

Body size and host plant specialization: a relationship from a community of herbivorous insects on *Ficus* from Papua New Guinea

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ABSTRACT. The relationships between body size and host specificity were studied in leaf-chewing and sap-sucking insect communities, including 792 species, feeding locally on 15 species of *Ficus* in a lowland rain forest in Papua New Guinea. A negative correlation between body size and host specificity, i.e., the tendency for large species to feed on numerous *Ficus* hosts and those smaller to have a more restricted host range, was found within both the sap-sucking and the leaf-chewing community. A more detailed analysis, which divided herbivorous species into three sap-sucking and four leaf-chewing guilds, revealed that the correlation between body size and host specificity was caused by differences in these traits between the guilds, while no such correlation was detected within any of the guilds. As the changes in feeding mode, defining various guilds, were unique evolutionary events, it is uncertain whether there is a functional relationship between feeding mode, body size and host specificity, or whether their correlation is only coincidental. It is suggested that, in the sap-sucking community at least, the positive body size versus host specificity correlation is a coincidental by-product of the causal relationship between the feeding mode and both the body size and host specificity. The causes of analogous patterns in a leaf-chewing community require further investigation. Methodological problems in the analysis of tropical insect communities, dominated by rare species, are discussed.

KEY WORDS: Auchenorrhyncha, Coleoptera, herbivorous guilds, leaf-chewers, Lepidoptera, Orthoptera, phloem-feeders, root-feeders, xylem-feeders, wood-borers

INTRODUCTION

Analyses performed on herbivorous insects have suggested, with varying degrees of persuasion, that polyphagy might be associated with large body size

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(Basset 1997, Gaston 1988, Gaston & Lawton 1988, Gaston & Reavey 1989, Lindstrom *et al.* 1994, Loder *et al.* 1998, Wasserman & Mitter 1978), but also concluded that further study was needed to explain any functional basis of this correlation.

The correlation between body size and host plant specialization has been well documented in regional insect faunas, but all such analyses were restricted to Lepidoptera in temperate areas (Gaston & Reavey 1989, Lindstrom *et al.* 1994, Loder *et al.* 1998, Wasserman & Mitter 1978). Within communities, the generality of the body size versus host specificity relationship is far from established, as it has been addressed by only a few studies. A significant relationship was revealed in a noctuid community from Europe (data from Rejmanek & Spitzer 1982, analysed by Gaston 1988) and in one of the two communities of bracken insects studied in Britain by Gaston & Lawton (1988). Basset's (1997) study revealed the same pattern in a tropical, arboreal community of leaf-chewing insects, but in separate analyses of Coleoptera and Lepidoptera the correlation was significant only in the former case.

It appears that there is a tendency for more specialized species to be smaller than polyphages, but that it exists only in certain taxa and communities. The paucity of data makes it difficult to specify the conditions requisite for this relationship, and prevents any explanation of its underlying mechanisms. Recently, Loder *et al.* (1998) tested several hypotheses, using the macrolepidopteran fauna of Britain, but were unable to find unequivocal support for any single explanation.

Broadening the scope of the analysis from the usual Lepidoptera to include more taxa representing diverse guilds, and altering its emphasis to the community patterns may provide further insight into this problem. Tropical communities are particularly suitable for such studies since their high species richness, wide range of body sizes, and the large number of plant resources available to them makes the analysis of any community patterns more sensitive. Following this rationale, the present study explores the body size versus host specificity relationship within various guilds of leaf-chewing and sap-sucking insects and discusses possible explanations of its presence or absence within each of them. It analyses a large (65 000-individual), diverse (792-species) and, taxonomically, broadly defined sample, including externally feeding herbivores from Coleoptera, Lepidoptera, Orthoptera, Phasmatodea, and Hemiptera–Auchenorrhyncha, from the community on 15 species of *Ficus* hosts in a lowland rain forest in New Guinea.

METHODS

Study area and insect sampling

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 Mts

and bounded by Gogol and Sempì rivers. Fieldwork was concentrated in primary and secondary lowland forests near Baitabag, Ohu and Mis villages, and in a coastal area near Riwo village (145°41-8'E, 5°08-14'S, *c.* 0–200 m). The average annual rainfall in the Madang area is 3558 mm, with a moderately dry season from July to September, mean air temperature is 26.5 °C and varies little throughout the year (McAlpine *et al.* 1983).

Among a conservative 48 species of *Ficus*, occurring in the area of the study (G. Weiblen, *pers. comm.*), 15 locally abundant species (*F. bernaysii* King, *F. botryocarpa* Miq., *F. conocephalifolia* Ridley, *F. copiosa* Steud., *F. dammaropsis* Diels, *F. hispidioides* S. Moore, *F. microcarpa* L., *F. nodosa* Tejasm. & Binn., *F. phaeosyce* Lauterb. & K. Schum., *F. pungens* Reinw. ex Bl., *F. septica* Burm. f., *F. tinctoria* G. Forst., *F. trachypison* K. Schum., *F. variegata* Bl., and *F. wassa* Roxb.) were selected for the study of their insect fauna (see Basset *et al.* 1997 for details). All externally feeding leaf-chewing herbivores (Coleoptera, Lepidoptera, Orthoptera and Phasmatodea) and all adults of sap-sucking Hemiptera–Auchenorrhyncha were collected. The insects were sampled from the foliage of the *Ficus* trees individually, by hand or by the use of an aspirator. They were collected during *c.* 500 person-days of fieldwork by five collecting teams with usually three people per team. Insect collecting continued from July 1994 to March 1996 for leaf-chewing insects and from July 1995 to June 1996 for those sap-sucking. Sampling effort was recorded as the time spent searching the foliage of each of the *Ficus* species for insects, which was approximately proportional to the leaf area examined. Sampling effort was identical for all *Ficus* species studied.

In the laboratory, all leaf-chewing insects were provided with fresh foliage of the *Ficus* species they were collected from and kept on it until they fed or died. Only the individuals that fed were considered in the analyses, to exclude transient species from the samples. Caterpillars were reared to adults whenever possible. All sap-sucking insects collected from the foliage were retained in the analyses since there were no simple feeding tests for sap-sucking insects, which could be performed in laboratory conditions on excised leaves.

All insects were assigned to morphospecies on the basis of their external morphology; the morphology of male genitalia was used for some leaf-chewing and all sap-sucking species. In critical groups, which included most of the Typhlocybinæ as well as several species complexes in other taxa, all specimens were routinely dissected and assigned to morphospecies using characters on genitalia. The assignment of morphospecies was later verified by specialist taxonomists and voucher specimens deposited in Bishop Museum, Honolulu.

Definition of guilds

Leaf-chewing insects were classified in the following guilds: (i) species with wood-boring larvae and foliage-feeding adults, which included all species of Cerambycidae and one species of Buprestidae (larval wood-borers thereafter); (ii) species with root-feeding larvae and foliage-feeding adults, which included all species of Curculionidae and most of the Chrysomelidae (larval

root-feeders); (iii) species with larvae feeding on the foliage and adults feeding on various plant resources other than leaves, or not feeding on alive plants, which included all Lepidoptera (larval leaf-chewers); (iv) species with both larvae and adults feeding on leaves, which included all Orthoptera and Phasmatodea and some species of Chrysomelidae, particularly the Galerucinae *Atyssa* and *Sastra* (life-long leaf-chewers). Sampling, as well as subsequent estimates of host specificity and body size, concerned only stages feeding on foliage.

The Auchenorrhyncha is probably paraphyletic (Sorensen *et al.* 1995) so that the two component, monophyletic taxa, the Fulgoromorpha and Cicadomorpha, were analysed separately. The Fulgoromorpha are all phloem-feeders. Within the Cicadomorpha, the following three guilds were recognized (see Novotny & Wilson 1997, for details): (i) mesophyll cell-feeders: Cicadellidae: Typhlocybinae; (ii) xylem-feeders: Cercopoidea, Cicadoidea, Cicadellidae: Cicadellini (*sensu* Hamilton 1983; Cicadellinae *sensu* Young 1968) and Mileewini (their position is uncertain; they were treated as xylem-feeders, based on the present field observations); (iii) phloem-feeders: the remaining Cicadomorpha. Only adults were collected and analysed in sap-sucking groups.

As in almost any other study, the above guilds are in fact 'taxon-guilds' (*sensu* Simberloff & Dayan 1991), i.e. groups of species defined both by their food resource and phylogenetical lineage (taxon), as certain taxa of leaf-chewers (e.g., molluscs) and sap-suckers (e.g., Sternorrhyncha) were not studied.

Estimation of body size and host specificity

In both leaf-chewing and sap-sucking insects, body length (excluding wings, any processes and ovipositor) and thorax width was measured. Only adults were measured in Auchenorrhyncha, Coleoptera, Orthoptera and Phasmatodea, and only caterpillars were measured in Lepidoptera. For both leaf-chewing and sap-sucking insects, the body length multiplied by body width was used as an index of the species' body size.

In leaf-chewing insects, average body length was estimated from 10 measurements whenever possible, but only the largest available measurement was used for caterpillars, in order to approach the size of the last instar. Body width to length ratio was measured on a macro-photograph of a single specimen and multiplied by the average body length to estimate body width. All measurements were performed on dry, mounted specimens; only caterpillars were measured when alive.

In sap-sucking insects, body length and width of two males and two females were measured whenever possible, and the average was calculated from these measurements. Alcohol-preserved material was used for measurements.

The host specificity of each species was quantified as the variance of its distribution among the 15 *Ficus* species. 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, was used as the host specificity parameter. This index is considered to be the best way of standardization of variance with respect to the mean (see Lepš 1993 for its detailed evaluation). Its value is minimum for an equitable distribution (i.e., indiscriminate polyphagy) and is increasing with increasing host specificity. Many species were too rare to derive any sensible estimates of their host specificity. Since the species' host specificity was measured as its distribution among 15 host trees, all species collected as less than 15 individuals were excluded from the analyses of host specificity.

The species abundance, host specificity and body size had positively-skewed distributions, which were difficult to normalize. Therefore, the Spearman's correlation (r_s) and Kruskal–Wallis test were used in the analysis. The relationship between host specificity and body size was also fitted by the locally weighted regression scatter-plot smoothing (LOWESS; the tension 0.5 was used; Cleveland 1979) which, unlike the standard regression, can be used to explore non-linear trends in the data.

RESULTS

The sampling effort amounted to the total of 370 h and 6831 tree-inspections for the leaf-chewing and to 316 h and 4573 tree-inspections for the sap-sucking insects (it is estimated that the actual number of individual *Ficus* trees sampled was > 1000 in both groups). The combined samples from all the 15 species of *Ficus* were used for the analysis. They consisted of confirmed feeding records for 13 193 individuals from 348 species of leaf-chewing insects and distribution records for 52 079 individuals from 444 species of sap-sucking insects.

Many species were rare in the samples, so that the exclusion of species collected as less than 15 individuals reduced the number of species from 348 to 92 in the leaf-chewing insects, from 200 to 78 in the Cicadomorpha, and from 244 to 98 in the Fulgoromorpha. In the reduced data set, the Lloyd's index of host specificity was tested for dependence on the species abundance (i.e., the sample size). There was no significant abundance versus host specificity correlation in any of the eight guilds analysed ($|r_s| < 0.2$ and $P > 0.05$ in all cases).

Leaf-chewing insects

Body size increased in the sequence larval root-feeders = larval leaf-chewers < larval wood-borers = life-long leaf-chewers (Table 1). The relative differences in body size remained the same in the reduced data set, but the significance of differences involving larval leaf-chewers changed (Table 1, Figure 1a). The guilds differed also in their host specificity. On average, the larval wood-borers and life-long leaf-chewers were less specialized than the other two guilds (see Table 1 for the significance of all pair-wise differences).

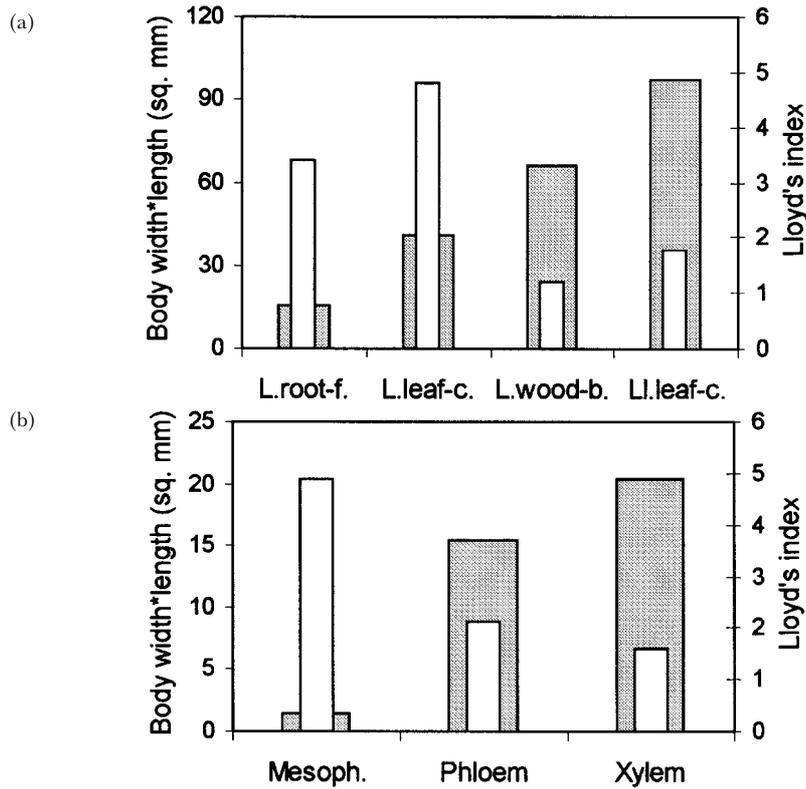


Figure 1. Body size and host specificity of the (a) leaf-chewing and (b) sap-sucking guilds. The median for body size (body length * width; stippled bars) and host specificity (Lloyd's index; open bars) is given for each guild: larval root-feeders, larval leaf-chewers, larval wood-borers, life-long leaf-chewers, mesophyll-cell, phloem- and xylem-feeders.

Table 1. Differences among guilds of leaf-chewing insects in abundance, body size and host specificity. The median and the range for 50% of cases around the median (in brackets) are reported; values followed by different letters are significantly different ($P < 0.05$, Dunn's pair-wise comparisons; Kruskal-Wallis test significant, $P < 0.001$, in all cases).

Variable	Data set	Larval root-feeders	Larval leaf-chewers	Larval wood-borers	Life-long leaf-chewers
Abundance	complete	6 a (1-42)	3 a (1-15)	1 a (1-7)	5.5 a (2-13)
Body size	complete	12.3 a (6.5-20.8)	27.5 a (2.8-56.6)	65.4 b (38.3-130.9)	119.2 b (66.4-198.3)
Body size	reduced	15.8 a (10.6-23.8)	40.7 b (27.5-73.1)	66.4 bc (30.9-89.6)	97.0 c (47.2-169.1)
Host specificity	reduced	3.4 ab (2.3-5.3)	4.8 a (2.6-8.0)	1.2 c (1.1-1.50)	1.8 bc (1.5-2.5)
S	complete	72	138	73	66
S	reduced	29	37	11	15

Abundance: the number of individuals per species; body size: body length * width, in mm^2 ; host specificity: Lloyd's index; S: number of species; reduced data set: species collected as $n \geq 15$ individuals.

The correlation between body size and host specificity was negative and significant for the leaf-chewing insects as a whole ($r_s = -0.357$, $P < 0.01$, $n = 92$ species; Figure 2a), but it was not significant within any of the guilds (Table 2). The overall correlation between body size and host specificity remained significant when abundance of the species was used as a covariable (Pearson's $r = -0.347$, $P < 0.01$).

There was a weak, but significant, positive correlation between body size and abundance in the whole data set on leaf-chewers, mostly caused by a strong correlation within the larval leaf-chewing guild (Table 3).

Sap-sucking insects

In Cicadomorpha, the body size increased in the sequence mesophyll-feeders < phloem-feeders < xylem-feeders; the xylem-feeding species were also more abundant than the species from the other two guilds (Table 4). In the reduced data set, these patterns were not detectable; instead, only the mesophyll-feeders were significantly smaller and more host specific than the other two guilds (Table 4, Figure 1b).

The correlation between body size and host specificity was negative and highly significant for the Cicadomorpha as a whole ($r_s = -0.572$, $P < 0.001$, $n = 78$ species; Figure 2b), but it was not significant within any of the three guilds (Table 2). The correlation between body size and host specificity was negative and significant also in the Fulgoromorpha ($r_s = -0.281$, $P < 0.01$, $n = 98$ species; Figure 2c). The body size versus host specificity correlations for both Cicadomorpha and Fulgoromorpha remained significant when abundance was used as a covariable (Pearson's $r = -0.584$ and -0.257 , respectively; $P < 0.05$).

The correlation between body size and abundance was negative and significant in the xylem-feeders, positive, but marginally not significant, in the phloem-feeders and non-existent in the mesophyll-feeders (Table 3).

DISCUSSION

Sources of bias

The differences in protocols used to estimate body size for sap-sucking and leaf-chewing insects reflect the preferred methodologies of the first and second author, respectively, rather than optimum solutions for respective insect groups. More importantly, this study avoids potential bias given by the use of wing span (used in all previous studies; see review by Loder *et al.* 1998) as the index of body size in Lepidoptera, instead of the ecologically relevant size of the last instar of the caterpillars. This convenient practice is dubious due to a low proportion (48%) of variation in the larval size accounted for by the wing span, reported by Gaston & Reavey (1991) and found also in the present data (authors' unpubl. data).

The host specificity was estimated as the local use of the 15 species of *Ficus*. This approach provided much finer resolution than in other studies, where all

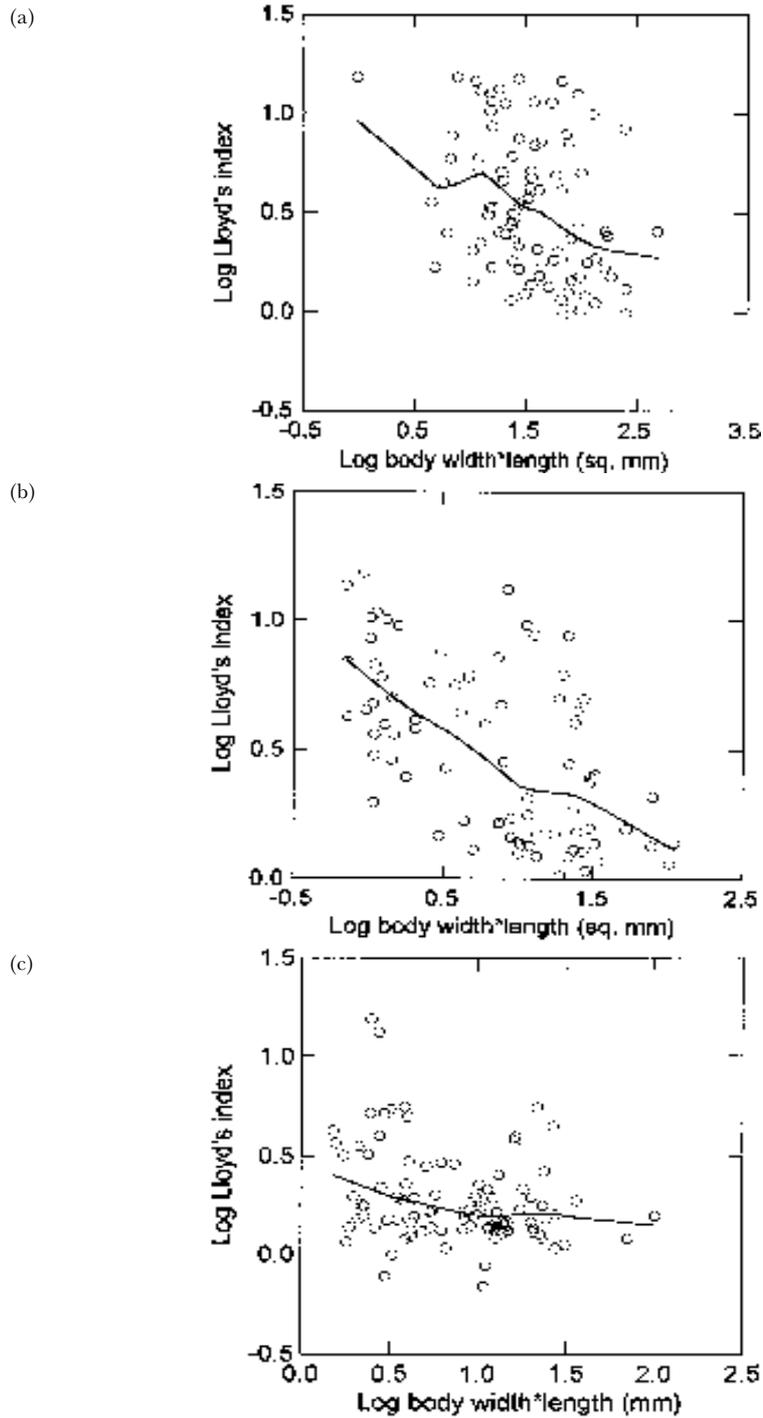


Figure 2. Relationship between body size and host specificity in (a) leaf-chewing insects, (b) sap-sucking Cicadomorpha, and (c) sap-sucking Fulgoromorpha. \log_{10} body size and log host specificity indices are plotted and a trend-line fitted by LOWESS regression.

Table 2. Spearman's correlation (r_s) between body size and host specificity. Reduced data set; see Tables 1 and 4 for sample sizes (S).

Guild	r_s	P
Mesophyll cell-feeders	-0.300	0.11
Phloem sap-feeders	-0.408	0.07
Xylem sap-feeders	-0.219	0.26
Larval root-feeders	-0.164	0.40
Larval leaf-chewers	-0.061	0.72
Larval wood-borers	-0.373	0.26
Life-long leaf-chewers	-0.421	0.12

Table 3. Spearman's correlation (r_s) between body size and abundance. Complete data set; see Tables 1 and 4 for sample sizes (S).

Guild	r_s	P
Mesophyll cell-feeders	0.036	0.75
Phloem sap-feeders	0.231	0.06
Xylem sap-feeders	-0.463	>0.01
Cicadomorpha total	0.054	0.14
Larval root-feeders	0.201	0.09
Larval leaf-chewers	0.344	>0.01
Larval wood-borers	-0.018	0.88
Life-long leaf-chewers	-0.105	0.40
Leaf-chewers total	0.121	0.03

Table 4. Differences among guilds of sap-sucking insects in abundance, body size and host specificity. The median and the range for 50% of cases around the median (in brackets) are reported; values followed by different letters are significantly different ($P < 0.05$, Dunn's pair-wise comparisons; Kruskal-Wallis test significant, $P < 0.001$, in all cases).

Variable	Data set	Mesophyll	Phloem	Xylem
Abundance	complete	6 a (1-31)	7 a (1-19)	22 b (4-229)
Body size	complete	1.6 a (1.1-2.5)	12.0 b (5.6-23.7)	23.6 c (12.0-53.1)
Body size	reduced	1.4 a (1.1-2.6)	15.4 b (9.8-24.5)	20.4 b (9.5-30.3)
Host specificity	reduced	4.9 a (3.8-7.5)	2.1 b (1.5-5.5)	1.6 b (1.3-2.4)
S	complete	82	69	49
S	reduced	30	20	28

Abundance: the number of individuals per species; body size: body length * width, in mm²; host specificity: Lloyd's index; S: number of species; reduced data set: species collected as $n \geq 15$ individuals.

species feeding on congeneric plants were usually treated summarily as specialists (Gaston 1988, Lindstrom *et al.* 1994, Wasserman & Mitter 1978). However, the host plant range of genuine polyphages, such as many acridids or aphrophorids, was greatly underestimated, as no information was available on their host plants other than *Ficus*. Ideally, local plant use, not the published information of the insect's host plant ranges, should be considered (Fox & Morrow 1981), and all plant species present in the study area should be examined.

Rarity of many species poses a serious problem for reliable estimation of their host specificity. The minimum sample size of 15 individuals, used here,

is a compromise between conflicting needs to describe adequately the host range of more polyphagous species and to retain specialist species in the analysis. Obviously, 15 individuals is insufficient for the quantification of host preferences of species feeding on numerous *Ficus* spp. A higher threshold could however exclude many specialists which are collected from only a small proportion of the host plants studied and are therefore rare in the composite sample. Another problem, particular to sap-sucking insects, are false host records represented by non-feeding tourist individuals. In order to alleviate this bias, a quantitative host specificity index, describing distribution of individuals among hosts, was used, rather than the number of host plants.

The differences in the body size among the three sap-sucking guilds, found in the original data, were distorted in the reduced data set, including only common species. The positive abundance versus body size correlation in phloem-feeders resulted in the over-representation of large species in the data set restricted to abundant species, while a negative abundance versus body size correlation produced the opposite bias in xylem-feeders. As a consequence, the originally significant difference in body size between these two guilds disappeared in the reduced data set. Similarly, a positive abundance versus body size correlation in larval leaf-chewers caused discrepancies between the complete and reduced data sets for leaf-chewing insects. The higher abundance of xylem-feeding species than those from the other two guilds led also to the over-representation of the xylem-feeders in the reduced data set; they made up 36% of its species, whilst there was only 25% of xylem-feeding species in the original data. These artifacts illustrate dangers inherent in the analyses of incomplete data, be they a result of insufficient sampling, not recording rare species at all, or data filtering, excluding them *a posteriori*. Conceivably, the reduced data could be biased also with respect to the host specificity, had there been a correlation between this trait and the species abundance. Any such bias cannot be quantified, since the host specificity estimates for rare species are not available.

The positive correlations between body size and host specificity in the present study were revealed by using species as independent data points. As such, they can be interpreted in functional terms, viz. that large species have a broader resource basis available in the studied community. However, this correlation cannot be interpreted as a tendency for the two traits, viz. body size and host specificity, to evolve in parallel. In order to test such a hypothesis, evolutionarily independent changes in these traits would have to be analysed, instead of their values possessed by individual species. There are several techniques for such analysis (e.g. Brooks & McLennan, 1991) but they are not applicable here since the significant differences, found between the guilds, were too few for any statistical analysis. Within guilds, no relationships between body size and host specificity were significant even when the analysis was performed on species as independent points, i.e., with the number of degrees of freedom greatly inflated.

Host specificity and body size: the effect of feeding mode

The community-wide tendency for larger species to feed on more species of *Ficus* was a consequence of simultaneous changes in body size and host specificity among guilds. In the leaf-chewers, the larval root-feeders had the smallest body size and were relatively host-specific, while the life-long leaf-chewers had the largest body size and were among the two less specialized guilds; in the Cicadomorpha, the mesophyll-feeders were at the same time the most specialized and with the smallest body size among the three guilds.

The absence of any body size versus host specificity relationship within guilds suggests that between-guild differences are crucial, with a particular feeding mode being more likely associated with either large body size and low host specificity, or vice versa. There is some evidence for causal relationships that could generate such a pattern, at least in the Auchenorrhyncha. Their host specificity may be influenced by the amount and diversity of secondary metabolites, which is decreasing in the sequence mesophyll cells > phloem sap > xylem sap (Mullin 1986, Raven 1983, Risebrow & Dixon 1986). The xylem-feeders indeed tend to be polyphagous (Press & Whittaker 1993), while phloem-, and especially mesophyll-feeding species are usually more host specific (Claridge & Wilson 1981, Cobben 1988, Wilson *et al.* 1994, Wood 1993). At the same time, particular feeding modes may constrain body size of sap-sucking insects. The mesophyll-feeders may be small because they feed by piercing and emptying individual plant cells, and there may also be energetic constraints, preventing the evolution of small xylem-feeders (Karban 1986, Novotny & Wilson 1997). The xylem-feeders indeed tend to be larger and the mesophyll-feeders smaller than the phloem-feeding Auchenorrhyncha (Novotny & Wilson 1997). Unfortunately, these hypotheses on the constraints on the body size and host specificity associated with particular feeding mode cannot be tested empirically. The mesophyll-feeding arose only once and the xylem-feeding probably twice during the evolution of Auchenorrhyncha (Novotny & Wilson 1997); clearly, the evolution has not generated enough independent data points for a thorough analysis.

In the leaf-chewing insects, there are reasons for larval wood-borers to be large and polyphagous. In the larval stage, they feed on a nutritionally extremely poor diet, which is often associated with large, energetically more advantageous, body size (Mattson 1980). In their adult stage, they perform only maturation feeding on the leaves. In many herbivorous insects, such maturation feeding by adults tends to be less specific than feeding by larvae (e.g., Jolivet & Hawkeswood 1995). However, there are no *a priori* reasons why the members of the other leaf-chewing guilds should be of particular body size and/or degree of host specificity. The interpretation of differences between feeding guilds of the leaf-chewing insects in the body size and host specificity is difficult for the same reasons as in the Auchenorrhyncha. Again, in the reduced data set, each guild was heavily dominated by a single insect lineage:

most of the larval root-feeders were chrysomelids, most of the life-long leaf-chewers acridids, all the larval-feeders lepidopterans, and all the larval wood-borers cerambycids. Interestingly, Basset *et al.* (1994) report differences in the intraspecific range of body size associated with different feeding modes in the herbivorous insects.

Host specificity and body size: the effect of body size range

An alternative explanation of the patterns found here is that the range of body sizes, included in the analysis, is important, rather than the guilds themselves. It is known that other correlates of body size, such as population density, can be detected only across a wide range of body sizes (Currie 1993). The combined analysis of all the guilds indeed encompasses a wider range of body sizes than the analyses of individual guilds. For example, the body size distributions of the mesophyll cell- and xylem-feeders, as well as of the larval root-feeders and the life-long leaf-chewers, almost do not overlap. Further, a significant correlation between body size and host specificity found in the Fulgoromorpha supports this explanation. There, all species belong to the same, phloem-feeding, guild, but span across a wider range of body sizes (body length from 1.7 to 15.9 mm) than the phloem-feeders in the Cicadomorpha (body length from 1.9 to 10.2 mm).

For similar reasons, it cannot be excluded that a significant correlation between body size and host specificity exists even within the guilds, but could not be detected in the restricted data set, which only was available for the analysis. For instance, the body size index in the complete sample of the 137 lepidopteran species ranged from 1.4 to 414.6 mm², while in the reduced sample of 37 species, which were abundant enough to estimate their host specificity, the body size index ranged only from 5.8 to 251.4 mm². Restricted data sets from other guilds exhibited similarly narrowed ranges of body size. This explanation is also supported by the fact that all seven within-guild correlations between body size and host specificity were negative, although none of them was significantly different from zero.

The present study found a correlation between body size and host specificity, previously reported from some insect regional faunas and temperate communities, in a large, tropical community of insect herbivores. It demonstrated that differences between the guilds generated such correlation. These differences can reflect a functional relationship between feeding mode, host specificity and body size. However, alternative explanations that they were merely coincidental, or artifacts caused by different sensitivity of the analysis for data with different ranges of body size, can not be ruled out.

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LITERATURE CITED

- BASSET, Y. 1997. Species abundance and body size relationships in insect herbivores associated with New Guinea forest trees, with particular reference to insect host-specificity. Pp. 237–264 in Stork, N.E., Adis J.A. & Didham, R.K. (eds). *Canopy arthropods*. Chapman & Hall, London.
- BASSET, Y., NOVOTNY, V. & WEIBLEN, G. 1997. *Ficus*: a resource for arthropods in the tropics, with particular reference to New Guinea. Pp. 341–361 in Watt, A., Stork, N. E., Hunter, M. (eds). *Forests and insects*. Chapman & Hall, London.
- BASSET, Y., SPRINGATE, N. D. & SAMUELSON, G. A. 1994. Feeding habit and range of body size: a case study in Papua New Guinea using arboreal leaf-beetles and weevils (Coleoptera: Chrysomelidae, Curculionidae). *Bulletin de la Societe Entomologique Suisse* 67:347–361.
- BROOKS, D. R. & MCLENNAN, D. A. 1991. *Phylogeny, ecology, and behavior*. University of Chicago Press, Chicago. 434 pp.
- CLARIDGE, M. F. & WILSON, M. R. 1981. Host plant associations, diversity and species-area relationships of mesophyll-feeding leafhoppers of trees and shrubs in Britain. *Ecological Entomology* 6:217–238.
- CLEVELAND, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association* 74:829–836.
- COBBEN, R. H. 1988. What we really know about host selection in Auchenorrhyncha? Pp. 81–92 in Vidano, C. & Arzone, A. (eds). *Proceedings of the 6th Auchenorrhyncha meeting, Turin, 7–11 Sept. 1987*. IPRA, Turin.
- CURRIE, D. J. 1993. What shape is the relationship between body size and population density? *Oikos* 66:353–358.
- FOX, L. R. & MORROW, P. A. 1981. Specialization: species property or local phenomenon? *Science* 211:887–893.
- GASTON, K. J. 1988. Patterns in the local and regional dynamics of moth populations. *Oikos* 53:49–57.
- GASTON, K. J. & LAWTON, J. H. 1988. Patterns in body size, population dynamics, and regional distribution of bracken herbivores. *American Naturalist* 132:662–680.
- GASTON, K. J. & REAVEY, D. 1989. Patterns in the life histories and feeding strategies of British macrolepidoptera. *Biological Journal of the Linnean Society* 37:367–381.
- GASTON, K. J. & REAVEY, D. 1991. The use of adult wing span as an estimate of final larval size in Lepidoptera. *Entomologist's Gazette* 42:161–163.
- HAMILTON, K. G. A. 1983. Classification, morphology and phylogeny of the family Cicadellidae (Rhynchota: Homoptera). Pp. 15–37 in Knight, W. J., Pant, N. C., Robertson, T. S. & Wilson, M. R. (eds). *Proceedings of the first international workshop on leafhoppers and planthoppers of economic importance*. CAB, London.
- JOLIVET, P. & HAWKESWOOD, T. J. 1995. *Host-plants of Chrysomelidae of the world: an essay about the relationships between the leaf-beetles and their food-plants*. Backhuys Publishers, Leiden. 281 pp.
- KARBAN, R. 1986. Prolonged development in cicadas. Pp. 222–235 in Taylor, F. & Karban, R. (eds). *Evolution of insect life histories*. Springer, New York.
- LEPS, J. 1993. Taylor's power law and measuring variation in the size of populations in space and time. *Oikos* 68:349–356.

- LINDSTROM, J., KAILA, L. & NIEMELA, P. 1994. Polyphagy and adult body size in geometrid moths. *Oecologia* 98:130–132.
- LODER, N., GASTON, K. J., WARREN, P. H. & ARNOLD, H. R. 1998. Body size and feeding specificity: macrolepidoptera in Britain. *Biological Journal of the Linnean Society* 63:121–139.
- MATTSON, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 20:97–117.
- MCALPINE, J.R., KEIG, G. FALLS, R. 1983. *Climate of Papua New Guinea*. CSIRO and Australian National University Press, Canberra. 200 pp.
- MULLIN, C.A. 1986. Adaptive divergence of chewing and sucking arthropods to plant allelochemicals. Pp. 175–209 in Brattsten, L.B. & Ahmad, S. (eds). *Molecular aspects of insect-plant associations*. Plenum Press, New York.
- NOVOTNY, V. & WILSON, M.R. 1997. Why are there no small species among xylem sucking insects? *Evolutionary Ecology* 11:419–437.
- PRESS, M. C. & WHITTAKER, J. B. 1993. Exploitation of the xylem stream by parasitic organisms. *Philosophical Transactions of the Royal Society, London, B* 341:101–111.
- RAVEN, J. A. 1983. Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Advances in Ecological Research* 13:135–234.
- REJMANEK, M. & SPITZER, K. 1982. Bionomic strategies and long-term fluctuations in abundance of Noctuidae (Lepidoptera). *Acta Entomologica Bohemoslovaca* 79:81–96.
- RISEBROW, A. & DIXON, A. F. G. 1986. Nutritional ecology of phloem-feeding insects. Pp. 421–448 in Slansky, F. Jr. & Rodriguez, J. G. (eds). *Nutritional ecology of insects, mites, spiders, and related invertebrates*. J. Wiley & Sons, New York.
- SIMBERLOFF, D. & DAYAN, T. 1991. The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22:115–143.
- SORENSEN, J. T., CAMPBELL, B. C., GILL, R. J. & STEFFEN-CAMPBELL, J. D. 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-Pacific Entomologist* 71:31–60.
- WASSERMAN, S. S. & MITTER, C. 1978. The relationship of body size to breadth of diet in some Lepidoptera. *Ecological Entomology* 3:155–160.
- WILSON, S. W., MITTER, C., DENNO, R. F. & WILSON, M. R. 1994. Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. Pp. 7–113 in Denno, R. H. & Perfect, T. J. (eds). *Planthoppers: their ecology and management*. Chapman & Hall, New York.
- WOOD, T. K. 1993. Diversity in the New World Membracidae. *Annual Review of Entomology* 38:409–435.
- YOUNG, D. A. 1968. *Taxonomic study of the Cicadellinae (Homoptera: Cicadellinae). Part 1, Proconiini*. Smithsonian Institution Press, Washington DC, USA. 287 pp.