

Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity

Nigel E. Stork* and Peter S. Grimbacher

Rainforest Cooperative Research Centre at James Cook University, Cairns, 4870 Queensland, Australia

There remains great uncertainty about how much tropical forest canopies contribute to global species richness estimates and the relative specialization of insect species to vertical zones. To investigate these issues, we conducted a four-year sampling program in lowland tropical rainforest in North Queensland, Australia. Beetles were sampled using a trap that combines Malaise and flight interception trap (FIT) functions. Pairs of this trap, one on the ground and a second suspended 15–20 m above in the canopy were located at five sites, spaced 50 m or more apart. These traps produced 29 986 beetles of 1473 species and 77 families. There were similar numbers of individuals (canopy 14 473; ground 15 513) and species (canopy 1158; ground 895) in each stratum, but significantly more rare species in the canopy (canopy 509; ground 283). Seventy two percent of the species (excluding rare species) were found in both strata. Using *IndVal*, we found 24 and 27% of the abundant species ($n \geq 20$ individuals) to be specialized to the canopy and the ground strata, respectively, and equivalent analyses at the family level showed figures of 30 and 22%, respectively. These results show that the canopy and the ground strata both provide important contributions to rainforest biodiversity.

Keywords: biodiversity; canopy crane; Coleoptera; species richness; specialization; tropical forest insects

1. INTRODUCTION

Tropical forest insects dominate the number of described and estimated species on Earth. Understanding the degree of insect specialization to vertical zones, host plants and other resources within tropical forests is of central importance to global species richness estimates (Erwin 1982; Stork 1988, 1993; Hammond 1995; Ødegaard 2000; Novotný *et al.* 2002). The first use of knockdown insecticides (canopy fogging) to collect samples of tropical forest canopy insects (Erwin & Scott 1980; Adis *et al.* 1984) revealed a previously unparalleled level of species richness of Coleoptera and subsequently led to Erwin's supposition that the canopy is twice as rich in species as the ground (Erwin 1982). However, to date there have been few studies that have accurately quantified the vertical stratification of insects within tropical forests.

One such study of 4025 beetle species collected over 12 months from an Indonesian tropical forest (Hammond 1990; Stork & Brendell 1990) suggested that only 8–13% of these beetles are canopy specialists (Hammond *et al.* 1997). Other canopy–ground comparisons within tropical rainforest have suggested that most insect activity is located in the top few metres of the canopy (Sutton *et al.* 1983), and that insects are more abundant and speciose in the canopy than the understory (Basset *et al.* 2001; Charles & Basset 2005). However, this contrasts with other studies on Lepidoptera and Formicidae which suggest that the ground layer is as speciose as the canopy (DeVries *et al.* 1997; Brühl *et al.* 1998; Schultze *et al.* 2001).

Despite poor consensus as to whether the canopy or the ground contributes more to global biodiversity, numerous

studies on arthropod groups including Collembola (Rogers & Kitching 1998), Lepidoptera (DeVries *et al.* 1997; DeVries & Walla 2001; Schultze *et al.* 2001), Formicidae (Longino & Nadkarni 1990; Brühl *et al.* 1998), Chrysomelidae (Charles & Basset 2005), *Drosophila* (Diptera; Tanabe 2002) and a range of insect orders (Basset *et al.* 2001), have unequivocally shown that arthropod assemblages in the canopy are very distinct from those that inhabit the ground zone. These differences are likely to be determined by a range of factors including resource availability, microclimate preferences and predator avoidance (Haddow *et al.* 1961; Kato *et al.* 1995; Brühl *et al.* 1998; Rogers & Kitching 1998; Schultze *et al.* 2001; Tanabe 2002; Basset *et al.* 2003). The degree of specialization to resources and physiological tolerances to microclimate are, therefore, likely to be particularly important in structuring arthropod assemblage differences between the canopy and the ground.

Our inability to determine how different vertical strata contribute to global biodiversity is the result of three major methodological problems with previous studies. First, few studies have incorporated methodologies that allow equal sampling effort in the canopy and near the ground. For example, although canopy fogging can sample vast numbers of arthropods in the canopy, such a technique cannot be used to sample the insect fauna of the ground layer. Second, few studies have used ecologically diverse or species-rich taxa to assess arthropod assemblages and it is difficult to extrapolate these results with confidence for other insect taxa. Third, few have tested vertical stratification data using robust and appropriate statistics that incorporate abundance. As far as we are aware, no study has adequately addressed all three areas of concern.

* Author for correspondence (nigel.stork@jcu.edu.au).

This study focuses on the distribution of insects between the canopy and the ground of an Australian tropical lowland rainforest. Here we have been careful to use a methodology that allows equal sampling of the canopy and the ground. We have used Coleoptera as our target taxon as this is by far the most species-rich order of insects (Hammond 1992; Nielson & Mound 1999) and, since this is arguably the most ecologically diverse order of insects (Lawrence *et al.* 2000), extrapolations for other insect taxa may be possible. We have also used appropriate statistics that incorporate abundance to test the hypotheses that (i) the canopy is richer in species than the ground and (ii) that a higher proportion of these species are strata specific.

2. MATERIAL AND METHODS

This study was conducted in lowland tropical rainforest (complex mesophyll vine forest type 1a (Tracey 1982)), under or close to the Australian canopy crane (40 m asl, 16°17' S, 145°29' E), approximately 140 km North of Cairns in North Australia. The canopy is topographically quite varied ranging from 10 to 35 m in height and at least 90 species of tree of 10 cm dbh of 35 families have been identified in the hectare of forest directly below the canopy crane. Insects were sampled using a 1700 mm long, 1700 mm high Malaise trap modified to also act as a flight interception trap (FIT). Collecting pans containing a 40% solution of propylene glycol were placed either side of the base of the central net to provide the FIT samples. In this way insects flying into the central net would either fly upwards and be caught in the Malaise bottle or fly/drop downwards and collect in the FIT. Pairs of traps, one suspended 15–20 m in the canopy and one directly underneath on the ground, were located at five sites, each 40–60 m from each other. Canopy traps were suspended from different species of trees. Aluminium frames with plastic covers were built for the traps to ensure that they maintained their shape and sampling efficiency. Malaise traps were washed once a year and replaced if damaged. Traps were run for two weeks a month from March 2000 to February 2004 (except July and October 2001, March 2002 and May 2003, while two samples were obtained in August 2000). This strategy generated five replicate canopy FIT, canopy Malaise, ground FIT and ground Malaise samples, during each of the 45 sampling periods. Beetles were removed from the samples, point mounted, labelled and sorted to families and morphospecies by both authors, using reference collections and expert advice where necessary (see acknowledgments).

For most analyses temporal data were pooled and differences among strata (and sometimes trapping methodology) were compared. Differences in the number of individuals, total species richness, rare species (singletons, and doubletons) and species (excluding rare species), were compared between strata using traps as replicates (but pooling trapping methodology), ANOVA statistics, and $\log(x+1)$ transformations of the data. Multi-dimensional scaling ordination (MDS), and cluster analysis were used to represent the patterns of similarity in beetle species composition among traps from the ground and the canopy (based on $\log(x+1)$ transformations of the entire species abundance data and a Bray–Curtis distance measure). The statistical significance of beetle assemblage differences between canopy and ground samples was tested with analysis

Table 1. Total number of individuals and species caught in five combined Malaise/FIT traps over four years from the ground and the canopy.

	canopy	ground
individuals	14 473	15 513
species	1185	895
singletons	340	186
doubleton species	169	97
species excluding singletons and doubletons	649	612

of similarity using the data described above. The identification of species specialist to the canopy or ground strata was made using the indicator value, *IndVal* procedure (Duf rene & Legendre 1997; McGeoch *et al.* 2002). This method combines species abundances with their frequency of occurrence at various groups of sites and in this study is based on their relative (square root-transformed) abundances and fidelity to the canopy or ground. *IndVal* is a symmetric indicator and is maximum when all individuals of a species are found at a particular type of site. The statistical significance of the *IndVal* statistics was assessed using a randomization procedure (5000 randomizations). *IndVal* statistics were separately calculated for each trapping method, trapping methods combined, each of the four years of sampling (year = March–February), cumulatively across years and for beetle families. Species accumulation curves and species richness estimators (Chao 1, ACE, ICE), were performed using ESTIMATES (v. 7.5, Colwell 2005).

3. RESULTS

Over four years, the canopy–ground samples from the Australian tropical lowland rainforest site produced 29 986 beetles sorted to 1473 species within 77 families (table 1). There were surprisingly similar numbers of individuals in each stratum (canopy 14 473; ground 15 513), and these differences were not statistically significant (ANOVA, d.f._{1,4}, $p=0.783$). Of all the species caught, 78.6% (1158) were in canopy traps and 60.8% (895) were in ground traps, however, these differences were not statistically significant (ANOVA, d.f._{1,4}, $p=0.131$). A high proportion of species (39.4%) were shared by both strata, and when singletons and doubletons were excluded, this figure was proportionally even higher (72.0%). There were significantly more rare species in the canopy than near the ground (ANOVA, d.f._{1,4}, singletons $p=0.048$, doubletons $p=0.011$) and in particular more in canopy FITs than ground FITs (ANOVA, d.f._{1,4}, singletons $p=0.027$, doubletons $p=0.003$). Rare species largely contributed to the differences in species totals among strata, as when they were removed, the number of species in ground and canopy samples were very similar (table 1), (ANOVA, d.f._{1,4}, $p=0.322$). The FIT component of the traps collected a higher proportion of the individuals and species than the Malaise trap component (figure 1). Non-parametric species richness estimators Chao 1, ACE and ICE (Colwell 2005) predict total species richness figures of 2118–2200 species suggesting that 67–70% of the beetle fauna has so far been sampled. However, total species richness estimators continued to rise with year by year increasing sample size (data not presented here) demonstrating the unstable nature of all of

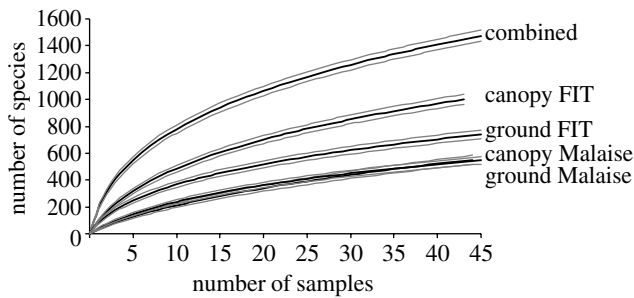


Figure 1. Species accumulation curves (dark lines) and 95% confidence intervals (light lines) for each trapping method, strata and combining both factors. Samples represent two week trapping intervals, conducted almost every month, over four years. Curves are the product of 50 randomizations (Colwell 2005).

the species richness estimators used in ESTIMATES (v. 7.5, Colwell 2005).

Ordination of this dataset by stratum and sampling method shows the striking differences between canopy and ground beetle assemblages, irrespective of differences between trapping method (figure 2). The differences between beetle assemblages from the canopy and the ground were highly significant (ANOSIM Global $R=0.424$, $p<0.001$). A cluster analysis based on degree of similarity (Bray–Curtis) among the beetle assemblages collected in both the Malaise traps and FITs, showed clear separation of sites into canopy and ground groups while there was no evidence of spatial autocorrelation among sampling sites (figure 3). Despite the clear partitioning of assemblages by vertical strata, canopy and ground assemblages showed compositional similarity in the 30–40% range. Up to 238 species (84.3% of all individuals) surpassed the abundance threshold ($n\geq 20$ individuals) to be included in *IndVal* analyses. We found 24% (range 24–26) of the canopy species and 27% (range 16–29) of the ground species were identified as specialists of those strata, depending on trapping method used (figure 4a). These proportions remained fairly constant over the four years sampling was conducted (figure 4b). Over time, additional species reaching the analysis threshold were identified as stratum specialists at a similar proportional rate (figure 4c) to overall species stratum-specialist allocations (figure 4a,b).

A similar *IndVal* analysis at the family level (and at subfamily level for Scarabaeidae, Staphylinidae and some Curculionidae; table 2) showed that of 64 Families (including 19 subfamilies) with 20 or greater individuals, 19 (30%) were canopy specialists and 14 (22%) were ground specialists. These specialist families usually had species that were also specialists of the particular stratum, but collectively were from diverse feeding guilds (allocation of families to feeding guild according to Hammond (1990) and Lawrence *et al.* (2000)) including herbivores, predators, fungivores and saprophages and mixtures of these guilds. There were few stratum specialist herbivore families and surprisingly more fungivorous (or largely fungivorous families).

4. DISCUSSION

Our results unequivocally show that (i) both the canopy and the ground are equally species-rich, and (ii) they share many species. The evidence presented here therefore does

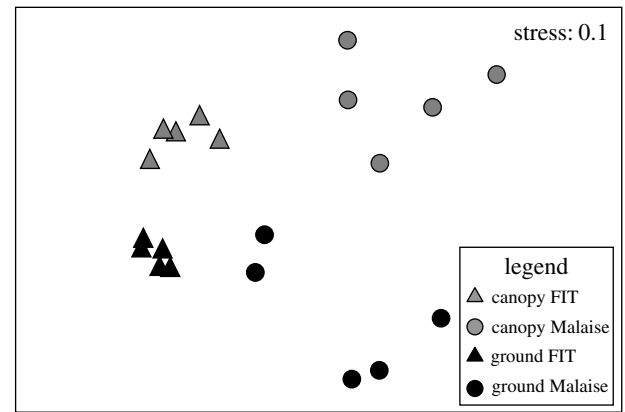


Figure 2. Multi-dimensional scaling ordination of the Australian rainforest beetle assemblage according to trap position and type (temporal data pooled). Each point represents the species composition of a trap. Points spaced closer together are more similar in species composition.

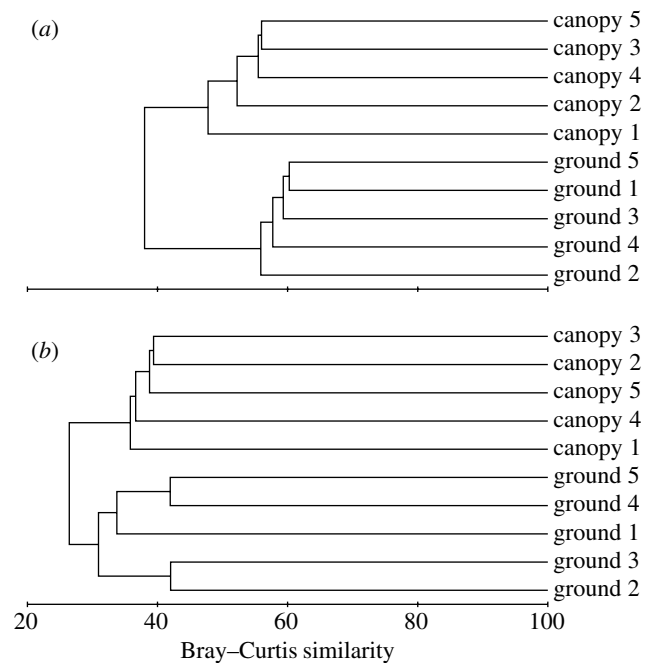


Figure 3. Dendrogram of a cluster analysis showing the degree of similarity in the beetle assemblage sampled over 4 years, among the five sampling sites and vertical strata for (a) FITs, and (b) Malaise traps.

not support the notion that most species are exclusively found in the canopy (Erwin 1982). Insect associations with the canopy or ground are likely to vary along a sliding scale, with some entirely associated with a particular stratum and others equally split between strata. These patterns are likely to reflect the specific biology of the species concerned and may even change with season (Devries & Walla 2001), although we have not addressed this possibility here. Our finding that there was vertical stratification in the beetle assemblage concurs with those for other tropical forest insect taxa (Longino & Nadkarni 1990; DeVries *et al.* 1997; Brühl *et al.* 1998; Rogers & Kitching 1998; Basset *et al.* 2001; Schultze *et al.* 2001; Tanabe 2002; Charles & Basset 2005).

Our results show that similar proportions (24–27%), of those species common enough to assess, were sufficiently strongly associated with the canopy or ground layer to be

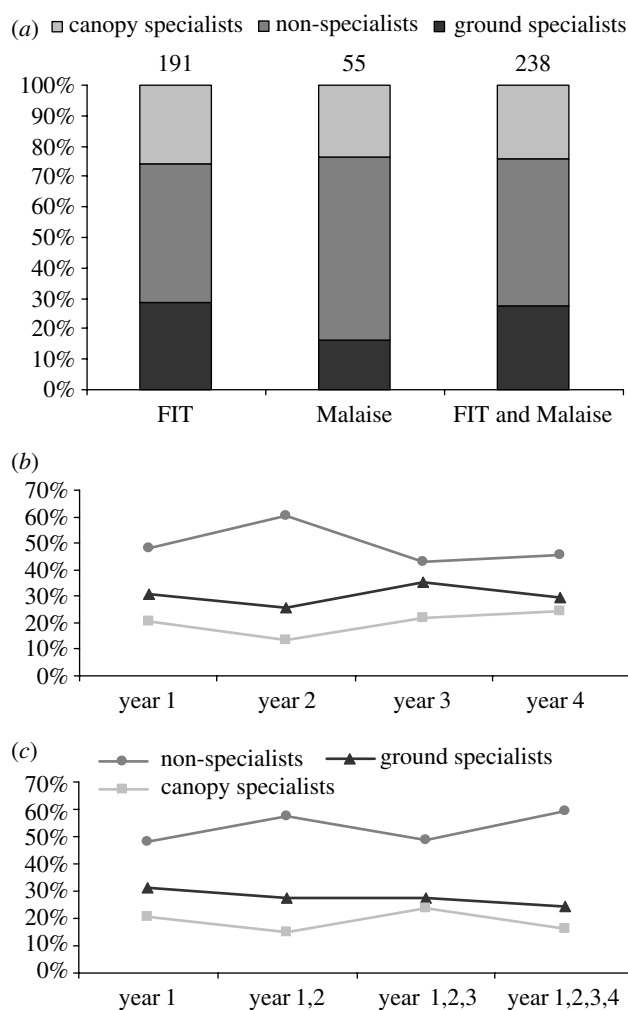


Figure 4. Proportions of species that are statistically significant indicators of the canopy, ground or not statistically significant (i.e. are neither canopy or ground stratum specialists) using *IndVal*, (a) for all species where number of individuals $n \geq 20$ (total number of species is over each column), (b) as (a) but separately for each year (year 1 $n = 58$, year 2 $n = 58$, year 3 $n = 96$, year 4 $n = 61$), and (c) as (a) but cumulatively across years for 'new' species only (species not previously classified from previous year(s), year 1 $n = 58$, year 1, 2 $n = 47$, year 1, 2, 3 $n = 84$, year 1, 2, 3, 4 $n = 49$).

considered to be specialists of these strata. However, even among the 115 'non-specialist' species, 42 species were three times more abundant in one stratum than the other. The absence of any spatial autocorrelation among assemblages caught from canopy-ground pairs of sites suggests that the vertical stratification patterns among beetle assemblages are robust. The statistical method we have used to determine stratum specialization (*IndVal*) provides an unbiased assessment of species' fidelity to vertical strata but was only used for species with 20 or more individuals. Even though this accounted for 84.3% of the individuals, it included only 16.2% of all the species. However, there is some evidence that the patterns observed for the abundant species may also hold true for rarer species as figure 4c shows that the proportions of species classified as canopy or ground specialists did not change when additional species reached the analysis threshold of 20 or more individuals each year.

What are the causes of vertical stratification? First, there are differences between the canopy and the ground in the kinds of resources and their quality and quantity.

For example, the canopy is where most leaves, flowers and fruits appear, while the ground is where these resources and dead wood accumulate and decompose. As a result, canopy insects should be more likely to be associated with key canopy processes such as herbivory, and pollination, whereas ground-based insects should be more likely to be associated with decomposition. Family and feeding ecology data from this study, however, do not support this theory. Second, the microclimate of the canopy layer differs strongly from the ground. The upper canopy is exposed to more solar radiation, experiences much stronger wind velocities and temperature extremes, and is less humid than the ground (Pinker 1980; Walsh 1996; Szarzynski & Anhuf 2001; Turton & Siegenthaler 2004). Third, behavioural traits (e.g. differences in predator avoidance; Schultze *et al.* 2001) may be important.

Our finding that 72% of the more common species are found in both strata shows that the beetle faunas are in many ways much more similar than might have been expected. We have two possible explanations for this. First, although there are some differences in the quality and quantity of resources between the canopy and the ground, there are also some similarities. We found support for this theory as among the families identified as canopy- or ground-specialists (52% of families with $n \geq 20$ individuals), there was no clear discrimination between vertical strata based on feeding ecology. At the resource level living wood is found in both strata and the ground zone contains other plant resources such as leaves, although in lower volumes than the canopy. Fungi are also present in both canopy and ground strata, although sometimes in different forms. Second, life-history constraints may force many canopy-dwelling species to spend time near the ground. The forest canopy has a much greater level of variation in humidity and temperature than the ground, and is therefore a challenging environment for beetle larvae, which are usually less protected from desiccation than adult beetles. This is reflected in the observation that some of the adult canopy-dwelling beetles have ground-based beetle larvae (Lawrence *et al.* 2000).

We were surprised to find that although more species were caught in the canopy than the ground, this difference was the consequence of there being many more rare species in the canopy. To our knowledge, this is the first time that this has been demonstrated although rare species are an important component of all tropical insect assemblages (Novotný & Basset 2000). We explore three possible explanatory hypotheses. First, it is possible that greater wind velocities present in the canopy (Walsh 1996; Szarzynski & Anhuf 2001) may have resulted in canopy traps capturing more 'tourists' (*sensu* Moran & Southwood 1982) just blowing by. We are unable to assess the likelihood of this hypothesis due to the absence of species' distributional data. The second possibility, which is related to the first, is that the difference in the abundance of rare species in the canopy and ground could be due to possible differences in the flight strategies of beetles in these strata. The presence of more rare species in the canopy could be the consequence of long-distance migratory flight and therefore, these species represent a much larger, geographically speaking, species pool, whereas the more abundant species represent local dispersal for new food resources. We have not tested this hypothesis further here. The third hypothesis is that the

Table 2. Numbers of individual beetles, the ratio of those collected in canopy to ground traps, and significance levels (those in bold $p < 0.05$) of *IndVal* analyses at the family level (and subfamily for Scarabaeidae, Staphylinidae and some Curculionidae). Number of species, number of canopy specialists and number of ground specialists record the total number of individual species and those species recognized as indicators of the canopy or the ground using *IndVal*. Trophic guild provides an assessment (or possible trophic guilds) for each family and is based on Hammond (1990) and Lawrence *et al.* (2000); H=herbivore; P=predator; F=fungivore; X=xylophage; S=saprophage; ?P=possibly predatory; F, (P) most of the family are fungivores but a few species are predators; ? unknown feeding guild.

family	number of individuals	canopy : ground ratio	<i>p</i> -value (canopy)	<i>p</i> -value (ground)	number of species	number of canopy specialists	number of ground specialists	trophic guild
Rhysodidae	6	83 : 17	0.1102	0.9778	2			F
Carabidae	113	41 : 59	0.7730	0.2422	26			P
Hydrophilidae	25	28 : 72	0.7378	0.2730	7			S, (P)
Histeridae	510	54 : 46	0.3102	0.6996	12	2		P
Hydraenidae	3	0 : 100	1.0000	0.0844	1			H
Ptiliidae	171	20 : 80	0.9702	0.0338	8		1	F
Leiodidae	987	19 : 81	1.0000	0.0040	15		5	F
Scydmaenidae	521	27 : 73	1.0000	0.0052	31		3	P
<i>Staphylinidae</i>								
Aleocharinae	674	39 : 61	0.8352	0.1724	109		1	P, F,
Euaesthetinae	6	33 : 67	0.7310	0.4918	1			P
Omaliinae	2	0 : 100	1.0000	0.2236	2			P, S
Osoriinae	275	53 : 47	0.2912	0.6994	17	1	1	S
Oxytelinae	20	30 : 70	0.7732	0.2976	3			S
Paederinae	211	38 : 62	0.8874	0.1148	16		2	P
Pselaphinae	521	27 : 73	1.0000	0.0044	86		3	P
Scaphidiinae	578	17 : 83	1.0000	0.0038	15		6	F
Staphylininae	551	25 : 75	0.9540	0.0592	34		1	P
Tachyporinae	194	37 : 63	0.8672	0.1466	20		1	P, S, F
Lucanidae	3	100 : 0	0.2154	1.0000	3			X
Passalidae	1	0 : 100	1.0000	0.5064	1			X
Bolboceratidae	26	12 : 88	0.9970	0.0306	3			S
Ceratocanthidae	2	50 : 50	0.7708	0.7904	1			S?, F?
<i>Scarabaeidae</i>								
Aphodiinae	5	60 : 40	0.5000	0.7820	2			S
Cetoniinae	120	96 : 4	0.0030	1.0000	6	2		H, (S, X)
Dynastinae	2	100 : 0	0.2228	1.0000	1			H, S, X
Melolonthinae	343	56 : 44	0.2146	0.7972	14	2	2	H
Rutelinae	35	91 : 9	0.0134	0.9910	4			H (S, X)
Scarabaeinae	672	18 : 82	1.0000	0.0074	9		3	S
Eucinetidae	3	100 : 0	0.0850	1.0000	1			F
Clambidae	1	0 : 100	1.0000	0.4988	1			F
Scirtidae	35	80 : 20	0.0106	0.9940	8			S
Buprestidae	43	63 : 37	0.4060	0.6524	9			H, (X)
Byrrhidae	1	0 : 100	1.0000	0.4976	1			H
Limnichidae	5	20 : 80	0.9972	0.0978	2			?S/H
Psephenidae	6	100 : 0	0.0822	1.0000	2			H
Ptilodactylidae	38	24 : 76	0.8104	0.1996	3			F, (S)
Chelonariidae	2	100 : 0	0.2206	1.0000	1			?S
Callirhipidae	2	100 : 0	0.2350	1.0000	1			X
Eucnemidae	748	43 : 57	0.6682	0.3246	34	2	1	F/X
Throscidae	759	80 : 20	0.0038	1.0000	3	2		?F, ?X
Elateridae	722	32 : 68	0.9710	0.0286	38	1	1	H, X, P, S
Lycidae	30	37 : 63	0.8806	0.1460	5			?P, ?F/X
Lampyridae	1	100 : 0	0.5022	1.0000	1			P
Cantharidae	43	42 : 58	0.7888	0.2658	6			P, (H)
Nosodendridae	106	20 : 80	0.9972	0.0110	1		1	S/F
Dermostidae	325	94 : 6	0.0042	1.0000	8	2	1	S
Anobiidae	944	88 : 12	0.0202	0.9824	23	4		X, (F)
Jacobsoniidae	10	70 : 30	0.1794	0.9182	1			S?, F?
Trogossitidae	5	40 : 60	0.7968	0.2626	2			?
Cleridae	219	78 : 22	0.0138	0.9890	14	2		P, (H)
Melyridae	44	59 : 41	0.1096	0.8988	7			P
Sphindidae	390	16 : 84	0.9972	0.0110	2		1	F
Nitidulidae	1905	25 : 75	1.0000	0.0030	46	4	4	F, S, H, (P)

(Continued.)

Table 2. (Continued.)

family	number of individuals	canopy : ground ratio	<i>p</i> -value (canopy)	<i>p</i> -value (ground)	number of species	number of canopy specialists	number of ground specialists	trophic guild
Monotomidae	147	63 : 37	0.0890	0.9064	3			S, F
Silvanidae	32	41 : 59	0.8630	0.1636	5			F, S
Passandridae	4	100 : 0	0.0816	1.0000	2			P
Cucujidae	1	100 : 0	0.4938	1.0000	1			F, (P)
Laemophloeidae	60	95 : 5	0.0044	1.0000	18			F, (S)
Propalacticidae	26	85 : 15	0.0270	0.9958	6			F
Phalacridae	200	45 : 56	0.7754	0.2226	17	1	2	H, F
Cryptophagidae	56	54 : 46	0.5216	0.4994	5		1	F
Languriidae	101	93 : 7	0.0032	1.0000	7	1		F, H
Erotylidae	5	80 : 20	0.3542	0.9166	3			F
Biphyllidae	127	33 : 67	0.9862	0.0254	4		1	F
Bothrideridae	2	100 : 0	0.5044	1.0000	2			P, (F)
Cerylonidae	244	45 : 55	0.8490	0.1552	7	1		F
Discolomatidae	5	20 : 80	0.9770	0.1940	2			F
Endomychidae	104	19 : 81	0.9918	0.0116	10		1	F
Coccinellidae	294	71 : 29	0.0040	1.0000	35	2		P, (H)
Corylophidae	1884	45 : 55	0.8026	0.2022	23	2		F
Latridiidae	346	40 : 60	0.5238	0.4906	6	2		F, (H)
Mycetophagidae	5	100 : 0	0.0198	1.0000	1			F
Ciidae	67	31 : 69	0.9258	0.0794	8			F
Melandryidae	29	90 : 10	0.0126	1.0000	8			F, (X)
Mordellidae	1368	75 : 25	0.0080	0.9962	32	1	1	H, (F, X)
Rhipiphoridae	5	100 : 0	0.0202	1.0000	2			P
Zopheridae	187	58 : 42	0.1898	0.8270	21	1	1	F, (P)
Tenebrionidae	103	78 : 22	0.0232	0.9816	39			S, F
Oedemeridae	23	35 : 65	0.8454	0.2200	5			H, (X)
Pyrochroidae	18	17 : 83	0.9562	0.0758	1			S?, F?
Salpingidae	20	95 : 5	0.0134	1.0000	8			?F
Anthicidae	110	7 : 93	1.0000	0.0048	4		1	S, (?P)
Aderidae	272	56 : 44	0.3000	0.7072	16	1		?S, ?H
Scaptidae	193	80 : 20	0.0048	0.9972	6	2		?X, ?F
Cerambycidae	219	60 : 40	0.1140	0.8940	52	1	1	X, (H)
Chrysomelidae	2547	68 : 32	0.0886	0.9192	70	5	1	H
Anthribidae	404	66 : 34	0.0314	0.9686	57	1	1	F, (H)
Attelabidae	4	75 : 25	0.3730	0.9084	2			H
Brentidae	65	65 : 35	0.0716	0.9434	12			X
Apionidae	2	100 : 0	0.2110	1.0000	2			H
<i>Curculionidae</i>								
other Curculionidae	2918	57 : 43	0.1832	0.8066	241	3	13	H, (X)
Platypodinae	413	56 : 44	0.3370	0.6758	8	3		X, X/F
Scolytinae	4412	39 : 61	0.8480	0.1682	53	7	3	X, X/F

canopy is more heterogeneous in structure than the ground, and thus there are more rare species. However, the species composition data (Bray–Curtis measure of similarity) do not support this interpretation as the degree of variation within canopy and ground groups was very similar.

The tropical forest canopy is poorly known and yet is of significance to so many fields of environmental concern (Ozanne *et al.* 2003). Our results show that the canopy does have a large number of species, although probably not exclusively two-thirds of all insect species as had been suggested (Erwin 1982), and is therefore home to an important component of forest biodiversity. These results also confirm that the ground stratum provides an equally important component of biodiversity that is often overlooked (Hammond 1990). Insect assemblages from the canopy and ground strata of tropical rainforest share many species, and certainly cannot be considered independent from each other.

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