VARIATION IN BEETLE (COLEOPTERA) DIVERSITY AT DIFFERENT HEIGHTS OF TREE CANOPY IN A NATIVE FOREST AND FOREST PLANTATION IN SABAH, MALAYSIA

A. Y. C. Chung, V. K. Chey,

P. O. Box 1407, Forest Research Centre, Forestry Department, 90715 Sandakan, Sabah, Malaysia

P. Eggleton, P. M. Hammond

Natural History Museum, Cromwell Road, London SW7 5BD, UK

&

M. R. Speight

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

CHUNG, A. Y. C., CHEY, V. K., EGGLETON, P., HAMMOND, P. M. & SPEIGHT, M. R. 2001. **Variation in beetle (Coleoptera) diversity at different heights of tree canopy in a native forest and forest plantation in Sabah, Malaysia.** Mist-blowing from a tower was used to investigate the beetle species richness, abundance and composition at three different canopy levels in a regenerating native forest and a forest plantation of *Acacia mangium.* Species richness and abundance did not differ between levels in the forest but their numbers decreased from bottom to top level in the forest plantation. CCA (canonical correspondence analysis) showed that there was a distinct difference in species composition between sites but not between canopy levels. The study also provided some general information on the canopy Coleoptera assemblages in the forest and forest plantation: Chrysomelidae and Curculionidae were highly abundant in the forest while in the forest plantation, Tenebrionidae and Elateridae were the most abundant families. Overall, vertical stratification of the fauna was less pronounced here than in other published studies.

Key words: Coleoptera - species richness - abundance - composition - canopy levels

CHUNG, A. Y. C., CHEY, V. K., EGGLETON, P., HAMMOND, P. M. & SPEIGHT, M. R. 2001. **Variasi kepelbagaian kumbang (Coleoptera) pada ketinggian kanopi pokok yang berbeza di hutan asli dan ladang hutan di Sabah, Malaysia.** Kekayaan spesies, kelimpahan serta komposisi kumbang di tiga paras kanopi yang berbeza di hutan asli dan ladang hutan *Acacia mangium* telah dikaji menggunakan teknik semburan kabus dari sebuah menara. Kekayaan spesies serta kelimpahan tidak menunjukkan perbezaan antara paras kanopi di hutan asli tetapi kedua-dua parameter ini berkurang dari paras bawah ke paras atas kanopi di ladang hutan. CCA (*canonical correspondence analysis*) menunjukkan perbezaan yang ketara dalam komposisi spesies antara hutan asli dan ladang hutan tetapi tidak ketara antara paras kanopi. Kajian ini juga memperihalkan maklumat berkenaan kumbang-kumbang di kanopi: Chrysomelidae dan Curculionidae amat melimpah di hutan asli manakala Tenebrionidae dan Elateridae paling melimpah di ladang hutan. Secara keseluruhan, penstrataan menegak fauna ini tidak ketara berbanding dengan kajian-kajian lain.

Introduction

Tropical forest canopies harbour rich assemblages of insects. Thus it has been suggested that these comprise a major portion of the global insect species richness (Erwin 1982, Basset & Kitching 1991). Many of the insect species found in the canopy do not exist in any other habitats (Davis *et al.* 1997). Stork (1991) recorded an average of 616.7 species of arthropods from approximately 2400 individuals by insecticide fogging of a single Bornean lowland rain forest tree. Erwin and Scott (1980) obtained more than 945 species of beetles, also through fogging, on *Luehea seemannii* trees in Panama. In Venenzuela, Davies *et al.* (1997) collected 978 species of beetles comprising 6132 individuals from six rain forest trees. Extrapolations from this kind of data, although gathered from only a few trees, along with assumptions about the levels of specialisation of herbivores and truly arboreal species, have led to expectations of high numbers of species within the canopy and also to a steep increase in the estimation of the total global biodiversity (Bruhl *et al.* 1998). However, many of the assumptions and methodologies used are open to criticism (May 1988, 1995, Hammond 1994, 1995, Speight *et al.* 1999).

Many early canopy studies focused on taxonomic inventories (e.g. Brown 1961, Sutton & Hudson 1980) and medical importance (Haddow *et al.* 1961) but today, they address a wider range of ecological issues (e.g. Davis *et al.* 1997). Interest in the canopy has increased at a remarkable rate in the 1990s, as various new methods are used to gain access to the canopy. Some of the methods used are spikes-and-belt methods, single-rope techniques, towers, cranes, walkways, dirigibles and canopy rafts (Lowman *et al.* 1993, Moffett 1993, Fukuyama *et al.* 1994). Sampling in the canopy has involved the use of knock-down insecticides, various flight interception traps, light traps, Malaise traps, baited traps and hand-collecting (Basset *et al.* 1997).

Beetles occupy a large and varied number of niches. The niche of a beetle species is a result of evolution that has been driven by the availability of food and also protection against extreme weather and predators (Evans 1977). Different beetle groups may occupy different levels of canopy. Parker (1995) defined canopy as the combination of all leaves, twigs and small branches in a stand of vegetation, and this definition is used here. It departs from other concepts that are restricted to the uppermost covering of vegetation, that is, the "roof" of the forest, the layer above the living limbs of the larger stems. The rain forest canopy can be classified into a number of subhabitats (Whitmore 1984). In this study, however, the canopy is divided into three simple levels due to the limitation of the sampling method. A number of researchers have investigated various assemblages of arthropods in different habitats (e.g. Hammond 1990, Nadkarni & Longino 1990, Stork & Brendell 1993, Mawdsley 1994) but relatively few have attempted to compare the diversity of various niches in different environmental conditions and in different strata of the canopy (Davis *et al.* 1997, Bruhl *et al.* 1998).

This study focused on the vertical stratification of beetles and we investigated the composition, species richness and abundance of the beetle assemblages at different canopy levels to answer the following questions:

(1) Are there distinct species richness, abundance and compositional differences in the Coleoptera assemblage between different vertical levels within a habitat and between habitats?

(2) Are certain families or feeding groups of beetles better represented at each level?

Materials and methods

Study sites

Two sites were chosen in Sabah, East Malaysia; one in a native forest and the other in a forest plantation. The distance between the two sites is approximately 90 km.

1. The arboretum, Sepilok (regenerating native forest)

The arboretum site consists of an area of 106.7 ha at 15–45 m asl. Situated adjacent to the Kabili-Sepilok Forest Reserve, it was gazetted as an arboretum in 1971. The vegetation of the area consists of logged-over lowland dipterocarp forest that includes good regenerating stands of naturally occurring forest species such as *Shorea* spp., *Parashorea* spp. and *Dipterocarpus* spp. The arboretum was partially logged between 1950s and 1960s. The mean temperature is about 27 °C and the mean annual rainfall around Sandakan is 3148 mm. The average daily sunshine is about 6–7 hours with the highest average in April and the lowest in January. Lee and Berhaman (1992) gave a detailed account of the Sepilok arboretum. The arboretum was chosen because of the practicality of setting-up a tower. It would have been logistically difficult and time-consuming to set up the tower at the Kabili-Sepilok Forest Reserve. Moreover, the orang-utans in the reserve might disturb the tower.

2. The *Acacia mangium* plantation, Segaliud Lokan (forest plantation)

The plantation area is located in the northern most part of the Segaliud-Lokan Forest Reserve (5° 37' N, 117° 35' E) and is about 100 km (by road) south-west of Sandakan. Plantation activities began in 1988 and by 1998, more than 180 ha have been planted since, of which about 100 ha were dedicated to acacias. Prior to plantation, the area was classified as a lowland dipterocarp forest. Other main plantation species include *Paraserianthes falcataria*, *Gmelina arborea* and various indigenous species. The *A. mangium* site chosen for the study is located within a 20-ha area planted in 1989 at 3 × 3 m spacing. The undergrowth in the plantation was dominated by the fern, *Nephrolepis pilosula* (Davalliaceae). In some parts of the acacia plantation, the fern grew to 1.5 m height. The plantation was about 8 years old when sampling was conducted.

Sampling procedure

An aluminium alloy tower was used to gain access to different levels of canopy (Figure 1). The height of the tower was 20 m, which allowed access to the crowns of younger trees. The tower was held in place by steel cables at each side. It was highly compact and portable and took only about a day to install (with four people working).

Three replicates were chosen at each study site. In the forest, it is almost impossible to sample from one tree alone at different levels of the forest. The trees normally
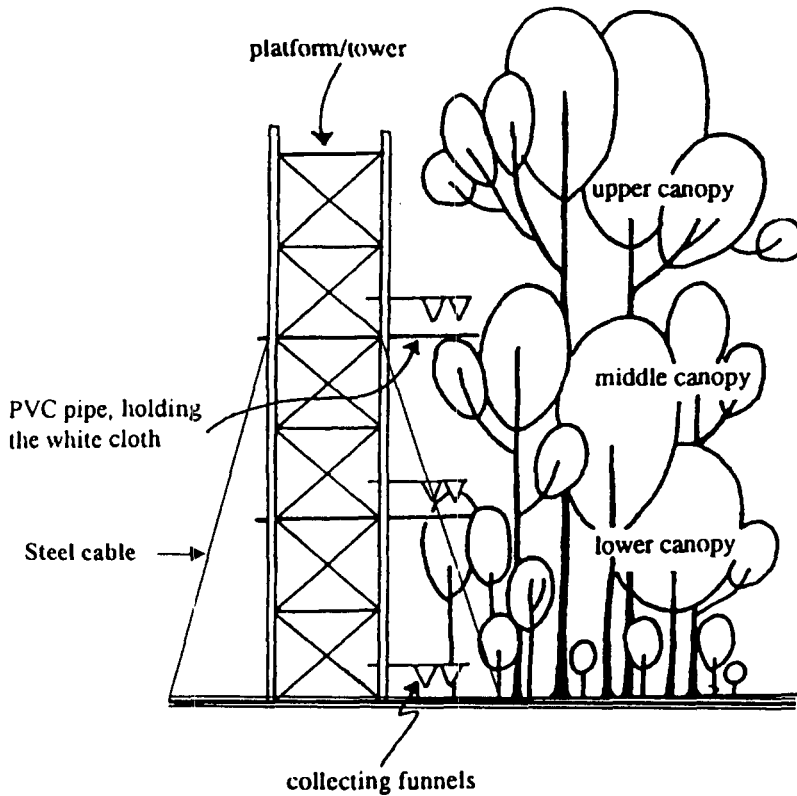
Figure 1. The set up of the aluminium alloy tower (20 m). The height of each canopy level varies between sites and replicates. The arboretum has a higher canopy compared with the acacia plantation. Variation between replicates in a site is subject to the presence of leaves and branches along the vertical profile. However, effort was taken to ensure that the height of each level was within a standard range (see Table 1).

grow very near each other and there is overlapping of vegetation at different canopy levels. Therefore, the vertical profile of each sampling replicate was taken and not a single tree species.

In this study, three levels of each replicate were investigated: canopy bottom, middle and top. The precise height of each level varied, depending on the profile of the replicate (Table 1). The height of each level was not entirely consistent because for a vegetational profile like the rain forest, it is difficult to obtain a fixed level or point that has a comparable density of leaves for mist-blowing. Five collecting-cloth funnels of 1-m diameter, with killing bottles attached, were hung under each level of the canopy. The vegetation at the different levels was sprayed from the tower using a mist-blower (Maruyama MD300), from the top to the bottom. Each level of the tree was mist-blown for one minute. The discharge rate of the mist-blower was 25 ml min^{-1} and the mist extended to a maximum height of 10 m (Chey 1994). The chemical used was Pybuthrin 2/16 (Roussel Uclaf), an environmentally-benign, pyrethroid-based insecticide. Knocked-down insects dropped through the funnels into attached killing bottles containing 75% ethanol solution. The funnels were monitored for about one hour and beetles that were trying to escape were brushed down the funnel with a

Table 1. Botanical descriptions and other remarks on the replicates in stratified vertical sampling of the Coleoptera assemblage at the arboretum in Sepilok and acacia plantation

(a) Arboretum, Sepilok

Replicate	Tree species	Vernacular name	Family	Dbh (cm)	Height (m)	Level(s) of canopy	Height of each canopy level
1	*Gracinia mangostana*	Kandis	Guttiferae	25	13	Bottom, middle	Bottom = 3–5 m
	Glochidion rubrum	Obah nasi	Euphorbiaceae	26	15	Top	Middle = 9–11 m
	Parashorea tomentella	Urat mata beludu	Dipterocarpaceae	20	17	Top	Top = 15–17 m
	Endospermum peltatum	Senduk-senduk	Euphorbiaceae	20	15	Top	
2	*Cratoxylum formosum*	Geronggang	Hypericaceae	24	22	Top	Bottom = 3–5 m
	Litsea sp.	Medang	Lauraceae	15	15	Bottom, middle	Middle = 8–10 m
	Parashorea tomentella	Urat mata beludu	Dipterocarpaceae	52	35	Top	Top = 17–23 m
	Dryobalanops lanceolata	Kapur paji	Dipterocarpaceae	20	26	Bottom, middle	
	Shorea leprosula	Seraya tembaga	Dipterocarpaceae	30	30	Top	
3	*Parashorea tomentella*	Urat mata beludu	Dipterocarpaceae	16	12	Middle	Bottom = 3–5 m
	Parashorea tomentella	Urat mata beludu	Dipterocarpaceae	27	20	Top	Middle = 8–9 m
	Madhuca pubicalyx	Nyatoh	Sapotaceae	28	11	Bottom, middle	Top = 15–17 m
	Parashorea tomentella	Urat mata beludu	Dipterocarpaceae	12	9	Middle	
	Shorea smithiana	Seraya timbau	Dipterocarpaceae	18	15	Top	

(b) Acacia plantation

Replicate	Tree species	Vernacular name	Family	Dbh (cm)	Height (m)	Level(s) of canopy	Height of each canopy level
1	*Acacia mangium*	Acacia	Leguminosae	21	17	Top	Bottom = 3–4 m
	Acacia mangium	Acacia	Leguminosae	9	13	Bottom, middle, top	Middle = 6–9 m
	Acacia mangium	Acacia	Leguminosae	12	10	Bottom, top	Top = 12–16 m
2	*Acacia mangium*	Acacia	Leguminosae	27	18	Top	Bottom = 4–5 m
	Acacia mangium	Acacia	Leguminosae	17	13	Bottom, middle, top	Middle = 6–8 m
							Top = 12–15 m
3	*Acacia mangium*	Acacia	Leguminosae	22	14	Bottom, middle, top	Bottom = 3–5 m
	Acacia mangium	Acacia	Leguminosae	25	20	Bottom, top	Middle = 7–9 m
							Top = 12–14 m

soft paint brush. Spraying was conducted on windless mornings between 8:00 and 9:00 a.m. Cloth sheets were placed beneath the funnels at the top and middle levels of canopy to prevent insect mix-up in funnels below. Sampling was carried out between July and October 1998, which was in between the dry season (March–May) and wet season (November–February) in Sabah.

Sorting and identification of specimens

Specimens were classified to family level (some to subfamily level) and were sorted to morphospecies. Coleoptera specialists at the Natural History Museum, London, carefully checked the specimen sorting in this study to provide sufficient quality control. In most biodiversity studies, morphospecies sorting has been considered a robust tool (Stork 1991, Stork & Brendell 1993, Floren & Linsenmair 1998) because of the lack of taxonomic knowledge of insects as well as time constraints.

Analyses of data

A commercial statistic program for computers, SPSS 1997, was used for statistical analyses. The Levene Test was applied to see if the data fulfilled the assumption of homogeneity of variance, and if not, appropriate transformations were carried out. In this study, the Tukey's HSD (honestly significant difference) test was used to assess post-hoc differences between means subsequent to an ANOVA. The chi-square test was used to assess the independence of variables in categorical data.

Species composition data were analysed with a canonical correspondence analysis (CCA) using the computer software PC-ORD version 3.04 for Windows. CCA was used in combination with DCA (detrended correspondence analysis) to infer whether the measured environmental variables can account for the major variation in the species data (Ter Braak 1986). Rules for the interpretation of species-sample biplots (DCA) or species-sample-environment triplots (CCA) followed Ter Braak (1986), Jongman *et al.* (1995) and Kent and Coker (1997).

Eigenvalues were used in DCA and CCA. They are values that represent the relative contribution of each ordination axis to the explanation of the total variation in the data. There is one eigenvalue for each ordination axis, and the size of the eigenvalue for an axis is a direct indication of the importance of that axis in explaining the total variation within the data set (Kent & Coker 1997). The significance of an eigenvalue can be tested with a Monte Carlo randomisation test.

Canonical coefficients and intraset correlation coefficients were used to interpret the ordination axes. Both coefficients relate to the rate of change in community composition per unit change in the corresponding environmental variable. However, in the former coefficient, it is assumed that other environmental variables are held constant, whereas in the latter coefficient, the other environmental variables are assumed to co-vary with the corresponding environmental variable (Ter Braak 1986).

Results and discussion

Family richness, abundance and composition

In total, 43 families were recorded. In both sites, there was no significant difference in the number of families recorded between levels (arboretum, $\chi^2 = 3.3$, p > 0.05; acacia plantation, $\chi^2 = 1.2$, p > 0.05). Families recorded in the sampling and also their trophic groups are shown in Appendix 1.

A total of 32 families were recorded at the arboretum in Sepilok. The five most prominent groups sampled are shown in Figure 2 along with their proportions of species and abundance at different canopy levels. There was no significant difference in the proportions of respective families between levels except for the abundance proportion of Chrysomelidae which was greater at the bottom level (Table 2a). Three chrysomelid subfamilies were recorded, with Galerucinae (12 species from 21 individuals) being dominant.

In the acacia plantation, 31 families were recorded. The five most prominent groups are shown in Figure 3, along with their proportional representation at different levels. The proportions of each family at different levels were not significantly different, except for Tenebrionidae (Table 2b), which was proportionally more abundant at the bottom level. Tenebrionids feed on a variety of materials, mostly of plant origin. The comb-clawed tenebrionids, Alleculinae, were fairly common. Five species were recorded in the acacia plantation, but only one species was recorded in the arboretum. Adult Alleculinae were often associated with foliage and flowers.
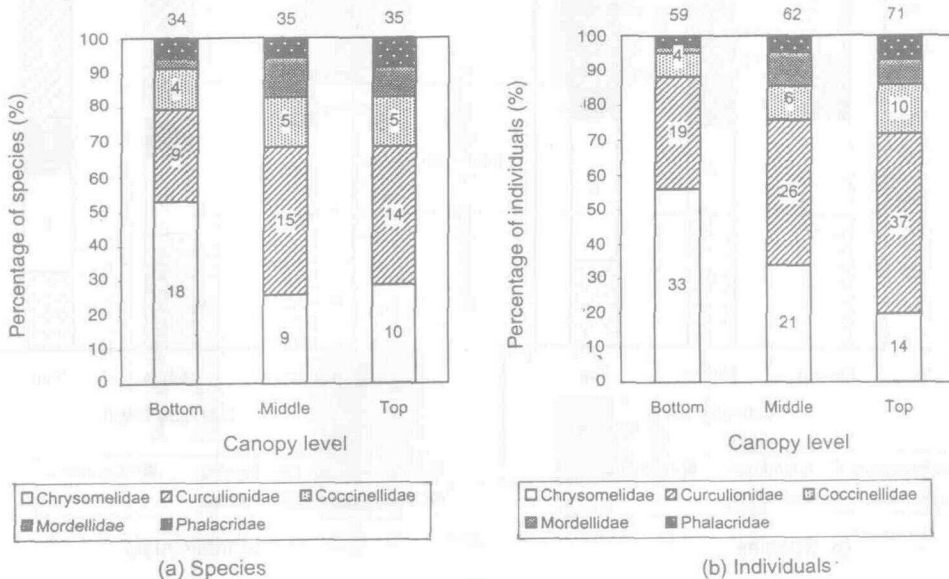

(a) Species   (b) Individuals

Figure 2. Proportions of (a) species and (b) individuals of the five dominant families in the arboretum. The total number of the five groups is given above the respective bar. The numbers within the bar are for the respective families. Only families with large proportions are shown.

Table 2. Chi-square values of dominant Coleoptera families at different levels of the canopy at the arboretum in Sepilok and the acacia plantation

(a) Arboretum, Sepilok

Family	χ^2	
	Species	Individuals
Chrysomelidae	3.95	8.15*
Curculionidae	2.00	6.03
Coccinellidae	0.14	2.80
Mordellidae	1.75	3.50
Phalacridae	0.29	1.40

(b) Acacia plantation

Family	χ^2	
	Species	Individuals
Tenebrionidae	4.46	9.74*
Elateridae	1.00	3.74
Phalacridae	2.67	1.50
Corylophidae	2.00	4.31
Anthicidae	0.67	1.90

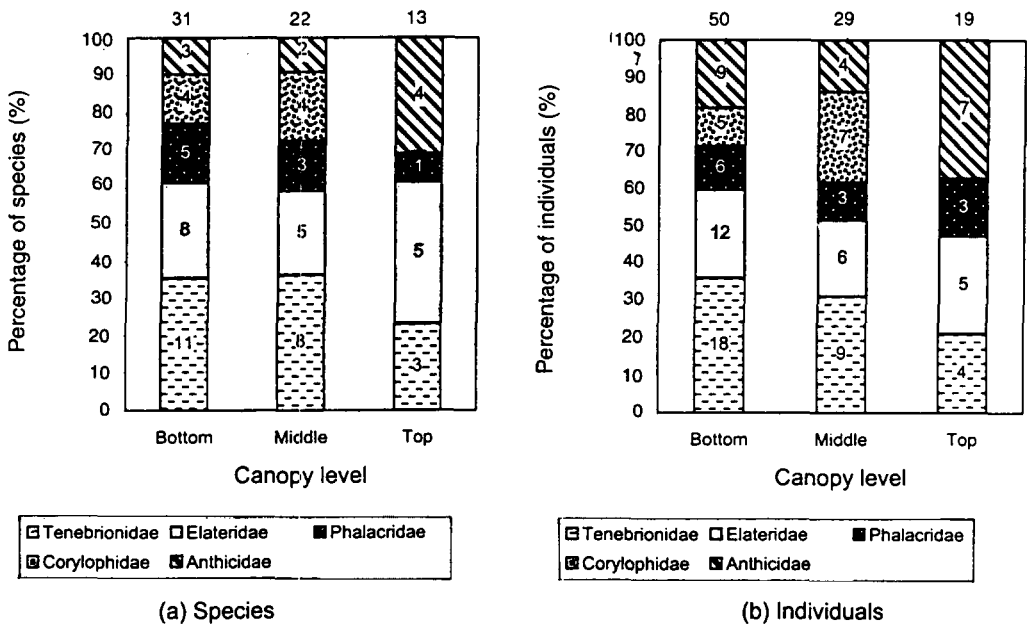* denotes significant at $p < 0.05$

Figure 3. Proportions of (a) species and (b) individuals of the five dominant families in the acacia plantation. The total number of the five groups is given above the respective bar. The numbers within the bar are for the respective families.

Only one family (Phalacridae) was common among the five most dominant families at both sites. However, the two sites did not have any similar species of this family, suggesting a high level of variation between the sites. Many phalacrids are often associated with flowers or vegetation, feeding on pollen, smuts and spores of other fungi (Thompson 1958, Lawrence 1982). The difference in the dominant Coleoptera families between the two sites also suggests that vegetation type may be important in determining the composition of certain coleopteran groups in an area. The availability of food resources also determines the presence of certain groups. Davis *et al.* (1997) reported that most of the arboreal rain forest dung beetles were found between 5 to 20 m-height because that was where most arboreal sources of dung could be expected to accumulate.

Stratification of species and abundance within site

The arboretum had 147 species from 279 individuals while the acacia plantation had 107 species from 188 individuals. There was a significant decline in the number of species and individuals collected from the bottom to top level in the acacia plantation (ANOVA, Tukey's HSD, p < 0.05) but there was no significant diff in the arboretum (Figure 4).
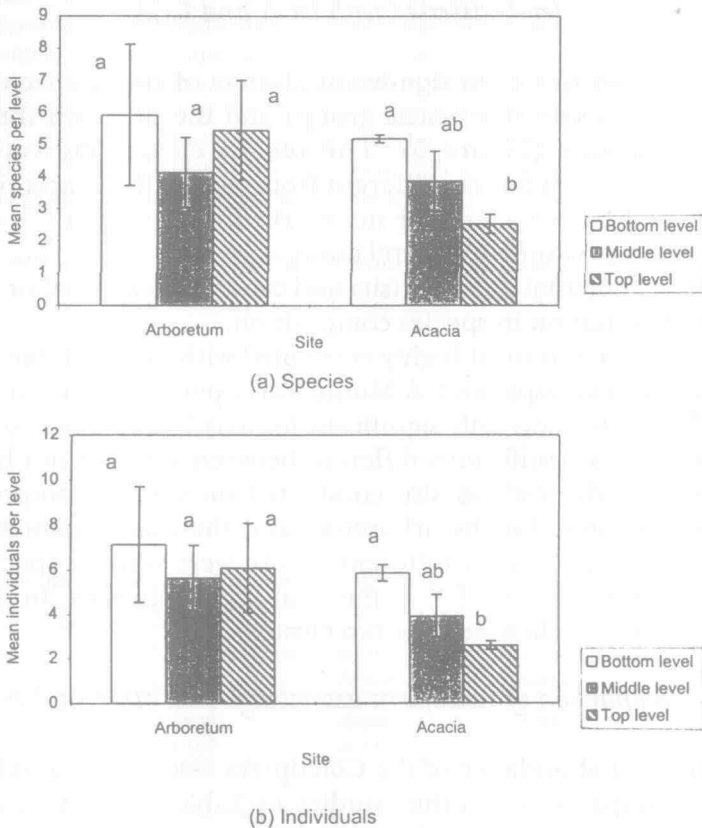

(a) Species

(b) Individuals

Figure 4. Mean Coleoptera species and individuals per level (with standard error) collected at different canopy level in the arboretum and the acacia plantation. Bars with the same letter within a study site are not significantly different (Tukey's HSD, p < 0.05).

The number of insects captured in this study is low compared to the enormous captures from rain forests reported by, for example, Stork (1991) and Davies *et al.* (1997). This is because the mist-blowing here was confined to a small part of the canopy with fewer collecting funnels compared with the fogging technique. In canopy-fogging, the whole tree is usually fogged and more than 20 collecting funnels (depending on the size of the canopy) are placed underneath the tree canopy (Stork *et al.* 1997). Another reason for the low capture rate is the relatively low penetration of mist-blowing into tree canopies (Chey *et al.* 1998).

In the arboretum, 13 to 20 species (9–14%) were found exclusively at one level while in the acacia plantation, it was within the range of 7 to 15 species (6–14%). There was no significant difference in the number of species found exclusively between levels in the arboretum and the acacia plantation. Hammond *et al.* (1997) reported that around one quarter of the estimated 6425 beetle species present in an intensively studied 500-ha area of lowland rain forest in Sulawesi were found at the tree-crown level. However, almost half of these are 'tourists' as far as the canopy level is concerned, and half of the 'resident' canopy species are likely to be canopy specialists, i.e. between 8 and 13% of the total beetle assemblage of the study area.

Species composition between sites and between canopy levels assessed with DCA and CCA

The CCA triplot shows two main significant clusters of beetle species composition: one on the right-hand side (the acacia group) and the other on the left-hand side (the arboretum group) (Figure 5). The results clearly indicate that species composition in the arboretum was different from that in the acacia plantation. CCA eigenvalues for the first two axes were not markedly lower than the eigenvalues for DCA, and all species-environment correlations were high (Table 3a), indicating that the measured environmental variables (site and canopy level, or either one) explained a major part of the variation in species composition.

Within the CCA, site was most highly correlated with axis 1 (Table 3b). Axis 2 was highly correlated with canopy level. A Monte Carlo permutation test was performed on axes 1 and 2. The test was only significant for axis 1 (Table 3c), showing that the beetle composition was significantly different between sites but not between canopy levels. The Monte Carlo test was also conducted on species composition between canopy levels within sites (for the arboretum and the acacia plantation separately) and it was again not significantly different. There were only 12 species in common between sites, amounting to just 5% of the total species number. In the CCA triplot, these species were located between the two clusters.

Comparison of Coleoptera assemblage with other studies

The proportions of abundance of the Coleoptera assemblage at different levels in this study were compared with other studies in Table 4. Many of the Coleoptera specimens in Sutton and Hudson (1980) and Sutton *et al.* (1983) were collected at level 4 (25–30 m), which was not sampled in this study due to the limitation of the tower. Obviously, Coleoptera vary greatly in their vertical distribution within and between sites.
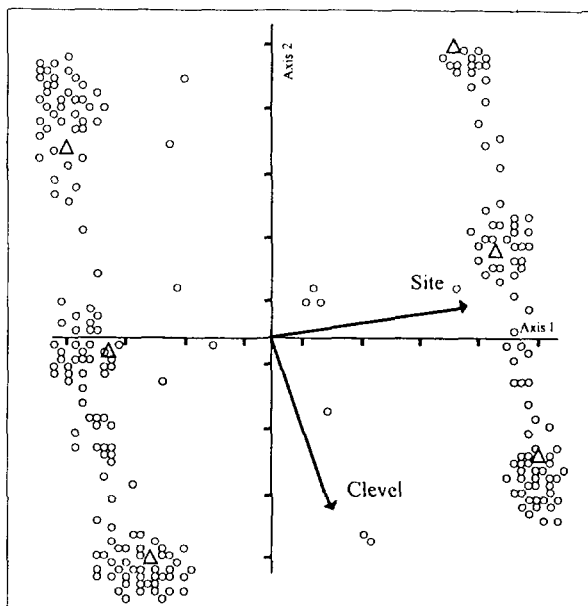
Figure 5. The distribution of 244 species of Coleoptera collected through mist-blowing at different levels of the canopy in the arboretum and the acacia plantation. Canonical correspondence analysis (CCA) ordination triplot with mist-blown samples (Δ), beetle species (o), and site (arboretum and acacia) and canopy level (bottom, middle and top) as environmental variables (arrows). Species located at the right-hand side of the triplot are mostly from acacia. Those on the left-hand side are mainly arboretum species. Similarly, the environmental variable for the canopy level, labelled as 'Clevel', shows that species located at the lower part of the graph are mainly from the bottom level of the canopy.

Table 3a. Comparison of eigenvalues by DCA and CCA of Coleoptera species composition data (see Figure 5) and the correlation coefficients of CCA

	Axis 1	Axis 2
	Eigenvalues	
DCA	0.933	0.709
CCA	0.899	0.669
	Correlation coefficients	
CCA	0.995	0.978

Table 3b. Coleoptera species composition data from Figure 5: canonical coefficients and the intraset correlations of environmental variables with the first two axes of CCA

Axis variable	Canonical coefficients		Correlation coefficients	
	Axis 1	Axis 2	Axis 1	Axis 2
Site	-0.913	-0.241	-0.985	-0.175
Clevel	0.167	-0.811	0.293	-0.956

Table 3c. The Monte Carlo test results at 99 permutations

Axis	Variable	p value
Axis 1	Site	≤ 0.010
Axis 2	Clevel	0.070

Table 4. Percentage of Coleoptera abundance at different canopy levels. Figure in parenthesis is the percentage when level 4 is taken into account.

Site	Percentage of Coleoptera abundance (%)				Sampling method	Source
	Level 1 (1-5 m)	Level 2 (8-10 m)	Level 3 (15-20 m)	Level 4 (25-30 m)		
Rain forest, Zaire	8 (5)	15 (9)	77 (46)	(40)	Sticky traps	Sutton & Hudson (1980)
Rain forest, Panama	63 (38)	21 (13)	16 (10)	(39)	Actinic traps	Sutton *et al.* (1983)
Rain forest, P. N. Guinea	25 (11)	30 (13)	45 (20)	(56)	Actinic traps	– ditto –
Rain forest, Temburung, Brunei	58 (39)	21 (14)	21 (14)	(33)	Actinic traps	– ditto –
Rain forest, Labi, Brunei	29 (18)	27 (17)	44 (27)	(37)	Actinic traps	– ditto –
Sepilok Arboretum, Sabah	38	28	33	+	Mist-blowing	This study
Acacia plantation, Sabah ++	49	32	21	+	Mist-blowing	This study

+ In this study, sampling was conducted only up to 20 m due to limitation of the tower.
++ In acacia, levels 2 and 3 were lower: level 2 = 6–9 m, level 3 =12–16 m.

Sutton and Hudson (1980) reported that flying insects are most abundant in the upper canopy levels in a lowland rain forest in Zaire, with Staphylinidae, Platypodidae, Scolytidae and Elmidae as the abundant Coleoptera families. The authors elaborated that Staphylinidae covered more than half of all the beetle specimens collected, even though this family is predominantly ground associated. White (1983), however, noted that staphylinids are among the most proficient fliers of all beetles. All adult Elmidae are aquatic and are found at canopy level only as tourists. Sutton and Hudson (1980) suggested the high abundance of Scolytidae was due to nuptial flights as they had flown to the upper canopy to aid dispersal and to mate. Sutton and Hudson (1980) had demonstrated that the vertical distribution of scolytid beetles in the forest of Côte d'Ivoire correlates with differing evapopreferenda. Brown (1961) reported that there appear to be a tendency towards some vertical stratification of Scolytidae in light-trapping on a high tower in Mpanga Forest, Uganda. Sutton *et al.* (1983) concluded that flying insects in the rain forests are not always concentrated in the upper canopy, although there is a tendency for this to occur when topography and forest structure are simple. Although sampling was conducted in the same type of forest the authors observed that a different family, Dryopidae (mostly aquatic species), emerged as the most abundant group. The differences in results (in terms of proportions and dominant families) between these studies (Sutton & Hudson 1980, Sutton *et al.* 1983) and ours are likely to be due to the sampling time and method employed. The study by Sutton *et al.* (1983) focused on beetles attracted to light during nocturnal flights and have little bearing on the composition of resident beetle assemblage in the canopy.

The result from Sutton and Hudson (1980) was based on sampling with sticky traps, which were operated for 23 hours. For the present study, mist-blowing was used, and only in the morning. Sutton and Hudson (1980) divided the high abundance of insects from the upper canopy into two components: (1) insects flying from lower levels, engaged in mating swarms and dispersal and (2) insects staying permanently in the upper canopy. The first component is unlikely to be present significantly in this study as insect nuptial flights most typically occur around sunset and sunrise (Haddow & Corbet 1961).

Factors affecting species richness and abundance at different levels

In this study, the decline of the Coleoptera fauna in species richness and abundance from bottom to top level was obvious in the acacia plantation but not in the arboretum. There are various abiotic factors which change from the upper to the lower canopy and this may have an effect on the composition of the Coleoptera assemblage. The upper (outer) regions of the canopy are subjected to extreme variation of heat, light, humidity and wind velocity which are tolerated by relatively few 'resident' species. However, these effects may penetrate only a relatively short distance below the 'roof' of the rain forest so that much of the upper canopy as defined in this present study was little affected.

In the arboretum, the situation is similar to that of a rain forest where the canopy is dense and it is possible that variation in abiotic factors between most parts of the three levels we studied was relatively low compared to the acacia plantation. In the acacia plantation, the canopy is very open and the effects of extreme variation in abiotic factors may have extended further into the upper, middle and even the lower layers of the canopy.

Constraints of canopy stratification in this study

There were a few difficulties encountered during this study. One of them was determining truly equivalent top, middle and bottom levels in each replicate. A standard measurement (e.g. height above the ground) could not be applied, especially at the arboretum as some trees grew straight and only branched off at the upper canopy. Therefore, the replicates had to be selectively chosen, especially when looking for trees with branches and leaves at the bottom and middle levels.

Mixing of insects of varying levels might have occurred even though a piece of white cloth was put between the strata during sampling. This was because of the difficulty of completely segregating each level, especially in areas with multiple branches. The noise produced by the mist-blower also might have frightened many of the beetles away before the insecticide could reach them.

Conclusion

Despite some limitations in the sampling technique, the results in this study showed some differences in the species richness, abundance and composition of arboreal beetles between a regenerating native forest and a forest plantation. Such results are essential in evaluating the impact of environmental changes on a habitat, from the

perspective of an arboreal insect group. The declining numbers of species richness and individuals of beetle fauna in the plantation, from bottom to top level, showed that the canopy of the plantation is less favourable due to the factors highlighted in this paper. Species composition, however, was not distinctly different between canopy levels within site. The high number of species with very few individuals is common in tropical beetle fauna and this can contribute to the insignificant differences of various hypotheses in statistical analyses.

Acknowledgements

References

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

BASSET, Y., SPRINGATE, N. D., ABERLENE, H. P. & DELVARE, G. 1997. A review of methods for sampling arthropods in tree canopies. Pp. 27–52 in Stork, N. E., Adis. J. & Didham, R. K. (Eds.) *Canopy Arthropod*. Chapman & Hall, London.

BROWN, K. W. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda–observations on Coleoptera. *Transactions of the Royal Entomological Society of London* 113: 353–355.

BRUHL, C., GUNSALAM, G. & LINSENMAIR, K. E. 1998. Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. *Journal of Tropical Ecology* 14: 285–297.

CHEY, V. K. 1994. Comparison of Biodiversity Between Plantations and Natural Forests in Sabah Using Moths as Indicators. D. Phil. thesis, Oxford University. 284 pp.

CHEY, V. K., HOLLOWAY, J. D., HAMBLER, C. & SPEIGHT, M. R. 1998. Canopy knock-down of arthropods in exotic plantations and natural forest in Sabah, north-east Borneo, using insecticidal mist-blowing. *Bulletin of Entomological Research* 88: 15–24.

DAVIES, J. G., STORK, N. E., BRENDELL, M. J. D. & HINE, S. J. 1997. Beetle species diversity and faunal similarity in Venenzuelan rain forest tree canopies. Pp. 85–103 in Stork, N. E., Adis, J. & Didham, R. K. (Eds.) *Canopy Arthropod*. Chapman & Hall, London.

DAVIS, A. J., HUIJBREGTS, J., KIRK-SPRIGGS, A. H., KRIKKEN, J. & SUTTON, S. L. 1997. The ecology and behaviour of arboreal dung beetles in Borneo. Pp. 417–432 in Stork, N. E., Adis, J. & Didham, R. K. (Eds.) *Canopy Arthropod*. Chapman & Hall, London.

ERWIN, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists' Bulletin* 39: 74–75.

ERWIN, T. L. & SCOTT, J. C. 1980. Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the canal zone of Panama. *The Coleopterists' Bulletin* 34(3): 305–322.

EVANS, G. 1977. *The Life of Beetles.* George Allen & Unwin Ltd., London. 232 pp.

FLOREN, A. & LINSENMAIR, K. E. 1998. Non-equilibrium communities of Coleoptera in trees in a lowland rain forest of Borneo. *Ecotropica* 4: 55–67.

FUKUYAMA, K., MAETO, K. & KIRTON, L. G. 1994. Field test of a balloon-suspended trap system for studying insects in the canopy of tropical rain forests. *Ecological Research* 9: 357–360.

HADDOW, A. J. & CORBET, P. S. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda–swarming activity above the forest. *Transactions of the Royal Entomological Society of London* 113: 284-300.

HADDOW, A. J., CORBET, P. S., GILLETT, J. D. *et al.* 1961. Entomological studies from a high tower in Mpanga Forest, Uganda.(12 papers in) *Transactions of the Royal Entomological Society of London* 113: 249–368.

HAMMOND, P. M. 1990. Insect abundance and diversity in the Dumago-Bone National Park, North Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. Pp. 197–254 in Knight, W. J. & Holloway, J. D. (Eds.) *Insects and the Rain Forests of South East Asia (Wallacea)*. The Royal Entomological Society of London.

HAMMOND, P. M. 1994. Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London* B 345: 119–136.

HAMMOND, P. M. 1995. Described and estimated species numbers: an objective assessment of current knowledge. Pp. 29–71 in Allsopp, D., Hawksworth, D. L. & Colwell, R. R. (Eds.) *Microbial Diversity and Ecosystem Function*. CAB International.

HAMMOND, P. M., STORK, N. E. & BRENDELL, M. J. D. 1997. Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. Pp. 184–219 in Stork, N. E., Adis, J. & Didham, R. K. (Eds.) *Canopy Arthropod*. Chapman & Hall, London.

JONGMAN, R. H. G., TER BRAAK, C. J. F. & VAN TONGEREN, O. F. R. (Eds.). 1995. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge. 299 pp.

KENT, M. & COKER, P. 1997. *Vegetation Description and Analysis–a Practical Approach*. John Wiley & Sons, New York. 363 pp.

LAWRENCE, J. F. 1982. Coleoptera. Pp. 482–553 in Parker, S. P. (Ed.) *Synopsis and Classification of Living Organisms*. McGraw-Hill Book Co., London.

LEE, Y. F. & BERHAMAN, A. 1992. The Sabah Forestry Department's arboretum at Sepilok, Sandakan. *Sandakania* 1: 23–36.

LOWMAN, M. D., MOFFETT, M. & RINKER, H. B. 1993. A new technique for taxonomic and ecological sampling in rain forest canopies. *Selbyana* 14: 75–79.

MAWDSLEY, N. A. 1994. Community Structure of Coleoptera Assemblage in a Bornean Tropical Forest. Ph.D. thesis, University of London. 307 pp.

MAY, R. M. 1988. How many species are there on earth? *Science* 241: 1441–1449.

MAY, R. M. 1995. Conceptual aspects of the quantification of the extent of biological diversity. Pp. 13–20 in Hawksworth, D.L. (Ed.) *Biodiversity–Measurement and Estimation*. Chapman & Hall, London.

MOFFETT, M. W. 1993. *The High Frontier: Exploring the Tropical Rain Forest Canopy*. Harvard University Press, Cambridge, MA. 192 pp.

NADKARNI, N. M. & LONGINO, J. T. 1990. Invertebrates in canopy and ground organic matter in a neotropical montane forest, Costa Rica. *Biotropica* 3(22): 286–289.

PARKER, G. G. 1995. Structure and microclimate of forest canopies. Pp. 73–106 in Lowman, M. D. & Nadkarni, N. M. (Eds.) *Forest Canopies*. Academic Press, London.

SPEIGHT, M. R., HUNTER, M. D. & WATT, A. D. 1999. *Ecology of Insects: Concept and Applications*. Blackwell Science, Oxford. 350 pp.

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

STORK, N. E., ADIS, J. & DIDHAM, R. K. (Eds.). 1997. *Canopy Arthropod*. Chapman & Hall, London. 567 pp.

STORK, N. E. & BRENDELL, M. J. D. 1993. Arthropod abundance in lowland rain forest of Seram. Pp. 115–130 in Edwards, I. D., MacDonald, A. A. & Proctor, J. (Eds.) *Natural History of Seram, Maluku, Indonesia*. Intercept Ltd., Andover.

SUTTON, S. L., ASH, C. P. J. & GRUNDY, A. 1983. The vertical distribution of flying insects in lowland rain forests of Panama, Papua New Guinea and Brunei. *Zoological Journal of the Linnean Society* 78: 287–297.

SUTTON, S. L. & HUDSON, P. J. 1980. The vertical distribution of small flying insects in the lowland rain forest of Zaire. *Zoological Journal of the Linnean Society* 68: 111–123.

TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67(5): 1167–1179.

THOMPSON, R. T. 1958. Coleoptera Phalacridae. *Handbook for the Identification of British Insects* 5(5): 1–16.

WHITE, R. E. 1983. *A Field Guide to Beetles of North America.* The Peterson Field Guide Series, Houghton Mifflin Company, Boston. 368 pp.

WHITMORE, T. C. 1984. *Tropical Rain Forest of the Far East.* Clarendon Press, Oxford. 352 pp.

Appendix 1. Details of species and individuals (in brackets) of Coleoptera families sampled through stratified vertical sampling using a mist blower at the Sepilok arboretum and acacia plantation (R = replicate; canopy level: B = bottom, M = middle, T = top).

No.	Family	Trophic group	Arboretum R1 B	R1 M	R1 T	R2 B	R2 M	R2 T	R3 B	R3 M	R3 T	Total	Acacia R1 B	R1 M	R1 T	R2 B	R2 M	R2 T	R3 B	R3 M	R3 T	Total
1	Carabidae	Pr.(etc)	1(1)			1(1)			1(1)			3(3)					1(1)		1(2)		1(1)	1(4)
2	Histeridae	Pr					1(1)					1(1)										0(0)
3	Staphylinidae	Pr	2(4)	1(1)		1(1)	1(1)		2(2)			4(9)										0
	Aleocharinae*	Pr, F, etc	2(4)			1(1)	1(1)		2(2)			4(9)										
	Paederinae*					1(1)	1(1)		2(2)			3(6)										
4	Psclaphidae	Pr	1(1)									1(1)										
5	Lucanidae	X,(etc)										1(1)										
6	Scarabaeidae	S,H,X										0										
	Aphodiinae*	S										0										
7	Ptilodactylidae	S, F										0										
8	Limnichidae	?S/H										0										
9	Buprestidae	X, H							1(1)			1(1)										
10	Elateridae	H, X, Pr, S	1(1)			1(2)	1(1)	2(5)	1(2)			4(11)	3(7)	2(2)	2(2)	2(2)	2(2)	2(2)	3(3)	2(2)	1(1)	16(23)
11	Eucnemidae	F/X										0	1(2)	2(4)	1(2)	2(2)	1(1)					5(11)
12	Dermestidae	S		1(1)								1(1)						1(1)				1(1)
13	Anobiidae	F, X	1(1)				2(2)					3(3)					1(1)					1(1)
14	Cleridae	Pr, (H, Pa)	1(1)	1(1)					1(1)			2(3)										0
15	Melyridae	Pr	3(4)				1(2)	1(1)				4(7)										0
16	Nitidulidae	F, S, H, (Pr)		1(1)								1(1)		1(1)								1(1)
17	Phalacridae	H, F	2(2)	2(3)			3(5)					6(10)	2(2)	2(2)	1(2)		1(1)		3(4)		1(1)	9(12)
18	Sphindidae	F	1(1)									1(1)										0
19	Silvanidae	F, S	1(1)	2(2)	2(2)	1(1)		1(1)				3(7)										0
20	Biphyllidae	F										0			1(1)							1(1)
21	Languriidae	F, H, (etc)	2(3)				1(1)					3(4)		1(1)		1(1)						2(2)
22	Erotylidae	F			1(1)			1(1)				2(2)										0
23	Corylophidae	F		1(1)			1(1)		1(1)			3(3)	1(1)	1(1)					4(12)	4(6)		7(20)
24	Coccinellidae	Pr, (H)		3(3)	4(7)		1(1)	2(2)	4(4)	1(2)		13(19)	2(2)	1(1)	1(1)							3(4)
25	Discolomidae	F	1(1)		2(3)							3(4)			1(1)	1(1)				1(1)		2(3)
26	Colydiidae	F, (Pr)										0	1(1)	1(1)								2(2)
27	Mycetophagidae	F										0				2(2)						2(2)
28	Cisidae	F										0	1(1)							1(1)		2(2)
29	Monotomidae	X, H, S	1(1)									1(1)										0
30	Mordellidae	H, F, X		3(4)		1(1)	1(2)	2(2)			1(3)	7(12)								2(2)		2(2)
31	Anthicidae	?S,				1(1)		1(1)				1(2)	1(4)	2(2)	3(3)	3(4)	1(1)		1(1)	1(1)	1(4)	6(20)
32	Pedilidae	?S					1(1)	1(1)				2(2)										0
33	Aderidae	?S, ?H	2(2)	1(1)								3(3)	1(1)			1(1)	1(1)			1(1)	1(1)	4(5)
34	Lagriidae	S, ?H										0		1(1)				1(1)				2(2)
35	Tenebrionidae	S, F	2(2)					3(3)				5(5)	5(5)	3(3)		4(8)	1(1)	2(3)	5(6)	5(5)		16(31)
	Alleculinae*	?X, ?H	1(1)					1(1)				2(2)	1(1)	2(2)		2(2)	1(1)	1(2)	4(4)	2(2)		5(14)
	Remainder*	S, F, (etc)	1(1)					2(2)				3(3)	4(4)	1(1)		2(6)		1(1)	1(2)	3(3)	1(1)	11(18)
36	Cerambycidae	X	1(1)							1(1)		2(2)	1(1)									1(1)
37	Chrysomelidae	H	15(30)	9(21)	8(10)	3(3)		1(3)	1(1)		1(1)	30(69)		2(3)	1(3)			1(1)		1(1)		3(8)
	Eumolpinae*	H	6(15)	4(13)	1(1)	2(2)		1(3)				8(34)		2(3)	1(3)			1(1)		1(1)		3(8)
	Galerucinae*	H	6(11)3(6)	3(3)	1(1)							12(21)					1(1)		1(1)			2(2)\
	Cryptocephalinae*	H	3(4)	2(2)	4(6)			1(1)			1(1)	10(14)										0
38	Anthribidae	F, (H, etc)	2(2)									2(2)	1(1)		1(1)	1(1)	1(1)	1(1)	2(4)	1(1)	4(10)
39	Attelabidae	H			2(2)					1(1)		3(3)										0
40	Brenthidae	X										0	1(1)									1(1)
41	Curculionidae	H, X		1(1)	1(18)	9(19)	11(19)	11(16)	6(8)	2(3)	29(84)										0
	Otiorhynchinae*	H			1(18)	9(19)	11(19)	9(14)	5(7)	2(3)	25(80)										0
	Rhyncophorinae*	H, X					1(1)				1(1)										0
	Reminder*	H, X		1(1)			1(1)	1(1)			3(3)										0
42	Scolytidae	X, XF						1(1)			1(1)	1(1)								1(1)	2(2)
43	Platypodidae	XF	1(1)			1(1)						2(2)										0
	Total (species)		41	25	20	20	17	29	15	11	5	147	20	21	10	22	10	12	21	22	8	107
	Total (individuals)		60	39	43	31	26	42	16	14	8	279	28	24	14	29	10	14	31	26	12	188

* Subfamily/tribe/other remaining taxa that form the above family.

*Note: The trophic guild (food) of each family follows Hammond (1990). It is based on the more important feeding cycle of the beetle, which is mainly the larval stage: F = fungivorous; H = herbivorous; Pr = predacious; Pa = parasitic; S = saprophagous; X = xylophagous; XF = xylomycetophagous. Where more than one type of feeding is represented, the relevant symbols are separated by commas and placed in approximate order of importance. Trophic guilds with very few members are placed in parentheses.