# PATTERNS OF BEETLE SPECIES DIVERSITY IN NEW GUINEA RAIN FOREST AS REVEALED BY CANOPY FOGGING: PRELIMINARY FINDINGS

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ABSTRACT. Canopy fogging with a pyrethrum-based insecticide was used in a comparative study of the structure and diversity of insect communities in two genera of oak trees (family Fagaceae) at study sites of 500, 1200–1400 and 2000–2200 m elevation along a transect through primary rain forest in Papua New Guinea (ca. 7° S latitude). Eight trees were fogged (two individuals of *Castanopsis acuminatissima* at each of the three study sites and two *Lithocarpus celebicus* at 500 m). Insects were collected in  $1m^2$  trays suspended beneath the trees and identified to morphospecies. The trees yielded 4840 individual beetles representing 633 species in 54 families. Diversity (measured by  $\alpha$ ) was highest at the 2000–2200 m study site, lowest at 1200–1400 m and intermediate at 500 m. There was 22–31% overlap in the beetle fauna of conspecific trees at the same site. Overlap between sites ranged from 2–12%. These trends are being studied from additional trees at each of the three sites.

#### INTRODUCTION

Tropical rain forests have long been regarded as the most diverse biological communities on earth. However, the true dimension of this diversity remains poorly understood. Erwin (1982), on the basis of canopy fogging studies in Panama, hypothesized that insect communities in the rain forest canopy were so diverse that the total number of insect species in the world was as high as 30 million. He subsequently raised this estimate to 50 million (Erwin, 1988). Others, on the basis of canopy fogging studies and other evidence, have suggested a figure of 5–10 million (Stork, 1988; Gaston, 1991). These different estimates have fueled a lively debate and prompted us to commence our study in New Guinea.

We were interested in diversity of insects within a community ( $\alpha$  diversity) and between communities ( $\beta$  diversity). Most previous studies have focussed solely on  $\alpha$  diversity and have neglected turnover ( $\beta$  diversity), a key determinant of overall diversity. For example, Pimm and Gittleman (1992, based on Mares, 1992) noted that Amazonia, thought to be the biologically most diverse place on earth, had high  $\alpha$  diversity but low  $\beta$ diversity and was overall less diverse than a mixture of adjacent communities.

We chose a study design that involved fogging multiple individuals of the same tree (*Castanopsis acuminatissima*) along an altitudinal transect. At each site we also fogged trees in related and unrelated genera. We focussed primarily on oaks because they occur over a wide altitudinal range in New Guinea and are well represented in our study sites. In addition oaks are virtually cosmopolitan in distribution and their associated insect communities have been well studied in temperate regions (Stork, 1988). We can therefore potentially compare patterns of insect diversity within the same plant family across a wide range of latitudes and altitudes.

We have fogged a total of 51 trees (including 36 oaks). However, we have completed the analysis of beetle samples only for the first eight trees. That information forms the basis for this preliminary paper.

### STUDY SITES

Field work was based at the Wau Ecology Institute in Papua New Guinea and involved three sites along an altitudinal transect in northeastern New Guinea (ca. 7°S, 146°E): Oomsis (500 m), Wau (1200 m) and Biaru Road (2000-2100 m). The Oomsis site receives an estimated 4000 mm of rainfall annually. Rainfall is fairly continuous throughout the year but is particularly heavy from May to October. The mean annual temperature at this site is ca. 25°C with little annual variation. The Wau site is in a drier zone and receives only 1900 mm of rainfall annually. Rainfall is slightly seasonal with approximately 60% of the annual total occurring from November to February. Mean annual temperature at Wau is ca. 22°C. The Biaru Road site has an annual weather pattern similar to Wau but is much wetter, receiving an estimated 2500-3500 mm of rainfall. It is also much cooler with a mean temperature of ca. 16°C (Gressitt and Nadkarni, 1978).

## **TREES FOGGED**

We fogged eight trees in the family Fagaceae (oaks): two *Castanopsis acuminatissima* (Bl.) A.DC. at each of the three sites and two *Litho-carpus celebicus* (Miq.) Rehd. at the 500 m site (Table 1). *Castanopsis acuminatissima* occurs

Tree	Site	Elevation (m)	Tree species	Date	Total species	Total individuals	Mean length	SD
1	Biaru	2,100	C. acuminatissima	19-09-87	234	1,829	2.45	1.61
2	Biaru	2,100	C. acuminatissima	20-09-87	151	642	2.84	1.86
3	Wau	1,200	C. acuminatissima	15-10-87	82	336	2.61	1.67
4	Wau	1,200	C. acuminatissima	04-11-87	86	299	2.49	1.80
5	Oomsis	500	L. celebicus	03-03-88	101	314	2.09	1.28
6	Oomsis	500	L. celebicus	04-03-88	77	329	2.67	1.50
7	Oomsis	500	C. acuminatissima	05-03-88	99	595	2.92	2.15
8	Oomsis	500	C. acuminatissima	05-03-88	125	496	3.23	2.99

TABLE 1. Details on total species and individuals of insects collected from 13 1-m<sup>2</sup> trays suspended beneath trees, including mean length (mm) and standard deviation.

throughout New Guinea from nearly sea level to at least 2200 m and is found mainly on ridge crests. It is extremely abundant at elevations from ca. 900–1600 m and at the Wau study site comprised up to 80% of forest biomass. It becomes progressively rarer towards the extremes of its altitudinal range. *Lithocarpus celebicus* occupies much the same range as *C. acuminatissima* and is comparatively uncommon. Both species are found in early successional to mature forest (Soepadmo, 1972; Streimann, 1983).

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## METHODS

We selected trees for fogging that seemed healthy, had no epiphytes or understory, 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 cubic meters.

Trees were fogged at 0600 hrs (when the air was almost still) for 15 minutes using Pyranone<sup>®</sup> mixed with kerosene to form a 5% solution that was delivered by a Curtis Dynafog model 2610 ("Golden Eagle") fogger with the fog density dial set on "5". The fogger was operated manually at canopy level from an adjacent tree. This method killed all insects in the canopy; no living insects were found in branches subsequently removed from fogged trees.

Insect samples were collected in 13 shallow plastic trays, each  $1m^2$  in area, suspended on ropes beneath each tree. Each tray was numbered individually and had an 8 cm diameter aluminum funnel inserted in the center, flush with the tray surface. A 125 ml Nalgene<sup>®</sup> 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 most of the insects dropped from the tree within 20–30 minutes of fogging. Each sample bottle was labeled with tray and tree number. To ensure good preservation, the alcohol was changed 4–5 times in the month following collection.

After the samples were collected the positions of the trays and the outline of the canopy were mapped and the height and bole of the tree were estimated. These measures were used to compute canopy volume by multiplying canopy area (from outline map) by canopy thickness (tree height minus bole).

In the laboratory all beetle specimens were removed from the samples, mounted, labeled (same details as sample bottles), individually numbered 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 labeled specimens to ensure accuracy. All beetles and tree voucher specimens are deposited in Bishop Museum.

## RESULTS

We obtained a total of 4840 individual beetles representing 633 species in 54 families (Table 1). Six of these families had more than 25 species each, viz. Aderidae (37 spp.), Anthribidae (26 spp.), Chrysomelidae (55 spp.), Corylophidae (32 spp.), Curculionidae (70 spp.), Staphylinidae (70 spp.). These six families comprised 65% of all individuals. Nine families were each represented by only one species, viz. Biphyllidae, Cleridae, Discolomidae, Inopeplidae, Merophysiidae, Mycetophagidae, Ptinidae, Rhizophagidae and Trogositidae.

Three hundred and twenty one (50.7%) species were represented by single individuals ("singletons"). The percentage of singleton species for individual trees ranged from 48.3% to 62.6% and did not show any obvious trend with elevation or tree species. The 321 singleton species represented only ca. 6.6% of total individuals. Treating each tree separately, no more than 20.1% of all individuals on a given tree were represented by singletons (Table 2). SELBYANA

			Insects					
Tree no.	Elevation (m)	Tree species	Total singletons	Total individuals	% singletons	α		
1	2,100	C. acuminatissima	113	1,829	6.2	71.3		
2	2,100	C. acuminatissima	93	642	14.5	62.3		
3	1.200	C. acuminatissima	50	336	14.9	34.6		
4	1,200	C. acuminatissima	48	299	16.1	40.4		
5	500	L. celebicus	63	314	20.1	51.6		
6	500	L. celebicus	47	329	14.3	31.6		
7	500	C. acuminatissima	62	595	10.4	33.9		
8	500	C. acuminatissima	76	496	15.3	53.8		

TABLE 2. Details on number and percentage of insect species represented by single individuals ("singletons").

 $\alpha$  diversity (Magurran, 1988) was highest at the 2100 m site, lowest at 1200 m and intermediate at 500 m (Table 2). Turnover (measured by the Jacard coefficient; Magurran, 1988) was extremely high with little overlap in species composition between the various sites (Table 3). Within a site overlap averaged only about 25% even when trees were close together. At 1200 m, for example, the two *C. acuminatissima* fogged were less that 50 m apart, yet only ca. 31% of the beetle fauna of these trees is shared.

The mean length of canopy beetles was 2–3 mm with no differences between the different sites (t test;  $p \gg 0.10$ ). 77.5% of total beetles were less than 3 mm in length (Table 1).

## DISCUSSION

Our results are similar to those obtained from other fogging studies. Beetle diversity in the New Guinea rain forest canopy is very high, and similar to that found by Stork (1991) for a lowland species of *Castanopsis* in Borneo (one tree yielded 396 individuals representing 103 species). Most of this diversity is composed of rare species—"singletons". Turnover is also very high, in part because nearly half the species are singletons. There is a strong relationship between the number of individuals and the number of species of beetles on a tree and this also can be explained by the large number of singletons. Graphs of cumulative species vs. cumulative tray totals show no obvious tendency to reach an asymptote even when samples from trees of the same species from the same site are combined. Preliminary analysis of samples (ca. 3000 beetles) from six additional *C. acuminatissima* trees at 1200–1400 m shows this same persistent relationship.

The key to understanding patterns of canopy beetle diversity obviously involves understanding the role of singletons in the canopy community. If a high percentage of these species occur only on a given species of tree then Erwin's estimates of diversity may be of the right order of magnitude. However, if these rare species are primarily tourists then overall diversity would be much less than indicated. There is an obvious limitation in attempting to extrapolate too much from results obtained from two conspecific trees at three sites and a more detailed understanding of this relationship must await analysis of additional samples. Basset and Kitching (1991) provide further discussion of the problems of understanding rare species in rain forests.

However, the general pattern of seemingly infinite cumulative species-area curves is characteristic of species-rich communities—e.g. plant communities on Mt. Kinabalu in Borneo (Kitayama, 1991, especially fig. 3). The lowland plants at the base of Mt. Kinabalu are mostly wide-ranging species that form very diverse com-

TABLE 3. Similarity in the beetle fauna of fogged trees as measured by the Jacard coefficient.

Tree no.	1	2	3	4	5	6	7	8
1		0.23	0.04	0.05	0.05	0.02	0.04	0.04
2		_	0.04	0.04	0.04	0.03	0.05	0.03
3			-	0.31	0.10	0.10	0.12	0.11
4				_	0.09	0.08	0.09	0.07
5						0.22	0.16	0.14
6							0.17	0.14
7								0.24
8								_

munities and unless the area studied is huge, a species-area plot is unlikely to show an asymptote. Possibly this same pattern occurs in the insect communities we studied. We designed our study with this possibility in mind. We have determined that there is relatively high turnover between sites. We intend in our future analysis to focus on turnover between tree species (related and unrelated). However, final resolution of this problem will depend on detailed studies of host specificity. Our colleague, Yves Basset is now working on host specificity of leaf-chewing insects on C. acuminatissima. We hope that our ongoing analysis, coupled with Basset's ecological studies, will provide new insights into the different components of diversity.

The relationship between diversity and altitude is rather difficult to explain. In general, insect diversity is thought to increase with altitude into mid-montane elevations (ca. 500-1000 m) and then slowly decline, although some data sets show a simple decrease in diversity with altitude (Holloway et al., 1990; Holloway and Stork, 1991; Wolda, 1987). The same trend has been suggested for plants, but has yet to be proven (Gentry, 1988). In canopy fogging in Sulawesi, Stork and Brendell (1990) found "little similarity in the [beetle] faunas at low (200-400 m), mid (1150 m) and high (1760 m) altitude sites" and a general "decrease in diversity with altitude." However, we found highest diversity at the highest elevation. This unexpected finding may simply reflect phenological differences between trees at the various sites (reflecting seasonal differences between the sites). Additional trees at the various sites were fogged at other times of the year and analysis of these samples will provide more definitive conclusions.

The consistently small size of the canopy beetles is interesting (Table 1) and approximate sizes found in Panama (Erwin and Scott, 1980), Brazil (Erwin, 1983), and Australia (Basset and Kitching, 1991). Basset and Kitching (1991) provide further discussion of this trend.

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