

Vertical distribution of beetles in a tropical rainforest in Sulawesi: the role of the canopy in contributing to biodiversity

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Abstract. 1. The extent to which forest canopies contribute to global biodiversity, and the degree of strato-orientation shown by forest insects, remain open questions. The vertical distribution of nocturnal flying beetles in tropical rainforest in Sulawesi was examined, and the extent to which stratum preferences occurred, in order to establish the relative importance of the forest canopy in shaping rainforest communities.

2. Samples were collected using actinic light traps set from the high canopy (30 m) to ground level. 11,692 specimens collected over one lunar month were sorted to 701 species within 65 families. The greatest abundance, species richness and diversity were recorded in the canopy, with a decrease in all measures towards the ground. The sample was analysed at family and species level, with correlation analysis showing the greater number of canopy specialist families and species found in the canopy compared to the ground. 56% of more abundant species showed no stratum preference, and of those species that did, 39% were specific to the canopy and 5% to the ground layer.

3. The structure of samples from each level of the forest showed remarkable uniformity in terms of numbers of singletons and doubletons as a proportion of the total sample. This suggested conformity of species assemblage structure, and underlying processes shaping these assemblages, at different heights.

4. The study was examined in relation to other literature on the vertical distribution of insects in tropical forests. As with other studies, many of the more common species were distributed throughout the forest, although in the present study a significant portion showed stratum preferences, and the majority of these showed strato-orientation to the forest canopy. This work reiterates the need to sample through multiple dimensions in order to accurately measure species richness and diversity in tropical forests and estimate global biodiversity, and the importance of maintaining the dimensional integrity of the forest when conserving rainforest ecosystems.

Keywords: biodiversity, Coleoptera, conservation, species richness, tropical forest insects, vertical stratification

INTRODUCTION

The spatial complexity of rainforest has long been understood as a determinant of the high species richness and diversity found there (Wallace 1869, Richards 1952). The heightened vertical profile of many tropical forests compared to temperate ones allows for niche-partition along the canopy-ground ecotone, thereby resulting in increased speciation and diversity (August 1983, Davis *et al.* 1997). Arthropods in tropical forests are known to be dominant in terms of species number and also play an important role in many ecological processes (Didham *et al.* 1996). The difficulty of access to the high forest canopy has been a determinant in the majority of rainforest studies being ground-based (Sutton 2001), despite the apparent importance of the canopy in influencing community structure (see papers in Stork *et al.* 1997, Linsenmair *et al.* 2001, Basset *et al.* 2003a) and contributing to global biodiversity (Erwin 1982, Erwin 1991, Stork 1988, Ødegaard 2000). Insects, with fine-scale niche requirements and high species richness, make ideal organisms for examining the role of spatial complexity in determining rainforest diversity.

The current state of knowledge of canopy invertebrates has been extensively reviewed by Basset (2001) and Basset *et al.* (2003b). The possible causes of vertical stratification are many-fold (see Smith 1973, Basset 1992, Le Corff & Marquis 1999, Basset *et al.* 2003b): light levels vary considerably between the canopy and understorey (Yoda 1974, Théry 2001) as does the quality of light (Endler 1993); variation in wind (Sutton & Hudson 1980); changes in forest architecture (Lawton 1983, Fowler 1985); resource availability (Beccaloni 1997, DeVries *et al.* 1999, Blüthgen *et al.* 2000, Schulze *et al.* 2001, Novotny *et al.* 2003, Brehm 2007); the distribution of organic matter (Nadkarni & Longino 1990); leaf characteristics (Lowman 1985, Basset 1992, Ribeiro & Basset 2007); behaviour and flight patterns (Brown *et al.* 1997); flowering and pollination patterns (Boulter *et al.* 2005, Kitching *et al.* 2007); and predation pressures (Cisneros & Rosenheim 1998). Studies have shown that low wind speeds and convective air currents in tropical forests lead to the spreading of pheromones that aids intraspecific vertical stratification with males being located at higher strata than females (Schal 1982) – studies tend to focus on interspecific vertical stratification whereas lack of clear stratification in certain taxa may relate to such intraspecific mechanisms.

Studies of vertical distribution in tropical forest arthropods are still limited, although previous studies have shown that many groups of arthropods are not equally distributed along vertical gradients (Sutton 1989, Basset *et al.* 2003b), with the majority showing equal degrees of specialisation of species in both canopy and ground habitats (Preisser *et al.* 1998, De Dijn 2003, DeVries *et al.* 1997, DeVries & Walla 2001, DeVries *et al.* 1999, Intachat & Holloway 2000, Schulze *et al.* 2001, Schulze & Fiedler 2003). Coleoptera have been used to investigate vertical distribution in insects (e.g. Rowe & Potter 1996, Davis & Sutton 1998, Boiteau *et al.* 1999, Lucky *et al.* 2002, Wagner 2003) and have been demonstrated to be exemplar organisms in revealing patterns and processes in ecological studies (Hammond 1990). Studies have shown that less than 15% of the beetle species may be restricted to the canopy as adults, with a larger percentage only found in the understorey, with the majority stratum generalists (Hammond *et al.* 1997, Basset *et al.* 2003b) – i.e. that arthropod samples taken from the canopy would tend to be less species rich than a comparable sample from the understorey (De Dijn 2003).

Studies on other (non-Coleopteran) groups of insects have shown relative abundance of major invertebrate taxa to be the same in the canopy and ground organic matter (Nadkarni & Longino 1990). Studies of ants have shown equal distribution of species in ground, understorey and canopy (25% in each) with clear stratification demonstrated (Brühl *et al.* 1998), although other studies have shown high abundance of ants in tropical forest canopies (Davidson 1997, Davidson *et al.* 2003). Work on termites has shown that although the ground fauna is richer than that of the canopy, the canopy does contribute significantly to the total species richness of the overall assemblage (Roisin *et al.* 2006). Overall, current evidence suggests that herbivore and gall-forming species tend to be more abundant and diverse in forest canopies (Basset *et al.* 1992, Basset 2001, Ribeiro & Basset 2007) as are sap-sucking insects (De Dijn 2003).

The relative importance of the rainforest canopy compared to other strata of the forest, in terms of specialist species restricted to this one stratum, has been much debated (Hammond *et al.* 1997, Basset *et al.* 2003b). Clearly the degree to which species are restricted to a specific stratum will have important implications for the conservation of tropical forests and other dimensionally rich ecosystems (Hammond *et al.* 1997, Leksono *et al.* 2005) and determination of the vertical ranges of forest insects must be an important first step in any study of forest community dynamics. The results presented here contribute to this discussion in presenting data on night-flying beetles from the forest of Sulawesi, and examining the degree to which strata (or layer) specialists exist within the fauna and, if so, whether these are canopy- or ground-based.

MATERIALS & METHODS

The sampling site was located in lowland rainforest in the Morowali district of eastern central Sulawesi, Indonesia (1°51'S, 121°30'E). The site was ca. 12 km inland at 5 m asl. The collection site was beside the Soluwo River, and the canopy had an uneven main canopy leaf layer between 20 and 30 m above ground level. *Syzygium syzygioides* (Miq.) Merrill & Perry was a common main canopy tree, and had an abundance of climbing palms (*Daemonorops*, *Korthalsia*, and *Calamus* being dominant).

Four actinic light traps were suspended from a semi-emergent *Syzygium* (see Rees 1983, for details of trap set-up), at 30 m, 20 m, 10 m and 1 m. The deployment resembled that used in Zaire, Panama, Papua New Guinea and Brunei (Sutton & Hudson 1980, Sutton *et al.* 1983). The light traps were essentially the same 8 watt ultraviolet-rich fluorescent tube traps to those designed by Sutton (1980). The 30 m and 20 m traps were located in the forest canopy, with the 30 m trap located within the crown of the *Syzygium* (Myrtaceae) and the 20 m trap was ca. 2 m above the crown of a *Garcinia* species (Guttiferae). The 10 m trap was at least 5 m clear of any foliage and located in free space. In subsequent discussion, comparison between canopy and ground will be made by comparing samples in the traps at 30 m and 20 m (forest canopy) to the trap at 1 m (essentially ground level).

The traps were operated continuously from 19.00 to 22.00 hours between 14 February and 16 March 1980, and for trial periods before and after these dates. Microclimatic and lunar data were collected and will be discussed in a subsequent paper (Sutton *et al.* in prep.).

In order for valid conclusions to be reached from the present study, and an accurate picture of species assemblages at each stratum of the forest be established, rigour in species sorting was of paramount importance (Hammond 1994). All specimens were mounted and identified by experts at the Natural History Museum (London) and elsewhere (see Acknowledgements) over many years, and the same thoroughness and accuracy was applied as has been used for other collections maintained by the museum (e.g. Hammond 1990, Hammond *et al.* 1997). The present study followed the degree of rigour and integrity eschewed by Hammond (1994) by using the fullest use of 'hands on' knowledge of the groups in question. There can therefore be a high level of confidence that the species identification on which the present paper is based is of the highest possible standards, an essential factor if realistic and representative data are required for analysis.

The specificity of beetles to different heights was measured in two ways in this study: the ratio of individuals in canopy compared to ground traps (and vice versa) and correlation between abundance and height for each species and family. One method of indicating 'bioindicator value' for a range of taxa is the indicator value (*IndVal*) as developed by Dufrène & Legendre (1997), which combines measures of habitat specificity (testing whether species show affinity for one habitat within the ecosystem) and habitat fidelity (testing whether patterns are repeated across different sites) (see also McGeoch *et al.* 2002). Stork & Grimbacher (2006) used this method to assess the strato-orientation of Coleoptera in Australian rainforest. The lack of replication (i.e. repeat values) between sites in the current study meant that the second aspect of *IndVal*, the fidelity measure (B_{ij}), could not be examined. The current data could not therefore be subjected to full analysis using *IndVal*, and only the specificity measure, A_{ij} (Dufrène & Legendre 1997) could be tested, where

$$\text{Specificity measure: } A_{ij} = N_{\text{individuals}_{ij}} / N_{\text{individuals}_i}$$

$N_{\text{individuals}_{ij}}$ is the mean number of species i in one habitat type j (in this case either the canopy or the ground), and $N_{\text{individuals}_i}$ is the sum of the mean number of individuals of species i over all groups (i.e. all habitats sampled, in this case all trap heights). Effectively this is the ratio of individuals at one strata compared to individuals in all strata, calculated for each species in turn, expressed as a percentage. Habitat specification is therefore simplified as a ratio rather than as *IndVal*. The specificity measure (A_{ij}) was calculated by combining data from the two canopy traps (20 m and 30 m) by taking the mean abundance from these traps for each species and comparing this to the ground trap (1 m).

Correlation with trap height was calculated using the Pearson coefficient (r). Data were $\log(x+1)$ transformed prior to analysis, and only species with sufficient abundance were used (see Results below). Correlation analysis was used in order to give a clear cut-off for stratum preferences already evident within the data, and to support specificity measures (see above). The pitfalls of using multiple statistical tests in ecological studies have been widely discussed (Moran 2003, García 2004). Corrections can be applied that adjust significance levels in order to limit spurious results (García 2004). In the current data, it is assumed that the occurrences of species tested are independent and so individual testing using correlation at species and family levels can be justified. It is possible that the abundance of species may be linked (e.g. predators and prey and other interactions), although given the paucity of information about individual species it is beyond the scope of the current paper to statistically investigate this further. Given that the correlation calculations are used to support other clear evidence showing stratum preferences, and the choice of species investigated is itself conservative (i.e. rare species are not included), corrections are not applied here as significance levels would be decreased to the extent of not being useful (see Moran 2003). The majority of values when indicated as significant are in any case at lower than the $P < 0.05$ level applied, with the majority at $P < 0.01$ ($Cr = 0.95, n > 10$).

RESULTS

The number of individuals collected during the 1-month sampling period was 11,692 sorted to 701 species within 65 families, with certain functionally or taxonomically important families divided further into 21 subfamilies (Table 4). The number of individuals in the total collection and number of species was ca. half that collected by Stork & Grimbacher (2006), who use the value $n \geq 20$ for calculation of *IndVal*, and so here we use $n \geq 10$ as the cut-off for correlation analysis, i.e. in proportion to that used by Stork & Grimbacher (discussed below).

The canopy contained the largest number of individuals and species (Table 1). Alpha diversity increased greatly from ground to canopy, with little increase in SD, but with only slight increase in Shannon (Table 1) which reflected the similar evenness measures (E) at each height (which were relatively high reflecting the lack of dominance by any one species or group of species; see also Figure 1). Adjacent sampling heights showed the largest similarity in species composition, with the least between canopy and ground samples (Table 2). The similarities between adjacent heights was more consistent between pairs of heights using the Sorensen (C_N) index than with Morisita-Horn (C_{mH}), which reflects the sensitivity of the C_{mH} index to the more abundant species (Magurran 2007). The species-accumulation curves for each height were remarkably similar to each other (Figures 1a-d) and to the overall species-accumulation curve for the entire sample (Figure 1e). Although the largest number of rare species (singletons and doubletons) was found in the canopy, as a proportion of the total sample at each height, the results were remarkably consistent (Table 3) with an average of 51 singletons and 14 doubletons, reflecting the similarity in species-accumulation curves noted above. Results from the total sample showed slightly depressed values, but only slightly, demonstrating the large number of rare species (59% of the full sample).

Specialisms for canopy vs. ground were calculated using the full data, including samples

taken from before and after the main 1-month trapping period, totalling 11,723 individuals sorted to 701 species (i.e. all species used in main analysis were present in extended sample). The degree to which species showed an affinity for the canopy compared to the ground was analysed using a subset of the total data, but including singletons and doubletons (i.e. rare species) by comparing abundance in the canopy (traps at 20 m and 30 m) to the ground (1 m trap), resulting in a subset of 646 species (55 species only being located at 10 m – mainly singletons and doubletons). 155 species (24% of total) were shared between strata and 491 species were not shared (76% of total) i.e. showing strong habitat preference. Of those not shared, 86% were canopy specialists (65% of total number of species) and 14% were ground specialists (11% of total number of species). When rare species (singletons and doubletons) are removed from the analysis, the strong canopy-affinity continues to be persuasive, with 48% of species not shared between strata, and of these 96% showing a canopy specialism and only 4% showing a ground affinity. When comparing these values the full sample, excluding singletons and doubletons, 46% are canopy specialists and 2% ground specialists.

Specialisms within families, subfamilies, and individual species (Table 4) were calculated by Pearson correlation of abundance vs. trap height. To remove the possible effects of tourist species (Sutton 1989, Hammond 1990, Hammond *et al.* 1997), analysis was carried out on a subset of the total data, excluding less abundant species, following the methods of Stork & Grimbacher (2006). Due to the logistical growth in abundance for habitat specialists between heights (i.e. large numbers in one habitat but rapid reduction in numbers along the ecotone gradient), data were $\log(x+1)$ transformed prior to analysis (see also Stork & Grimbacher 2006). Analysis was only carried out on more abundant species ($n \geq 10$, see Materials & Methods).

Table 4 shows 57 species that have a habitat affinity based on correlation analysis (50 canopy and 7 ground). This analysis used $n \geq 10$ (representing 129 species), and so of this number 39% are canopy and 5% ground specialists. 56% of species showed no specific stratum preference. These results tally with the results that use data for less abundant species, with only a slight reduction in canopy specialism recorded with increased abundance of individual species. These values are different to those recorded by Stork & Grimbacher (2006), who recorded 24 and 27% of the abundant species specialized to the canopy and ground strata respectively. At the family level, 32 families overall showed a positive r -value (canopy affinity) whereas 5 showed a negative value (ground affinity). This more rigorous approach to strata specialists showed the same importance of the canopy fauna compared to the ground as the more general analysis of the whole sample.

Table 1. Total number of individuals (N), species richness (S), diversity indices (alpha, α and Shannon, H'), and evenness (E) for assemblages of Coleoptera at different heights in rainforest in Sulawesi, and for total sample.

height (m)	N	S	alpha		Shannon		E
			α	SD	H'	SD	
1	1,571	224	71.45	4.77	3.84	0.45	0.71
10	2,108	256	76.33	4.77	3.81	0.04	0.69
20	2,946	324	92.68	5.15	3.76	0.39	0.65
30	5,049	464	124.42	5.78	4.05	0.03	0.66
total	11,692	701	163.69	6.18	4.23	0.02	0.65

SD = standard deviation of diversity indices
total = calculations for total sample

Table 2. Similarities between samples collected by actinic light trap at different heights (1 m, 10 m, 20 m, 30 m) in rainforest in Sulawesi, measured using (a) Sorensen (C_N), and (b) Morishita-Horn (C_{mH}) indices.

(a) C_N

	1 m	10 m	20 m
10 m	0.6165	-	-
20 m	0.4146	0.6230	-
30 m	0.2798	0.3803	0.5593

(b) C_{mH}

	1 m	10 m	20 m
10 m	0.7985	-	-
20 m	0.5255	0.8389	-
30 m	0.2875	0.3948	0.5879

Table 3. The number of rare species (singletons and doubletons) and commoner species (remainder) at different heights from ground to canopy both in total numbers and as a proportion of total number of species at each height. Mean percentages are given with SD. The number of rare and commoner species in total sample (all heights combined) is also shown.

height (m) number of species	1	10	20	30			total sample
singletons	123	128	160	225			326
doubletons	33	36	47	66			89
remainder	68	92	117	173			286
% of total number of species					mean	SD	
% singletons	55	50	49	48	51	2.88	47
% doubletons	15	14	15	14	14	0.30	13
% remainder	30	36	36	37	35	3.10	41

DISCUSSION

Our results from the Sulawesi night-flying coleopteran fauna show a clear dominance of canopy species compared to those found at ground level, although 56% of the more common species show no clear stratum preference. The evidence presented here supports to a degree the assertion that most species are found in the rainforest canopy and that canopy faunas play an important role in shaping global biodiversity (Erwin 1982), although we agree with the assertion that the canopy should be seen as providing the opportunity for a continuum of niche-diversification options from ground to canopy, and that the majority of species are not restricted to the canopy (Hammond *et al.* 1997, Basset *et al.* 2003b). Clearly, however, the canopy does play an important role in shaping the communities examined here. The data are particularly persuasive given that only the commoner species ($n \geq 10$) were used in the analysis, with 50 species showing canopy affinity whereas only 7 showed a preference for the ground, although the pattern holds up when singletons and doubletons are also included. With rare species excluded, our results showed 48% of species not shared between strata, in contrast to the results of Stork & Grimbacher (2006) who showed 24-27% of common species not shared and 72% of species found in both strata, with no canopy affinity demonstrated in the Australian fauna.

Table 4. Numbers of individual beetles, the ratio of those collected in the canopy (traps at 20 m and 30 m) compared to the 1 m trap, and the Pearson correlation (r) of abundance relative to trap height analysed at the family level (and subfamilies for Carabidae, Hydrophilidae, Staphylinidae, Scarabaeidae, and Curculionidae). r is calculated for more abundant families and subfamilies only ($n \geq 10$) and is starred if statistically significant ($P < 0.05$, 2 d.f., 1-tailed test). In each case data are $\log(x+1)$ transformed (see text). Specialisms are indicated based on significant r -values (i.e. negative correlation indicates ground specialism, g; positive correlation indicates canopy specialism, c). Number of canopy and ground specialist species is calculated by correlation (r) for each species (trap height vs. abundance at each height) ($P < 0.05$, 2 d.f., 1-tailed test). Trophic guild gives an indication of feeding where known, based on Hammond (1990) and Lawrence *et al.* (2000), and following Stork & Grimbacher (2006). H = herbivore; P = predator; F = fungivore; X = xylophage; S = saprophage; ?P = possibly predatory; H, (X) most of the family are herbivores but a few species are xylophages; ? = unknown feeding guild.

Family	Number of Individuals	Canopy: Ground Ratio	r	Specialism	Number of Species	Number of Canopy Specialists	Number of Ground Specialists	Trophic Guild
Carabidae								
Paussinae	6	100 : 0	-		1			?P
Cicindelinae	1		-		1			P
other Carabidae	527	76 : 24	+0.9841*	c	51	3		P
Hydrophilidae								
Georyssinae	50	35 : 65	-0.6941		1			H
Sphaeridiinae	4	100 : 0	-		3			P, S
other Hydrophilidae	609	28 : 72	-0.6981		16			S, (P)
Histeridae	1	100 : 0	-		1			P
Hydraenidae	16	10 : 90	-0.7271		1			H
Leiodidae	240	21 : 79	-0.9000*	g	3		1	F
Scydmaenidae	3	33 : 67	-		3			P
Staphylinidae								
Aleocharinae	32	53 : 47	+0.6152		15			P, F
Omalinae	79	14 : 86	-0.6869		2			P, S

Family	Number of Individuals	Canopy: Ground Ratio	<i>r</i>	Specialism	Number of Species	Number of Canopy Specialists	Number of Ground Specialists	Trophic Guild
Osoriinae	2		-		2			S
Oxytelinae	1144	40 : 60	-0.9221*	g	10		2 ⁺	P
Paederinae	50	70 : 30	+0.9883*	c	14	1		P
Pselaphinae	188	81 : 19	+0.8761		24	2		P
Scaphidiinae	2	0 : 100	-		1			F
Staphylininae	1	0 : 100	-		1			P
Lucanidae	4	100 : 0	-		3			X
Passalidae	3	33 : 67	-		1			X
Scarabaeidae								
Aphodiinae	27	33 : 67	-0.7873		4		1	S
Melolonthinae	47	96 : 4	+0.9939*	c	8	2		H
Rutelinae	31	71 : 29	+0.7655		3			H (S,X)
Scarabaeinae	3	0 : 100	-		2			S
Scirtidae	142	91 : 9	+0.9172*	c	15	2		S
Buprestidae	4	50 : 50	-		2			H, (X)
Limnichidae	103	60 : 40	-0.0879		5			?S/H
Ptilodactylidae	5	100 : 0	-		4			F, (S)
Chelonariidae	2	100 : 0	-		1			?S
Callirhipidae	1	0 : 100	-		1			X
Eucnemidae	4	100 : 0	-		4			F/X
Elateridae	58	89 : 11	+0.9780*	c	17	1		H,X,P,S
Lycidae	18	100 : 0	+0.9981*	c	13			?P, ?F/X
Lampyridae	48	100 : 0	+0.9843*	c	6	1		P
Cantharidae	45	91 : 9	+0.8845		3	1		P, (H)
Ptinidae	1	100 : 0	-		1			X, (F)
Trogossitidae	19	100 : 0	+0.8597		2			?
Cleridae	4	33 : 67	-		4			P, (H)

Family	Number of Individuals	Canopy: Ground Ratio	<i>r</i>	Specialism	Number of Species	Number of Canopy Specialists	Number of Ground Specialists	Trophic Guild
Melyridae	12	100 : 0	+0.8676		3			P
Prionoceridae	25	100 : 0	+0.9934*	c	1	1		?
Nitidulidae	3187	86 : 14	+0.8715		29	2		F,S,H, (P)
Silvanidae	289	48 : 52	+0.1314		15	1	2	F,S
Cucujidae s.l.	25	50 : 50	+0.2794		12			F, (P)
Phalacridae	77	90 : 10	+0.9560*	c	10	2		H,F
Cryptophagidae	2	100 : 0	-		2			F
Languridae	43	72 : 28	+0.9514*	c	6			F,H
Erotylidae	17	73 : 27	+0.6318		6			F
Biphylidae	2	0 : 100	-		1			F
Cerylonidae	3	100 : 0	-		2			F
Endomychidae	212	95 : 5	+0.9580*	c	4	2		F
Coccinellidae	8	56 : 44	-		5			P, (H)
Corylophidae	44	85 : 15	+0.8547		8	1		F
Latridiidae	13	69 : 31	+0.9236*	c	3			F, (H)
Mycetophagidae	86	68 : 33	+0.9571*	c	5			F
Ciidae	1	0 : 100	-		1			F
Mordellidae	8	56 : 44	-		5			H, (F,X)
Ripiphoridae	1	100 : 0	-		1			P
Zopheridae	73	80 : 20	+0.9574*	c	8			F, (P)
Tenebrionidae	292	92 : 8	+0.9651*	c	51	4		S,F
Oedemeridae	2	100 : 0	-		1			H, (X)
Salpingidae	2	100 : 0	-		2			?F
Anthicidae	201	58 : 42	+0.5904		16	2		S, (?P)
Aderidae	96	98 : 2	+0.9957*	c	32	1		?S, ?H
Scraptiidae	15	80 : 20	+0.2267		1			?X, ?F
Cerambycidae	30	75 : 25	+0.7573		16			X, (H)

Family	Number of Individuals	Canopy: Ground Ratio	<i>r</i>	Specialism	Number of Species	Number of Canopy Specialists	Number of Ground Specialists	Trophic Guild
Chrysomelidae	2068	97 : 3	+0.9798*	c	71	12**		H
Anthribidae	4	100 : 0	-		2			F, (H)
Brentidae	21	56 : 44	+0.2604		9			X
Apionidae	5	100 : 0	-		3			H
Curculionidae								
Platypodinae	86	66 : 34	+0.9920*	c	4	2		X, X/F
Scolytinae	673	50 : 50	-0.3169		28	3	1	X, X/F
other Curculionidae	329	93 : 7	+0.9875*	c	56	4		H, (X)
Halplidae	2		-		2			?
Dytiscidae	148	50 : 50	+0.4324		15			P
Gyrinidae	1	0 : 100	-		1			P
Bostrichidae	2	33 : 67	-		1			X
Elmidae	14	37 : 63	-0.0525		4			H
Monotomidae	2	100 : 0	-		2			S,F
Propalticidae	2	0 : 100	-		2			F
Lymexylidae	42	80 : 20	+0.5778		3			X/F
Myceteridae	1	100 : 0	-		1			?S
Meloidae	2	100 : 0	-		2			P/S/H

*Significant result ($P < 0.05$, 2 d.f., 1-tailed test)

+Both species in genus *Carpelimus* (P.M. Hammond ident.)

**Chrysomelid data separated into subfamilies: 9 species in Galerucinae, 3 in Eumolpinae (S. Shute ident.)

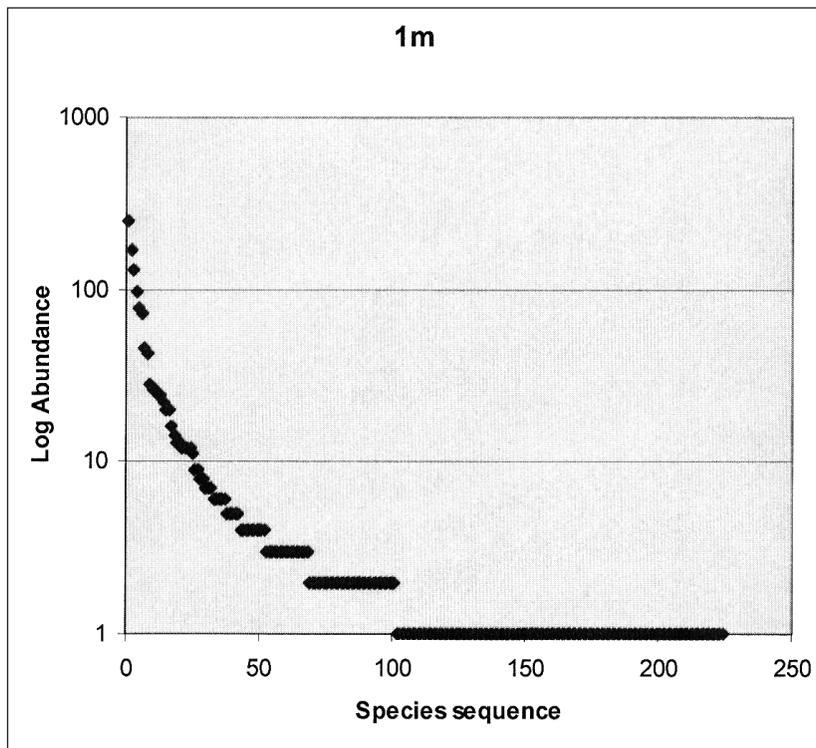


Figure 1a. Rank-abundance curve of Coleoptera collected at 1 m by actinic light trap in Sulawesi rainforest.

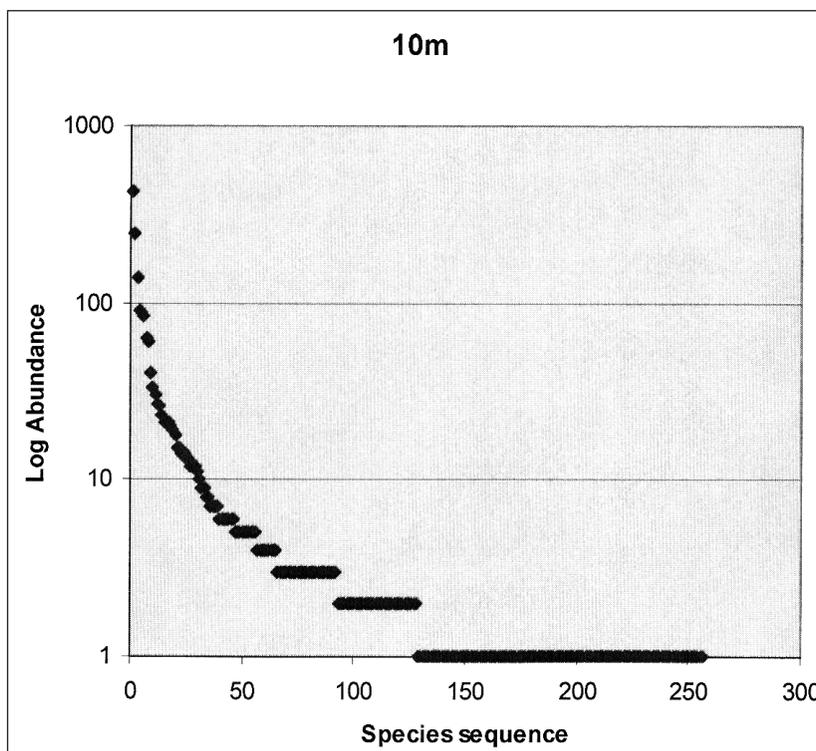


Figure 1b. Rank-abundance curve of Coleoptera collected at 10 m by actinic light trap in Sulawesi rainforest.

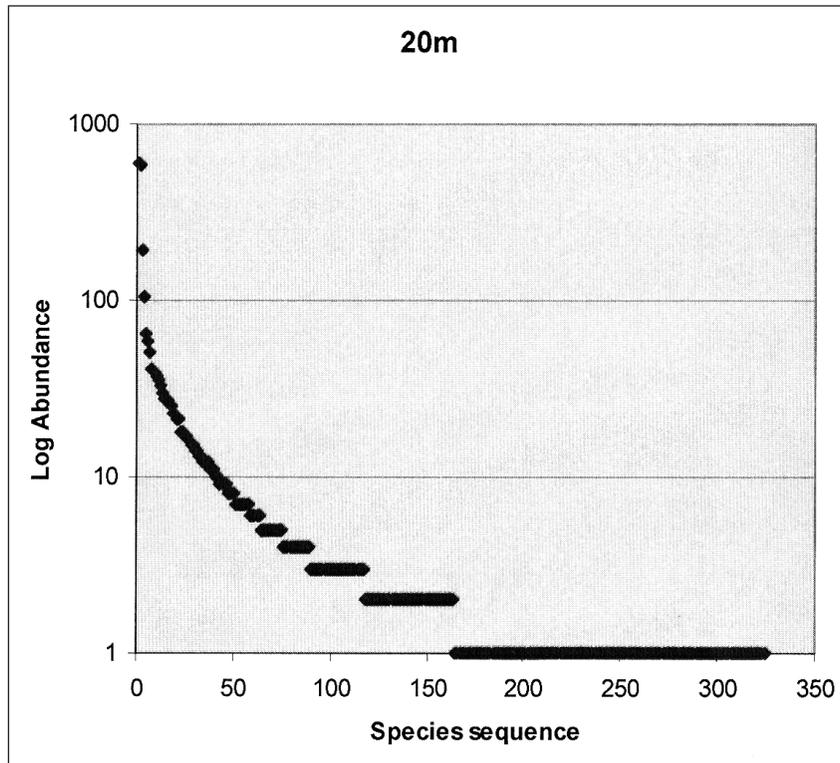


Figure 1c. Rank-abundance curve of Coleoptera collected at 20 m by actinic light trap in Sulawesi rainforest.

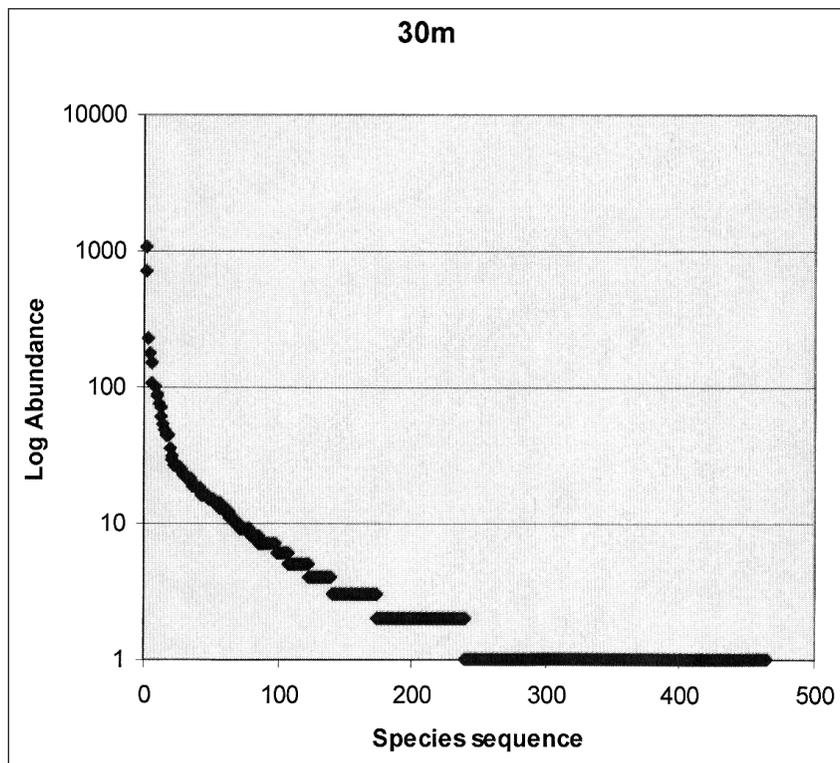


Figure 1d. Rank-abundance curve of Coleoptera collected at 30 m by actinic light trap in Sulawesi rainforest.

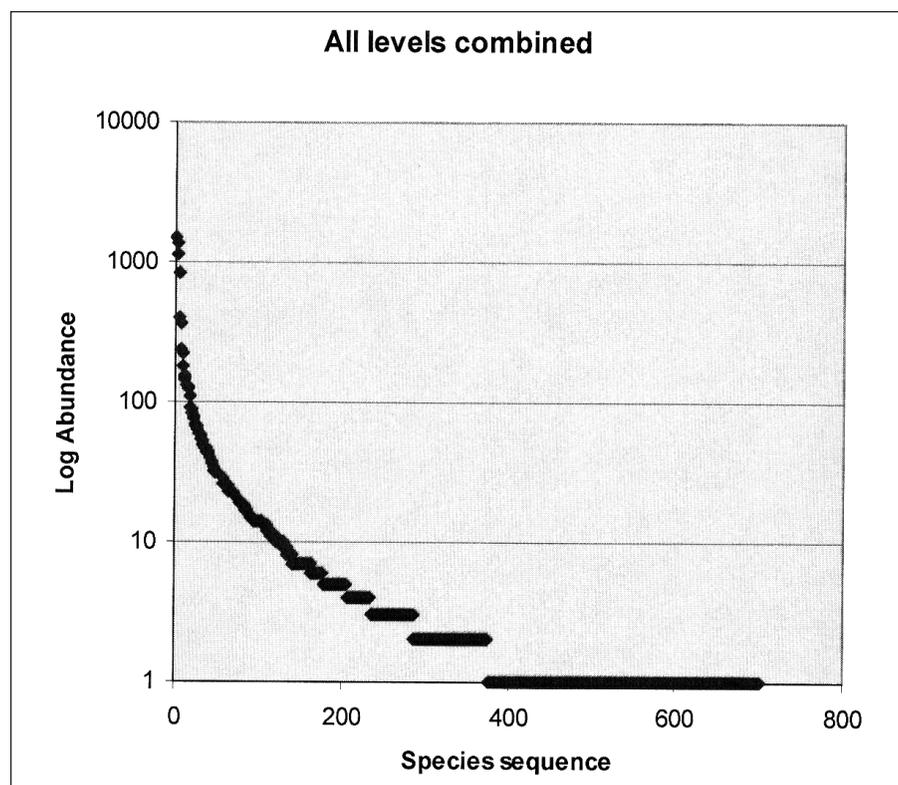


Figure 1e. Rank-abundance curve of Coleoptera collected in total collection (data from individual heights combined) by actinic light trap in Sulawesi rainforest.

Our results also differ from the Australian fauna (Stork & Grimbacher 2006) in the even distribution of singletons and doubletons between all strata (Table 3). Although the canopy showed the largest species richness and abundance values, the distribution of singletons was remarkably consistent between different levels. The Australian coleopteran assemblage, in contrast, showed higher numbers of singletons in the canopy, an effect that Stork & Grimbacher (2006) attributed to greater wind velocities capturing more tourist species, differences in flight strategies, or greater heterogeneity in canopy structure to the ground resulting in more rare species. Other work has made the association between increases in rare species and greater habitat heterogeneity (Leksono *et al.* 2005) showing greater number of singletons at lower strata and linking this to the greater diversity in shrub and tree species found there.

In comparison with other studies on beetle communities, results vary with forest type and geographical location. Kato *et al.* (1995) showed that Tenebrionidae and Nitidulidae were the most abundant families in the canopy, with Staphylinidae and Carabidae most abundant at ground level. Overall the study showed that many more night-flying insects occur at canopy level rather than below it, with mass attraction of phloem-feeders, ovule-feeders and seed-feeders at canopy level (Kato *et al.* 1995). Moeed & Meads (1984) showed fewer beetles in traps at 22 m compared to lower strata in New Zealand forest using traps of a modified intercept design, and linked insect abundance to bird predator distribution. Wolda *et al.* (1998) showed a higher

species richness at lower levels of the forest although more individuals were found in the canopy and there were clear-cut differences between the faunas caught in the canopy compared to those caught at ground level. Ulyshen & Hanula (2007) also showed significant differences between ground and canopy and discreet faunas within each, with 29% and 31% of species exclusively captured in the canopy and near the ground respectively. In other work carried out in Sulawesi, Hammond (1990) showed only 10% of Coleoptera to be restricted to the canopy, with a high proportion not being able to be assigned to any given stratum, and all but ants having higher densities on the ground compared to the canopy, with ants being equally distributed through all strata. A later account of this work (Hammond *et al.* 1997) indicates that between 8% and 13% of the study area's beetle species were more or less exclusively tree-crown dwelling, although in this case stratum preferences were identified using samples taken using a variety of different methods (canopy fogging being dominant): when stratum preferences were examined using samples taken by the same trapping method (Malaise traps), 37.6% of species were categorized as canopy specialists, 33% as stratum generalists, and 19% as ground specialists (Hammond *et al.* 1997). The current study shows a stronger canopy affiliation compared to the ground, in contrast to the above studies.

The present study is limited to night-flying coleopterans attracted to light traps. Light traps are frequently used in biodiversity research (Schulze & Fiedler 2003) although criticisms have been made of their use. Assertions have been made that they: selectively rather than randomly sample populations; attract insects from distance from traps that makes assertions regarding stratum preference difficult; are affected by wind velocity; and that catches are affected by surrounding structure (e.g. density of vegetation) (Sutton & Hudson 1980, Bowden 1982, Hammond *et al.* 1997). Effects of lunar cycle are also known to affect catches (Muirhead-Thomson 1991, Yela & Holyoak 1997). Examining each of these criticisms in turn in relation to this current work, trapping method clearly affects the species composition in samples, although this is true of any other field method in animal ecology (Southwood & Henderson 2000) and tropical forests in general (Barker & Pinard 2001). Standardization of trapping methods and consistent application between different sites is clearly important, with each method having different strengths and weaknesses (Basset *et al.* 1997). The observation in the current study of remarkable consistency in assemblage structure at each height suggests that this form of trapping is successful in consistently sampling the available fauna. In terms of the distance that insects are drawn to the trap, the power of the bulbs used in this study were much lower than those of other studies which drew insects from a wider area (Bowden 1982) – the bulbs in the present study were selected to minimize attraction from neighbouring vegetation layers. Recent work with low-power bulbs has shown that differences in catches between light traps and Malaise traps (i.e. a passive trapping method) are far less pronounced than previously thought (Hammond *et al.* 1997). In our analysis the clear separation of canopy, ground, and intermediate species, both in the full data set and also when rare species are removed, suggests that the trapping method did not result in significant mixing of species from different habitats and, although some cross-attraction between habitats may have occurred, this was not severe enough to interfere with the validity of our results. For most of each trapping period there was no measurable wind and, where there was, it took the form of short-lived gusts lasting between 3 and 45 seconds (Rees 1983) and so this abiotic factor was unlikely to bias sample data. As to the question of vegetation density, the site had a semi-continuous leaf layer between 20 and 30 m and a well developed understorey rich in Palmae-rattans. Careful citing of the traps within the tree crown would have overcome the problem of differences in foliage density to some degree, and any obscuring effect of foliage may to

some extent be offset by reflected light from leaves although precisely how this affects flying insects is unclear (Sutton 1983). Clearly, we cannot predict the effect of foliage density on trap efficiency although the uniformity of data from different layers of the forest in terms of species composition and relative numbers of rare species suggests again that this variable had limited effect on the data. Finally, the effects of the lunar cycle and variation in trap efficiency were overcome by collecting throughout a full lunar cycle, negating any changes in sky luminosity over this period (Bowden 1982).

Clearly a major criticism of the current study is the lack of spatial replication employed in the sampling. The dangers of pseudoreplication have been widely reported in the literature (e.g. see Barker & Pinard 2001, for a useful summary). The current study sampled at four levels on one tree over a one-month period. Given the constraints imposed on the sampling at the time (a short-term expedition with limited resources and time to do a more expensive sampling regime with greater replication), it can be argued that the benefits of a realistic sample size and the ability to perform a thorough and exhaustive identification of the material to species level outweighs (or at least compensates for) lack of spatial replication. Clearly if species sorting is limited by large sample size, the analysis of stratum preferences, and other ecological work, is compromised. Ideally both replication and comprehensive sorting of material should go hand-in-hand, although such studies are limited. Stork & Grimbacher (2006) showed replication of similar patterns at different spatial scales, and so it is possible that patterns shown in the current study would be endorsed by further replication. More work would be needed to show if the patterns shown in the current study hold up to further scrutiny, although the current data do provide a base-line and point of reference for future studies.

The exact reasons for the vertical stratification noted here and the specialisms in the canopy fauna in particular, and differences between this and other studies (e.g. Stork & Grimbacher 2006), can only be speculated upon. Differences in vertical stratification patterns may depend both on local conditions (Sutton *et al.* 1983) as well as the differences in food supply for the organisms in question (Le Corff & Marquis 1999, Brehm 2007). The individual response of species to environmental and biological conditions encountered in the understorey and canopy may result in the current complex picture of stratum preferences within insect groups (see review in Le Corff & Marquis 1999). Differences in the degree of vertical stratification may also be a result of local topography – where the landscape is relatively flat, greater vertical stratification of insects may occur compared to sites adjacent to steep slopes or more rugged terrain (Sutton *et al.* 1983) where there may be greater mixing of different layers within the forest. Biogeographical and evolutionary origin (i.e. Gondwanan vs. Laurasian) may also influence diversity, guild, and taxonomic structures (Arias *et al.* 2008). It is possible that the different biogeographical origins of the faunas have led to different community structures and patterns between Australia and Sulawesi, but more extensive studies are needed to explore this further; differences in sampling technique and other methodological differences could also explain the divergent results. An important limitation of most studies is that they rely on the study of adult specimens, with other stages of the life cycle rarely studied (Hammond 1990, Basset & Samuelson 1996), which is also true of the current study. Ideally knowledge of larval distribution should complement that from extensive collecting regimes for the adult stage (Kitching *et al.* 2003, Brehm 2007). Further analysis of guild structure and feeding specialisms within the current data may shed further light on the results, although ultimately only detailed bottom-up studies of individual species-

specific distribution patterns based on life history data of the type summarized by Kitching *et al.* (2003), working in combination with extensive sampling programmes, will shed true light on the underlying forces that shape insect distribution and determine vertical stratification patterns.

The majority of studies, including the present one, show clear stratification of insects. The results presented here show that the canopy plays a crucial role in determining the species richness and diversity of tropical forests, both as a habitat with specific biotic and abiotic characteristics enabling canopy specialists to evolve, but also as one end of a continuum from ground to canopy that provides a level of complexity enabling niche diversification and increased species richness. Although, as with other studies, we show that many of the more common species are distributed throughout the forest, a significant portion show stratum preferences and the majority of these are to the forest canopy. The present study reiterates the need to sample through multiple dimensions for accurate measurement of species richness and diversity in tropical forests (DeVries *et al.* 1997, Davis & Sutton 1998). Evidence of canopy specialism and greater preference for that stratum suggests that the canopy should be a focus of conservation in its own right, as well as part of the overall management of forest ecosystems.

ACKNOWLEDGEMENTS

Our thanks to numerous taxonomists who ensured that the Sulawesi beetle collection was kept in view and in constant gestation over many years, and who helped sort the collection with expertise and ensured the highest degree of accuracy in species identification, especially Peter Hammond and Sharon Shute. Max Barclay was of enormous help gaining access to the collection, in offering advice, and in maintaining the taxonomic integrity of the project. Chris Rees and Charles Fletcher were instrumental in the development of the Sulawesi material, and Chris Bowden helped to initially sort the material. The collections were made possible by the super-human efforts of the Operation Drake team. Our thanks to Charles Fletcher, Ray Aldridge, Laurence Cook, Nigel Stork, John Willott, Yves Basset, and an anonymous reviewer for their helpful comments on earlier drafts of this manuscript.

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