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Patterns of beetle species diversity in *Castanopsis acuminatissima* (Fagaceae) trees studied with canopy fogging in mid-montane New Guinea rainforest

A. Allison, G.A. Samuelson and S.E. Miller

ABSTRACT

Canopy fogging with a pyrethrum-based insecticide was used to study the structure and diversity of beetle communities in eight *Castanopsis acuminatissima* (Bl.) A.DC. (Fagaceae) trees at elevations of 1200–1400 m in the Wau Valley, Papua New Guinea. Arthropods were collected in 1-m^2 trays suspended beneath the trees, sorted to Order and all beetles were identified to morphospecies. The eight trees yielded 3977 individual beetles representing 418 morphospecies in 53 families. The mean number of beetle morphospecies per tree was 114 (range 82–155). Of these morphospecies, 199 (47.6%) were represented by single individuals, and only 62 (14.8%) were represented by 10 or more individuals. Approximately 25% of the species on each tree were tree-specific, although those species represented only ca. 5–10% of the individuals. The similarity of the beetle fauna between trees, as measured by the Jaccard coefficient, ranged from 12 to 31%. This study is part of a much larger canopy fogging project in which 51 trees at study sites of 500 m, 1200–1400 m and 2100–2250 m have been fogged. Preliminary analysis of these samples indicates that diversity is similar at sites at 500 m and 1200–1400 m, but higher at 2100–2250 m.

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INTRODUCTION

Canopy fogging techniques were originally developed to control pests. Gagné was one of the first to recognize the applicability of these techniques to study the diversity of insects in native forest trees (Gagné, 1979). This led to further similar studies and in 1980 Erwin reported on his canopy studies in Panama (Erwin and Scott, 1980). The debate that this work sparked on the magnitude of global species richness (Erwin, 1982; Stork, 1988, 1993; May, 1990; Gaston, 1991, Hodkinson and Casson, 1991; Hammond, 1992; 1994; Hodkinson, 1992) prompted us in 1987 to commence a canopy fogging study of rainforest trees along an altitudinal transect from 500–2200 m in New Guinea.

In order to put patterns of diversity into clear perspective it is necessary to measure both within-habitat diversity (alpha-diversity) and between-habitat diversity, also known as turnover (beta-diversity) (Whittaker, 1975). To achieve this our experimental design emphasized a single species of tree, *Castanopsis acuminatissima* (Fagaceae). We fogged this species, together with related (*Lithocarpus* and *Nothofagus*) and unrelated genera (of Burseraceae, Clusiaceae, Dipterocarpaceae, Elaeocarpaceae, Grossulariaceae, Juglandaceae, Lauraceae, Phyllocladaceae, Rosaceae, Sapindaceae) at study sites located at 500 m (Oomsis), 1200–1400 m (Wau Valley) and 2100–2200 m (Biaru Road). We have now fogged a total of 51 trees and obtained more than 45 000 beetle specimens. The preliminary analysis of beetle samples from the first eight trees has been completed (two trees of *C. acuminatissima* from each of the three study sites and two trees of *Lithocarpus celebicus* at 500 m) (Allison *et al.*, 1993b). In this paper we report on the preliminary analysis of insect samples from eight *C. acuminatissima* trees (including two trees from the earlier analysis) at the same elevation in the Wau Valley.

STUDY SITES

Field work was based at the Wau Ecology Institute in Papua New Guinea. Part of the field work was conducted in remnant *Castanopsis* forest approximately 1 km east of Wau Ecology Institute on the road to the former New Guinea Goldfields mine at Nami (1250 m). The remaining work was conducted on the lower slopes of Mt Missim on a ridge between Poverty and Sandy Creeks (1250–1350 m).

The Wau Valley generally receives ca. 1900 mm of rainfall annually. There is a slight seasonal pattern with ca. 60% of the annual total occurring from November to April under the influence of the north-west monsoons. The period from May to October, when the south-west tradewinds form the dominant weather pattern, is sometimes very dry (<25 mm of rainfall per month). The mean annual temperature at

Table 11.1 Details of total number of species and individuals and mean body length (± S.D.) of beetles collected from a total of 126 1-m^2 trays suspended beneath trees

Tree	*Date*	*Total species*	*Total individuals*	*Mean (S.D.) body length (mm)*	*Total no. of trays used*
3*	15–10–87	82	335	2.66 (1.62)	13
4	04–11–87	86	300	2.51 (1.74)	13
9*	07–08–88	99	404	2.84 (1.74)	13
10	18–08–88	155	800	2.89 (2.46)	17
11	18–08–88	154	547	2.55 (1.63)	16
12	19–08–88	129	696	2.30 (1.35)	15
13	19–08–88	132	493	2.40 (1.65)	16
14	20–08–88	106	402	2.39 (1.28)	23

* Trees 3 and 9 are the same tree sampled 10 months apart.

1230 m (Wau Ecology Institute) in the Wau Valley is 22°C with little annual variation (Gressitt and Nadkarni, 1978). The vegetation in the area is generally classified as mid-montane rainforest (van Valkenburg and Ketner, 1994).

Study trees

We fogged eight trees of *Castanopsis acuminatissima* over a 2-year period (Table 11.1). C. *acuminatissima* occurs throughout New Guinea from nearly sea level to at least 2200 m and, like many tropical fagaceous trees, is found mainly on ridge crests (Soepadmo, 1972; Streimann, 1983; van Valkenburg and Ketner, 1994). It is extremely abundant in the Wau Valley and occurs in both primary and secondary forest. In some areas it appears as a monospecific dominant. It is the only species of *Castanopsis* in New Guinea, although there are a large number of related species to the west in Indonesia and south-east Asia, including a number of species that occupy subtropical and temperate environments (Soepadmo, 1972).

Our original sampling design called for 10 trays per tree, but to guard against the possibility of samples being lost, we used at least 13 trays for each tree and obtained a total of 126 tray samples (Table 11.1).

METHODS

Our methods are described in full in Allison *et al.* (1993b) and are summarized here. We selected trees for fogging that seemed healthy, had no epiphytes or understorey, did not have flowers or fruit, and had

a canopy that did not intermingle with adjacent trees. Each of the trees was 20–25 m tall and had a canopy volume of ca. 3000–4000 m^3.

Trees were fogged at 06:00 h (when the air was almost still) for 15 minutes using Pyranone® mixed with kerosene to form a solution of 5% active ingredient that was delivered by a Curtis Dynafog model 2610 fogger with the fog density dial set on '5'. The fogger was operated manually at canopy level from an adjacent tree. No living insects were found on branches subsequently removed from fogged trees.

Insect samples were collected in shallow plastic trays (126 in total), each 1 m^2 in area, suspended approximately 1 m above the ground beneath each tree. Each tray was numbered individually and had an 8-cm diameter aluminium funnel inserted in the centre, flush with the tray surface. A 125-ml Nalgene® bottle approximately half full of 70% ethanol was attached to the base of each funnel. Paint brushes (ca. 5 cm wide) were used to sweep the insect samples into the bottles for preservation. Trays were left in place for 2 hours after fogging although our impression was that most of the insects dropped from the tree within 20–30 minutes of fogging. Each sample bottle was labelled with tray and tree number. To ensure good preservation, the alcohol (70% ethanol) was changed at least four times in the month following collection.

In the laboratory all beetle specimens were removed, mounted and identified to morphospecies. Where possible our morphospecies concepts have been verified by specialists in each family. All information was entered into a computer database and reconciled with labelled specimens to ensure accuracy. All beetles and tree voucher specimens are deposited in the Bishop Museum, Hawaii. Beetles were measured from the anterior-most part of the head to the apex of the elytra, except for species with hidden heads for which the anterior edge of the pronotum was used and weevils for which the anterior edge of the eye was used. For species with more than a few individuals, several individuals, determined by inspection to be of average size, were measured. Mass was calculated from the equation derived by Schoener (1980) for Costa Rican rainforest beetles.

RESULTS

The eight trees yielded 3977 individual beetles representing 418 morphospecies in 53 families (Table 11.1). The total number of species on each of the trees ranged from 82 to 155. Four families had more than 25 species each: Chrysomelidae (39), Staphylinidae (39), Curculionidae (37) and Coccinellidae (29), together comprising 34% of total species richness. They each had more than 200 individuals and together were represented by 1885 individuals (47% of the total). The only other family with more than 200 individuals was Attelabidae which had 431

individuals (but only three species), more than Curculionidae (206), Coccinellidae (229), but less than Chrysomelidae (601) and Staphylinidae (849). These five families comprised 58% of total individuals. Eleven families were represented by single species (number of individuals in parentheses): Lampyridae (1), Merophysiidae (1), Rhizophagidae (1), Sphindidae (1), Hydrophilidae (2), Trogositidae (2), Alleculidae (3), Bostrichidae (4), Endomychidae (6), Eucnemidae (6) and Mycetophagidae (114).

There was no correlation between the number of collecting trays used beneath a tree and the number of individual beetles recorded from that tree (simple linear regression, $R^2 < 0.04$, $n = 8$). In other words, the variance in numbers of individuals per tree masked any effect from differing numbers of trays. Therefore, to simplify analysis we simply report on the total insect sample recorded from each tree.

Slightly fewer than half the species (199, 47.6%) were represented by single individuals ('singletons') and 19.9% (83) were represented by two individuals, with declining numbers represented by three or more individuals. Only 62 species (14.8%) were represented by 10 or more individuals (Figure 11.1). More than half the beetle species (55.3%) were found on only one tree and fewer than one-third were found on three or more trees (Table 11.2).

A separate analysis was performed on chrysomelids (herbivores) and staphylinids (predominantly predators; four species of omaliines, thought to be pollen-feeders, were excluded from this analysis). Patterns were similar to the overall trend described above, except that singletons comprised only 33.3% of chrysomelids (13 of 39 species) and 51.4% of staphylinids (18 of 35 species) (Figure 11.1).

Table 11.2 Distribution of beetle species on eight *Castanopsis acuminatissima* trees from ca. 1200–1400 m elevation in the Wau Valley, Papua New Guinea

Total no. of trees on which beetle species were recorded	*No. (%) of beetle species*
1	232 (55.3)
2	70 (16.8)
3	41 (9.8)
4	30 (7.2)
5	14 (3.4)
6	7 (1.7)
7	13 (3.1)
8	12 (2.9)

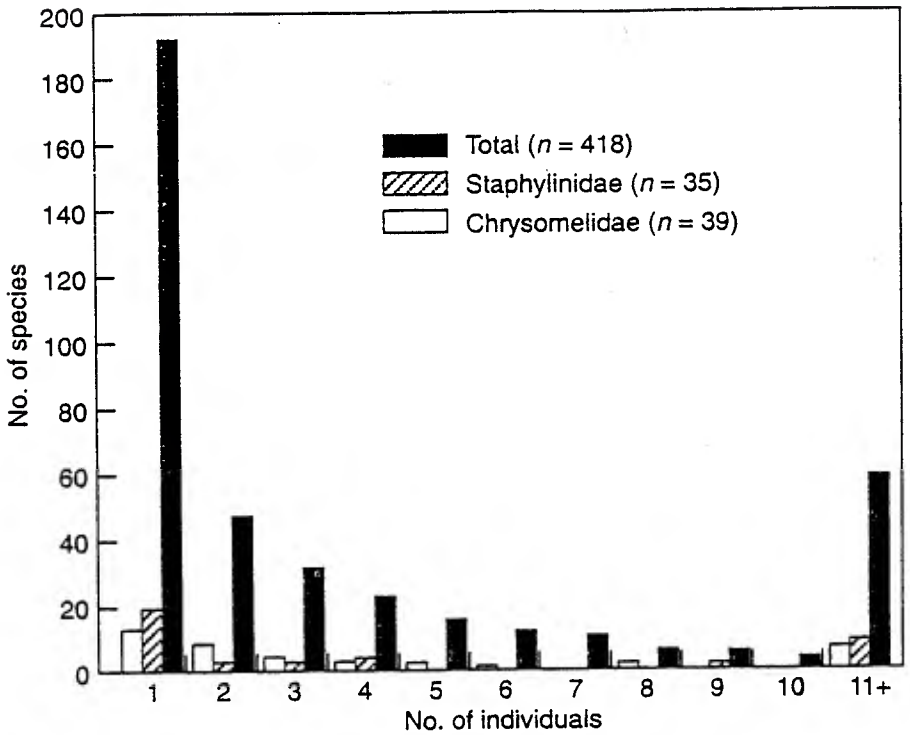

Figure 11.1 Comparison of numbers of individuals per species for all eight trees at 1200–1400 m. Categories are all beetles, Staphylinidae (except Omaliinae) and Chrysomelidae.

Although there was a large number of singleton species, they comprised only 5.0% of total individuals. The percentage of singletons on individual trees ranged from 10.1 to 17.2% (Table 11.3). These higher figures include species occurring as singletons on individual trees. However, about half these species occur on more than one tree and therefore are not treated as singletons in the overall sample (Table 11.2).

The species diversity of the tree samples as measured by the Q-statistic ranged from 32.31 to 68.72 (Table 11.3). (Q is used instead of α because the underlying species-abundance distribution did not follow the log-series; the Q-statistic is a non-parametric distribution based on the inter-quartile slope of the cumulative species abundance curve; Magurran, 1988.) Higher measures of diversity reflect lower total numbers of individuals in the sample.

The similarity in the beetle faunas of the various trees, as measured by the Jaccard coefficient, C_J (Magurran, 1988), ranged from 0.12 to 0.37 (Table 11.4). Trees 3 and 9, the same individual tree fogged about 10 months apart, had a Jaccard coefficient of 0.30, similar to the 0.31 for trees 3 and 4 (fogged 20 days apart and separated by a distance of ca. 50 m). The greatest similarity between samples, and the only samples

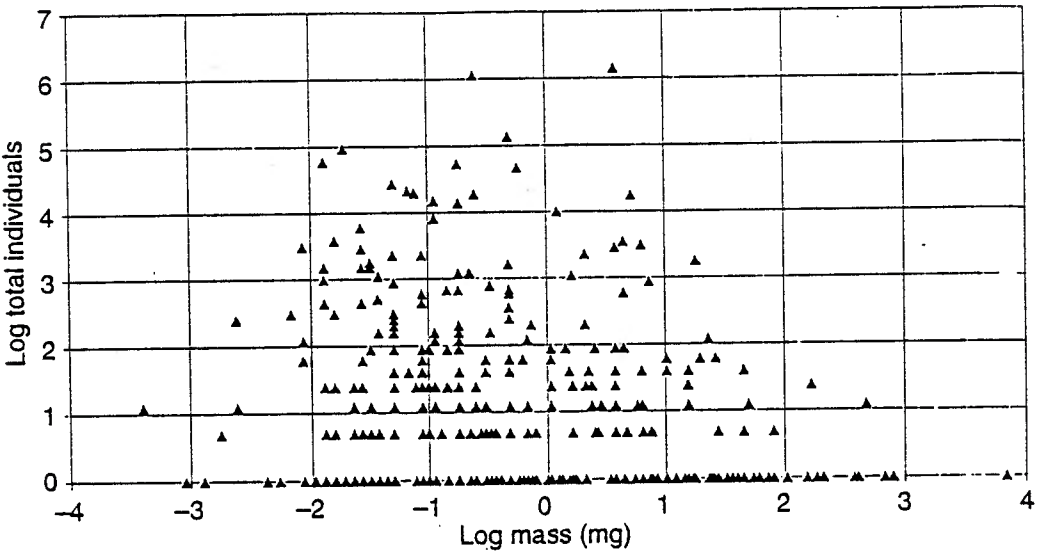

Figure 11.2 Double logarithmic plot of body mass versus abundance for beetles from eight trees at 1200–1400 m. Body mass was calculated from length using the formula for Costa Rican rainforest beetles derived by Schoener (1980).

with a Jaccard coefficient above 0.31, were from trees 10 and 11. These trees were ca. 15 m apart and were fogged at the same time.

Mean length of beetle species in the overall sample was 2.86 mm and ranged from 0.50 to 22.0 mm (SD = 2.23). Mean length of beetles in each of the tree samples ranged from 2.30 to 2.89 mm (Table 11.1). In a double logarithmic plot of abundance–body mass, the data points fall within an approximately triangular-shaped zone, as observed for many other assemblages (Gaston *et al.*, 1993a,b) (Figure 11.2). Blackburn *et al.* (1990) examined similar samples from Brunei (Morse *et al.*, 1988) and concluded that this pattern was caused by a preponderance of middle-sized species. However, it is not clear whether the observed patterns of size and abundance result from biological processes, or from statistical or sampling properties common to distributions of any collection of objects subject to optimal design constraints (see also Gaston *et al.*, 1993b).

DISCUSSION

Our results are similar to those obtained from other canopy fogging studies (Erwin and Scott, 1980; Erwin, 1983; Stork and Brendell, 1990; Stork, 1991; Allison *et al.*, 1993b). A prominent feature common to these studies is that there is a strong relationship between the number of individuals and the number of species, primarily because a high percentage (47.6% in our study) of the species are singletons. Our figure is lower than

Table 11.3 Details of number and percentage of beetle species represented by single individuals ('singletons')

Tree No.	*Total singletons*	*Total individuals*	*Singletons (%)*	*Q-statistic*
3	51	336	15.2	32.31
4	48	300	16.0	38.23
9	44	404	10.9	38.23
10	85	800	10.6	68.72
11	58	547	10.6	46.89
12	70	696	10.1	45.81
13	78	493	15.8	58.26
14	69	402	17.2	42.78

Table 11.4 Similarity of the beetle faunas of eight *Castanopsis acuminatissima* trees in the Wau Valley, Papua New Guinea using the Jaccard coefficient

	Tree 4	*Tree 9*	*Tree 10*	*Tree 11*	*Tree 12*	*Tree 13*	*Tree 14*
Tree 3	0.31	0.30	0.19	0.22	0.19	0.19	0.16
Tree 4		0.23	0.19	0.17	0.20	0.14	0.12
Tree 9			0.22	0.23	0.19	0.18	0.18
Tree 10				0.37	0.29	0.30	0.26
Tree 11					0.29	0.32	0.32
Tree 12						0.32	0.32
Tree 13							0.29

that reported by Morse *et al.* (1988) from Brunei (57.8%), but higher than that reported by Basset and Kitching (1991) from Australia (35.7%). The reasons for this variation are undoubtedly complex and probably reflect differences in the insect communities as well as differences is sampling methodology and effort. Our results and those of Basset and Kitching (1991) are based on single tree species. Morse *et al.* (1988) sampled single individuals of 10 species of lowland trees and their samples may include greater beta-diversity. In any case, it is the generally high percentage of singleton species in canopy fogging samples (assumed to include the total insect fauna of the tree canopy) that led to the extremely high estimates of the diversity of the rainforest canopy insect fauna advanced by Erwin and others (Erwin, 1982, 1988; Stork, 1988). However, in our study, of the species recorded from individual trees as singletons, approximately half occurred on other trees, sometimes in reasonably large numbers.

The ecology of singleton species can be better understood by documenting their presence and absence on other related and unrelated species of trees. Our experimental design allows for this comparison. At 1200–1400 m we fogged four *Lithocarpus* trees and one tree each of *Engelhardia mersingensis*, *Callophyllum* sp., *Prunus* sp., and *Carpodetus arboreus*. Beetle species that have no particular affinity to *C. acuminatissima* or fagaceous trees in general should show up on some of these unrelated species of trees. Other species may occur only on fagaceous trees. Analysis of these data is necessary to better assess the true number of species that are restricted to *C. acuminatissima*. Our preliminary results indicate that herbivores (the leaf-chewing family Chrysomelidae) are far less likely to occur as singletons than are predators (non-omaliine Staphylinidae) (Figure 11.1). General insect predators might be expected to occur widely throughout the forest on any available leaf substrate while leaf-chewers are more likely to be restricted to a given species of tree because of specialized adaptation to leaf chemistry and other factors. Farrell and Erwin (1988), in a study of Peruvian canopy beetles, found that Chrysomelidae were more closely associated with individual 'forest types' than were Staphylinidae (singletons were excluded from their analysis). On balance, we would therefore predict that predators would be more likely to occur as singletons. This is consistent with our results but is something that requires further analysis.

Montane forests in Papua New Guinea are not stable ecosystems but are constantly subjected to natural disturbances, including landslides, drought, fire and storms (Johns, 1986; van Valkenburg and Ketner, 1994). *Castanopsis acuminatissima* appears to be well adapted to this successional regime (van Valkenburg and Ketner, 1994). Insects associated with successional forests that include *Castanopsis* would therefore be expected to have a high dispersal capacity. A high percentage of the singleton species recorded in this study may represent dispersing individuals that are not otherwise associated with this tree species.

Another important component of diversity is turnover (beta-diversity). Our experimental design allows us to compare the canopy insect fauna of *C. acuminatissima* at different elevations. Preliminary results suggest that turnover is very high between the three elevational study sites (Allison *et al.*, 1993b). Pair-wise Jaccard coefficients between *C. acuminatissima* trees at different elevations (500 m, 1200–1400 m and 2100 m) averaged ca. 0.06 compared with 0.24 for the eight trees sampled at 1200–1400 m, a four-fold difference.

Comparison of beetle diversity (Q-statistic) in our study trees at three elevations confirms the conclusion of our previous altitudinal transect (Allison *et al.*, 1993b). Table 11.5 shows that diversity is similar at the 500 m and 1200–1400 m sites and higher at the 2100 m site. This relationship between diversity and altitude needs more examination (see

Table 11.5 Comparison of the beetle faunas of *Castanopsis acuminatissima* at different elevations using the Q-statistic. (See Allison *et al.*, 1993a for details of trees 1, 2, 7 and 8.)

Elevation (m)	*Tree no. (s)*	*Q-statistic*
2100	1	103.31
2100	2	67.36
1200–1400	3, 4, 9, 10–14	32–68 (see Table 11.2)
500	7	43.24
500	8	53.25

Allison *et al.*, 1993b). It is possible that it represents phenological differences between trees at the various sites, but could also be because of greater topographical and habitat heterogeneity at higher altitudes (N. Stork, personal communication).

As mentioned earlier, one tree was fogged twice and is included in this analysis as trees 3 and 9. The total number of individuals and species increased slightly in the second fogging, presumably indicating that beetles had rapidly recolonized the tree. The fauna of the recolonized tree was as similar to the original fauna (Jaccard coefficient = 0.30) as the original tree (no. 3) was to tree 4 located close by (Jaccard coefficient = 0.31) and fogged 20 days later. These findings are consistent with predictions of island biogeography theory (MacArthur and Wilson, 1967) that species number remains fairly constant but that species composition changes during turnover events.

With the exception of Erwin and Scott (1980), Gagné (1979) and several temperate studies (Barnard *et al.*, 1986; Blackburn *et al.*, 1993; Gaston *et al.*, 1993a), published canopy fogging studies are not based on multiple foggings of the same tree species at the same site, making statistical evaluation difficult. Also, early studies did not segregate the overall samples from individual trees (the insects were collected on large sheets rather than multiple replicate small trays). Thus, our study and others in this volume (Floren and Linsenmair, 1997, Chapter 16; Mawdsley and Stork, 1997, Chapter 6; Stork and Hammond, 1997, Chapter 1; Wagner, 1997, Chapter 9, this volume) are among the first to report data from multiple individual conspecific trees from the same site with subsampling by replicate trays.

To our knowledge the only other species of *Castanopsis* that has been fogged was that reported by Stork (1991) from lowland Borneo. One tree yielded 396 individuals representing 103 species. This compares with an average of 497 individuals (range 300–800) and 117 species (range 82–155) from our eight trees. This is slightly higher than the mean of

112 species that we earlier reported from our 500-m study site (two trees) and lower than the mean of 192 species for the 2100–2200 m study site (two trees) (Allison *et al.*, 1993b).

The distributional patterns of individual species are extremely complex and will require detailed analysis to understand and summarize. That is beyond the scope of this paper and will be forthcoming as we complete analysis of additional samples. Elsewhere, we have discussed the implications of this issue to overall estimates of species numbers (Basset *et al.*, 1996a).

To further refine our understanding of the role of singletons it will be necessary to study the feeding ecology of individual species. Such work has been undertaken by our colleague, Yves Basset, as part of a comprehensive study of the feeding ecology of the insect fauna on 10 species of trees in the Wau Valley, including *C. acuminatissima* (Basset, 1994, 1997, Chapter 12, this volume; Basset *et al.*, 1996b and unpublished data).

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