and mean of the sample, respectively, was used as the seasonality parameter (SE1). This index is con-

sidered to be the best way to standardise variance with respect to the mean (Lepš 1993; see also McArdle and Gaston 1995). The SE1 value is minimum for an equitable distribution and increases with increasing unevenness; species characterised by low/high SE1 are reported as those with low/high seasonality. One serious drawback of the SE1 statistic is that it only characterises variance and does not incorporate any information on the temporal sequence of individual sampling periods. Consequently, erratic short-term changes in abundance cannot be distinguished from more persistent, and more interesting, seasonal trends. To redress this problem, another index, the circular statistic (Batschelet 1981), was used to study the changes in abundance over time. The abundance of a species in each sampling period was expressed as a vector. Its length was proportional to the species' abundance and its angle was $(p/36) \times 360$ degrees, where p was the serial number of the sampling period (1, 2, ..., 36). The seasonality is given by the length of the mean vector (SE2), resulting from the addition of the 36 vectors, characterising sampling periods. The seasonal optimum is given by the angle of the mean vector, transformed back to the weeks of the year (cf. Wolda and Chandler 1996). One serious drawback of the SE2 statistic is that it can underestimate the seasonality for species having more than one seasonal maximum as the opposite vectors (e.g., those for the sampling periods no. 1 and 19, i.e. with the angles 10° and 190°) cancel each other out. Since both the SE1 and SE2 indices have disadvantages, it is prudent to use them simultaneously.

Seasonal distribution was also measured by two parameters introduced by Wolda (1979), season length (SL) and the seasonal maximum (SM). The season length is 1 year minus the longest stretch of 10-day sampling periods in which the species was not observed. The seasonal maximum is the number of individuals found in the three consecutive 10-day sampling periods with maximum abundance, divided by the average number of individuals per 30 days for the whole year. The seasonal maximum thus ranges from 1 (constant abundance throughout the year) to 12.2 (all individuals concentrated within a single 30-day period).

Host specificity was estimated as the variance of the species' distribution among 15 species of *Ficus*, quantified again by Lloyd's index (SP).

It was not possible to keep sampling effort exactly the same for all 36 sampling periods. When comparing composite community characteristics, such as density or species richness, the data were always standardised to identical sampling effort. The number of species was standardised to a common sample size by rarefaction (Hurlbert 1971). Uneven sampling effort was ignored in the analyses of relative differences between species (e.g. in their SE1 or SE2 values) since all species were likely to be influenced in a similar way.

Many species were too rare to derive any sensible estimates of their seasonality or host specificity. Since seasonality was measured as the distribution of species among 36 sampling periods, all species collected as less than 36 specimens were excluded from all analyses. In some analyses, the more restrictive minimum sample of $N \geq 120$ (ten specimens per month) was applied. The species abundance (N), seasonality (SE1) and host specificity (SP) had very skewed distributions which were normalised by double \log_e transformation. The hypothesis of normal distribution could not be rejected for the original SE2 and the transformed SE1, SP and N data ($P > 0.05$, Kolmogorov-Smirnov test with the Lilliefors' correction). The relationships between seasonality, host specificity and abundance were explored by locally weighted regression scatter plot smoothing (LOWESS; the tension 0.65 was used; Cleveland 1979) which, unlike the standard regression, can be used to explore non-linear trends in the data. Pearson's (multiple) correlation (r) and ANOVA were also used.

Results

Altogether 61,777 individuals and 491 species, representing 20 auchenorrhynchan families were collected from the 15 *Ficus* species during 1 year (Appendix 2).

Many species of Auchenorrhyncha were rare in the samples: 109 species were represented by only a single individual, while only 139 species had sample size $N \geq 36$ individuals, and 79 species $N \geq 120$ individuals.

The number of sampling periods in which each species was recorded was strongly correlated with its abundance ($r = 0.758$, $P < 0.001$, $n = 139$). Most species were present during more than half of the year; the median length of species' presence was 23 sampling periods (i.e. about $7\frac{1}{2}$ months). Almost all abundant species were present for most of the year. For instance, the median for the 79 species with sample size $N \geq 120$ was 29 sampling periods (i.e. about $9\frac{1}{2}$ months; Fig. 2). Among these most abundant species, 62 had $SL > 30$, which means that the longest period of time they were absent was $1\frac{1}{2}$ months or less. Despite their almost continuous presence, most of the species varied greatly in abundance over the course of the year. The population dynamics of most species were characterised by a single peak of abundance. Among the 79 species with $N \geq 120$, only 4 species were distributed so evenly round the year to have $SM < 2$, while 18 species had $SM > 5$ (Fig. 3).

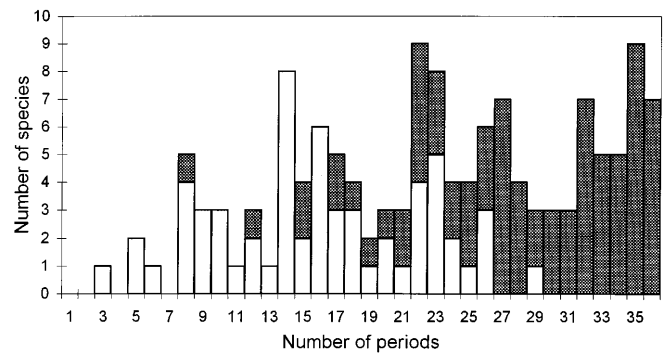


Fig. 2 Number of 10-day periods during which a species was recorded in the adult stage (open bars species with sample size $36 \leq N < 120$; cross-hatched bars species with $N \geq 120$)

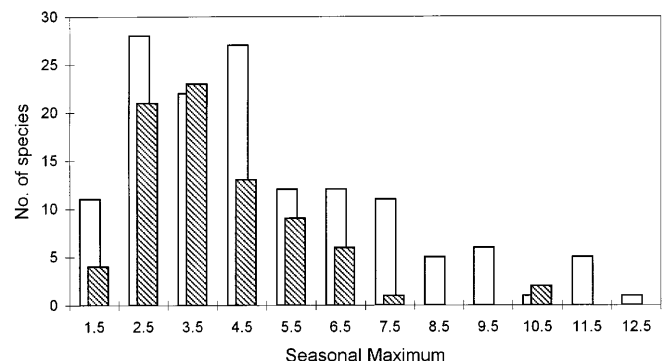


Fig. 3 Distribution of the seasonal maximum values for Auchenorrhyncha on *Ficus* (hatched bars) and in a lowland rainforest in Panama (open bars; data from Wolda 1982). Only species with total sample $N \geq 120$ are analysed

The total abundance and species richness of Auchenorrhyncha also exhibited considerable variability during the year. The dry season was characterised by lower numbers of individuals and species than the wet season (Fig. 4). Most of the species had their peak abundance (Fig. 5A) as well as their overall abundance (characterised by the mean vector; Fig. 5B) concentrated in the wet season, while many, even those otherwise abundant, species were absent during the dry season (Fig. 5A).

The two seasonality indices, SE1 and SE2, were significantly, but not very tightly, correlated with each other ($r = 0.642$, $P < 0.001$, $n = 139$). There was no significant correlation between the seasonality (SE1, SE2) and sample size ($r = -0.117$ for SE1 and $r = -0.099$ for SE2; $P > 0.1$, $n = 139$). Their LOWESS regressions on sample size were also not significant.

The overall correlation between the host specificity (SP) and abundance (N) was not significant ($r = -0.158$, $P = 0.062$, $n = 139$). However, the LOWESS regression showed a negative correlation between host specificity and abundance, limited to the most abundant species ($N > 300$). The fitted LOWESS model (Fig. 6) was statistically significant ($P = 0.044$, effective $df = 1.55$, analysis of deviance performed in the S+ statistical package).

There was a significant correlation between seasonality (SE1, SE2) and host specificity (SP), even after the effect of sample size had been removed using N as a covariable ($r = 0.538$ for SE1 and $r = 0.321$ for SE2,

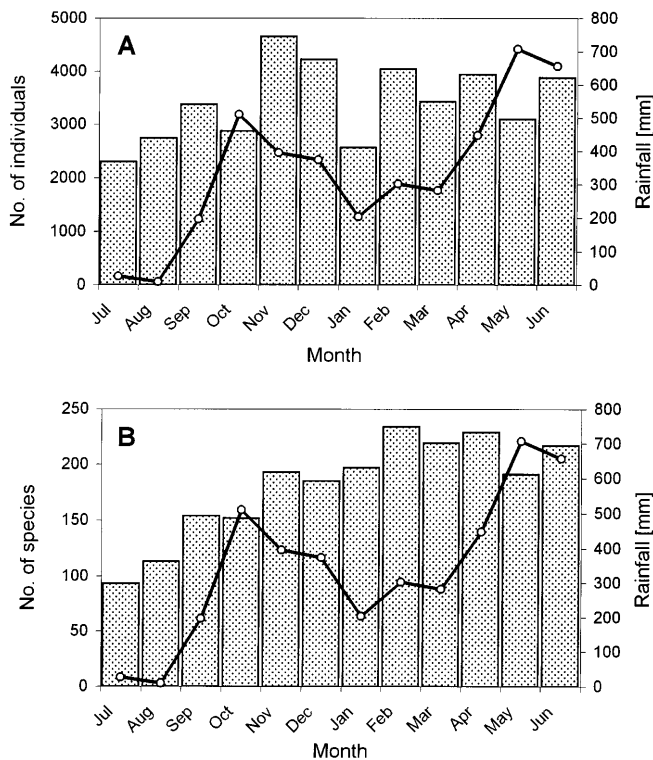


Fig. 4 Number of individuals (A) and species (B) of Auchenorrhyncha collected monthly during the study period (line rainfall data)

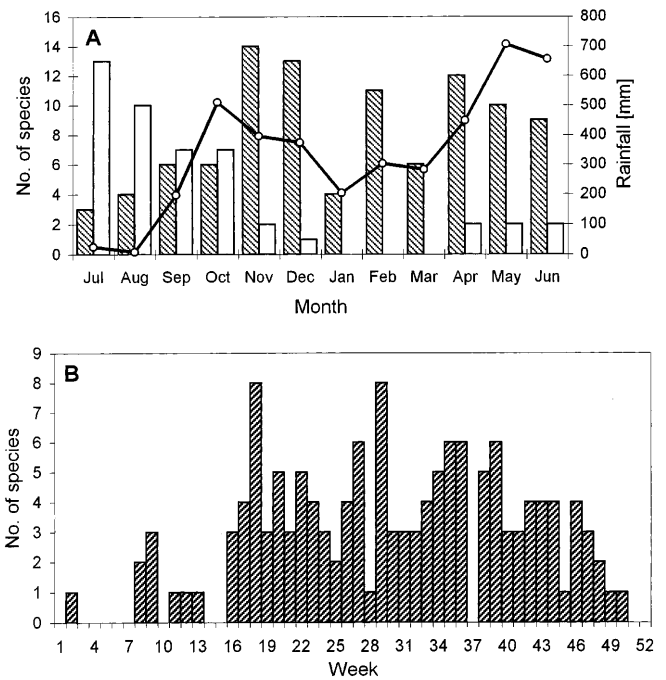


Fig. 5 Number of species reaching an abundance peak (hatched bars) and number of species absent (open bars) during each month (A) and with their mean vector pointing to each week (weeks numbered from the first week in July 1996, i.e. the start of the study) (B). Only species with total $N \geq 120$ included in A. Peak abundance and mean vector are defined in Materials and methods (line rainfall data)

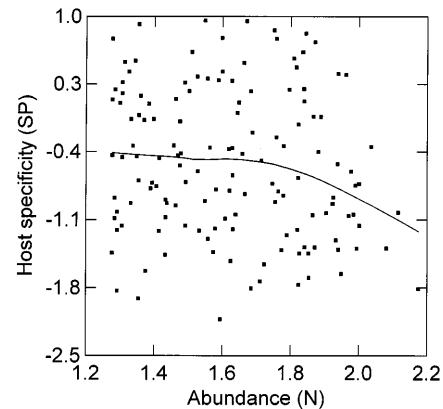


Fig. 6 Relationship between the abundance (N) and the host specificity (SP) for auchenorrhynchan species. Both axes are double log_e transformed; the LOWESS regression is fitted to the data

$P < 0.001$, $n = 139$). This correlation was found throughout the whole range of both variables (Fig. 7).

Species in the mesophyll-feeding guild showed a significantly higher seasonality (SE1, but not SE2) than the phloem- and xylem-feeders. This difference could be explained entirely as a result of the higher host specificity of the mesophyll-feeders (Table 1) and the overall correlation between host specificity and seasonality. No difference in seasonality (SE1) between the guilds was detected when host specificity (SP) was used as a covariable (ANOVA, $P > 0.4$).

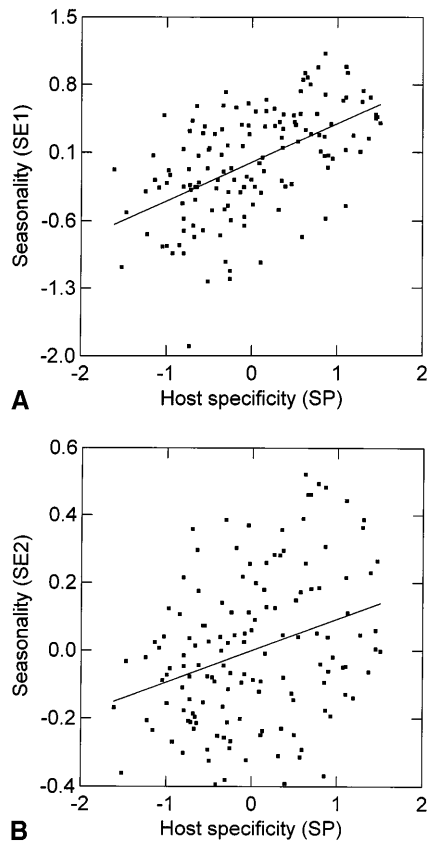


Fig. 7 Relationship between host specificity (SP) and seasonality (SE1, **A**; SE2, **B**) of Auchenorrhyncha on *Ficus*. Residuals after regression on the number of specimens collected are shown

Table 1 Seasonality, host specificity and abundance of species from various feeding guilds: SE1, SE2 seasonality indices, SP host specificity index, N number of specimens per species [mean calculated from the original (SE2) and normalised (SE1, SP and N) data is given for each guild], n number of species analysed. Values significantly different from the other two guilds are italicised ($P < 0.05$, ANOVA, Tukey multiple comparisons)

Guild	SE1	SE2	SP	N	n
Mesophyll	4.9	0.56	3.9	157.6	23
Phloem	2.6	0.46	1.6	137.2	92
Xylem	2.7	0.43	1.7	305.3	24

Discussion

Sample size and sampling artefacts

The sampling intensity was relatively high (61,777 specimens per year) and concentrated on a small and well-defined subset of rainforest habitats, the foliage of 15 species of *Ficus*. Still, 22% of the species in the samples were represented by a single individual and only 86 species (18%) by more than 100 individuals. Although the proportion of singletons was lower than in most studies of arboreal insects in the tropics (e.g. Morse et al. 1988; Basset and Kitching 1991; Novotny 1993;

Robinson and Tuck 1996; Allison et al. 1997; most studies detailed in Stork et al. 1997), rare species still represented an important part of the community. Two even more extensive samples of the tropical Auchenorrhyncha, obtained by light trapping, exhibited similar patterns: despite the sample size of 87,547 and 89,039 individuals, 23% and 20% of species were singletons, and only 9% and 20% of species were collected as $N > 100$ individuals (Wolda 1982 and 1980, respectively). With such abundance patterns, it is difficult to define the boundaries of the community considered. In the absence of feeding experiments and field observations, it is difficult to decide which of the rare species are only transient (tourists) and which feed on a given host tree (Basset and Samuelson 1996). A purely pragmatic approach was adopted here: all species with sufficient sample size were included in the “community” analysis. The resultant inclusion of common transient species and the exclusion of rare genuine members of the community could not be avoided. Further, transient species may bias host specificity estimates. The SP index, based on quantitative distribution data, is less sensitive to such bias than estimates based merely on the presence or absence of the herbivore species on each of the plant species studied.

In quantitative descriptions of the distribution of individuals among sampling periods or host plants, genuine effects of species abundance on seasonality and host specificity must be carefully disentangled from the statistical effects of sample size on the SE1 and SP indices. All estimates of variance in the species’ distribution, both spatial (e.g. among the host plants) and temporal (seasonality), are sensitive to sample size (Wolda 1979; Lepš 1993; Gaston and McArdle 1994). There is thus always a possibility of spurious correlation of the seasonality and host specificity indices with the species’ abundance. The only remedy to this problem is the exclusion of inadequately sampled species from the analyses. This step necessitates a substantial sampling effort in order to obtain representative data for rare species. Any restriction of a community analysis to only the most abundant species is highly undesirable since such analysis would concern only patterns peculiar to these species, rather than those typical of the whole community. In this study, species found as $N < 36$ individuals were excluded from all analyses using the seasonality (SE1, SE2) and host specificity (SP) indices. This threshold was sufficient to remove a positive correlation between the N and the SE1, SE2 and SP values for small sample sizes, where such correlation is always suspect. The analysis was therefore limited to only 139, i.e. 29% of species. The same approach was used e.g. by Spitzer and Lepš (1988) in the analysis of temporal variability of insect populations (with an $N \geq 5$ threshold). The negative correlation between sample size (N) and host specificity, detected in the present data among the most abundant species, is unlikely to be a statistical artefact since the correlation concerns only high values of N .

The monthly samples had to be adjusted a posteriori to equal sample size by rarefaction. This algorithm is based on the assumption that each individual is collected independently of the others so that the opposite process, i.e. the reduction of the sample size, can proceed by random resampling of the original sample (Hurlbert 1971). The aggregated distribution of insects on *Ficus* trees (V. Novotny and Y. Basset, in preparation) violated this assumption so that the rarefaction probably overestimated the number of species. However, it is unlikely that this resulted in important bias because the adjustments of sample sizes were relatively small (the largest sample was twice the size of the smallest one).

In all analyses, species are treated as independent data points. Such an approach implies that the species traits analysed do not have any phylogenetic component, which is an unrealistic assumption (Harvey and Pagel 1991). Consequently, the correlation between host specificity and seasonality, found in the present study, cannot be interpreted as a tendency for these two traits to evolve in concert. However, the analysis is still valid as the means of description of existing community patterns.

Patterns of seasonality

The overall seasonality is distinctly lower in tropical than in temperate ecosystems and most of the tropical species are present during most of the year. In five communities studied in Panama by Wolda (1983), the proportion of species present year-round ranged from 37 to 73%. This is consistent with the present results, showing a prevalence of species constantly present among the abundant, i.e. well-sampled, species (cf. also Flint and Masteller 1993). Almost constant presence of adults in many species indicates that these species may have overlapping generations. No data are, however, available on the voltinism of Auchenorrhyncha species from *Ficus* trees, as data on their larvae were not collected. Seasonally restricted occurrence of even the most abundant species, for example as reported by Casson and Hodkinson (1991) for a hemipteran rain forest community from Sulawesi, may be an artefact caused by small sample size.

Despite a low average seasonality, the seasonal patterns of tropical insects are very diverse, ranging from very synchronised, short-term appearances to year-round presence. Previous studies (reviewed by Wolda 1988) indicate that almost all insect species in the tropics exhibit large seasonal changes in their abundance and often have one or more clear-cut peaks in abundance. Wolda (1988) reports only 7.5% of species as non-seasonal in the Homoptera from Panama, while in the present data, only 5% of species can be classified as non-seasonal (defined as species with $SM < 2$). Rain forest insects attain their peak abundance most often in the wet season (e.g., Wolda 1980), as was found in the present study. This tendency is reflected also by maximum spe-

cies richness reported for insect communities during the wet season. In Panama, this was the case for Auchenorrhyncha (Wolda 1980, 1982) psocids (Broadhead 1983) and the herbivores collected from *Luehea seemannii* trees (Erwin and Scott 1980). The peak in species richness is often accompanied by a peak in insect biomass (Erwin and Scott 1980; Smythe 1982; Broadhead 1983; Kato et al. 1995).

Not surprisingly, rainfall seasonality can have a marked effect on the seasonality of insect communities. For instance, the lowland rain forest on Barro Colorado Island (Panama) has a more severe dry season than the area of the present study (cf. Fig. 1 in Wolda 1982 and in this study), and this difference is paralleled by the more seasonal auchenorrhynchan community in Panama than in Papua New Guinea, as indicated by comparison of the SM values from Wolda's (1982, Fig. 7) data with those in Fig. 3 (median is in the 3.0–3.9 range for *Ficus* and in the 4.0–4.9 range for Panama; difference between the medians is significant, $P = 0.011$, Mann-Whitney test). A similar correlation between climate and the seasonality of insect communities was found elsewhere in the tropics (e.g., Barlow and Woiwod 1990; Wolda and Broadhead 1985; Wolda and Chandler 1996; Yule and Pearson 1996; cf. Basset 1991 for a subtropical community). The question of which environmental factors serve as environmental cues driving population dynamics of insects is out of the scope of this study since seasonality data from more than 1 year and/or controlled experiments would be needed for such an analysis (cf. Wolda 1989; Wolda and Wright 1992).

Life history correlates of seasonality

The correlation between seasonality and host specificity in the present study was highly significant for both the seasonality characteristics, SE1 and SE2. This congruence is not trivial since, as discussed above, each of the indices captures a different aspect of seasonality, which is also reflected by their rather low mutual correlation. Therefore, it can be safely concluded that species feeding on many *Ficus* hosts are distributed less seasonally than the more specialised species. This relationship can be readily interpreted in terms of the resource base, especially young foliage, available to them throughout the year. Young leaves are a high-quality, rare and short-lived resource for herbivores (Aide 1993; Coley and Aide 1991; Scriber and Slansky 1981). Sap-sucking insects often prefer young foliage because growth means increased translocation of nutrients via phloem and, to some extent, xylem vessels (Press and Whittaker 1993; Raven 1983). Most tropical woody plants as well as the whole forest communities display seasonal variation in the presence of new leaves (Opler et al. 1980; van Schaik et al. 1993) so it is probably safe to assume that a wider host plant range enables the exploitation of subsequent flushes of new foliage on different host plants and, consequently, a non-seasonal population dynamics.

The 15 species of *Ficus* studied here differ from one another in the timing of the production of new leaves (personal observation; cf. Spencer et al. 1996). Further, the expansion of new leaves, together with the abundance of host trees, i.e. traits relevant to the resource base, were shown to be important determinants of the species richness in the auchenorrhynchan communities supported by the 15 species of *Ficus* (V. Novotny and Y. Basset, in preparation). Therefore, a direct functional relationship may connect low seasonality and host specificity in *Ficus* herbivores. The positive correlation between seasonality and host specificity is also important methodologically as it can produce a sampling bias against specialists, especially in snapshot samples taken from insect communities.

The species of *Ficus*, unlike most other rainforest trees, do not have their reproduction cycles synchronised within populations (Janzen 1979; Milton et al. 1982) so that at any time of the year, a certain proportion of trees is producing flowers and fruits. The translocation of nutrients via phloem, preceding flower and fruit formation, may create similar periods of high host plant quality for sap-sucking insects to that accompanying the growth of new leaves (Waloff 1980; Mattson 1980). However, it is not clear whether these dynamics of reproduction, peculiar to *Ficus*, have any effect on the seasonality of their herbivores.

Differences in host specificity among the three feeding guilds, represented in the Auchenorrhyncha, have been noted previously (Novotny and Wilson 1997) and were also documented for the *Ficus* fauna studied here (V. Novotny and Y. Basset, in preparation). Xylem-feeders tend to be polyphagous (Press and Whittaker 1993), while phloem-, and especially cell-feeding species are usually more host specific (Claridge and Wilson 1981; Cobben 1988; Wood 1993; Wilson et al. 1994). Nothing is known about general differences among these guilds in their seasonality, but the present study indicates that the high seasonality discovered in the mesophyll-feeding guild does not require any special explanation, being the result of the general relationships between host specificity and seasonality found across the whole auchenorrhynchan community. On a wider scale, Basset (1991) found differences in seasonality among various insect guilds on a subtropical tree; fungal-feeders and epiphyte-grazers exhibited lower seasonality than leaf-chewers and sap-suckers.

The negative correlation between host specificity and abundance, detected among the most abundant species, was rather weak. However, its direction conforms with the theoretical expectation that by being able to utilise more than one host plant at a time, polyphagous species have a large resource base which could support higher population densities.

Information on other life history correlates of seasonality in tropical insects is very scarce. Wolda (1982) found that the species with more pronounced seasonality changed more in abundance from year to year. Their distribution throughout the year may buffer short-term

variability in resources, leading to lower year-to-year variance. This mechanism is analogous to that proposed for polyphagous species, which can buffer changes in host plant quality by switching to other host species and are therefore expected to exhibit low between-year variability in their abundance (MacArthur 1955; cf. Redfearn and Pimm 1988).

In summary, various seasonality characteristics, estimated for the Auchenorrhyncha on *Ficus* trees, are in general concordance with those already reported for other rainforest insects (Wolda 1988). Detailed information on life histories of constituent species is needed if the observed patterns are to be explained. The present study is only a small step in this direction and its results, such as the correlation of seasonality with host specificity, await further testing.

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Appendix 1 Species of *Ficus* studied (identifications by C.C. Berg)

F. bernaysii King, *F. botryocarpa* Miq., *F. conocephalifolia* Ridley, *F. copiosa* Steud., *F. dammaropsis* Diels, *F. hispidoides* S. Moore, *F. microcarpa* L., *F. nodosa* Teysm. & Binn., *F. phaeosyce* Laut. & K. Schum., *F. pungens* Reinw. ex Bl., *F. septica* Burm., *F. tinctoria* Forst., *F. trachypison* K. Schum., *F. variegata* Bl., *F. wassa* Roxb.

Appendix 2 The number of specimens/species from various families of Auchenorrhyncha collected on the foliage of *Ficus* spp.

Achilidae (52/11); Aphrophoridae (10,692/17); Cercopidae (621/9); Cicadellidae (18,753/188); Cicadidae (165/11); Cixiidae (122/13); Delphacidae (873/21); Derbidae (9,066/119); Dictyopharidae (967/3); Flatidae (7,166/24); Fulgoridae (383/5); Issidae (3,226/14); Kinnaridae (1/1); Lophopidae (2,149/5); Machaerotidae (3/1); Meenoplidae (170/5); Membracidae (574/13); Nogodinidae (225/3); Ricaniidae (6,045/20); Tropiduchidae (520/8).

References

- Aide TM (1993) Patterns of leaf development and herbivory in a tropical understorey community. *Ecology* 74: 455–466
- Allison A, Samuelson GA, Miller SE (1997) Patterns of beetle species diversity in *Castanopsis acuminatissima* trees studied with canopy fogging in mid-montane New Guinea rain forest. In: Stork NE, Adis JA, Didham RK (eds) *Canopy arthropods*. Chapman & Hall, London, pp 222–234
- Barlow HS, Woiwod IP (1990) Seasonality and diversity of Macrolepidoptera in two lowland sites in the Dumoga-Bone National Park, Sulawesi Utara. In: Knight WJ, Holloway JD (eds) *Insects and the rain forests of South East Asia* (Wallacea). Royal Entomological Society of London, London, pp 167–172
- Basset Y (1991) The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecol Entomol* 16: 265–278
- Basset Y, Kitching RL (1991) Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecol Entomol* 16: 391–402
- Basset Y, Samuelson GA (1996) Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. In: Jolivet P, Cox ML, Hsiao TH (eds) *Chrysomelidae biology*, vol 2. Ecological studies. SPB, Amsterdam, pp 243–262
- Basset Y, Aberlenc H-P, Springate ND, Delvare G (1997a) A review of methods for collecting arthropods in tree canopies. In: Stork NE, Adis JA, Didham RK (eds) *Canopy arthropods*. Chapman & Hall, London, pp 27–52
- Basset Y, Novotny V, Weiblen G (1997b) *Ficus*: a resource for arthropods in the tropics, with particular reference to New Guinea. In: Watt A, Stork NE, Hunter M (eds) *Forests and insects*. Chapman & Hall, London, pp 341–361
- Batschelet E (1981) *Circular statistics in biology*. Academic Press, London
- Bowman DMJS, Woinarski JCZ, Sands DPA, Wells A, McShane VJ (1990) Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: the response of birds, butterflies and reptiles. *J Biogeogr* 17: 227–239
- Broadhead E (1983) The assessment of faunal diversity and guild size in tropical forests with particular reference to Psocoptera. In: Sutton SL, Whitmore TC, Chadwick AC (eds) *Tropical rain forest: ecology and management*. Oxford, Blackwell, pp 107–120
- Casson DS, Hodkinson ID (1991) The Hemiptera (Insecta) communities of tropical rain forest in Sulawesi. *Zool J Linn Soc* 102: 253–275
- Claridge MF, Wilson MR (1981) Host plant associations, diversity and species-area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain. *Ecol Entomol* 6: 217–238
- Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. *J Am Stat Assoc* 74: 829–836
- Cobben RH (1988) What do we really know about host selection in Auchenorrhyncha? In: Vidano C, Arzone A (eds) *Proceedings of the 6th Auchenorrhyncha meeting*, Turin, 7–11 September 1987. IPRA, Turin, pp 81–92
- Coley PD, Aide TM (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, London, pp 25–49
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst* 27: 305–335
- Erwin TL, Scott JC (1980) Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. *Coleopter Bull* 34: 305–322
- Flint OS, Masteller EC (1993) Emergence composition and phenology of Trichoptera from a tropical rain-forest stream at El-Verde, Puerto-Rico. *J Kans Entomol Soc* 66: 140–150
- Gaston KJ, McArdle BH (1994) The temporal variability of animal abundances: measures, methods and patterns. *Phil Trans R Soc Lond B* 345: 335–358
- Hamilton KGA (1983) Classification, morphology and phylogeny of the family Cicadellidae (Rhynchotha: Homoptera). In: Knight WJ, Pant NC, Robertson TS, Wilson MR (eds) *1st international workshop on leafhoppers and planthoppers of economic importance*. CAB, London, pp 15–37
- Harvey PM, Pagel MD (1991) *The comparative method in evolutionary biology*. Oxford University Press, New York
- Hodkinson ID, Casson D (1991) A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biol J Linn Soc* 43: 101–109
- Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–586
- Janzen DH (1979) How to be a fig. *Annu Rev Ecol Syst* 10: 13–51
- Janzen DH (1992) Caterpillar seasonality in a Costa Rican dry forest. In: Stamp NE, Casey TM (eds) *Ecological and evolutionary constraints on caterpillars*. Chapman & Hall, London, pp 448–477
- Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T (1995) Seasonality and vertical structure of light-attracted insect communities in a Dipterocarp forest in Sarawak. *Res Popul Ecol* 37: 59–79
- Lepš J (1993) Taylor's power law and measuring variation in the size of populations in space and time. *Oikos* 68: 349–356
- MacArthur RH (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533–536
- Mattson WJ (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11: 119–161
- McAlpine JR, Keig G, Falls R (1983) *Climate of Papua New Guinea*. CSIRO and Australian National University Press, Canberra
- McArdle BH, Gaston KJ (1995) The temporal variability of densities: back to basics. *Oikos* 74: 165–171
- Milton K, Windsor DM, Estrubi M (1982) Fruiting phenologies of two neotropical *Ficus* species. *Ecology* 63: 752–762
- Morse DR, Stork NE, Lawton JH (1988) Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecol Entomol* 13: 25–37
- Novotny V (1993) Spatial and temporal components of species diversity in Auchenorrhyncha (Insecta: Hemiptera) communities of Indochinese montane rain forest. *J Trop Ecol* 9: 93–100
- Novotny V, Wilson MR (1997) Why are there no small species among xylem sucking insects? *Evol Ecol* 11: 419–437
- Opler PA, Frankie GW, Baker HG (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowland of Costa Rica. *J Ecol* 68: 167–188
- Perry DR (1978) A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155–157
- Press MC, Whittaker JB (1993) Exploitation of the xylem stream by parasitic organisms. *Phil Trans R Soc Lond B* 341: 101–111
- Raven JA (1983) Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Adv Ecol Res* 13: 135–234
- Redfearn A, Pimm SL (1988) Population variability and polyphagy in herbivorous insect communities. *Ecol Monogr* 58: 39–55
- Reich PB (1995) Phenology of tropical forests: patterns, causes, and consequences. *Can J Bot* 73: 164–174
- Robinson GS, Tuck KR (1996) Describing and comparing high invertebrate diversity in tropical forest – a case study of small moths in Borneo. In: Edwards DS, Booth WE, Choy SC (eds) *Tropical rainforest research – current issues*. Kluwer, Dordrecht, pp 29–42
- Schaik CP van, Terborgh JW, Wright JS (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu Rev Ecol Syst* 24: 353–377
- Scriber JM, Slansky F Jr (1981) The nutritional ecology of immature insects. *Annu Rev Entomol* 26: 183–211

- Smythe N (1982) The seasonal abundance of night-flying insects in a Neotropical forest. In: Leigh EG Jr, Rand AS, Windsor DM (eds) *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington, Smithsonian Institution Press, pp 309–318
- Sorensen JT, Campbell BC, Gill RJ, Steffen-Campbell JD (1995) Non-monophyly of Auchenorrhyncha (“Homoptera”), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropteroidea Hemiptera (s.l.) and a proposal for new monophyletic suborders. *Pan Pac Entomol* 71: 31–60
- Spencer H, Weiblen G, Flick B (1996) Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia. *J Biogeogr* 23: 467–475
- Spitzer K, Lepš J (1988) Determinants of temporal variation in moth abundance. *Oikos* 53: 31–36
- Stork NE, Adis JA, Didham RK (eds) (1997) *Canopy arthropods*. Chapman & Hall, London
- Waloff N (1980) Studies on grassland leafhoppers (Auchenorrhyncha, Homoptera) and their natural enemies. *Adv Ecol Res* 11: 81–215
- Wilson SW, Mitter C, Denno RF, Wilson MR (1994) Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. In Denno RH, Perfect TJ (eds) *Planthoppers: their ecology and management*. Chapman and Hall, New York, pp 7–113
- Wolda H (1979) Seasonality parameters for insect populations. *Res Popul Ecol* 20: 247–256
- Wolda H (1980) Seasonality of tropical insects. 1. Leafhoppers (Homoptera) in Las Cumbres, Panama. *J Anim Ecol* 49: 277–290
- Wolda H (1982) Seasonality of leafhoppers (Homoptera) on Barro Colorado Island, Panama. In: Leigh EG Jr, Rand AS, Windsor DM (eds) *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington, Smithsonian Institution Press, pp 319–330
- Wolda H (1983) Spatial and temporal variation in abundance in tropical animals. In: Sutton SL, Whitmore TC, Chadwick AC (eds) *Tropical rain forest: ecology and management*. Blackwell, Oxford, pp 93–105
- Wolda H (1988) Insect seasonality: why? *Annu Rev Ecol Syst* 19: 1–18
- Wolda H (1989) Seasonal cues in tropical organisms. Rainfall? Not necessarily! *Oecologia* 80: 437–442
- Wolda H, Broadhead E (1985) Seasonality of Psocoptera in two tropical forests in Panama. *J Anim Ecol* 54: 519–530
- Wolda H, Chandler DS (1996) Diversity and seasonality of tropical Pselaphidae and Anthicidae (Coleoptera). *Proc K Ned Akad Wet* 99: 313–333
- Wolda H, Wright SJ (1992) Artificial dry season rain and its effects on tropical insect abundance and seasonality. *Proc K Ned Akad Wet* 95: 535–548
- Wood TK (1993) Diversity in the New World Membracidae. *Annu Rev Entomol* 38: 409–435
- Young DA (1968) Taxonomic study of the Cicadellinae (Homoptera: Cicadellinae). Part 1: Proconiini. Smithsonian Institution Press, Washington, DC
- Yule CM, Pearson RG (1996) Aseasonality of benthic invertebrates in a tropical stream on Bougainville Island, Papua-New-Guinea. *Archiv Hydrobiol* 137: 95–117