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THE COMPOSITION AND RICHNESS OF THE TREE-CROWN COLEOPTERA ASSEMBLAGE IN AN AUSTRALIAN SUBTROPICAL FOREST

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Abstract. The assemblage of beetles (Insecta: Coleoptera) present in the canopy of subtropical rainforest at Lamington National Park, Queensland, Australia was sampled using a pyrethroid insecticide as a knockdown agent. 110 m^2 of canopy sampled yielded 2,269 Coleoptera of 454 species. The species richness, taxonomic composition and trophic guild composition of these canopy beetle samples was compared with those of similar samples from other regions. The Queensland samples prove to be more species rich than samples from the U.K., but less species rich than ones from tropical sites, e.g., Brunei and Panama. In taxonomic and trophic guild composition the Queensland samples most closely resemble those from the U.K., and least closely resemble those from Panama. The most notable features of the Lamington beetle samples are the high proportion (21.1 %) of xylophagous pecies, and the strong representation of species of Corylophidae (5.9 %), Anthribidae (4.8 %) and Pselaphidae (3.3 %). *Accepted 11 November 1996.*

Key words: Arthropods, Coleoptera, rainforest, canopy, ecology, species richness, trophic groups, Australia.

INTRODUCTION

Rain forest canopies harbour exceptionally rich assemblages of arthropods (Erwin 1982; Stork 1988, 1991; Wilson 1992; Stork *et al.*; in press). Although borne of studies of Neotropical (Erwin & Scott 1980; Erwin 1982, 1983, 1990; Adis *et al.* 1984, Adis & Schubart 1984) and south-east Asian forests (Stork 1987a, 1987b, 1988, 1991; Stork & Brendell 1990, 1993; Hammond 1990; Hammond *et al.*, in press), this generalisation appears to apply also to the hereto little studied canopies of Australian rainforests (Basset 1990, Lowman 1982). Since 1988 the arthropod fauna of the canopies of Australian rainforests has been the subject of investigation using, inter alia, insecticide knockdown techniques already used so effectively elsewhere. Results so far presented have described techniques, study sites and results obtained at ordinal level (Kitching *et al.* 1993), the impact of drought on the size and composition of the canopy fauna (Kitching & Arthur 1992), and preliminary analyses of specificity in the arthropod assemblages associated with selected species of tree (Kitching & Zalucki, in press). Other studies in Australia have looked at the insect assemblages (Lowmann 1982, Basset 1990), and in particular ants, in other forests (Majer 1990, Majer & Recher 1988).

An important part of this programme of work has been to examine the representation in rain forest canopy samples of major groups, emphasising faunistics and ecological roles. The present paper examines the taxonomic and guild structure of one of the largest components, the assemblage of Coleoptera, from canopies of subtropical rainforest in south-East Queensland. Coleoptera have featured prominently in canopy studies published to date (see references above). One reason for this is that large numbers of species are to be found within any fauna (Hammond 1992) or even at a single site, making it relatively easy to detect faunistic and ecological patterns. In addition, the Coleoptera are trophically diverse, unlike, say the Lepidoptera, and large samples of beetles contain species representing many different components of the natural communities of which they form part. Finally, many of the Coleoptera present in canopy samples are 'canopy specialists' and not merely 'tourists' (Hammond 1990, 1992, 1995; Stork 1987a, 1988; Gaston *et al.* 1993; Hammond *et al.*, in press).

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METHODS AND STUDY SITES

A full account of the field methods used, together with descriptions of the study sites, is presented in the first paper of this series (Kitching *et al.* 1993). The relevant parts of this account are summarised here.

Study site. The area of forest studied is located around the 'Wishing tree track', just west of O'Reilly's Guesthouse, adjacent to Lamington National Park, south-east Queensland (28°13'S, 153°07'E). The forest is largely undisturbed notophyll vine forest, with a small proportion of more disturbed forest resulting from human activities 20 to 30 years ago. These more disturbed sites were clearly identifiable by the presence of the understorey tree *Acradenia euodiiformis*, highly characteristic of disturbance in this vegetation type.

Rainfall in the area is distributed throughout the year, with a summer peak in February and March (ca 500 mm per month) and a winter minimum in August (ca 100 mm per month). Mean maximum temperatures range from 16°C in July to 25°C in January, and mean minima from 8°C in July to 16°C in January.

The vegetation of the region has been described by McDonald & Whiteman (1979) and McDonald & Thomas (1990). The forest is a complex notophyll vine forest following the classification of Webb (1959), and is a 'Subtropical Rainforest, *Argyrodendron actinophyllum* alliance, Suballiance 11 (*Caldcly-via-Cryptocarya erythroxylon-Orites-Melicope octandra-Acmena ingens*)' of Floyd (1990). Seventy-four woody species were recorded from transects taken through the plots. The canopies were dominated by species such as *Geossois benthamina*, *Lophostemon conferta*, *Argyrodendron actinophyllum*, *Ficus watkinsiana*, *Baloghia lucida* and *Pseudowienmannia lachnocarpa*. The commonest understorey species were *Acradenia euodiiformis*, *Synoum glandulosum*, *Dysoxylon rubrum*, *Wilkeia* spp. and *Triunia youngiana*.

All plots selected for sampling were in forest with closed canopy, and were otherwise located randomly within the 1 km x 1 km study area. The precise location of sampling sites was guided by the need to centre each 10 x 10 m quadrat around a canopy tree with horizontal branches suitable for suspending the spraying device used for sampling. Between two and four tree species formed the canopy within each plot. The canopy trees involved (i.e., those above 15 m in height) were: *Geossois benthamina* (Cunoniaceae), at 6 plots, *Baloghia inophylla* Euphorbiaceae), *Caldclyvia paniculosa* (Cunoniaceae), *Planchonella australis* (Sapotaceae) and *Quintinia verdonii* (Escalloniaceae), all at 3 sites each, *Ficus watkinsiana* (Moraceae) at 2 sites, and *Acmena smithii* (Myrsinaceae), *Acradenia euodiiformis* (Rutaceae), *Argyrodendron actinophyllum* (Sterculiaceae), *Cryptocarya* sp. (Lauraceae), *Diploglottis australis* (Sapindaceae), *Lophostemon confertus* (Myrtaceae), *Orites excelsa* (Proteaceae), *Stenocarpus salignus* (Proteaceae) and *Syzygilum crebrinerve* (Myrtaceae), all at one site each. The overall floristic similarity among the study plots was assessed as 0.50+/-0.064 (Morisita Horn index of similarity) (see Kitching *et al.*, 1993, for details).

Field methods. At each sampling site a 10x10 metre area was marked out, orientated north-south. A line was thrown into the canopy using a sling-shot, and a central rope and pulley put in place. A head-high web of cords was established from which ten half-metre square collecting hoops were suspended. Each site was then sprayed twice, for 5 minutes on each occasion, using a Stihl SG-17TM backpack sprayer delivering the insecticide Pyrethrin 2EL(tm). The first spray was delivered from the ground with the mist directed at the lower canopy and understorey, and the second spray, 24 hours later, was delivered in the upper canopy with the sprayer suspended from the central rope. For the present analyses data from the upper and lower collections have been combined.

At nine sites ten funnels (occasionally with an 'extra' to allow for accidents) were employed. At one site twenty funnels were used. Samples were collected up after a three-hour 'drop time', and returned to the field laboratory. Full details of the sampling method and study sites are given by Kitching *et al.* (1993).

Sorting and analysis. Samples were sorted to ordinal level in the field laboratory. Subsequently, adult Coleoptera were card-mounted or pinned and sorted to species (by PMH and NES) at the university laboratory. For most groups, aided in some cases by study of male genitalia or other sexual characteristics, sorting was considered to be reliable. Of the few uncertainties remaining, most related to limits of certain of the species of corticariine Lathridiidae and eumolpine Chrysomelidae. As stressed by Hammond (1994), the quality of datasets such as the one discussed below depends first and foremost on the accuracy with which species have been sorted.

Following the definitions used by Hammond (1990) all species of Coleoptera were assigned to one

or other of 5 feeding 'Guilds': herbivores, xylophages, fungivores, saprophages and predators. As far as possible, this was done on an individual basis, species by species. Where the feeding habits of life stages was considered to differ, emphasis was placed on the larvae. As stressed by Hammond (1994), the possible margins of error in how species are allotted to feeding 'guilds' should be recognised (see also Stork 1987a). Considerable uncertainty remains as to the appropriate feeding 'guild' for some 20% or so of the Lamington Coleoptera species. For example, a high proportion of the Curculionidae in these samples are members of the Cryptorrhynchinae, and most of these were allocated to the xylophage category, although their feeding biology is uncertain. Assignations of species to feeding guilds for the U.K. sample are likely to be rather more accurate, while for the Panama sample assignations are likely to be less so, as the only data available were numbers of species present per family-group.

The system of 'family-groups' (i.e., either families or subfamilies, depending on their size and homogeneity) employed for the analysis follows that of Hammond (1990), with a few minor exceptions, these being that no subgroups of Carabidae, Hydrophilidae, Scarabaeidae or Tenebrionidae are used here. For the Panama sample (Erwin & Scott 1982) used for comparison, no data were available for individual subfamilies of Staphylinidae or for separate families of Curculionoidea, except Anthribidae.

In general, the taxonomic groups used here are equivalent to those employed by Lawrence & Britton (1991), except that several groups regarded by them as subfamilies are recognised as families here, for convenience. These 'families' are Scaphidiidae, Ptinidae, Lagriidae, Bruchidae, Apionidae, Scolytidae and Platypodidae. In addition, unlike Lawrence & Britton (l.c.) Alticinae and Zeugophorinae are recognised here, again for convenience, as distinct subfamilies of Chrysomelidae. Note also that family names and limits employed here differ in some instances to those of Erwin & Scott (1980) (see caption to Table 1).

RESULTS

The 110 m^2 of canopy sampled at Mt Lamington yielded 2,269 Coleoptera assigned to 454 species, belonging to 64 'familiy-groups' (Table 1). The number of species represented is high compared to the number (200) in samples taken in the U.K. from 818 m^2 of canopy (Hammond & Owen, in press; Stork & Hammond, in press), but lower than those reported for tropical samples from, for example, Brunei, with 859 species (4043 individuals) from 200 m^2 of canopy (Stork, 1991, also see Table 1), Sulawesi, with 1176 species (9158 individuals) (Stork & Brendell 1990; see also Hammond & Stork, in press), and Panama, with 956 species (7735 individuals) (Erwin & Scott 1980, see also Table 1). Direct comparison between these samples is hampered by the large differences between them in a number of important features, including the number of tress sampled, area of canopy sampled, number and seasonal spread of individual foggings, the fogging technique itself, and sample sizes.

The taxonomic composition of the Australian samples is similar in a number of respects to that of most fogging samples from forest canopies in other continents, most notably in the dominance of Curculionidae, Staphylinidae and Chrysomelidae (Tables 1 and 2). Compared in more detail with samples from sites in Panama, Brunei and the U.K., the greatest similarity, in terms of rank correlation (Table 3), is with the U.K. (rank correlation value = 0.70), and least with Panama (rank correlation value = 0.46). Compared with both Panama and Brunei (tropical forests), the representation in the Lamington samples of Ptiliidae, Lathridiidae and Scraptiidae is particularly high, and with respect to Panama (but not Brunei) that of Corylophidae, Anthribidae and Pselaphidae is also very high. In comparison with the U.K., the greatest differences are the better representation at Lamington of Corylophidae, Anthribidae, Pselaphidae and Tenebrionidae and the poorer representation of Cryptophagidae. As might be expected, some of these differences are attributable to differences of forest type sampled, namely moist tropical forest in Brunei and Panama, subtropical forest at Lamington, and moist temperate forest in the U.K. However, part of the explanation is also likely to be found in overall faunistic between the various biogeographical regions in question.

The numbers of Australian species currently described in each family of Coleoptera (Lawrence & Britton 1991) are unlikely to reflect at all accurately the genuine pattern of representation of these families in the continent. It is probable that most species remain undescribed and that the descriptive effort to date ist biased towards the larger and more "apparent" (Hammond 1990, 1995) of them. However, available data on the proportional representation of

TABLE 1. Coleoptera in canopy fogging samples from subtropical rainforest in Lamington National Park, Australia, with comparative data from other forests and woodlands. The Lamington data are for 110 m^2 of mixed canopy (see methods). The Brunei data are for 200 m^2 of canopy from 10 trees of 5 species (Stork, 1991). The Panama data are from the canopies of 19 individual trees of *Luehea seemannii* (Erwin & Scott, 1980). The U.K. data are for 818 m^2 of mixed deciduous canopy, mostly of the English Oak (Quercus robur) (Hammond & Owen, in press). The 'family-groups' (families and subfamilies) used and the feeding 'guild' definitions are those used by Hammond (1990). The guilds recognised are herbivores (H), xylophages (X), fungivores, including slime-mould feeders (F), saprophages (S) and predators, including parasitoids (P). Where 'f' is placed in parentheses this indicates xylomycophagy. As a result of further taxonomic investigation of the samples, the Brunei data differ in some details from those provided by Stork (1991). The Panama data do not include subfamily assignments for the Staphylinidae, and the Panama 'Curculionidae' (Erwin & Scott 1980) include Apionidae, Attelabidae and Brentidae. The Panama Nilionidae (Erwin & Scott 1980) are included here in Tenebrionidae. The Panama species listed as 'Cucujidae' (Erwin & Scott 1980) are probably largely or entirely equivalent to the Laemophloeidae and Silvanidae of the other sites, and some of the Panama species lisred as Cryptophagidae are likely to be equivalent to the Languriidae (in part) of samples from other sites (see asterisks). The Panama 'Colydiidae' may also include some Cerylonidae and/or Bothrideridae. Following the comments made by Erwin & Scott (1980) the number of species of Curculionidae senu lato given for Panama is ca 250, and the number of species of Staphylinidae is ca 164, an allowance of 50 extra species having been given for the Aleocharinae.

Taxa	Australia		Brunei	Panama	U.K.	'Guild'
	inds.	spp.	spp.	spp.	spp.	
Aderidae	19	9	45	11	1	S
Anobiidae	3	3	11	14	5	X,F
Anthicidae	2	2	12	15	0	S,?P
Anthribidae	58	22	39	11	0	F,H,X
Biphyllidae	3	1	0	1	0	F
Bruchidae	0	0	0	6	0	H
Buprestidae	0	0	17	14	2	H,X
Byrrhidae	1	1	0	0	0	H
Byturidae	0	0	0	1	0	H
Cantharidae	29	11	10	19	10	P
Carabidae	20	11	9	41	7	P
Cerambycidae	25	10	18	62	3	X
Cerylonidae	0	0	0	0	1	F
Chelonariidae	0	0	2	0	0	S
[Chrysomelidae	404	30	97	205	10	H]
Alticinae	243	16	15	66	8	H
Cassidinae	0	0	1	11	0	H
Chlamisinae	0	0	1	2	0	H
Chrysomelinae	9	1	0	2	0	H
Clytrinae	0	0	2	2	0	H
Cryptocephalinae	6	4	6	30	1	H
Eumolpinae	139	5	33	36	0	H
Galerucinae	7	4	35	41	1	H
Hispinae	0	0	4	9	0	H
Lamprosomatinae	0	0	0	1	0	H
Zeugophorinae	0	0	0	5	0	H
Cisidae	16	4	6	9	2	F
Clambidae	6	1	0	0	0	F
Cleridae	5	4	10	12	1	P
Coccinellidae	63	13	20	36	9	P,etc.
Colydiidae	9	3	7	5	1	F,etc.
Corylophidae	97	27	31	10	3	F
Cryptophagidae	52	4	0	*9	12	F
Cucujidae	0	0	0	*18	0	F,etc.
[Curculionidae	381	89	148	c.250	27	H,X]
Apionidae	35	8	14	?	5	H
Attelabidae	44	4	14	?	3	H
Brentidae	1	1	5	?	0	(F)
Curculionidae	301	76	115	?	19	H,X
Dermestidae	0	0	0	6	0	S
Discolomidae	0	0	1	0	0	F
Dryopidae	0	0	8	0	0	S
Dytiscidae	0	0	1	1	0	P

Taxa	Australia inds.	Australia spp.	Brunei spp.	Panama spp.	U.K. spp.	'Guild'
Elateridae	14	11	27	12	7	H,X,P
Endomychidae	8	4	10	5	0	F
Erotylidae	0	0	3	9	0	F
Eucnemidae	1	1	6	11	1	?F,?X
Heteroceridae	0	0	0	1	0	P
Histeridae	12	2	1	3	0	P
Hydraenidae	1	1	1	0	0	P
Hydrophilidae	11	4	1	2	5	P,S
Lameophloeidae	9	5	4	*0	1	F,S
Lagriidae	0	0	5	7	0	S,H
Lampyridae	0	0	3	12	0	P
Languriidae	0	0	6	*14	0	F,H
Lathridiidae	305	10	1	3	13	F,H
Leiodidae	5	2	0	0	1	S
Limnichidae	0	0	2	1	0	H,?S
Lycidae	7	4	9	9	0	?P,?F
Lymexylidae	0	0	0	0	1	(F)
Melandryidae	21	12	0	14	5	F,X
Melyridae	141	7	8	2	3	P
Monommidae	0	0	0	1	0	S
Mordellidae	14	6	23	43	3	H,X,F
Mycetophagidae	2	1	1	0	0	F
Mycteridae	0	0	0	11	0	?F
Nitidulidae	17	3	15	22	4	S,H,F
Phalacridae	0	4	19	28	1	H,F
Platypodidae	1	1	2	2	0	(F)
Propalticidae	2	1	1	0	0	?F
Pselaphidae	33	15	29	7	3	P
Ptiliidae	31	14	4	0	10	S,F
Ptilodactylidae	0	0	4	35	0	S,?F
Ptinidae	0	0	6	0	1	S
Pythidae	3	3	0	0	0	X,S
Rhipiphoridae	0	0	0	1	0	P
Rhizophagidae	0	0	0	1	0	S,F,P
Salpingidae	13	5	0	0	3	?F
Scarabaeidae	8	3	4	3	1	S,H
Scaphidiidae	0	0	5	8	0	F
Scirtidae	3	1	7	12	4	S
Scolytidae	7	4	11	10	4	X,(F)
Scraptiidae	18	9	2	0	8	?X,?F
Scydmaenidae	8	8	12	3	0	P
Silvanidae	0	0	2	*0	0	F,?S
[Staphylinidae	320	55	116	c.164	22	P,S,F]
Aleocharinae	248	35	69	?	14	P,F
Euaesthetinae	3	2	1	?	0	P
Omaliinae	8	2	1	?	3	P,etc.
Osoriinae	9	3	8	?	0	S
Oxytelinae	4	3	7	?	2	S
Paederinae	42	6	27	?	0	P
Piestinae	1	1	0	?	1	S
Proteininae	3	1	0	?	0	P,S
Staphylininae	1	1	0	?	0	P
Steninae	1	1	2	?	0	P
Tachyporinae	0	0	1	?	2	P
Tenebrionidae	18	12	33	33	2	S,F
Tetratomidae	0	0	0	0	2	F
Throscidae	0	0	0	1	1	?F
Trogossitidae	0	0	0	7	0	P,?S
Zopheridae	1	1	0	0	0	F
?family	0	0	0	2	0	?
Total	2269	454	875	1255	200	–

TABLE 2. Rank correlation analyses among datasets representing the number of species across beetle families from canopies in Australia, Brunei, Panama and the U.K. (see text). The values of the Spearman rank correlation coefficients presented are significant at the <0.001 level.

	Australia	Brunei	Panama	U.K.
Subtropical forest, Australia	1			
Lowland tropical forest, Brunei	0.59	1		
Luehea canopies,	0.46	0.65	1	
Temperate woodland, U.K.	0.71	0.44	0.44	1

Coleoptera families in better-known faunas and in large samples taken from a range of sites in Australia and elsewhere, including many in the Tropics, may be used to gauge roughly the likely proportion of Australian species so far described in various of the families of Coleoptera. Using these data to rank beetle families in terms of actual species richness in the Australian fauna (see Table 4), the strong representation of such families as Pselaphidae and Tenebrionidae, and to a lesser degree also Anthribidae, Corylophidae and Ptiliidae in the Lamington samples, may be seen to reflect in some measure their probably strong representation in the Australian fauna as a whole.

Another series of comparisons with canopy samples from other regions may be made in terms of trophic guild composition. The feeding 'guilds' to which most members of the Coleoptera family-groups listed below are indicated in Table 1, and the proportional representation of Coleoptera species among these guilds for the Lamington canopy samples, along with the U.K. Brunei and Panama samples for comparison, are Indicated in Fig. 1. In most respects the Lamington samples exhibit the greatest similarity to those from the U.K., except that there are far fewer xylophagous species in the U.K. samples. In both of the tropical samples (Brunei and Panama) the proportion of herbivores is much higher, and the pro-

TABLE 3. Rank order of major beetle families in terms of species richness in canopy fogging samples from (A) Australia, (B) U.K., (C) Brunei, and (D) Panama. See Table 1 for sample details. The lists include the ten families with the most species for each of the 4 sites.

Taxa	Australia	U.K.	Burnei	Panama
Curculionidae	1	2	2	1
Staphylinidae	2	1	1	3
Chrysomelidae	3	5=	3	2
Corylophidae	4	18=	7	27=
Anthribidae	5	–	5	23=
Pselaphidae	6	18=	8	33=
Ptiliidae	7	5=	38=	–
Coccinellidae	8	8	11	7
Tenebrionidae	9=	25=	6	9
Melandryidae	9=	12=	–	15=
Lathridiidae	14=	3	53=	39=
Cryptophagidae	24=	4	–	29=
Cantharidae	11=	5=	22=	12
Scraptiidae	16=	9	46	–
Elateridae	11=	10=	9	19=
Aderidae	16=	29=	4	23=
Mordellidae	19=	18=	10	5
Cerambycidae	14=	18=	13	4
Ptilodactylidae	–	–	38=	8
Carabidae	11=	10=	25=	6
Phalacridae	24=	29=	12	10

portion of fungivores and predators lower. Again, many of these differences may reflect differences in resources present (at the time of sampling) in forests of different types, but some may also reflect differences in the respective regional species pools. For example, the proportionally, greater representation of Curculionidae in general in southern temperate regions (see Watt 1982, Gaston *et al.* 1992) as compared with other regions, may provide some of the explanation for the very high representation of xylophagous species in the Lamington canopy samples.

DISCUSSION

The extent to which the Lamington results are informative about the overall species richness of Coleoptera at this or other similar Australian sites is limited by the lack of available data with respect to the species not found in the canopy. As noted by Hammond (1991, 1995; Hammond *et al.*, in prep.), the proportion of beetle species occurring at a forest site that are likely to be present as adults in insecticide fogging samples from the canopy is likely to vary according to forest type. In moist temperate forests such as those in the U.K. even extensive sampling from the canopy is unlikely to obtain much more than 20 % of the beetle species present (Hammond & Owen, in press), whereas a higher proportion of the locally occurring species may be obtained from the canopy in many tropical forests. In a Sulawesi lowland rainforest (Stork & Brendell 1990, Hammond 1990) fogging samples from some 1500 m^2 of canopy contained adults of almost 25% of the beetle species estimated to occur in the 500-hectare area stu-

TABLE 4. Rank order of major beetle families in Australia in terms of species richness. A = described species (Lawrence & Britton 1991); B = all species, estimated by reference to checklists and sample data from many sources, including Australian and orher tropical sites; C = Lamington fogging samples. The lists include the 20 families with most species, for each of rhe 3 categories (A, B & C).

Taxa	A Described	B Projected	C Fogging
Curculionidae	1	1	1
Chrysomelidae	2=	3	3
Scarabaeidae	2=	6	32=
Carabidae	4	5	11=
Staphylinidae	5	2	2
Tenebrionidae	6	7	9=
Cerambycidae	7=	10	14=
Buprestidae	7=	12	–
Pselaphidae	9	4	6
Elateridae	10	9	11=
Cleridae	11	17	25=
Coccinellidae	12=	27	8
Melyridae	12=	26	20
Nitidulidae	12=	11	32=
Scydmaenidae	12=	8	19
Lycidae	16	31	25=
Anobiidae	17	25	32=
Anthicidae	18=	24	37=
Brentidae	18=	18	16=
Dytiscidae	20=	33	–
Histeridae	20=	16	37=
Hydrophilidae	22=	15	25=
Cantharidae	25=	28	11=
Anthribidae	25=	19	5
Aderidae	33=	22	32=
Corylophidae	36+	20	4
Ptiliidae	36+	21	7
Melandryidae	36+	52	9
Scraptiidae	36+	60=	16=

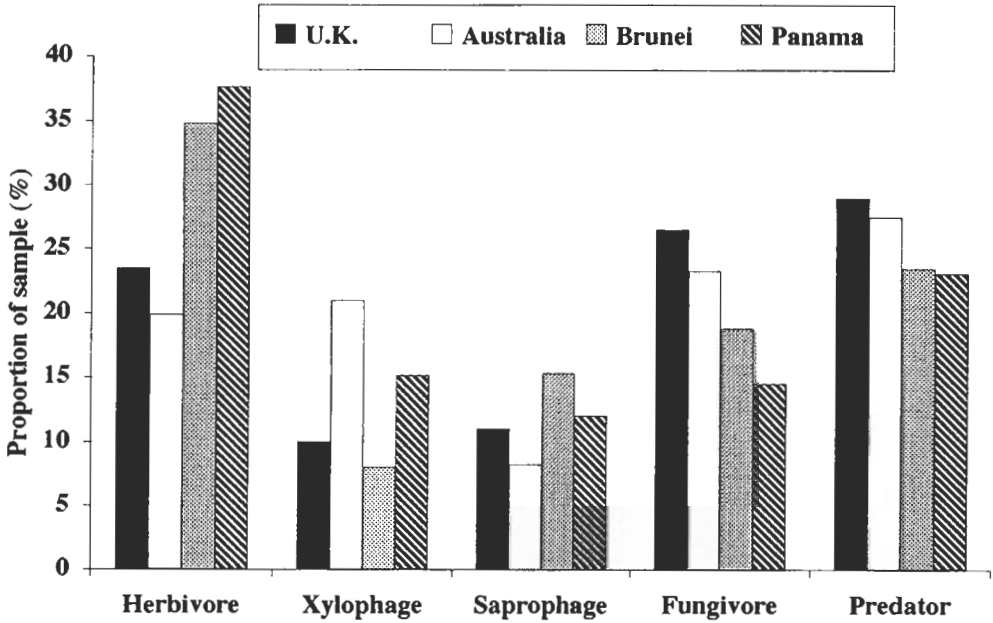

FIG. 1. Proportional representation of species of Coleoptera among feeding 'guilds' (as defined by Hammond 1990) in fogging samples from forest canopies in the U.K., Australia, Brunei and Panama.

died (Hammond *et al.*, in press). Dry tropical forests and some subtropical forests may reasonably be assumed to harbour less species-rich beetle assemblages at ground-level, so that a commensurately greater proportion of locally occurring species are found in the canopy. At Lamington, an informed guess might put this proportion at around 30%, so that the number of beetle species present at the site may be expected to be in excess of 1500 species. To what extent 1500 is an underestimate will depend on the pattern of accumulation of species in fogging samples. However, an increase in m^2 of canopy sampled by a factor of ten would be expected to at least double the figure of 454 (taken from 110 m^2), and a conservative figure for beetle species present at the Lamington site might thus be put at around 3000. In the absence of appropriate data the relationship between such local species richness figures and regional diversity of Coleoptera (see Westoby 1993) remains even more problematical.

Finally, the limited number of samples discussed here provides little direct evidence with respect to the controversy concerning the *absolute* richness of canopy arthropod assemblages and, more particularly, in the absence of intensive ground-level sampling, the *proportion* of locally occurring tropical or subtropical species that occur in the canopy and are canopy specialists (Erwin 1992, Hammond 1990, 1992, 1995; Hammond *et al.*, in prep.). Some of the more abundant species in the Lamington canopy samples (e.g., *Longitarsus victoriensis* Blackburn) appear to be 'stratum generalists', as they are also found readily at ground level, for example in Malaise and flight interception traps (Basset 1992, P.M. Hammond, unpublished). A number of others, e.g., Carabidae Tachyini, Hydrophilidae and Hydraenidae (aquatic or riparian in habits), and Ptiliidae (*Acrotrichis*, etc.), Leiodidae Catopinae, Staphylinidae (*Anotylus and Atheta*, etc.) and Scarabaeidae such as *Onthophagus* (associated with dung or other decaying matter), that feature in the Lamington canopy samples are almost certainly present as 'tourists'. Overall, some 20% of the 454 beetle species are likely to be strictly 'tourists' in terms of their occurrence in the canopy, while an uncertain proportion, probably well in excess of 50% of the remainder may be regarded as stratum generalists.

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REFERENCES

Adis, J., & H.O.R. Schubart. 1984. Ecological research on arthropods in central Amazonia forest ecosystems with recommendations for study procedures. Pp. 111–141 *in* Cooley, J.H., & F.B. Golley (eds.). Trends in Ecological Research for the 1980s. Nato Conference Series 1: Ecology. New York.

Adis, J., Lubin, Y.D., & E.G. Montgomery. 1994. Arthropods from the canopy of inundated and terra firme forests near Manaus, Brazil, with critical considerations on the pyrethrium-fogging technique. Studies on the Neotropical Fauna and Environment 19: 223–236.

Basset, Y. 1990. The arboreal fauna of the rain forest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: composition of the fauna. The Entomologist 109: 173–183.

Basset, Y., Springate, N.D., Aberlenc, H.P. & G. Delvare. (In press). A review of methods for sampling arthropods in tree canopies. *In* Stork, N.E., Adis, J., & R.K. Didham (eds.). Canopy Arthropods. London.

Erwin, T.L. 1982. Tropical forests: their richness in Coleoptera and other species. Coleopts Bull. 36: 74–75.

Erwin, T.L. 1983. Tropical forest canopies: the last biotic frontier. Bull. ent. Soc. Am. 30: 14–19.

Erwin, T.L. 1990. Canopy arthropod biodiversity: a chronology of sampling techniques and results. Revista Peru. ent. 33: 71–77.

Erwin, T.L. & J.C. Scott. 1980. Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal system: the fauna of the tree *Luehea seemanii* Triana and Planch in the Canal Zone of Panama. Coleopts Bull. 34: 305–322.

Floyd, A. 1990. Australian Rainforests in New South Wales, Volume 2. Chipping Norton, N.S.W.

Gaston, K.J. 1991. The magnitude of global insect species richness. Conservation Biology 5: 564–566.

Gaston, K.J., Blackburn, T.M., Hammond, P.M., & N.E. Stork. 1993. Relationships between abundance and body size: where do tourists fit? Ecological Entomology 18: 310–314.

Gaston, K.J., Warren, P.H., & P.M. Hammond. 1992. Predator: non-predator ratios in beetle assemblages. Oecologia 90: 417–421.

Hammond, P.M. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. Pp. 197–274 *in* W.J. Knight & J.D. Holloway (eds.). Insects and the rain forests of South East Asia (Wallacea). London.

Hammond, P.M. 1992. Species Inventory. Pp. 17–39 *in* B. Groombridge (ed.). Global biodiversity: status of the earth's living resources. London.

Hammond, P.M. 1994. Practical approaches to the estimation of the extent of biodiversity in speciose groups. Phil. Trans. R. Soc. B 345: 119–136.

Hammond, P.M. 1995. Described and estimated species number: an objective assessment of current knowledge. Pp. 29–71 *in* Allsopp, D., Colwell, R.R., & D.L. Hawksworth (eds.). Microbial diversity and ecosystem function. Wallingford.

Hammond, P.M., Brendell, M.J.D., & N.E. Stork. In press. Tree crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. *In* Stork, N.E., Adis, J., & R.K. Didham (eds.) Canopy Arthropods. London.

Hammond, P.M., & J.A. Owen. In press. The beetles of Richmond Park SSI-a case study. English Nature Science.

Kitching, R.L., & M. Arthur. 1993. The biodiversity of arthropods from Australian rain forest canopies: summary and the impact of drought. Selbyana 14: 29–35.

Kitching, R.L., Bergelson, J.M., Lowman, M.D., McIntyre, S., & G. Catruthers. 1993. The biodiversity of arthropods from Australian rain forest canopies: general introduction, methods, sites and ordinal results. Australian Journal of Ecology 18: 181–191.

Kitching, R.L., & J.M. Zalucki. (In press). The biodiversity of arthropods in Australian rain forest canopies: some results on the role of the tree species. *In* Booth, W., & S. Choy (eds.). Rain forest research: current issues. Amsterdam.

Lawrence, J.F., & E.B. Britton. 1991. Coleoptera (Beetles). Pp. 543–683 *in* CSRO Division of Entomology (ed.). The insects of Australia: a textbook for students and research workers. Second Edition. Vol. 2. Ithaca, New York.

Lowman, M. 1982. Seasonal variation in insect abundance among the Australian rain forests, with particular reference to the phytophagous types. Australian Journal of Ecology 7: 353–361.

McDonald, W.J.F., & M.B. Thomas. 1990. Flora of Lamington National Park. 2nd edition. Brisbane.

McDonald, W.J.F., & W.G. Whiteman. 1979. Moreton Bay Vegetation Map Series: Murwillumbah. Brisbane.

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

Stork, N.E. 1987b. Arthropod faunal similarity of Bornean rain forest trees. Ecological Entomology 12: 219–226.

Stork, N.E. 1988. Insect diversity: facts, fiction and speculation. Biol. J. Linn. Soc. 35: 321–337.

Stork, N.E. 1991. The composition of the arthropod fauna of Bornean lowland forest trees. Journal of Tropical Ecology 7: 161–180.

Stork, N.E., & M.J.D. Brendell. 1990. Variation in the insect fauna of Sulawesi trees whith season, altitude and forest type. Pp. 173–195 *in* Knight, W.J., & J.D. Holloway (eds.). Insects and the rain forests of South East Asia (Wallacea). London.

Stork, N.E., & M.J.D. Brendell. 1993. Arthropod diversity studies in lowland rain forest of Seram, Indonesia. Pp. 115–130 *in* Edwards, I.D., MacDonald, A.A., & J. Proctor (eds.). Natural history of Seram, Maluku, Indonesia. Andover.

Stork, N.E., & P.M. Hammond. In press. Sampling arthropods from tree-crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park (U.K.). *In* Stork, N.E., Adis, J., & R.K. Didham (eds.). Canopy Arthropods. London.

Stork, N.E., Adis, J., & R.K. Didham. In press. Canopy Arthropods. London.

Watt, J.C. 1982. New Zealand beetles. N.Z. Ent. 7: 213–221.

Webb, L.J. 1959. A physiognomic classification of Australian rain forests. J. Ecol. 47: 551–570.

Westoby, M. 1993. Biodiversity in Australia compared with other continents. Pp. 170–177 *in* Ricklefs, R.E., & D. Schluter (eds.) Species diversity in ecological communities, historical and geographical perspecitives. Chicago.

Wilson, E.O. 1992. The diversity of life. Cambridge, Mass.