

A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests

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Data are presented on the Hemiptera fauna of a moderately large and topographically diverse area of tropical rain forest in Sulawesi Utara, Indonesia. Insects were sampled using several methods at several sites over a 1-year period. The numbers of described and undescribed species captured is used to predict the number of extant species of both Hemiptera and total insects in the world. The global estimates of 1.84–2.57 million species of insect are much lower than the 10–80 million predicted by Erwin and Stork from a study of tropical Coleoptera. The reasons for believing that the lower estimates are more reliable are discussed.

KEY WORDS: Species numbers Hemiptera-Insecta tropical rain forest Sulawesi – Indonesia.

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INTRODUCTION

Biologists have long struggled to describe and catalogue the diversity of animal species found on the surface of the globe. Amongst many vertebrate groups, such as mammals and birds, the rates of discovery of new species are low and declining, suggesting that the majority of extant species are now known to science. However, amongst the insects the exploration of new tropical habitats continually yields a profusion of new species. For example, a recent study on a small group of plant-feeding bugs, the Psylloidea, in Panama, yielded almost as many new or recently described species as the number of new bird species (136) described between 1934 and 1985 (Brown & Hodkinson, 1988; Diamond, 1985). It is observations such as these that have led biologists to speculate as to the true number of living species of insect. At present there are about 1 million described species and earlier conservative estimates put the real total at around 3–5 million (May, 1986). Recent extrapolations, based on the numbers of beetles (Coleoptera) obtained by insecticidal fogging of rain forest canopy have suggested that the true total may number between 10 and 80 million species,

dependent on what assumptions are made about host plant specificity (Erwin, 1982, 1983; Stork, 1988).

This paper examines what conclusions might be drawn about insect diversity from an intensive study of the bug (Hemiptera) fauna of a moderately large and topographically diverse area of tropical rain forest in Sulawesi Utara, Indonesia. It provides estimates of the world bug and insect fauna for comparison with Erwin's & Stork's data but is based on a different set of organisms and what are felt to be more realistic assumptions. The study relies on detailed samples collected on the Royal Entomological Society of London expedition to Sulawesi (Project Wallace). We gratefully acknowledge the many participating hemipterists who gave us access to material, data and expertise and the many scientists who made available to us the numerous general samples of insects that we examined. We, however, retain full responsibility for all interpretations and conclusions presented.

MATERIALS AND COLLECTION METHODS

A composite list (Table 1) was compiled of all Hemiptera species, collected over a 1-year period (1985) using several sampling methods, at a number of sites in the Dumoga Bone National Park, Sulawesi Utara, Indonesia. Sampling method used included canopy fogging with insecticide, Rothamsted light trapping, malaise trapping at ground and canopy level, flight interception trapping, yellow-pan trapping, sweep netting and hand searching. Sites were chosen to represent a diversity of habitats, including an extended altitudinal transect from lowland to montane rain forest. Full details of all collecting methods and sites are given by Hodkinson & Casson (1987) and Casson (1988). The species list forms the basis of the subsequent analyses. The intensity of the sampling programme employed should have ensured that the Hemiptera sample obtained was representative of the general area and contained a significantly high proportion of the species present. We would not claim that we have obtained a complete set of the Hemiptera present but the rate of accumulation of previously unrecorded species in our reference collection had slowed to a trickle by the end of the study period. The general thrust of our argument would not be substantially altered even if we had underestimated the total number of species by 50%.

RESULTS AND ANALYSIS

Table 1 lists the number of described species in each of the families/superfamilies of Hemiptera together with the number of species recognized from North Sulawesi. Aquatic bugs belonging to the Gerromorpha and Nepomorpha (of Stys & Kerzhner, 1975), totalling around 3000 species, are excluded from the analysis as aquatic habitats were not sampled. Also smaller obscure and unrepresented families with fewer than ten species are omitted as they have little bearing on the conclusions. These, totalling fewer than 60 species, embrace the Termitaphididae, Idiostolidae, Hyocephalidae, Canopidae, Phloeidae, Lestoniidae, Serbanidae, Aphylidae, Xylastodoridae, Joppicidae, Viannaididae, Velocopedidae, Medocostidae, Omaniidae, Aepophilidae, Leotichiidae, Hysipterygidae and Stemmocryptidae. Numbers of described

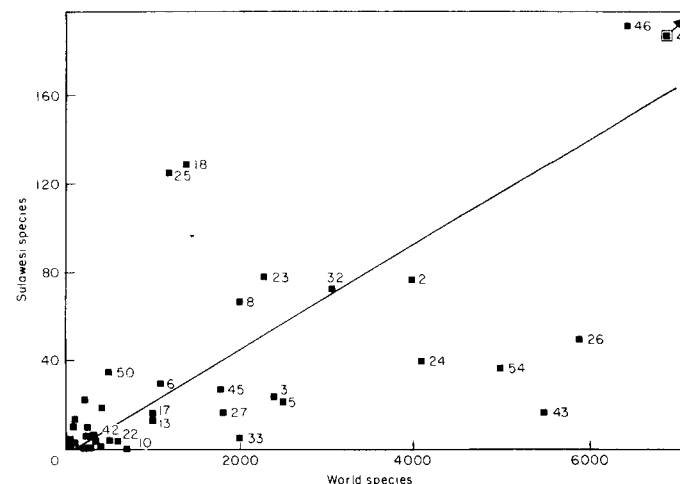


Figure 1. Relationship between the number of species of Hemiptera within families or superfamilies recorded from northern Sulawesi and the number of formally described species in that family.

species were taken from The Natural History Museum records updated, where possible, by a taxonomic specialist on the individual family. When a family occurred on Sulawesi an estimate was given of the percentage of the species collected that have formally been described. An estimate (guesstimate?) was also made for each family of the percentage of species that could be broadly classified as herbivores (feeding on living green plants, including seeds, flowers etc.), predators (feeding on other animals) and others (including fungal/detritus feeders). For the herbivores probable host-plant specificity was indicated as follows: (1) monophagous, restricted to species within a single genus; (2) oligophagous, restricted to one family; (3) narrowly polyphagous, feeding on just a few plant families; (4) broadly polyphagous, feeding on many plant families. Information on the percentage of species described and food preferences was derived from a questionnaire sent to various specialist hemipterists involved in the expedition and from the literature.

The relationship (Fig. 1) between the numbers of described species per family and the numbers of species in the Sulawesi sample shows a highly significant and relatively tight correlation ($r^2 = 0.88$, $n = 60$, $P < 0.001$). This suggests that the Sulawesi sample is a reasonably representative subset of the world fauna, although a strict χ^2 test for deviation from the 'expected' species composition, calculated from the known world faunal composition but based on the 1690 species known from Sulawesi, was statistically significant ($\chi^2 = 1402$, $n = 60$, $P > 0.05$). The relationship is defined by the regression equation $y = 0.024x - 3.62$ where the gradient represents an estimate of the number of Sulawesi Hemiptera species as a proportion of the world fauna. Hemiptera

TABLE 1. Species numbers, percentage of described species and feeding habits for the Hemiptera groups found in north Sulawesi

Group	World species	North Sulawesi species	Feeding habits				Specificity
			Undescribed	Herbivore	Predator	Other	
HOMOPTERA							
1. Coleorrhyncha	20	0					
Auchenorrhyncha							
2. Cicadoidea	4000	77	39	100	0	0	3
3. Cercopoidea	2380	24	50	100	0	0	2/3
4. Cicadelloidea	17000	498	90	100	0	0	1/2
5. Membracidea	2500	21	50	100	0	0	1/2
6. Cixiidae	1100	30	30	100	0	0	1/2
7. Teturometridae	70	0					
8. Delphacidae	2000	67	33	100	0	0	1/2
9. Eurybrachidae	180	0					
10. Fulgoroidea	700	0					
11. Achilidae	224	22	50	50	0	50	2
12. Tropiduchidae	350	5	50	100	0	0	2
13. Issidae	1000	13	50	100	0	0	2
14. Lygaeidae	120	2	50	100	0	0	2
15. Anomalidae	81	0					
16. Ricaniidae	360	5	50	100	0	0	2
17. Flatidae	1000	15	50	100	0	0	2
18. Derbidae	1350	129	80	50	0	50	3/4
19. Achilidae	19	3	100	50	0	50	2
20. Memphidae	100	11	50	100	0	0	2
21. Kinnaridae	42	0					
22. Dictyopharidae	570	4	50	100	0	0	2
Sternorrhyncha							
23. Psyllodea	2300	78	75	100	0	0	1
24. Aphidoidea	4100	40	25	100	0	0	1
25. Aleocharidae	1200	125	75	100	0	0	2/3
26. Coccinea	5900	50	30	100	0	0	3
HETEROPTERA							
27. Aradidae	1800	18		0	0	100	2
28. Psephenidae	40	0					
29. Colobathridae	70	0					
30. Berytidae	160	1		90	10	0	2
31. Maltidae	20	0					
32. Lygaeidae	3100	72	15	95	0	5	2/3
33. Pyrrhocoridae	420	1		95	5	0	2
34. Largidae	100	2		90	10	0	2
35. Stenocephalidae	40	0					
36. Coreidae	2000	5		100	0	0	2
37. Alydidae	250	5		100	0	0	2
38. Rhopalidae	150	0					
39. Urostylidae	100	0					
40. Acanthosomatidae	200	0					
41. Cydnidae	400	19	2	90	0	10	2
42. Plataspidae	500	4	2	100	0	0	2
43. Pentatomidae	5500	17	20	90	10	0	2/3
inc. Pentatomidae							
44. Thaumastocoridae	12	0					
45. Tingidae	1820	28	2	100	0	0	2
46. Miridae	6500	195	30	90	10	0	2/3
inc. Isometopidae							
47. Microphysidae	25	0					
48. Nabidae	370	6	2	0	100	0	
49. Phlokiophilidae	13	0					
50. Anthracoridae	500	35	2	0	90	10	
51. Cimicidae	80	0					
52. Polycetidae	31	0					
53. Pachynomidae	16	0					
54. Reduviidae	5000	36	20	0	95	5	
55. Saldidae	260	0					
56. Leptopodidae	30	0					
57. Diposoridae	23	2	2	0	100 ²	0	
58. Geratocombidae	45	0					
59. Schizopteridae	155	15	2	0	100	0	
60. Encicrphalidae	260	10	2	0	100	0	
Total	78656	1690					

TABLE 2. Host-plant specificity of herbivorous Hemiptera on Sulawesi. For explanation on specificity categories see text

Specificity category	Percentage of fauna
1	8.8
1/2	46.2
2/3	30.6
3	9.5
3/4	4.8

groups lying above the line are over-represented in the Sulawesi fauna relative to the world fauna: those lying below the line are under-represented. Amongst the larger groups, containing more than 500 species, the Cicadelloidea, Delphacidae, Cixiidae, Derbidae, Psylloidea, Aleyrodoidea, Miridae and Lygaeidae were over-represented. The Cicadoidea, Membracoidea, Cercopoidea, Fulgoroidea, Issidae, Flatidae, Dictyopharidae, Coccoidea, Aphidoidea, Pentatomoidea, Reduviidae, Plataspidae and Aradidae were under-represented.

The mean proportion of undescribed species weighted according to the number of species per family works out at 62.5%. The probable proportions of herbivores (87%), predators (7%) and others (6%) were calculated in a similar manner. The probable host-plant specificity of the herbivores is shown in Table 2 in which the numerical ratings correspond to the category numbers previously described. Responses to the questionnaire indicated that some families fall within two categories and these are given a double entry such as 1/2. No group fell within the strict 2 category. The 'average specificity' works out at 1.9, implying that the 'average' species uses a restricted but broadly spread range of host plants within a single family.

Insect groups for which reliable estimates of host specificity were not available were excluded from the calculations but together they represented less than 10% of the fauna and their omission should not unduly influence the conclusions.

INTERPRETATION AND DISCUSSION

Data on the Hemiptera fauna of Sulawesi provide a basis for the estimation of total Hemiptera and insect diversity. Erwin's well publicized estimates of the world beetle and insect faunas are based on extrapolations from the numbers of beetle species found on 19 specimens of a single neotropical tree species *Luehea seemannii*. May (1986) and Stork (1988) have already pointed out how sensitive the totals are to varying the assumptions made about the host-plant specificity of the beetles. The whole concept of applying host-specificity data and extrapolating from the fauna of single tree species is open to question. Twenty percent of beetle species collected from *Luehea* may be host specific but that does not mean they are specific to *Luehea*. There is a high level of vagrancy in tropical rain forest insects and a significant proportion of the fauna of any tree species comprises dispersing animals. For example, our work on the highly host-specific Psylloidea of Panama showed that a light trap hung in a particular tree caught over 70 species, none of which were specific to that tree! To interpret that sample

correctly one needs to know the identity of at least all the adjacent trees. In the Panama example one species appeared to originate from coastal mangrove swamp many kilometres away. The capacity for compounding errors when 19 trees are considered is immense. A large sample of different tree species is necessary to average out the effects of vagrancy between tree species. Specificity arguments, associating insects with particular tree species, are largely irrelevant when estimating the total number of insect species. Non-specific species, distributed between many hosts tend to be ignored. What matters is the total number of insect species present per area and the overall ratio of insect to tree species. For example, within an area there may be 1000 insect species and 500 tree species. Host plant relationships could be distributed with minimum equitability such that each tree would be fed on by just two completely specific insects or, with maximum equitability, such that each tree species was fed on by all 1000 insects. In both cases the number of insects and trees is the same but the conclusions that might be drawn from a knowledge of the fauna of just one tree would be quite different. Similarly, it is difficult to see how it can be argued that many predators or fungivores are specific to certain tree species. One must also question whether a sample obtained by canopy fogging alone is truly representative. Our data suggest that a variety of sampling techniques is required to obtain a truly representative sample of the fauna of a particular area.

In trying to arrive at a sensible global projection of the number of Hemiptera species two alternative approaches are worth considering. First one can regard the Sulawesi fauna as a sub-sample of the world fauna. By examining the ratio of undescribed to described species, an estimate of the global number of species can be extrapolated. Second, if we consider the number of tree species known from the Dumoga area to be c. 500, a reasonable assumption knowing that on the adjacent island of Borneo, with a tree flora of 1500 species (Mabberley, 1983), 1.2 ha plots can support up to 250 species (Whitmore, 1984), we can view this in a representative subset of the 50 000 known rain forest tree species and multiply the faunal count accordingly. There are, unfortunately, no good comparable floral surveys for Sulawesi (Whitten, Mustafa & Henderson, 1987).

The Sulawesi sample comprises 1690 species of Hemiptera of which 62.5% are undescribed. This is equivalent to one species for every 41 or 43 described species, dependent on whether terrestrial Hemiptera are considered alone or with the addition of the aquatic species. This represented one described Sulawesi species for every 109 or 114 described Hemiptera species. Multiplying these figures by 1690 gives an estimate of the total world number of Hemiptera of 184 000–193 000 species. Hemiptera have been shown to comprise 7.5% of all described insect species (Southwood, 1978) or about 10% of rain forest canopy insects (Stork, 1988). Multiplying by these factors produces estimates of 1.84–2.57 million for the total number of insect species.

Alternatively it can be argued that 500 species of Sulawesi tree produced 1690 \times 62.5% = 1056 new species of Hemiptera. By simple proportionality the 50 000 world species might produce 105 600 new species. When added to the 81 700 species already described this gives a grand total of 187 300 species of Hemiptera or a global insect fauna of 1.87–2.49 million species, a figure surprisingly close to the earlier estimate.

The above estimates of the number of extant insect species are very much lower than the figures of 10–80 million species predicted by Erwin and Stork. It

may be that beetles, with their more varied biologies, are intrinsically different and that the higher estimates are correct. However, several reasons convince us that our estimates are closer to the truth. They are:

- (1) The estimates are based on a large sample collected over a long period of time at many localities using several different sampling methods. It is not based on the fauna of a single tree species.
- (2) Assumptions are kept simple and extrapolation based on assumptions of host-plant specificity are avoided.
- (3) No assumptions are made about the relative richness of canopy and ground level fauna.
- (4) More realistic assumptions are made about the proportion of the group under study within the total fauna.
- (5) No single parameter used in the calculations is sufficiently sensitive to manipulation so as to produce large differences in the estimates obtained. Much of the variation in the beetle-based estimates derives from the sensitivity of the analysis to what in reality are arbitrary figures for the host-plant specificity of the beetles.

Nevertheless, it has been suggested that the Sulawesi forests may be less florally diverse than similar forests elsewhere (Whitten *et al.*, 1987). This may have influenced Hemiptera diversity. However, unlike much South East Asian rain forest, that on Sulawesi is not dominated by a single family of trees, the Dipterocarpaceae. Furthermore, Sutton (1983) presents evidence from light trapping at Morowali, Sulawesi that the numbers of Homoptera species are not markedly lower than at equivalent sites in Brunei and Panama. His Sulawesi data, together with that of Stork (1987) for Borneo, also add some support to our contentions. They show that the levels of similarity between the Hemiptera faunas on trees of the same species differ little from the faunal similarities between trees of different species. This suggests that only a relatively small proportion of the fauna captured was unique to any one tree species and that a significant element of the fauna is generally, if somewhat patchily, distributed. This corresponds with our data on the presumed host preferences of the Hemiptera fauna.

In conclusion, the number of insect species, while huge, may not be as staggeringly high as we have been led to believe. To paraphrase Prof. J. B. S. Haldane (or was it T. H. Huxley?) (Fisher, 1988), our Creator may have an inordinate fondness for beetles but maybe he shows a lesser predilection for bugs. It may be that the perceived number of insect species depends on the group from which the extrapolations are made!

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