Rare species in communities of tropical insect herbivores: pondering the mystery of singletons

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The host specificity, taxonomic composition and feeding guild of rare species were studied in communities of herbivorous insects in New Guinea. Leaf-chewing and sap-sucking insects (Orthoptera, Phasmalodea, Coleoptera, Lepidoptera and Hemiptera-Auchenorrhyncha) were sampled from 30 species of trees and shrubs (15 spp. of Ficus, Moraceae, six spp. of Macaranga and nine species of other Euphorbiaceae) in a lowland rain forest. Feeding trials were performed with all leaf-chewers in order to exclude transient species. Overall, the sampling produced 80062 individuals of 1050 species. The species accumulation curve did not attain an asymptote, despite 950 person-days of sampling. Rare species, defined as those found as single individuals, remained numerous even in large samples and after the exclusion of transient, non-feeding species. There was no difference among plant species in the proportion of rare species in their herbivore communities, which was, on average, 45%. Likewise, various herbivore guilds and taxa had all very similar proportions of rare and common species. There was also no difference between rare and common species in their host specificity. Both highly specialised species and generalists, feeding on numerous plants, contributed to the singleton records on particular plant species. Predominantly, a species was rare on a particular host whilst more common on other, often related, host species, or relatively rare on numerous other host plants, so that its aggregate population was high. Both cases are an example of the “mass effect”, since it is probable that such rare species were dependent on a constant influx of immigrants from the other host plants. These other plants were found particularly often among congeneric plants, less so among confamilial plants from different genera and least frequently among plants from different families. There were also 278 very rare species, found as one individual on a single plant species only. Their host specificity could not be assessed; they might have been either very rare specialists, or species feeding also on other plants, those that were not studied. The former possibility is unlikely since monophagous species, collected as singletons at the present sampling effort, would have existed at an extremely low population density, less than 1 individual per 10 ha of the forest.

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Insect communities in tropical rain forests appear to contain high numbers of rare species. Those collected as single individuals (singletons) often represent more than half of the species, even in large collections (Morse et al. 1988, Basset and Kitching 1991, Novotný 1993, Robinson and Tuck 1996, Allison et al. 1997, Stork et al. 1997). In addition to being a nuisance in the statistical analysis and interpretation of the data (e.g., Colwell and Coddington 1994, Robinson and Tuck 1996, Wolda 1996), these apparently rare species raise intriguing questions such as why there are so many of them, who they are, whether they are genuinely as rare as they appear to be in the samples, and if so, why.
With reference to communities of insect herbivores collected from particular plant species, rare species could, in theory, belong to one of the following categories: (a) transient, i.e., resting on the foliage but not feeding; (b) specialists/generalists inadequately sampled by inefficient sampling methods; (c) specialists with genuinely low population levels; (d) generalists feeding occasionally on the host examined but whose overall population levels may be relatively high when considered across all (numerous) host plant species occupied; (e) specialists feeding on the host examined but preferring, and more abundant on (a few) other, often closely related, hosts. The categories (a) and (b) represent sampling artefacts, (c) is an example of suffusive rarity, while (d) and (e) are examples of diffusive rarity sensu Schoener (1987).

Studies of insect herbivores feeding on tropical plants, particularly rainforest trees, are complicated by the high number of transient species (tourists sensu Moran and Southwood 1982; see also Janzen 1977, Moran et al. 1994, Basset 1997). This problem is compounded by the relative inadequacy of standard mass-collecting methods, such as pyrethrum knockdown, light- or Malaise-trapping. The host plants of the specimens obtained by these methods are difficult to trace with precision, and since they often involve the killing of the specimens, no rearing of or further experimentation with insects is possible (Basset et al. 1997a). Although the exclusion of transient species from the samples is the first, logical step in any community analysis, it can rarely be done in practice because of these methodological problems.

Insufficient seasonal or spatial replication of sampling can result in numerous species appearing rare because they were sampled in marginal times or places. The difficulty of organising long-term studies in the tropics with sufficient sampling effort (Janzen 1988, Erwin 1995) makes insufficient replicates a widespread problem.

Sampling problems notwithstanding, some species in the communities are genuinely rare. The study of differences between common and rare species in their ecology and life history appears to be a promising approach to understanding the causes of the species’ rarity (Kunin and Gaston 1993). Host specificity is one of the very relevant traits in such comparisons, since the patterns of host use determine the abundance and dynamics of resources available to herbivorous species.

The present analysis concentrates on rare species in the communities of herbivorous insects feeding on 30 species of shrubs and trees in a lowland rain forest in Papua New Guinea (PNG). Since it is based on extensive insect material, collected over three years of sampling from several thousands of trees, and involving numerous feeding tests on the collected insects, it overcomes some of the usual shortcomings, making analysis of the ecological characteristics of rare species possible.

Methods

Study area and host plants

The study area was situated in the lowlands of the Madang Province in PNG, extending from the coast to the slopes of the Adelbert Mts. Fieldwork was concentrated in primary and secondary lowland forests near Baitabag, Ohu and Mis Villages, and in a coastal area near Riwo village (145°41–48'E, 5°08–14'S, ca 0–200 m). The average annual rainfall in the Madang area is 3558 mm, with moderate dry season from July to September; mean air temperature is 26.5°C and varies little throughout the year (McAlpine et al. 1983).

Thirty locally abundant species of trees and shrubs, involving 15 species of Ficus (Moraceae), six species of Macaranga and nine species from nine other genera of Euphorbiaceae, were selected for the study (Appendix 1). The Moraceae and Euphorbiaceae, with 3000 and 5000 species worldwide, respectively (Heywood 1993), represent important components of tropical floras, including lowland rain forests in New Guinea (e.g., Oatham and Beehler 1998).

Ficus is an exceptionally large, pan-tropical genus (Berg 1989) and New Guinea is one of the main centres of its diversity, with 135 described species (Corner 1965). In the lowlands around Madang, there is a conservative estimate of 48 species of Ficus (G. Weiblen pers. comm.). Both in PNG (Höft 1992) and in the Madang area (pers. obs.), Moraceae other than Ficus are minor in species richness and biomass so our data on Ficus are also representative for the whole family of Moraceae.

There are 461 species of Euphorbiaceae reported from New Guinea, 73% of them endemic (van Welzen 1997). Macaranga is the largest genus of early successional (pioneer) trees in the world (Whitmore 1979). The main centre of its diversity is New Guinea, with 82 species described (van Welzen 1997). The other nine species of Euphorbiaceae, each from a different genus, included representatives of four, of five of its currently recognized subfamilies (Webster 1984).

Insect collecting

All externally feeding leaf-chewing insects (Orthoptera, Phasmatodea, Coleoptera and Lepidoptera) and one group of sap-sucking insects, the Auchenorrhyncha (of Hemiptera), were collected individually, by hand or by the use of an aspirator, from the foliage. Both adults and larval stages of the leaf-chewers and adults of the sap-sucking insects were collected. All 15 confamilial tree species were sampled simultaneously, for a period of at least one year. The leaf-chewing insects on Ficus were collected from July 1994 to March 1996 and on Euphorbiaceae from August 1996 to August 1997. The
sap-sucking insects on *Ficus* were collected from July 1995 to June 1996; no data are yet available for Euphorbiaceae.

Collecting effort was recorded as the time spent surveying the foliage of each of the tree species studied, which was approximately proportional to the leaf area examined. The number of tree inspections, i.e. a particular tree sampled at a particular time, was also recorded. For leaf-chewing insects, collecting effort varied from 22.9 to 25.6 h (average 24.7 h per species) on the *Ficus* hosts, and it was exactly 24.7 h per species on the Euphorbiaceae. For the sap-sucking insects, the sampling effort amounted to exactly 15.7 h on each *Ficus* host. In addition to regular sampling of all hosts, an exhaustive census of all sap-sucking insects from 191 individuals of *Ficus phaeosyce* was carried out at a single sampling site (Baitabag). The nearly complete sampling of the whole community was feasible since *F. phaeosyce* is a small understory shrub. Overall, these sampling protocols involved approximately 950 person-days of fieldwork and 25152 tree inspections.

### Processing of insect material

In the laboratory, all leaf-chewing insects were provided with fresh foliage of the species they were collected from and kept on it until they fed or died. Only the specimens which fed were considered in the analyses, to exclude transient species from the samples. Caterpillars were reared to adults whenever possible. Host preferences of the sap-sucking insects were inferred from the number of specimens collected on each tree species 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 also used in the characterisation of numerous, particularly sap-sucking, species. In critical groups, all specimens were routinely dissected and morphotyped using characters on genitalia. Various taxonomists later verified the assignment of morphospecies. Voucher specimens are deposited in Bishop Museum, Honolulu.

Feeding guilds of the leaf-chewing insects were consistent, to a large extent, with their classification to major taxa. Almost all Coleoptera fed on the foliage only during their adult stage, while all Lepidoptera only as larvae, and all Orthoptera and Phasmatodea throughout their life cycles. In beetles, species with wood-boring larvae included all species of Cerambycidae and Buprestidae, while species with root-feeding larvae included some Curculionidae and most of the Chrysomelidae.

Sap-sucking Auchenorrhyncha encompasses three guilds, those feeding on phloem sap, xylem sap and the mesophyll cells of leaf parenchyma, respectively. Species were assigned to their respective guilds following evidence on feeding modes for higher auchenorrhynch taxa (see Novotný and Wilson 1997). Further information on insect collecting, study site and plant species studies is detailed elsewhere (Basset et al. 1997b, Novotný et al. 1997, http://www.bishop.hawaii.org/bishop/natsci/ng/ngecol.html).

### Analysis of community samples

Throughout this study, rare species are defined as those represented by only a single specimen in the sample (singletons). Singletons represent such a large and conspicuous part of samples from any tropical insect community that they appear to be a natural choice when studying rare species. All species were divided into rare species (= singletons), common species (the first *s* most abundant species in the community, where *s* is the number of singletons), and the intermediate, i.e. all remaining, species. Depending on the analysis, both singletons and common species were defined for individual communities on different host plants (called “component communities” sensu Root 1973), or for the combined data set involving all 30 host plants (“compound community”). Species found as a single individual in component communities are called “local singletons”; those found as a single individual in the combined data set are called “unique singletons”. It should be noted that local singletons in all component communities have similar population densities since the sampling effort was almost identical for all 30 plants studied.

Species and singleton accumulation curves were estimated for the sequence of samples as they were collected in the course of time, as well as for the randomised sequence. For the latter, 500 random combinations of individual samples were created for each sample size, and the average number of species and singletons calculated from them.

The number of singletons was compared with that expected for a log-normal distribution of species abundance. Differences in the proportion of unique singletons and the remaining species in different guilds and taxa (orders, families) were tested by the $\chi^2$ test. Many species-poor families had to be excluded from the tests, or the analysis had to be performed on a higher, often superfamilial, taxonomic level.

### Host specificity

The host specificity was quantified by Lloyd’s index ($L$), quantifying the variance of the species’ distribution among the plant species studied:
L = \frac{S_X^2 - \bar{X}}{X^2} + 1,

where $S_X^2$ and $\bar{X}$ are variance and mean calculated from the number of individuals of a particular herbivore species, found on each of the 30 plant species studied. This index is considered to be the best way of standardisation the variance with respect to the mean (Lepsˇ 1993). Its value is minimum for an equitable distribution (i.e., indiscriminate polyphagy) and is increasing with increasing host specificity. Many species were too rare for the derivation of any plausible estimates of their host specificity. Potentially spurious correlation of host specificity, expressed by Lloyd’s index, with species abundance (i.e., sample size) was eliminated when species collected as less than 15 individuals were excluded from the analysis (Spearman $r = 0.11$, $P > 0.1$ for $n = 163$ species with $N \geq 15$ individuals).

The host specificity of those singletons which were also collected as at least 15 individuals on other plants was quantified by Lloyd’s index and compared with the host specificity of the same number of the most common species feeding on the same plant. In both cases, Lloyd’s index was calculated using only data from the remaining 29 plant species, not from the one studied. The values of Lloyd’s index for singletons and common species from each host plant species were compared by the Mann-Whitney test.

**Results**

**Number of rare species in communities**

Samples from leaf-chewing communities included 13172 individuals from 347 species feeding on the *Ficus* hosts and 14490 individuals from 383 species feeding on the euphorb hosts. Together, there were 606 leaf-chewing species, 180 (30%) of them unique singletons. Common species, i.e. the 180 most abundant species in the whole data set, included all species collected as 10 or more individuals. The sample from sap-sucking communities on *Ficus* included 52402 individuals from 444 species; 98 (22%) of them were unique singletons. Common species included all those collected as more than 58 individuals. The species accumulation curve for neither leaf-chewing, nor sap-sucking insects reached an asymptote (Fig. 1).

The species abundance distribution in both sap-sucking and leaf-chewing communities was not log-normal ($G$-test, $P < 0.001$), as the number of singletons observed (180 and 98 for leaf-chewing and sap-sucking insects, respectively) was higher than that expected for a log-normal distribution (142 and 77, respectively).

**Host specificity of rare species**

The host specificity of local singletons was compared with that of common species within communities of leaf-chewing insects, associated with particular plant species. Only one difference between singletons and common species was significant (Mann-Whitney test, $P < 0.05$), which was expected by chance, given the 30 tests, each on one plant species, performed. The median host specificity of common species was higher than that of singletons on 17 plant species, and smaller on 13 plant species, which again was not a significant difference (sign test, $P > 0.5$). When Lloyd’s host specificity values of all common species across the 30 communities were compared with those of all singletons, no significant difference was revealed either (Mann-Whitney test, $P > 0.5$, $n = 668$). In this instance, it should be noted that Lloyd’s values are not completely independent from each other, since the species which belonged to the common or singleton category on more than one host plant were included more than once, with Lloyd’s values describing their distribution among different subsets of 29 plants from the 30 studied.

The distribution of Lloyd’s values for local leaf-chewing singletons spanned a wide range of values, indicating that both highly specialised species and generalists contributed to the singleton records on a particular host (Fig. 2). The extremes were represented by...
Fig. 3. The number of unique singletons (black), shared local singletons (hatched) and other species (dotted) of leaf-chewing insects on different host plant species. Plant species abbreviated by the first letter of their generic and first two letters of their specific name; see Appendix 1 for full names.

*Fig. 5. Relationships of the number and the proportion of unique singletons with the number of host plant species sampled in the community of leaf-chewing insects. A regression $y = 27.66 + 43.71 \log x (R^2 = 0.996)$ was fitted for the number of singletons (circles) and $y = 0.465 x^{-0.1337} (R^2 = 0.993)$ for the proportion of singletons (diamonds) to extrapolate the respective trends for up to 50 plant species. Based on randomized species-accumulation curves.

The number of unique singletons in a sample from the leaf-chewing compound community was increasing with the expansion of sampling to an increasing number of plant species (Fig. 5). Increase in the number of singletons was slower than that in the total number of species because with the expansion of sampling, additional individuals of many, originally unique singleton species were found. As a consequence, the proportion of singletons was decreasing with the number of trees studied (Fig. 5). An extrapolation of this trend predicted a very slow decrease in the proportion of unique singletons with increasing sample size; for instance, 28% of singletons was expected for 50 plant species (Fig. 5).

Similar decrease in the proportion of singletons with increasing sample size was found also when the sampling was limited to conspecific trees, for example for sap-sucking insects on *Ficus phaeosyce* (Fig. 6). This decrease was rather slow as the percentage of singletons...
was decreasing in proportion to the logarithm of the number of individuals. The extrapolation of the linear trend found for *Ficus phaeosyce* predicted no singletons for the sample size of about 180000 sap-sucking insects from this plant species.

Other characteristics of rare species

The proportion of local singletons in the leaf-chewing communities (45% on average) did not differ among plant species ($\chi^2$ test, $P > 0.5$, $n = 30$). Similarly, the proportion of local singletons in the sap-sucking communities (32% on average) did not differ among *Ficus* species ($\chi^2$ test, $P > 0.5$, $n = 15$). There was a close correlation between the number of singletons and the number of other species in a community, both for leaf-chewing insects across 30 plants and sap-sucking insects across 15 *Ficus* spp. ($r = 0.820$ and 0.824, respectively; $P < 0.01$).

The relative abundance of unique singletons and other species was not different among sap-sucking guilds, leaf-chewing orders, nor among major sap-sucking and leaf-chewing families (Table 1). There were 278 leaf-chewing species identified at least to genus (see Miller et al. in press, for identifications of *Ficus*-feeding spp.). Among 124 genera, there were 14 large ones, each represented by at least five species. There was no difference between the proportion of singletons among species from these large and from small genera (13% and 19% of singleton species, respectively, $P > 0.1$, Fisher’s exact test, $n = 112$ spp. from large and 166 spp. from small genera). The present data were insufficient to examine whether certain genera exhibited a marked excess or lack of singletons as there were only two genera with more than ten species (*Rhyparida*, Chrysomelidae, with 19 and *Tmesisternus*, Cerambycidae, with 11 species).

Despite the large sample size of the data, it was not possible to investigate specific differences in temporal variability and body size of rare vs common species.

### Table 1. The number of unique singletons and other species in various herbivore guilds and taxa. Cicadellidae = Cicadellidae and Membracidae; Orthopteroids = Orthoptera and Phasmatodea; Notocnemidae = Notocnemidae, Lymantriidae, Notodontidae and Arctiidae; Pyraloidea = Pyralidae (incl. Crambidae); Caelifera = Acrididae, Pygromorphidae, Eu- masticidae. N.S. = differences among guilds or taxa not significant, $P > 0.05$, $\chi^2$ test.

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<th>Other spp.</th>
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Discussion

Similarly as in other samples from rainforest communities of insects (Erwin 1988, Janzen 1988, Hammond 1990, Stork 1993, Price et al. 1995, Orr and Haeuser 1996), species accumulation curves in the present study did not attain any asymptote and the proportion of rare species (singletons) was high. This was the case despite the large sample, containing more individuals than in any of the 11 major rainforest insect studies reviewed by Erwin (1995), and having the ratio of individuals to species higher than any of the seven studies reviewed by Erwin (1997). It is suggested here that the species richness in component herbivore communities, and the number of rare species in particular, is inflated by a steady influx of species from adjacent plants (“mass effect”, Shmida and Wilson 1985). This influx may be particularly important for herbivores in rain forests, where numerous plant species grow in close proximity. For instance, one-hectare plots of rain forests typically have from 60 to 150–300 species of large (dbh > 10 cm) trees (Gentry 1990, Richards 1996). It was also suggested that the species diversity of trees in rain forests was largely dependent on regional species richness and availability of potential migrants (Hubbell and Foster 1986). Many herbivorous insects present on the foliage are there only by accident and do not feed on it. For instance, such tourists made up 20% of leaf-chewing species collected from rainforest trees by Basset (1997) and their contribution to a high local species richness of rainforest insects is widely assumed, though rarely tested. One of the more interesting findings of the present study is that a high number and proportion of rare species, as well as a non-asymptotic species accumulation curve, characterise leaf-chewing communities, even after the tourist species have been excluded by feeding experiments.
In addition to tourist species, it is useful to recognise another category, viz. species which feed on a particular plant, but do not have resident, self-perpetuating populations on this plant species alone. These species may appear to be rare because (1) they were sampled on marginal host plants, rather than those considered to be optimal host plants, or (2) they are using several host plants, but are rare on each of them. These are also examples of the mass effect since such species, feeding on a particular plant, are dependent on a constant influx of immigrants from other plant species. In the present study, a majority of the species that were rare on a particular plant were indeed found also on other plants. There was a full range of host plant utilisation patterns represented among rare species, which included both almost monophagous and widely polyphagous species. The most frequent pattern of host plant use by rare species was intermediate, which involved simultaneous feeding on several plant species. Since numerous singletons may be sustained on at least some of their host plants by immigration only, there is no minimum threshold for their population density on these plants. In consequence, there may be many species reaching extremely low densities on some of their hosts, so that a large sampling effort would be needed to record them. This corresponds with a slow decrease in the proportion of singletons with increasing size of the samples taken from a particular plant species, as reported here. These results indicate that the number of rare species in samples will not approach zero for any practicable scheme of sampling rainforest communities of insects.

Any herbivore community on a particular plant may be considered to be composed of core species, which have sustainable populations on that plant, and from marginal samples of core communities feeding on each of the several tens to a few hundreds of locally coexisting plant species. These samples from other communities will, as any small samples, have a large proportion of rare species, thus contributing to high species richness of herbivores on each plant species. Since the importance of plant phylogeny to host selection by herbivores is well known (Farrell and Mitter 1993), it is not surprising that this overlap by rare herbivore species to other hosts, found here, was mainly with closely related plants.

The above considerations cannot be applied to unique singletons, which may be either very rare specialists on the host plants from which they were collected or species feeding on other plants, not studied presently. The latter is possible for some, if not a majority of these species, since herbivores from only a small fraction of local plant diversity were sampled (e.g., two plant families from a conservative 64 present at one of our study sites; L. Balun pers. comm.). The existence of monophagous singletons cannot be proven in principle, but it becomes increasingly unlikely with increasing sampling effort. For instance, a complete census of 191 shrubs of *P. phaeosyce* yielded 426 sap-sucking insects. Since there were, on average, 46 *P. phaeosyce* shrubs per hectare of the forest and the complete sample from this host included 4514 sap-sucking individuals, any monophagous species, collected as a singleton, would have had the population density of 2.2 individuals per 100 ha. Similar calculation for *F. wassa* and leaf-chewing insects (unpubl.) suggests that any species, monophagous on this host and collected as a singleton, had a density of 5.2 individuals per 100 ha. Such low densities suggest that most of the apparently rare species were probably feeding also on other hosts.

There were no differences in the proportion of rare species among various herbivorous guilds and families, neither between small and large insect genera. Various host plants also did not differ in the proportion of rare and common herbivores, both in the present study and in a study on another 10 rainforest trees (Basset 1997). Similarly, there were few differences in the number of rare species between plant families in the study by Hubbell and Foster (1986). Once again, this pattern suggests the significance of regional species pool and mass effect, rather than the effect of different life histories of either plants or insects. A constant proportion of rare species in the communities on various tree species indicates that the species richness of common and rare species was determined by the same factors. These included leaf palatability and leaf production for leaf-chewing insects, and tree density and leaf expansion for sap-sucking insects (Basset and Novotný 1999).

The inflated local (alpha) species richness due to the mass effect would decrease species turnover (beta diversity). Species locally co-existing in rainforest communities indeed appear to represent a large proportion of the regional species pools, at least in butterflies (Orr and Haeuser 1996, Robbins and Opler 1997) and woody plants (Foster and Hubbell 1990, Kochummen et al. 1990, 1992), where such comparisons could be performed.

**Conclusions**

Rare species are an important part of rainforest communities of insect herbivores. This conclusion is supported even by large samples containing only feeding individuals. Therefore, rare species cannot be excluded from community studies as an artifact or a group of marginal importance. Rather, they should be targeted as an interesting biological phenomenon, albeit one difficult to study.

It has been suggested that species may appear to be rare for various reasons, including sampling artifacts, polyphagy, as well as genuine rarity (categories a–e, listed in the Introduction). An analysis of 80000 insects...
and 30 host plants later, it is possible to discuss from where rare species originated, at least in the present study.

Transient, not feeding species (a) are an important part of any unfiltered data set (such as the samples of sap-sucking insects here), but even after they have been excluded, numerous rare, and feeding, species remain (as in the present leaf-chewing data).

Species, apparently rare because they were inadequately sampled by inefficient sampling methods (b) may represent a few cases, particularly of species restricted to inaccessible parts of mature trees of large, canopy species. It is doubtful whether any sampling method is free from bias with respect to at least some species or habitats (e.g., Basset et al. 1997a), but direct sampling of insects from the foliage performs well for externally feeding herbivores.

Specialists with genuinely low population levels (c) are probably very few. The sampling effort was such that species collected as singletons on their only host would have to have a very low population density. Generalists, feeding occasionally on the studied plants, but whose overall population levels may be relatively high when considered across all (numerous) host plants (d) and specialists, feeding on the host examined, but preferring and more abundant on other closely related plants (e) are the two by far most important sources of rare species in component communities. These are examples of diffusive rarity, found to be predominant also among rare bird species (Schoener 1987).

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**Appendix 1. Plant species studied**
