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THE BIODIVERSITY OF ARTHROPODS FROM AUSTRALIAN RAIN FOREST CANOPIES: SUMMARY OF PROJECTS AND THE IMPACT OF DROUGHT

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ABSTRACT. Studies of canopy arthropods in a number of Australian rainforest types have been in progress since 1983. Information on the variation in ordinal signatures and overall levels of abundance in tropical, subtropical and cool temperate sites is available, as are estimates of beta-diversity among sites within the subtropical forest. Species level studies on selected Orders are well advanced and current work focuses upon the Coleoptera, Psocoptera, Collembola and Lepidoptera.

A severe drought affected the tropical forests of North Queensland in 1991–1992. This had the impact of reducing insect numbers dramatically particularly in the high canopy. Significant declines in numbers of Diptera, Coleoptera, Lepidoptera and Collembola were recorded. A significant increase in the numbers of Psocoptera was noted. Impact appeared to be generally greater in the high than the low canopy. The possible mechanisms for these patterns are discussed.

INTRODUCTION

In 1988 two things were very clear to me: first, that Australians had finally realized that they were in possession of the only continental tropical rain forest in the "developed" world and, second, that arguments favoring conservation and advocating management of this rainforest based on the biodiversity of an area, although appealing, had very little data to back them up.

In spite of the justifiably great excitement generated by results published on the arthropod assemblages from rain forest canopies in the Neotropics and southeast Asia, the number of data sets available in 1988 was pitifully small. Although others have been added to this set since then our global information base is still lacking (Erwin 1982, 1983, Adis 1990, Stork 1987a, 1987b, Stork & Brendell in press, Hammond 1990, Basset & Kitching 1991). The few data sets available have created a healthy secondary industry (e.g., Stork 1988, May 1990, Adis 1990, Blackburn *et al.* 1990, Gaston 1991), with many delighted to rework, comment and criticize, many fewer to engage in the considerable effort (even pain), expense and frustration of trying to collect additional data sets.

In 1983, Meg Lowman initiated a long-term study of herbivorous insects in Australian rain forest canopy. Beginning in 1988, Lowman and I collaborated on a project which would examine general arthropod biodiversity of the canopy of subtropical rainforest adjacent to Lamington National Park in southeast Queensland.

This subtropical study was to provide a benchmark and trial run for studies which subsequently have extended to tropical sites at Cape Tribulation in the far north of Queensland and to cool temperate rain forest sites in northern New South Wales. Since 1988 the work has involved a range of co-workers: Meg Lowman, Sue McIntyre and Margaret Greenway as botanists, Joy Bergelsen as biometrician and a host of entomological and botanical taxonomists listed in full elsewhere. The work hereto has been largely supported through Earthwatch with additional funds from the Australian Geographical Society, the Melbourne-based Ian Potter Foundation and the Australian Research Committee.

As the early results of this work move (slowly) to publication (see below), I take this opportunity to present a summary of the work to date. In addition I present a short set of new data which, serendipitously, we were able to collect to exploit the extraordinary drought situation encountered in February 1992 in the coastal rainforests of Cape Tribulation, in dramatic contrast to our field work there in February 1991.

I. SUMMARY OF WORK IN PROGRESS

General Methods

We sample arthropods by spraying first the lower and then the upper canopy at each of our selected sites with a mixture of pyrethrins delivered from a simple backpack sprayer hauled into the canopy by rope. We do not use a fogging technique and the insecticidal mist produced is of larger droplet size, shorter lived and less visible than that of fog-generating machines. The details of our technique are described in Kitching *et al.* (in press) together with botanical, climatic and locational details of our three study forests.

Most of our work to date has focussed on selected 10 × 10 m^2 columns of forest with variously mixed canopies. Following each sampling exercise we have then carried out botanical surveys of each site by constructing vegetation profiles through each sampling point. We have sampled twenty sites from the subtropical forest in southeast Queensland and seven from the lowland tropical forests at Cape Tribulation. Work in the near monocultural *Nothofagus*-dominated cool temperate forest sites uses a variation on this general technique and is described in Kitching *et al.* (in press). Extensive herbarium material has been accumulated, of necessity, from the tropical sites, most of the subtropical and cool temperate woody plants can be identified in situ.

Most recently, we have moved in part away from this "mixed canopy block" approach to a "single tree" technique designed, ultimately, to quantify levels of tree specificity within the arthropod assemblages. So far we have focussed, for purely practical reasons, on understory species and have samples awaiting analysis from four species from the subtropical forest and a range of species from the tropical forest. The further analysis of these samples and the extension of the project to cover many species proceeds slowly while awaiting further funding.

Ordinal Signatures from Three Forest Types

In addition to presenting general information on methods and study sites, the paper by Kitching *et al.* (in press) illustrates and analyzes ordinal level differences across the three forest types studied, each based on summer (wet season) samples.

Among the insects there is a distinct cool-temperate to tropical change in the ordinal signature which was highly significant statistically. This trend was reflected, most obviously, in the decrease in the proportion of Collembola and an associated increase in numbers of Diptera. The former trend may reflect an association between abundance of Collembola and the level of occurrence and nature of epiphytes in the canopies. The increasing occurrence of Diptera in the tropical samples probably reflects the semi-aquatic nature of a majority of their larval stages and the increased moisture levels in tropical compared with more temperate canopies (see discussion of drought impacts below). The non-insectan arthropods similarly showed a clear south–north pattern with the ratio of spiders to mites increasing in favor of the spiders in more tropical samples.

This paper also compared numbers of insects and their ordinal profiles between high and low canopy samples from the subtropical and tropical sites. Both insects and non-insects showed a significant decrease in number from low to high samples in the subtropical forest. In the tropical samples only the insects showed this pattern; for non-insects high and low canopies numbers were not significantly different. The ordinal profile of the insects differed across the two layers in the subtropical forests only. The ordinal profiles of non-insects showed no such pattern.

Beta Diversity across Subtropical Sites

A manuscript has been prepared which calculates beta diversity coefficients (both Sørensen's Index and the Horn-Morisita Index) for Psocoptera, Coleoptera and woody plants among 13 of the subtropical sites studied (R. L. Kitching, J. Bergelson, N. Stork unpubl. results).

In summary there is a strong negative relationship between intersite similarity for Psocoptera when calculated on the basis of relative abundance of species (Horn-Morisita analysis) which is absent when calculated on presence or absence of species only (Sørensen Analysis). We take this to mean that the variation observed between sites captures population-level variation of the psocopterans involved but that our scale of study is at the within-assemblage level which does not pick up changes in species composition. Results for the Coleoptera show no relationships with distance.

There is a weak but significant relationship between the Horn-Morisita similarity for Coleoptera and that for woody plants suggesting beetle diversity roughly parallels woody plant diversity within a single patch of forest.

Psocoptera Studies

The Psocoptera in our canopy samples from the subtropical forest have been sorted to morphospecies. There are approximately 50 species involved, about half of which have been previously described. The cumulative discovery curve for these species across samples is curvilinear and apparently asymptotic allowing some estimate of the overall size of the fauna (Kitching in press, E. Schmidt & R. Kitching unpubl. results). Work extending these analyses to include samples from subtropical and tropical forest samples is in progress. An experiment comparing psocopteran diversity across bark types and different degrees of micro-epiphyte load will be carried out in December 1992 (D. Brown unpubl.).

Coleoptera Studies

The Coleoptera from 13 of our subtropical canopy samples have been sorted to morphospecies (N. Stork, P. Hammond, R. Kitching unpubl.). There are 440 morphospecies in these

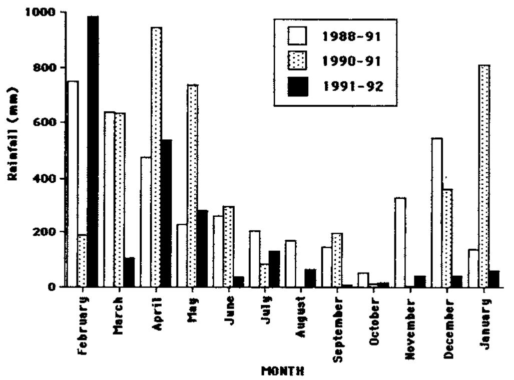

FIGURE 1. Climatic Data from "Pilgrim Sands," Cape Tribulation, North Queensland.

samples dominated by the Staphylinidae, Curculionidae, Lathridiidae and Chrysomelidae (Kitching in press). The cumulative species discovery curve remains linear. The morphospecies have been further classified into broad trophic guilds (saprophages, xylophages, fungivores, herbivores, predators) and log abundance vs. log size curves plotted for each. These results show the characteristic triangular plot identified by Lawton (1989, 1990).

Collembola Studies

It was initially surprising to us to observe the degree to which our subtropical samples were dominated, in terms of numbers of individuals, by the Collembola (Kitching in press). These samples have now been analyzed further and the Collembola samples further sorted to families, the Entomobryidae and Paronellidae to morphospecies (Sutrisno & P. Greenslade unpubl.). Twenty-one morphospecies were present in our high canopy samples and 26 in the low canopy. One species of *Epimetrura,* previously known only from single specimens from Borneo and China, dominated these samples and is undoubtedly a canopy specialist (Sutrisno & P. Greenslade unpubl.).

Some comparisons of Collembola diversity from the canopy with coincident samples of litter and from pitfall traps have also been made by Sutrisno and will be presented as part of his Masters' thesis.

Lepidoptera Studies

Lepidoptera are not well sampled by pyrethrum knockdown, so in February 1992 (in the tropical forest at Cape Tribulation) we carried out ten nights of intensive light trapping on a platform in the low canopy, shielded from beneath, and at two adjacent ground sites, shielded from above (D. Harmsen & R. Kitching unpubl.). Virtually all moths attracted to the light were captured, preserved and identified to morphospecies subsequently. Over 4,000 moths were represented by 490 morphospecies. These were dominated by the Noctuidae and Pyralidae. Size profiles showed a common peak across both ground and canopy samples but an additional, higher mode in the ground samples. These data are currently being analyzed and prepared for publication.

A parallel survey of moths in the subtropical forest is planned for the 1992–1993 summer.

II. The Impact of Drought on Tropical Canopy Assemblages

Introduction

In February 1992 our regular annual sampling expedition to the tropical rainforests of Cape Tribulation in North Queensland coincided not with the expected height of the wet season but with the culmination of an exceptional period of drought. Rainfall figures for the twelve months preceding the sampling period are presented in FIGURE 1 together with comparative figures preceding our 1991 sampling period and the longer term average rainfall for the period 1987–1991. All these figures are from records kept at "Pilgrim Sands," the base of our North Queensland operations. The low levels of rainfall experienced in the area from mid 1991 up to February 1992 were at levels not previously experienced since the 1940's (local anecdotal information).

The impact of the drought was evident as substantial wilting of leaves on many species of tree and widespread leaf loss to the point that a few tree species were almost completely defoliated. In particular withering and even death of epiphytic ferns was apparent.

We took the unexpected opportunity to estimate the impact of this drought on the canopy arthropods by resampling six sites previously sampled in February 1992. Exactly similar techniques were used across the two years.

Methods

General descriptions of the vegetation of the area are given by Jessup (1985) and in Kitching *et al.* (in press). The latter of these two papers also discusses in detail site selection and methods.

Essentially in each of six sites a 10 m × 10 m section of forest was marked out and a head-high "cats cradle" of light ropes strung within these limits. For each sampling event eleven 0.5 m^2

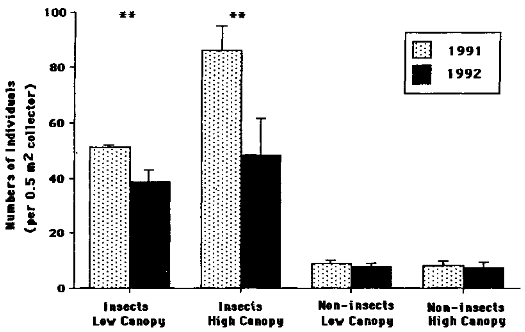

FIGURE 2. Total numbers of insects and non-insectan arthropods collected per 0.5 m^2 collecting funnel from rainforest canopy from six sites in 1991 and 1992 from Cape Tribulation, North Queensland. Counts are shown ± 1 standard error.

collecting funnels were hung throughout the area. A four to six minute treatment with pyrethrum insecticide delivered by a backpack mister was used on each sampling. Two samples were taken at each site: one with insecticide delivered from the ground and directed at the understory up to about 6 m in height, the second from the same mister suspended in the high canopy at 15 to 20 m. All samples were taken in the morning. These samples are referred to as "low canopy" and "high canopy," respectively.

Arthropods knocked down by the pesticide were brushed into central vials containing ethanol. These were removed three hours after the spraying event, returned to the laboratory, and sorted to Order.

Two of the six sites used in each year were located in littoral forest and four in lowland forest about two km from the coast. All samples were taken in the same ten-day window of time in each of the two years.

All results were converted to counts per collecting hoop (i.e., per 0.5 m^2) and these figures used for all further analyses.

Results

Two sets of results are presented here. FIGURE 2 shows the total numbers of insects and non-insectan arthropods collected in each of the two years. FIGURES 3 and 4 show the ordinal signatures for insects and non-insects from the two years.

NUMBERS OF INDIVIDUALS. As indicated in FIGURE 2 there was a marked decline in total numbers of insects in both the low and high canopy samples across the two years. Samples from the low canopy showed, on average, a 24% reduction in 1992 compared with 1991 ($t = 2.16$, $P = 0.058$). A greater decline was shown by the insects from the high canopy samples with a 44% decline from 1991 to 1992 ($t = 2.23$, $P = 0.05$). Numbers of non-insectan arthropods also declined in both low and high canopy samples but these did not lead to significant differences between the two figures.

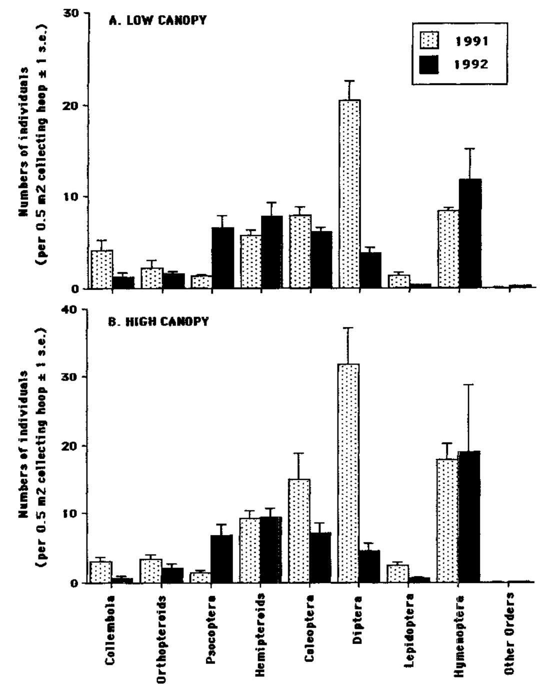

FIGURE 3. Numbers of insects in each Order collected per 0.5 m^2 collecting funnel from low and high rainforest canopy from six sites in 1991 and 1992 from Cape Tribulation, North Queensland. Counts are shown ± 1 standard error. Asterisks indicate significant differences between non-drought and drought years (see text).

ORDINAL SIGNATURES. Although declines in overall numbers of insects are shown clearly in the results, the differences between the two years are shown more dramatically when the ordinal signatures from the two sets of samples are compared (FIGURE 3). We carried out a two-way nested ANOVA on these data after applying a square root transformation to homogenize the variances. Each Order of insects and non-insects was used as the dependent variable, and canopy layer nested within sampling year was the treatment protocol. The six sites used in each year provided the replicated data in the analysis. TABLE 1 presents a summary of the results of this procedure.

The treatment variable "year" had a highly significant effect on five of the insect Orders. The

Collembola, Coleoptera, Lepidoptera and Diptera showed significant declines from 1991 to 1992 (that is, from non-drought to drought year) and the Psocoptera showed a significant increase in abundance between the two years. By level of significance, the ordering of the magnitude of the negative impacts was: Diptera > Lepidoptera > Collembola > Coleoptera. The positive impact on the Psocoptera was at a very high level of significance ($P = 0.0005$). Excluding the categories "other orders" and "Crustacea" and "other non-insects" in which actual counts were so low that we discount the significances as likely to represent Type I errors, Canopy Layer/Year interactions approached significance in four cases: hemipteroids ($P = 0.06$), Coleoptera ($P = 0.07$), Diptera ($P = 0.08$) and Lepidoptera ($P = 0.09$). Although not reaching the 0.05 level of significance, these results do confirm the indications apparent in FIGURE 3 that the impact of drought may well be greater in the more exposed upper canopy than the more protected lower canopy. They also reinforce the differences in overall insect abundance seen in FIGURE 2.

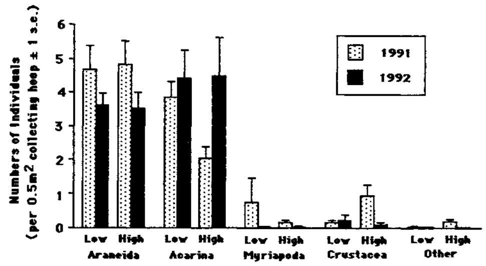

FIGURE 4. Numbers of non-insectan arthropods in each Order collected per 0.5 m^2 collecting funnel from low and high rainforest canopy from six sites in 1991 and 1992 from Cape Tribulation, North Queensland. Counts are shown ± 1 standard error.

Discussion

The severe impact of an acute drought in such a mesic environment as a tropical rainforest is, perhaps, not surprising. The particular value of our results, we believe, is that they document for the first time impact on the arthropod assemblage within the forest canopy and identify the differential impacts across arthropod groups. Negative impacts on the Collembola, Coleoptera, Diptera and Lepidoptera must be considered in the light of the likely susceptibility of each group to desiccation.

The Collembola are conventionally thought of as a group where the abundance and diversity closely reflects the environmental conditions of their habitats; humidity plays a particularly important role in this respect (Christiansen 1964, Fjellberg 1985, Kitching *et al.* in press, Sutrisno, Greenslade & Kitching in prep.). Even in unstressed forests the canopy Collembola are less abundant in high canopy compared with low canopy samples (Kitching *et al.* in press, Sutrisno, Greenslade & Kitching in prep.). Their relatively soft, lightly sclerotized cuticle presumably underlies this suceptibility to any drying influence (Greenslade 1991).

The Diptera dominate samples of arthropods in non-drought years (Kitching *et al.* in press). Their substantial decline in the drought year probably reflects the moist habitat associations of the larvae of most species (Brauns 1954, Colless & McAlpine 1991): associations with moist leaf litter, decomposing matter or free water. A further minor contribution may also be associated with a decline in the availability of flowers and fruits in the forest in response to the drought conditions although good corroborative evidence is lacking in this case.

Drought associated declines in numbers of Lepidoptera, as in the case of the Collembola,

TABLE 1. Results of the taxon by taxon analysis (see text for further details).

Taxon	Significant factor	F-ratio	LSD
Insecta			
Collembola	Year	df = 1,15 $P < 0.001$	1991 > 1992
Orthopteroids	None	df = 1,15 $P > 0.05$	–
Psocoptera	Year	df = 1,15 $P < 0.0001$	1992 < 1991
Hemipteroids	Canopy	df = 1,15 $P < 0.05$	High > Low
Coleoptera	Year	df = 1,15 $P < 0.05$	1991 > 1992
Diptera	Canopy	df = 1,15 $P < 0.0001$	1991 > 1992
Lepidoptera	Year	df = 1,15 $P < 0.0001$	1991 > 1992
Hymenoptera	None	df = 1,15 $P > 0.05$	–
Non-Insects			
Araneida	None	df = 1,5 $P > 0.05$	–
Acarina	None	df = 1,5 $P > 0.05$	–

may reflect the general desiccation-sensitivity of soft bodied insects—in this case lepidopterous larvae. Many species also feed in exposed positions on foliage and may, accordingly, be more susceptible to drying influences. Leaf and epiphyte death and wilting (observed commonly in the drought-stricken forest) may also have a negative effect on folivores whether they are external or internal feeders upon the leaves and stems.

The decline in Coleoptera abundance is of particular interest as the impact, although significant, is nowhere near as severe as for the other Orders described (a significance level of 0.049 compared with 0.0017, 0.0001 and 0.002—TABLE 1). This fits well with the idea that the high impact observed elsewhere is a measure of direct desiccation susceptibility as, a priori, one would expect the Coleoptera, with their highly sclerotized cuticles and great mobility, to be somewhat less effected than other groups. Their prominence as herbivores, nevertheless, may well have led to the observed decline produced indirectly through decline in the quality and quantity of their food resources.

The significant increase in the abundance levels of Psocoptera in the drought as opposed to the non-drought year is noteworthy as it is counter to the clear trend in other groups. There are several possible reasons for this trend but each can only be a hypothesis for testing at this stage. First, the Psocoptera, being exopterygotes, do not have a desiccation sensitive larval stage, in contrast to the Diptera or Lepidoptera, for instance. Second, the general decline in numbers of insects may indicate a relaxation of predatory pressure on the group, although the absence of a significant decline in our data in the key predatory group, the spiders, mitigates against this. Generalist vertebrate predators, principally birds, may also have reduced impact if, as anecdotal evidence suggests, they abandoned the insect-poor drought-affected forests for other foraging grounds. Last, and possibly of greatest significance, may be a drought-related reduction in fungi-induced pathogenicity. New (1987) notes several instances of fungal attack particularly on the eggs of Psocoptera in his review of the biology of the Order.

Overall the very dramatic impact of drought on the fauna of the rain-forest canopy points out the sensitivity of these ecosystems to environmental change. The enormous species richness we have come to associate with rainforest canopies, particularly in the tropics, is associated with the highly predictable, mesic environment which allows fine partitioning of resources and the gradual build-up of species as vegetation structure becomes more complex and associated habitats become available. This very complexity and the narrow niches assumed by the fauna become a liability when major impacts occur on the forest such that a disproportionate loss in individuals and, possibly, species richness may result. Occasional droughts such as the one monitored here may not be environmental disasters if, as was the case in 1991–1992, they are very occasional events. The situation may be quite different if on-going change is imposed upon the forest either through over-exploitation or global climatic change.

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LITERATURE CITED

ADIS J. 1990. 30 million arthropod—too many or too few? Journal of Tropical Ecology 6: 115–118.

BASSET Y. AND R. L. KITCHING. 1991. Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. Ecological Entomology 16: 391–402.

BLACKBURN T. M., P. H. HARVEY, AND M. D. PAGEL. 1990. Species number, population density and body size relationships in natural communities. Journal of Animal Ecology 59: 335–345.

BRAUNS A. 1954. Terricole dipteranlarven, Musterschmidt, Wissenschaftlicher Verlag, Göttingen, Frankfurt, Berlin.

CHRISTIANSEN K. 1964. Bionomics of Collembola. Annual Review of Entomology 9: 147–178.

COLLESS D. H. AND D. K. MCALPINE. 1991. Diptera (flies). Pp. 717–786 *in* Insects of Australia, 2nd ed. (C.S.I.R.O.). Melbourne University Press, Melbourne.

ERWIN T. L. 1982. Tropical forests: their richness in Coleoptera and other species. Coleopterists' Bulletin 36: 74–75.

———. 1983. Beetles and other arthropods of the tropical forest canopies at Manaos, Brasil, sampled with insecticidal fogging techniques. Pp. 59–75 *in* S. L. SUTTON, T. C. WHITMORE, AND A. C. CHADWICK, eds., Tropical rain forests: ecology and management. Blackwell Scientific, Oxford.

FJELLBERG A. 1985. Recent advances and future needs in the study of Collembola biology and systematics. Quaestiones entomologicae 21: 559–570.

GASTON K. J. 1991. The magnitude of global insect species richness. Conservation Biology 5: 283–296.

GREENSLADE P. 1991. Collembola (Springtails). Pp. 252–264 *in* Insects of Australia 2nd ed. (C.S.I.R.O.). Melbourne University Press, Melbourne.

HAMMOND P. M. 1990. Insect abundance and diversity in Dumoga-Bone National park, North Sulawesi, with special reference to the beetle fauna of lowland rainforest in the Toraut region. Pp. 197–260 *in* W. J. KNIGHT AND J. D. HOLLOWAY, eds., Insects and the rain forest of South East Asia (Wallacea). Royal Entomological Society of London, London.

JESSUP L. W. AND G. P. GUYMER. 1985. Vascular plants recorded from the Cape Tribulation area. Queensland Naturalist 26: 2–19.

KITCHING R. L. (in press) Biodiversity and taxonomy: impediment or opportunity? *In* C. MORITZ, ed., Conservation biology in Australia and Oceania. Surrey Beatty, Sydney.

———, J. M. BERGELSON, M. D. LOWMAN, AND S. MCINTYRE. (in press) The biodiversity of arthropods from Australian rain forest canopies: general introduction, methods, sites and ordinal results. Australian Journal of Ecology.

LAWTON J. H. 1989. What is the relationship between population density and body size in animals? Oikos 55: 429–434.

MAY R. M. 1990. How many species? Philosophical Transactions of the Royal Society of London B 330: 293–304.

NEW T. R. 1987. Biology of the Psocoptera. Oriental Insects 21: 1–109.

STORK N. E. 1987a. Guild structure of arthropods from Bornean rain forest trees. Ecological Entomology 12: 69–80.

———. 1987b. Arthropod faunal similarity of Bornean rain forest trees. Ecological Entomology 12: 219–226.

———. 1988. Insect diversity: facts, fiction and speculation. Biological Journal of the Linnean Society 35: 321–337.

——— AND M. J. D. BRENDELL. (in press) Arthropod diversity studies in lowland rain forest of Seram, Indonesia. *In* J. PROCTOR AND I. EDWARDS, eds., The natural history of Seram.