Local versus regional species richness in tropical insects: one lowland site compared with the island of New Guinea

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Abstract. 1. The overlap in species composition of Cercopoidea (Aphrophoridae, Cercopidae, and Machaerotidae), Flatidae, and Ricaniidae between two data sets, an almost exhaustive census from 13 *Ficus* species and a sample from diverse vegetation in the same area, led to the estimate for local species richness of 111 (SE 11.5) species (45 species of Cercopoidea, 36 species of Flatidae, and 30 species of Ricaniidae) at a lowland rainforest site in New Guinea.

2. Samples restricted to 13 species of *Ficus* contained 66 species, i.e. 59% of the estimated local species richness. This high proportion probably results from the high proportion of polyphagous and tourist (transient) species in the Cercopoidea, Flatidae, and Ricaniidae.

3. The two largest museum collections of New Guinean insects contained 327 species of Cercopoidea from New Guinea, including 23 of the 34 species collected in the field samples. This overlap led to the estimate of 483 (SE 97.2) species of Cercopoidea present in New Guinea.

4. The species found in the field samples were also 2.6 times more likely to be found in the museum collection than other species. This sampling bias can be due to a positive correlation between species local abundance and geographic distribution and/or similar patterns of species abundance at different sites.

5. The estimate of species richness of Cercopoidea in New Guinea increased to 1222 species when corrected for this sampling bias. Thus, only 4% of the New Guinean species were present locally, in the study area. Such high beta diversity is probably a consequence of the exceptional habitat and vegetation diversity in New Guinea, as well as its complex geological history.

Key words. Aphrophoridae, Cercopidae, Flatidae, herbivores, museum collections, Papua New Guinea, rainforest, Ricaniidae, species diversity, species turnover.

Introduction

The number of species is a key community characteristic but it is difficult to estimate for insect communities in the tropics (e.g. Price *et al.*, 1995; Basset & Novotny, 1999). Unsurprisingly, data on regional species richness of insects, which combine numerous local estimates, are almost non-existent for tropical areas (but see Gaston *et al.*, 1996). From New Guinea, such data are available only for cicadas (de Boer & Duffels, 1996) and butterflies (Parsons, 1999). In the temperate zone, insect faunas are fairly well known following decades of faunistic studies. The effort necessary to reach such coverage in the tropics would be considerably higher. Most tropical studies result in collections of unnamed morpho-species, which cannot be cross-referenced across studies or areas (e.g. Stork *et al.*, 1997). The integration of local studies into regional databases is thus slow in most insect groups (Holloway, 1983; Janzen, 1993; Kitching, 1993).

New data on beta diversity are crucial for better understanding of the dynamics of speciation in the tropics (Morell, 1996), better description of ecosystem heterogeneity on large spatial scales (Tuomisto *et al.*, 1995), better insight into the

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relative importance of local and regional determinants of the composition of tropical communities (Basset & Novotny, 1999), as well as for more informed decisions in nature conservation. For instance, poor understanding of beta-diversity patterns in rainforests is generating controversy about current extinction rates caused by logging (Mann, 1991).

Recent progress has been made in the study of the relative magnitude of local vs. regional richness of tropical trees (Condit *et al.*, 1996). Results indicate that locally coexisting species appear to represent a large proportion of the regional species pools (Foster & Hubbell, 1990; Kochummen *et al.*, 1990, 1992). Similar comparisons available for butterflies and parasitoid Hymenoptera also suggest low beta diversity (Gaston & Gauld, 1993; De Vries, 1994; Gaston *et al.*, 1996; Orr & Haeuser, 1996; Haeuser *et al.*, 1997; Robbins & Opler, 1997; Bartlett *et al.*, 1999).

Comparisons for taxonomically less well-known insect groups can only be derived indirectly. One feasible approach to the estimation of species richness in large, poorly known areas is analogous to capture–mark–recapture methods used to estimate population size. It is based on the comparison of data from large-scale but incomplete surveys with detailed samples available from a limited part of the studied area. The species richness of the large area is calculated from the number of species known from the detailed samples *recaptured* during the large-scale survey (Colwell & Coddington, 1994; Hammond, 1994). This approach has rarely been used, however, probably because it requires detailed samples from the focal area, as well as less intense sampling of wider areas. Because most studies use only one of these sampling protocols, few existing data sets meet these criteria. A related approach, used to derive regional or global species richness, is based on a comparison of species numbers in community samples with those known to taxonomists or represented in museum collections (Gaston, 1991; Hodkinson & Casson, 1991; Hodkinson, 1992). Methods based on this approach are potentially useful but they rest on a number of assumptions, which are yet to be tested (Hodkinson & Hodkinson, 1993; Colwell & Coddington, 1994; Hammond, 1994).

The aim of the work reported here was to use these methods to estimate local and regional species richness for several hemipteran taxa (Cercopoidea and Fulgoroidea: Ricaniidae and Flatidae) in New Guinea and to explore sampling biases of museum collections, in comparison with quantitative samples from ecological communities. The analysis is based on data obtained from two extensive sampling programmes and two large collections from New Guinea, housed at the Bishop Museum, Honolulu, Hawaii and The Natural History Museum, London.

Methods

Field samples

Two sampling programmes were completed: general sampling from diverse vegetation at a single rainforest site, and restricted sampling from 13 species of *Ficus* at several sites in the same area near Madang, Papua New Guinea. General sampling was performed within one square kilometre in the centre of Baiteta rainforest (145°45′E, 5°01′S; 50 m a.s.l.) (see Bowman *et al.*, 1990 for site description) during March–June 1993, March–June 1994, and April–July 1996. Insects were sampled by canopy fogging (5% Reslin Premium insecticide mixed with diesel) and UV light trapping. Seventy-three samples were obtained by fogging the crowns of a diverse range of tree species and two light traps were operated for a total of 110 nights at 37 locations in the canopy (maximum six nights at one location).

Ficus sampling was performed mainly at three sites, in lowland rainforests near Baitabag, Ohu, and Mis Villages (145°41–8′E, 5°08–14′S, 50–200 m a.s.l.) and in secondary locations nearby, including Baiteta. All main collecting sites were located within 30 km of the Baiteta forest. The 13 locally abundant species sampled were *F. bernaysii* King, *F. botryocarpa* Miq., *F. conocephalifolia* Ridley, *F. copiosa* Steud., *F. dammaropsis* Diels, *F. hispidioides* S. Moore, *F. nodosa* Tejsm. & Binn., *F. phaeosyce* Lauterb. & K. Schum., *F. pungens* Reinw. ex Bl., *F. septica* Burm. f., *F. trachypison* K. Schum., *F. variegata* Bl., and *F. wassa* Roxb. Insects were sampled from foliage by hand or using an aspirator. *Ficus* species were sampled simultaneously with equal effort, from July 1995 to June 1996. Sampling involved a total of 3960 tree inspections, i.e. a particular tree sampled at a particular time, representing 450 person-days of fieldwork.

All adult Auchenorrhyncha collected on *Ficus* were assigned to morphospecies. In critical groups, specimens were dissected and genital characters used. Completeness of sampling was evaluated for each family by inspection of the species-accumulation curves. Only taxa where zero or one new species was found in the last 500 individuals collected were retained for the analysis. These included Cercopoidea (Cercopidae, Aphrophoridae, and Machaerotidae), Flatidae, and Ricaniidae. Subsequently, only these taxa were studied in the material from the general sampling programme.

Museum collections

Unfortunately, it was not possible to apply the same methods of regional species richness estimation consistently to all three focal taxa. Museum collections could only be analysed for Cercopoidea as substantial portions of Flatidae and Ricaniidae material were on loan. Likewise, comparison with the taxonomic literature could only be performed for Flatidae, as there is no recent taxonomic revision of New Guinean species of Cercopoidea and Ricaniidae.

Morphospecies of Cercopoidea from the field samples were cross-referenced with the Bishop Museum and Natural History Museum collections. All pinned, unidentified material in the museum collections was also sorted to morphospecies and used alongside identified specimens. Comparisons were restricted to the island of New Guinea, i.e. excluding neighbouring islands. Flatidae were identified by John Medler and cross-referenced with the worldwide museum holdings of New Guinean flatids (Medler, in press).

The relationship between species' local abundance and regional distribution was explored, using Ricaniidae as a model group, by comparing the abundance in the *Ficus* samples with the number of New Guinean localities recorded in the Bishop Museum collection.

Estimates of species richness

Local species richness of focal taxa within the study area was calculated as:

$$S^*_{local} = S_g \ (S_f/S_{fg}) \qquad (1)$$

where S_g is the number of species in the general collection, S_f the number of species in the *Ficus* collection, and S_{fg} the number of species found both in *Ficus* and general collections. It was assumed that the proportion of the *Ficus* species recorded by general sampling was the same as the proportion of all locally present species recorded by this sampling and that the species collected on the 13 *Ficus* species represented their total fauna. As eqn 1 is analogous to the Lincoln index used to estimate population size from capture–mark–recapture data, the variance estimate for the Lincoln index (Poole, 1974) can be used to calculate the variance of S^*_{local}:

$$\mathrm{var}\,(S^*_{local}) = S_g \ S_f^2 (S_g - S_{fg})/S_{fg}^3 \qquad (2)$$

Similarly, New Guinean species richness was estimated as:

$$S^*_{regional} = S_m \ (S_s/S_{sm}) \qquad (3)$$

$$\mathrm{var}\,(S^*_{regional}) = S_m \ S_s^2 (S_m - S_{sm})/S_{sm}^3 \qquad (4)$$

where S_m is the number of species in the museum collection, S_s the number of species in the field samples (general and *Ficus* samples combined), and S_{sm} the number of species found in both field and museum collections. This requires that species collected in field samples are as likely to be present in the museum collections as other species found in New Guinea. This assumption was tested as proposed by Hodkinson and Hodkinson (1993) by comparing the proportion of species found simultaneously in both museum collections between two data sets, viz. species represented in the field samples $[P_1 = S_1/(S_1 + S_2 + S_3)]$ and species absent from the field samples $[P_2 = S_5/(S_5 + S_6 + S_7)$; see Table 1 for variables $S_1 - S_7]$. If species from field samples are equally likely to appear in the museum collections as the other species, both proportions will be the same $(P_1 = P_2)$. If the proportions are different, the ratio P_1/P_2 can be used as a correction factor to allow for a different probability of species present in and absent from the field samples to appear in the museum collections (Hodkinson & Hodkinson, 1993).

Results

Local species richness

Sampling of *Ficus* produced 48 507 Auchenorrhyncha from 437 species, with the number of species increasing steadily throughout the sampling programme (Fig. 1), particularly in the two largest families, Cicadellidae and Derbidae. Among species-rich taxa, only Cercopoidea, Flatidae, and Ricaniidae showed nearly asymptotic species accumulation curves. To collect the last new species, 794 individuals were needed in Flatidae 1831 in Cercopoidea and 1891 in Ricaniidae. These taxa together contained 20 969 individuals from 66 species (Table 2, Appendix).

General sampling collected 865 individuals and 62 species from the focal taxa (Table 2, Appendix). The species accumulation curve showed a rapid increase with sample size for insecticide fogging samples but was asymptotic for the light trap samples.

The *Ficus* and general collections of the focal taxa overlapped, with 37 of the 91 species in common (Table 2). Local species diversity, estimated using eqn 1, was 111 (SE 11.5) species (45 species of Cercopoidea, 36 species of Flatidae, and 30 species of Ricaniidae), suggesting that 81% of species present were collected (Table 2).

Regional species richness

Medler (in press), reviewing museum collections of Flatidae worldwide, reported 150 species from New Guinea. Among the 33 species from the field samples, 31 were examined by him and only one was undescribed and absent from his revision. This high proportion (97%) of described species in field samples suggests the total species diversity for Flatidae in New Guinea to be 155 species. This is probably too low, owing to sampling bias. Regrettably, the correction factor, allowing for a different probability of species from the field samples to be represented as described species in museum collections, could not be estimated as the complete museum collections were not available for study.

The Bishop Museum and Natural History Museum collections of New Guinea Cercopoidea contained 254 and 163 species respectively (Table 1), with a combined total of 327, including 23 of the 34 species found in field samples. Using eqn 3, this estimates the total species richness in New Guinea as 483 (SE 97.2) species.

Among the 23 species of Cercopoidea found both in field and museum collections, 15 species (65%) were common to Bishop Museum and Natural History Museum collections, while eight species were present in just one museum (Table 1). By contrast, among 304 species present in the museums alone, only 25% (75) of species occurred in both Bishop Museum and Natural History Museum and 229 species were unique to one collection (Table 1). The difference between 65% and 25% proportion is significant (Fisher's exact test, $P < 0.001$). The difference between these proportions indicates that species found in field collections were $P_1/P_2 = 2.64$ times more likely

Table 1. Species of New Guinean Cercopoidea classified to groups (S_1–S_7) according to whether they were found in the field samples (Samples), the Bishop Museum, and/or The Natural History Museum.

Variable	Samples	Bishop Museum	Natural History Museum	No. of species
S_1	Present	Present	Present	15
S_2	Present	Present	Absent	3
S_3	Present	Absent	Present	5
S_4	Present	Absent	Absent	11
S_5	Absent	Present	Present	75
S_6	Absent	Present	Absent	161
S_7	Absent	Absent	Present	68

Fig. 1. Species accumulation curves for Auchenorrhyncha on *Ficus*.

to be found in the museum collection than other species. This differential probability was used to correct the number of species present only in the museum collections from 304 to 804. The corresponding estimate of regional species richness, using eqn 3, was 1222 species of Cercopoidea for New Guinea.

There was a positive correlation between the abundance of Ricaniidae species in the *Ficus* samples and the number of localities recorded for them in the material from the Bishop Museum collection (Spearman $r = 0.785$, $P < 0.01$, $n = 18$ species).

Discussion

Methodological remarks

Methods of extrapolating species richness from focal areas to larger areas are conceptually straightforward but their validity depends on a number of assumptions. Here, it was assumed that the *Ficus* sampling was exhaustive, providing a census of the *Ficus* community, that species from *Ficus* were collected as frequently by general sampling as were species from other vegetation, and that species collected by the field sampling in the Madang area were as likely to be represented in the museum collections as those from other habitats and areas of New Guinea.

Exhaustive census of all species within insect communities is almost impossible, except on limited temporal or spatial scales. The rate of discovery of new species cannot therefore be expected to drop to zero at any stage of sampling (cf. Southwood, 1996). What is an acceptably low discovery rate is arbitrary but at one new species per 800–1900 individuals, achieved here, *Ficus* sampling was considered exhaustive for focal taxa.

By contrast, insecticide fogging was not exhaustive, with the last 100 individuals containing six additional species. The asymptote reached by the species-accumulation curve for light-trap data concerns only phototactic species. Because the proportion of these species in the focal taxa is not known, the results of light trapping were analysed only in combination with the fogging data.

The *Ficus* and general collections used different methods, and the areas sampled overlapped only partially. This could
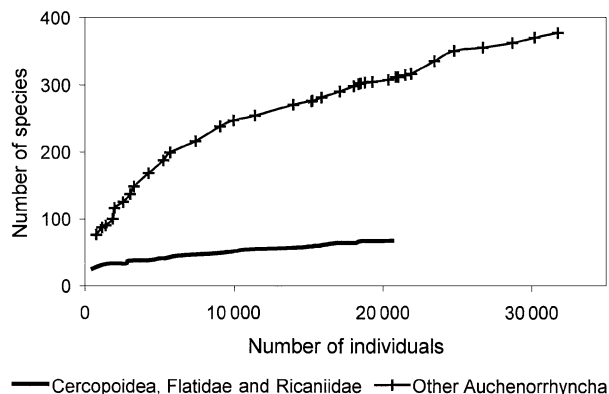
reduce the probability of some species being collected by *Ficus* and general sampling, thus overestimating local richness. The extent of this bias is difficult to estimate, but, as the methods used both targeted insects on the foliage and sites were similar, it is probably not serious. For instance, *Ficus* samples from two sites 7.5 km apart had almost identical composition. Among 33 species represented by at least six individuals, only three species were limited to one locality (the threshold of six individuals was used because a 6–0 distribution is significantly different from the equitable distribution between two localities; $P < 0.05$, binomial probability).

Extrapolation from local to regional richness is invalid if the species sampled at field sites were over-represented in museum collections compared with species from other areas of New Guinea. This was indeed the case, as revealed by the comparison of the field samples of Cercopoidea with the Bishop Museum and Natural History Museum collections. Such bias may result from Madang being prospected more exhaustively than other areas or by local abundance being correlated with widespread distribution and/or with abundance in other areas of New Guinea.

Although historically Madang was an important port and recently (1986–97) the Christensen Research Institute was a centre of biological research, the research of Auchenorrhyncha in this area was not exceptionally intense. The intensity of sampling in different provinces of Papua New Guinea and in Irian Jaya was compared as the number of known localities per species per $100\,000\,\text{km}^2$ of area recorded for 30 species of Flatidae by Medler (1989). The value for the Madang Province (4.1) was the ninth highest among 14 provinces, ranging from 0.6 (Gulf Province) to 9.4 (Central Province), suggesting an average intensity of exploration.

A positive correlation between local abundance and geographic distribution is a very widespread relationship (Brown, 1984; Gaston *et al.*, 1997) and could be responsible for the sampling bias. This correlation, found here for Ricaniidae, could reflect this pattern, but it could also be a sampling artefact, caused by differences in local abundance among species being consistent across large areas.

Table 2. Number of species (S) and individuals (N) in the *Ficus* (f) and general (g) collections, number of species present simultaneously in both collections (S_{fg}), total number of species in the two collections combined (S_s), and an estimate of the local species richness ($S*_{local}$) from eqn 1.

	S_f	N_f	S_g	N_g	S_{fg}	S_s	$S*_{local}$
Flatidae	23	6021	27	567	17	33	36
Cercopoidea	25	9244	20	241	11	34	45
Ricaniidae	18	5704	15	57	9	24	30
Total	66	20 969	62	865	37	91	111

Local and regional diversity

The *Ficus* collection contained a large proportion (59%) of the estimated local species of Cercopoidea, Flatidae, and Ricaniidae. Such a high percentage on only 13 congeneric plant species suggests that many species were tourists and/or polyphagous. Both factors are likely to be important. The proportion of transient, nonfeeding species in samples from rainforests is generally high (Basset & Samuelson, 1996) and many species of Flatidae are polyphagous (Medler, 1989). It is likely that xylem-feeding Cercopoidea are also polyphagous (Novotny & Wilson, 1997), while no reliable data are available for Ricaniidae.

The 33 species of Flatidae collected represented a high proportion (22%) of all known New Guinea species. Furthermore, there was only one previously undescribed species and two of unknown status in the field samples. This high proportion of described species produced an estimate of only 155 species of Flatidae in New Guinea, with 21% of these species present locally. The apparently high proportion may be an artefact caused by the sampling bias discussed above. The 97% of described Flatidae species in the samples is exceptionally high for a tropical insect group. This is due to the recent taxonomic revisions by Medler (1989, in press): only nine species (29%) were described previously.

The 34 species of Cercopoidea represented 10% of all New Guinean species, both described and undescribed, found in the Bishop Museum and Natural History Museum collections. The estimated local diversity (45 species) represents only 4% of the 1222 species estimated for the whole of New Guinea; however the value of species richness of New Guinea is very uncertain as indicated by the large standard error of the uncorrected estimate of 483 species (SE 97.2), which is probably compounded by an unknown error associated with the correction factor of $P_1/P_2 = 2.64$.

The ratio of local to regional diversity of Cercopoidea is low compared with other studies. Orr and Haeuser (1996) found one-third of the Bornean fauna of butterflies at a single locality and Haeuser *et al.* (1997) discovered two-thirds of the Bornean fauna in a single area including an elevational gradient. Robbins and Opler (1997) reported six studies, recording 600–1300 species of butterflies locally, in comparison with 7500 species for the neotropical region. In New Guinea, of 959

species of butterflies (Parsons, 1999), 373 were found along an altitudinal transect from 500 to 3000 m in a single valley (Parsons, 1991). Similarly, De Vries (1994) reported a high overlap, of ~50% of species, between butterfly faunas from three sites in Costa Rica and one in Panama. For zygopine weevils, 68 from 290 species were shared between La Selva (Costa Rica) and Barro Colorado Island (Panama) (Hespenheide, 1994). Some of these studies, however, are not directly comparable with the present results, which included only lowland rainforest habitat. The high beta diversity observed here is probably a consequence of the exceptional topographic, habitat and vegetation diversity of New Guinea (Paijmans, 1976; McAlpine *et al.*, 1983), as well as its complex geological history. Several tectonic blocks that now compose the island of New Guinea remain distinct centres of endemism (de Boer & Duffels, 1996; Polhemus, 1996).

Hodkinson and Casson (1991) estimated that there might be ~4760 species of Cercopoidea worldwide. This estimate was based on the total number of described species and an estimated 50% proportion of described species in local samples from Sulawesi. By comparison, the species richness of New Guinea (estimated 1222 spp.) would represent 26% of the global diversity. Such a high proportion is unlikely. The global richness given by Hodkinson and Casson (1991) is probably too low, due to the same sampling bias encountered here that led, when uncorrected, to the estimate of 483 species of Cercopoidea in New Guinea (i.e. 40% of the corrected estimate and 10% of the global diversity as estimated by Hodkinson and Casson, 1991).

In comparison, there are 959 species of butterflies (Papilionoidea) in New Guinea (Parsons, 1999), i.e. 5.5% of the global total of 17 500 species (Robbins, 1993; Robbins & Opler, 1997). In several other groups of organisms, including flowering plants, various invertebrates and vertebrates, approximately 5% of the world diversity occurred in New Guinea (Sekhran & Miller, 1996).

Many more regional estimates for various taxa and areas are needed before reliable estimates of continental or global species richness can be obtained. The spatial variation in species richness of various taxa is idiosyncratic so that long-ranging extrapolations are always a very risky exercise. Further, the magnitude of beta diversity can also vary spatially. This may be particularly true for New Guinea with its complex topography and history.

Acknowledgements

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Appendix: Species composition of the field samples

Aphrophoridae: *Interocrea* (4 spp.), *Liorhina disjuncta* (Walker), *Liorhina internigrans* (Jbi.), *Liorhina novabritanniana* (Lall.), *Liorhina suppressa* (Jbi.), *Liorhina* (11 spp.), genus unidentified (5 spp.); **Cercopidae**: *Aufidus* (3 spp.), *Cosmoscarta* (2 spp.), *Leptataspis* ?*discolor* Boisduval, *Literna*? sp., genus unidentified (2 spp.); **Machaerotidae**: *Machaerota humboldti* Lallemand; **Flatidae**: *Acrophaea dianata* Medler, *Atracis corticinus*? Distant, *Atracis pyralis* G.-M., *Atracis scissa* (Melichar), *Colgar asperum* Mel., *Colgar elatum* Medler, *Colgar missior* Medler, *Colgar orisum* Medler, *Colgar surrectum* Melichar, *Cromgar rubellum* Medler, *Dascanga novotnyi* Medler, *Neocromna bistriguttata* Stal, *Neocromna hastifera* (Walker), *Neodaksha agrossa* Medler, *Neosephena novara* Medler, *Papuanella destituta* Medler, *Papuanella papija* Medler, *Papuanella redaga* Medler, *Papuanella similata* Medler, *Papuanella* sp., *Paradaksha meeki* Distant, *Sephena besula* Medler, *Sephena intexa* Medler, *Sephena marena* Medler, *Sephena rosata* Medler, *Sephena rubrovenosa* Melichar, *Sosephena binoba* Medler, *Talopsus variabilis* Medler, *Talopsus* sp., *Taparella amata* Walker, *Taparella ambigua* Medler, *Trisephena anomala* Medler, *Trisephena rubeola* Medler; **Ricaniidae**: *Armacia hyalinata* (Donovan), *Ricania* sp., *Tarundia* cf. *glaucesenus* Melichar, genus unidentified (21 spp.).