

Diversity and abundance of insect herbivores collected on *Castanopsis acuminatissima* (Fagaceae) in New Guinea: Relationships with leaf production and surrounding vegetation

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Abstract. Insect herbivores were collected from *Castanopsis acuminatissima* (Fagaceae) at Wau, Papua New Guinea, by beating the foliage of 15 trees during four one-month sampling periods, each representing different leaf-flush events. The association of leaf-chewing beetles with *C. acuminatissima* was verified with feeding trials. Of 59 species of leaf-chewing beetles that were collected, 36 species could be used in feeding trials. Only 9 of these species fed on *C. acuminatissima*. A further 27 beetle species were tested in feeding trials but did not feed. Of these, 7 were specialists feeding on other tree species within the surrounding vegetation. Most beetle species collected from *C. acuminatissima* foliage were probably transient species, dispersing from other tree species. Path analyses showed that herbivore abundance during a particular sampling period was significantly influenced by rainfall, leaf flush of other conspecific trees and air temperature, but not so by the species richness of surrounding vegetation, number of surrounding conspecific trees and size (DBH) of trees sampled. The species richness of leaf-chewing beetles collected on particular study trees depended on that of the surrounding vegetation, thus supporting the hypothesis that most beetle species collected were transient. The abundance of insect herbivores on particular *C. acuminatissima* trees probably depends on a balance between the leaf flush of conspecific trees and that of the particular tree sampled. The results also emphasize the need to remove transient species in analyses of insect faunas of tropical trees, at the risk of analyzing species richness patterns derived from loosely defined "assemblages" of species.

INTRODUCTION

Recently, Moran et al. (1994) questioned whether the lack of information about the closeness of association between herbivorous insects and their putative hosts was not confusing the understanding of insect distribution on tropical trees. Indeed, most surveys of arboreal insects in tropical rain forests have been unable to provide information on the association and feeding specialization of insect herbivores and their presumed hosts (but see Marquis, 1991 and Basset, 1992). Strict rules need to be defined to delimit the boundaries of particular communities of arboreal insects in the tropics. Without this, there remains the risk of analyzing patterns derived from loosely defined "assemblages" of species, with little interesting biological meaning to be gained (Basset, 1997).

The distribution of insect herbivores on tropical foliage is influenced by numerous factors. In particular, local factors (as opposed to regional factors; see Cornell & Lawton, 1992 for further discussion) may be particularly important for insect herbivores of tropical rain forests (Basset, 1996). Such significant factors include rainfall (e.g. Wolda, 1978, 1989; Denlinger, 1980; Janzen, 1985), patterns of leaf production (e.g. Rockwood, 1974; Wolda, 1978; Clark & Clark, 1991; Basset, 1991; Aide, 1993), vegetational texture and background (e.g. Risch, 1981; Bach, 1984) and abundance of enemies (e.g. Whalen & Mackay, 1988; Majer, 1993). However, to date, studies examining the relative importance of these various factors on whole communities of herbivorous insects on tropical vegetation are few (e.g. Cytrynowicz, 1991; Lewinsohn,

1991; Marquis, 1991; Novotný, 1992; Basset, 1996; Novotný & Basset, 1998).

In 1987, an intensive programme of insect collecting on *Castanopsis acuminatissima* and on related species of Fagaceae in Papua New Guinea, was initiated by A. Allison of the Bishop Museum (Honolulu), using pyrethrum knockdown (Allison et al., 1993a, b, 1997). Sorting of the material and analyses are still in progress. This programme provided the opportunity to study the insect fauna of *C. acuminatissima* on a different scale and with a different methodology, for the purpose of assisting the interpretation of the data obtained by pyrethrum knockdown. The present contribution seeks to analyse patterns in abundance and species richness for insect herbivores collected on individual *C. acuminatissima* trees, with particular reference to the influence of leaf production and vegetational background on leaf-chewing beetles. The study focuses on leaf-chewing beetles as the emphasis of the fogging programme of the Bishop Museum is on beetles. Further, the relatively small scale of the insect collections, which were restricted to one year of field work and to insect herbivores, allowed to examine the closeness of association between a high proportion of the leaf-chewing beetles collected and *C. acuminatissima*.

MATERIAL AND METHODS

Study site and study trees

Sampling was performed on the lower slopes of Mt. Kaindi, within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7°24'S, 146°44'E, altitude 1,200 m). Mt. Kaindi has been cleared locally, leaving a mosaic of grasslands and for-

est patches, dominated by secondary forest (Van Valkenburg & Ketner, 1994). The main forest formations encountered on its slopes include lower and mid-montane rain forest (Johns, 1982). Wau Ecology Institute grounds include remnant and secondary forests, grasslands and coffee plantations (Gressitt, 1982; see Fig. 1). The climate is "humid to perhumid mesothermal with little or no water deficit" (McAlpine et al., 1983). Mean annual rainfall amounts to 1,900 mm and mean annual temperature to ca. 22°C (Allison et al., 1993b). The study area is detailed further by Gressitt & Nadkarni (1978) and Van Valkenburg & Ketner (1994).

Sampling was performed on 15 mature *Castanopsis acuminatissima* A. DC. (Fagaceae) trees growing within the grounds of Wau Ecology Institute. The genus *Castanopsis* includes about 120 species, most of them occurring in SE Asia (Soepadmo, 1973). *Castanopsis acuminatissima* is a medium-sized to large tree, up to 36 m tall, distributed from India to New Guinea, where it is very common. It grows in primary and secondary forests, from 300 to 2,500 m. In New Guinea it may form almost pure stands on ridges up to 1,500 m (Soepadmo, 1973). At the study site, *C. acuminatissima* appears to flush 2–3 times a year, as a relatively synchronous event (Basset, 1996). Study trees were designated as no. 1 to no. 15 and their location is indicated in Fig. 1. The main characteristics of these trees are summarized in Table 1. Most trees were between 15–20 m tall.

Insect collecting

Insect sampling was performed during four one-month periods, in December 1992, January, February and March 1993. Each study tree was sampled during each of these months, for one day, as follows: ten beating samples were taken at different heights within the crown, during day-time, targeting young foliage whenever present. The samples were taken by striking heavily five times with a stick the foliage above a large plastic funnel, fitted with a collecting jar filled with water at its base. The upper aperture of the funnel was 75 cm in diameter, the lower aperture 3 cm in diameter and the depth of the funnel 60 cm. Insects and falling debris were pushed gently into the collecting jar with a brush.

The contents of the jars were examined immediately in the laboratory. Insect herbivores (chewing and sap-sucking insects) were counted and stored in 70% alcohol. Leaf-chewing beetles (Chrysomelidae, some Curculionidae, Lagriidae, some Cerambycidae, etc.) were later dry-mounted at Bishop Museum, counted and assigned to morphospecies (hereafter "species").

Foliage beating of *C. acuminatissima* was part of a larger study examining insect abundance and species richness on ten different tree species at Wau (Basset, 1994, 1996, 1997). In particular, branch clipping samples were also obtained from *C. acuminatissima* trees other than the study trees discussed in this paper (procedure and results detailed in Basset, 1996). Accounts

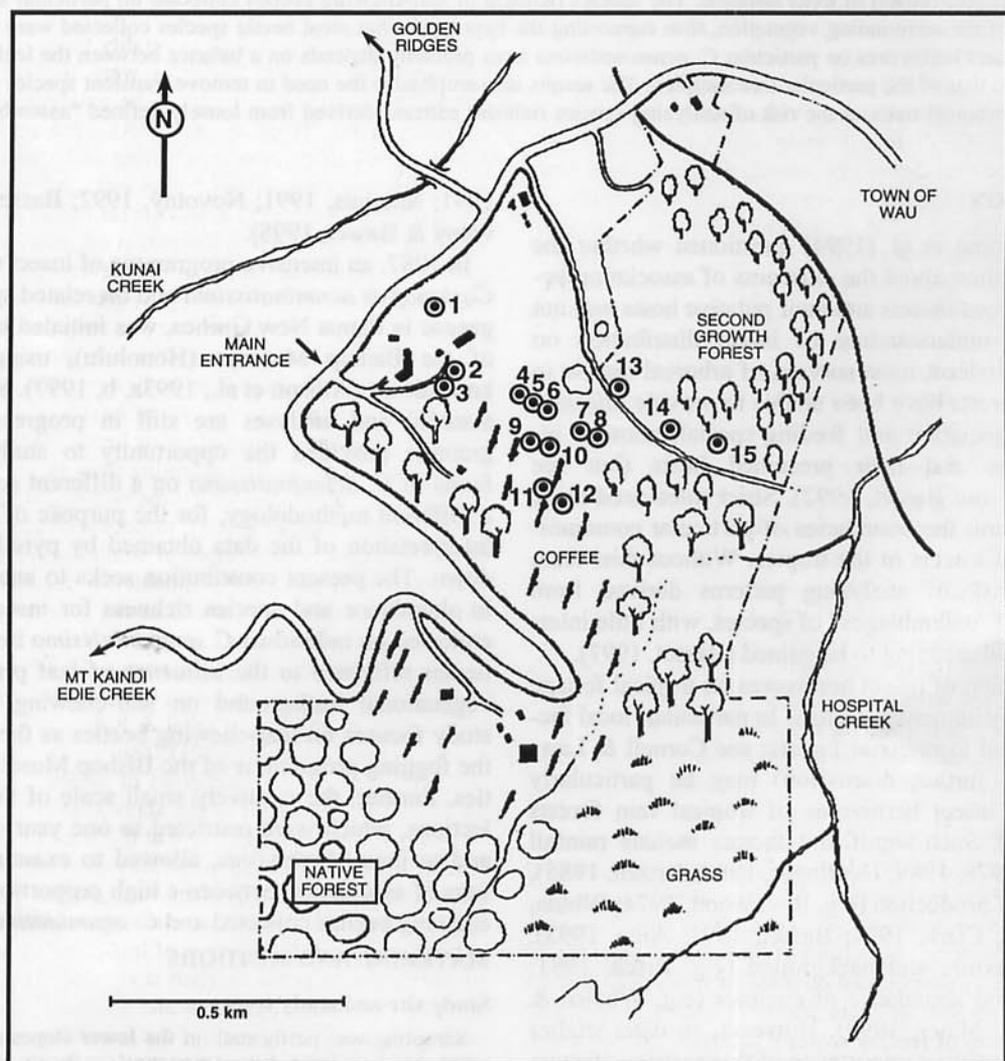


Fig. 1. The grounds of the Wau Ecology Institute and the location of the 15 *C. acuminatissima* trees sampled (modified from Gressitt, 1982).

TABLE 1. Main characteristics of the study trees. Diameter breast height (DBH) and surrounding vegetation within a radius of 12 m: aspect; no. of conspecifics (Consp.); no. of tree and shrub species (No. sp.); and no. of individual trees exceeding 6 m in height (No. trees).

Tree	DBH (cm)	Aspect of surrounding vegetation	Consp.	No. sp.	No. trees
1	18.3	Secondary forest, herb layer short	1	13	10
2	19.1	Open area, herb layer short	0	6	7
3	22.9	Open area, herb layer short	0	5	3
4	15.3	Open area, herb layer prominent	1	6	3
5	13.8	Open area, herb layer short	1	6	7
6	18.8	Open area, herb layer short	1	11	8
7	15.4	Regrowth area, herb layer short	2	9	7
8	16.7	Regrowth area	3	7	8
9	15.4	Open area, herb layer prominent	2	8	3
10	12.9	Open area, herb layer prominent	1	11	4
11	23.6	Open area, herb layer short	1	6	3
12	18.8	Open area, herb layer short	1	10	4
13	10.8	Secondary forest, herb layer prominent	0	11	7
14	14.3	Secondary forest, herb layer short	0	10	12
15	24.5	Open area, herb layer short	0	7	11

of the insect fauna foraging in *C. acuminatissima* trees are found in Allison et al. (1993a, b, 1997) and Basset et al. (1996).

To test whether the size of beating samples varied significantly, a series of ten samples were taken in March on the mature foliage of one tree (4 samples in lower crown, 3 in the mid-crown and 3 in the upper crown). Samples were taken as described above; the beaten foliage was also collected, dried immediately for 24 h at 100°C and the leaf area calculated by regression (Y. Basset, unpubl. data). On the tree, sample size was assessed visually as all leaves being vigorously shaken and likely to have their resident flying insects dislodged. The mean sample size (\pm s.e.) of these samples was 49.1 ± 4.2 g of dry foliage, corresponding to $8,735 \pm 745$ cm² of leaf area (double-sided). The relatively low standard error (8% of the mean) of samples taken from this tree, plus casual observation of other *C. acuminatissima* trees suggested that samples obtained with the beating procedure from this tree species did not vary much in size. Therefore, beating samples were considered as being roughly of the same sample size and insect abundance or species richness was not corrected according to sample size.

Assessment of insect specialization

Since knowledge of the ecology of most Papuan insects is fragmentary, specialization of adult insects had to be assessed from feeding trials in the laboratory. Live insects were stored in plastic vials, at room temperature and in conditions of near-saturated relative humidity. They were provided with fresh foliage of the tree species from which they were collected (10 species, see Basset, 1994), until they died or accepted food. In the latter case, they were then tested in random order for 24 h periods on the foliage of the 9 other study species. Feeding damage was scored visually, relative to insect body size, on a logarithmic scale, as follows: 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding. This procedure emphasized regular feeding in comparison with food-probing. Insects were assigned to four leaf-feeding categories according to the results of the feeding tests: (a) "specialists", i.e., insects tested on three or more plant species but which only fed on the plant they were collected from (sum of feeding scores <100); (b) "generalists", i.e., insects tested on three or more plant species and which fed on two or more plants belonging to different plant families (sum of feeding scores \geq 100); (c) "unknown specialization", i.e., insects which fed but, due to death, could not be tested on more than two plant species; and (d) "not feeding", i.e., insects which did not feed in the trials. Together, categories

(a), (b) and (c) are referred to as "proven feeders". The procedure, which has been proved to be reliable to assign species into specialist and generalist categories, is further discussed elsewhere (Basset, 1994; Basset & Samuelson, 1996).

Statistical methods

Insect data were tested for normality using the Kolmogorov-Smirnov-Liliefors test. Variables were $\log(x+1)$ transformed (natural base) whenever found to be non-normal ($p < 0.05$ in normality tests). Two-way ANOVAs were performed on the abundance of all herbivores, chewing and sap-sucking insects, testing for the interactions of trees and sampling periods. Several methods were used to assess the respective influence of host leaf flush and surrounding vegetation on insect variables. First, species accumulation curves of beetle species, leaf flush and species richness of surrounding vegetation (see below) were drawn. Second, clustering with the unweighted arithmetic average method (UPGMA) was used to infer both faunal similarity and vegetational similarity for study trees. The matrices used in the calculations (programme "R" of Legendre & Vaudor, 1991) were the abundance of leaf-chewing beetle species in each study tree at the end of the four sampling periods and the abundance of tree and shrub species within the surrounding vegetation next to each study tree (see below), respectively. Kulczynski's coefficient was used as a measure of similarity for these computations, since it is particularly suitable for quantitative data, does not include double-zeros, and does not give more weight to either abundant or rare taxa (Legendre & Vaudor, 1991).

Third, models describing the abundance and species richness of insect herbivores collected on *C. acuminatissima* were developed using path analysis (Sokal & Rohlf, 1981), with the programme "Piste" (Vaudor, 1991). Transformed values were used in the calculations and two types of analyses were performed. The first was an analysis of the abundance and species richness of herbivores in each study tree at the end of the four sampling periods (hereafter referred to as "long-term analysis"; number of observations = 15). Dependent variables for these models included: number of herbivores, chewing and sap-sucking insects, proven feeders; and of species of leaf-chewing beetles and beetle specialists recorded on each study tree. The second type of analysis examined abundance and species richness patterns in each study tree during each of the four sampling periods (hereafter this is termed "short-term analysis"; number of observations = 60). The true number of freedom for such an analysis is difficult to evaluate, but it must be $15 < df < 60$. Dependent

variables for the "short-term" analysis included the same as above, with the exception of the number of species of beetle specialists, which was too low in most cases to justify separate analysis.

Several independent variables were used in path and other analyses. First, two variables were derived from daily rainfall and air temperature which were available courtesy of Wau Ecology Institute: sum of rainfall and mean temperature for the previous 7 days before sampling (including the date of sampling). Second, variables related to study trees included: diameter at breast height (Table 1); percentage of leaf flush for individual trees at the date of sampling (see results, Table 3) and sum over the four sampling periods; leaf flush in other study trees during the period of sampling (sum of percentage leaf flush for other study trees during the sampling period). Third, variables describing the surrounding vegetation next to study trees were considered. Trees and shrubs exceeding 2 m in height and within a radius of 12 m of each *C. acuminatissima* tree studied were recorded (R. Höft pers. comm.; in total 53 plant species were recorded). Four variables were derived from this survey: number of conspecifics adjacent to study trees (Table 1); general aspect of vegetation ranked from 1 to 4 in increasing complexity (open area with short herb layer, open area with prominent herb layer, regrowth area, secondary forest; Table 1); species richness of surrounding trees and shrubs; and species richness of trees exceeding 6 m in height (Table 1).

RESULTS

General patterns of abundance and species richness

In total, 3,390 individuals of insect herbivores were collected from the 15 study trees. Most of the chewing insects consisted of Noctuidae, Geometridae, Tortricidae, Lymantriidae, Drepanidae and Gracillariidae, whereas the families Cicadellidae, Aphididae, Lygaeidae and Plataspidae were prominent among sap-sucking insects. The material also included 201 individuals of leaf-chewing beetles, which represented 59 species (34 species of Chrysomelidae, 17 of Curculionidae, 5 of Lagriidae, 2 of Attelabidae and 1 of Scarabaeidae). Only 9 species of leaf-chewing beetles were able to feed on *C. acuminatissima* (proven feeders: 4 Chrysomelidae, 3 Curculionidae, 1 Attelabidae and 1 Cerambycidae). Among these, there

were 5, apparently, specialist species (3 Chrysomelidae, 1 Curculionidae and 1 Attelabidae). These specialist species were all represented by at least 3 individuals in the collections. None of the study trees appeared to harbour all 5 specialist species (Table 2).

The rest of the species of leaf-chewing beetles either did not feed (27 species), or could not be tested (23 species). At least for 7 (26%) of the species tested but which did not feed, it was confirmed that those were specialists feeding on other tree species which were present in the surrounding vegetation and whose insect faunas were also under investigation in the study area (*Aleurites moluccana* Willd., *Ficus nodosa* Teys. & Binn. and *Pipturus argenteus* Wedd., see Basset, 1994, for further details). Of the 23 beetle species which could not be tested, 10 were also collected from tree species other than *C. acuminatissima* in the study area. Further, 16 of these species were represented as singletons and only 3 occurred as more than 3 individuals in the collections. At least one of these species, *Ophrida* sp. (Alticinae) feeds on members of the Anacardiaceae or Burseraceae (G.A. Samuelson, pers. comm.). These results suggest that most of the beetle species collected do not feed as adults on the foliage of *C. acuminatissima*.

When data were pooled for all trees and sampling periods, herbivore densities amounted to 5.65 ± 0.21 (s.e.) individuals per beating sample (of about 8,700 cm² of leaf area, $n = 600$), including 2.38 ± 0.09 chewing insects and 3.27 ± 0.18 sap-sucking insects. This appears to be within the range of herbivore densities reported at Wau, with perhaps the figure for leaf-chewing insects being slightly higher than average (see Basset, 1996). The abundance of all herbivores, of chewing and sap-sucking insects is detailed by study trees in Table 2, whereas this information is detailed further by sampling periods in Table 3, with details about the phenological status of the trees during sampling. A two-way ANOVA with transformed data showed that interactions accounting for tree, sampling period and tree * sampling period were all significant for

TABLE 2. Mean number of individuals (followed by s.e., in brackets) of all insect herbivores, chewing insects, sap-sucking insects collected per sample; and total number of individuals of leaf-chewing beetles (proven feeders only, Feeders), of species of leaf-chewing beetles (proven feeders plus species not feeding, Beetles) and of specialist leaf-chewing beetles (Spec.) recorded in each study tree.

Tree	Herbivores	Chewing	Sap-sucking	Feeders	Beetles	Spec.
1	3.70 (0.43)	2.20 (0.32)	1.50 (0.31)	0	11	0
2	3.20 (0.49)	1.40 (0.21)	1.80 (0.43)	0	5	0
3	5.28 (0.51)	1.65 (0.25)	3.63 (0.53)	1	9	1
4	6.63 (0.80)	2.40 (0.35)	4.23 (0.81)	3	9	2
5	4.55 (0.46)	2.10 (0.31)	2.45 (0.39)	3	9	3
6	6.75 (1.57)	1.60 (0.24)	5.15 (1.47)	4	10	3
7	5.58 (0.82)	2.10 (0.29)	3.48 (0.70)	1	7	1
8	4.75 (0.43)	2.30 (0.28)	2.45 (0.31)	1	3	0
9	6.05 (0.80)	2.80 (0.46)	3.25 (0.65)	2	15	0
10	6.23 (0.83)	2.90 (0.45)	3.33 (0.62)	5	8	1
11	8.33 (1.05)	3.25 (0.39)	5.08 (0.90)	20	9	4
12	4.40 (0.45)	2.15 (0.27)	2.25 (0.33)	4	11	2
13	6.30 (0.72)	2.93 (0.34)	3.38 (0.52)	11	13	2
14	6.00 (0.64)	2.60 (0.26)	3.40 (0.57)	5	12	2
15	7.03 (1.00)	3.28 (0.43)	3.75 (0.76)	3	8	1

TABLE 3. Mean number of individuals of all insect herbivores (first entry), of chewing insects (second entry), of sap-sucking insects (third entry) collected per sample and total number of beetle proven-feeders, of species of leaf-chewing beetles recorded in all samples, followed by phenological status (% of leaf flush, visual estimations) (fourth entry, separated by slashes), detailed by tree and study period. Means are followed by s.e., in brackets.

Tree no.	December 92	January 93	February 93	March 93
1	3.00 (0.67)	5.40 (1.22)	3.60 (0.76)	2.80 (0.44)
	1.10 (0.23)	3.20 (0.93)	2.40 (0.60)	2.10 (0.46)
	1.90 (0.72)	2.20 (0.80)	1.20 (0.49)	0.70 (0.26)
	0 / 1 / 1	0 / 5 / 20	0 / 2 / 0	0 / 4 / 0
2	4.60 (1.45)	2.10 (0.67)	1.90 (0.60)	4.20 (0.77)
	1.00 (0.21)	1.50 (0.52)	0.90 (0.31)	2.20 (0.47)
	3.60 (1.45)	0.60 (0.22)	1.00 (0.39)	2.00 (0.58)
	0 / 0 / 0	0 / 1 / 20	0 / 0 / 0	0 / 4 / 0
3	8.00 (1.22)	3.90 (0.75)	2.80 (0.36)	6.40 (0.72)
	0.60 (0.22)	2.40 (0.75)	1.60 (0.31)	2.00 (0.39)
	7.40 (1.16)	1.50 (0.31)	1.20 (0.25)	4.40 (0.70)
	0 / 0 / 5	0 / 4 / 20	0 / 2 / 0	1 / 3 / 0
4	13.40 (1.54)	4.00 (0.98)	5.20 (0.61)	3.90 (0.75)
	1.60 (0.34)	3.10 (0.80)	4.30 (0.63)	0.60 (0.27)
	11.80 (1.40)	0.90 (0.28)	0.90 (0.31)	3.30 (0.58)
	1 / 3 / 0	0 / 2 / 20	2 / 4 / 0	0 / 1 / 5
5	4.20 (1.02)	4.00 (0.76)	3.10 (0.90)	6.90 (0.53)
	1.10 (0.35)	2.90 (0.59)	2.10 (0.80)	2.30 (0.60)
	3.10 (0.95)	1.10 (0.31)	1.00 (0.35)	4.60 (0.76)
	0 / 0 / 5	0 / 4 / 20	1 / 3 / 0	2 / 3 / 0
6	19.40 (4.21)	2.10 (0.71)	2.70 (0.42)	2.80 (0.59)
	2.30 (0.45)	1.70 (0.68)	1.60 (0.27)	0.80 (0.39)
	17.10 (3.96)	0.40 (0.22)	1.10 (0.43)	2.00 (0.39)
	3 / 4 / 5	0 / 0 / 20	0 / 1 / 0	1 / 3 / 5
7	10.40 (1.91)	2.10 (0.72)	3.00 (0.92)	6.80 (1.37)
	2.50 (0.37)	1.40 (0.67)	1.60 (0.48)	2.90 (0.71)
	7.90 (1.92)	0.70 (0.30)	1.40 (0.56)	3.90 (0.96)
	1 / 4 / 0	0 / 2 / 20	0 / 0 / 0	0 / 2 / 0
8	5.20 (0.51)	5.30 (0.84)	3.70 (0.84)	4.80 (1.17)
	1.50 (0.27)	3.80 (0.63)	1.70 (0.42)	2.20 (0.55)
	3.70 (0.60)	1.50 (0.27)	2.00 (0.60)	2.60 (0.76)
	0 / 2 / 0	0 / 0 / 60	0 / 0 / 0	1 / 1 / 0
9	7.50 (1.62)	8.60 (1.33)	3.80 (2.08)	4.30 (0.72)
	1.30 (0.42)	6.80 (0.92)	1.40 (0.34)	1.70 (0.42)
	6.20 (1.36)	1.80 (0.53)	2.40 (1.89)	2.60 (0.60)
	0 / 3 / 0	2 / 5 / 60	0 / 1 / 0	0 / 3 / 0
10	3.30 (0.63)	5.20 (1.31)	5.00 (1.58)	11.40 (1.77)
	1.20 (0.29)	3.60 (1.01)	2.80 (1.23)	4.00 (0.63)
	2.10 (0.60)	1.60 (0.54)	2.20 (0.81)	7.40 (1.70)
	0 / 2 / 0	2 / 2 / 5	0 / 1 / 0	3 / 5 / 0
11	8.90 (2.68)	9.20 (1.86)	2.30 (0.56)	12.90 (1.24)
	1.80 (0.49)	4.50 (0.75)	1.50 (0.40)	5.20 (0.66)
	7.10 (2.65)	4.70 (1.42)	0.80 (0.25)	7.70 (1.24)
	1 / 4 / 0	8 / 5 / 20	0 / 0 / 0	11 / 4 / 0
12	5.60 (1.19)	4.40 (0.93)	3.60 (0.73)	4.00 (0.68)
	2.10 (0.59)	2.50 (0.73)	2.10 (0.46)	1.90 (0.41)
	3.50 (0.91)	1.90 (0.53)	1.50 (0.43)	2.10 (0.55)
	2 / 3 / 0	2 / 4 / 20	0 / 2 / 0	0 / 5 / 1
13	4.90 (0.78)	2.70 (0.67)	5.20 (0.90)	12.40 (1.03)
	2.30 (0.47)	1.50 (0.31)	3.30 (0.75)	4.60 (0.72)
	2.60 (0.62)	1.20 (0.47)	1.90 (0.41)	7.80 (1.00)
	1 / 5 / 1	0 / 3 / 20	1 / 4 / 0	9 / 3 / 5
14	5.30 (0.70)	3.70 (0.68)	5.70 (1.03)	9.30 (1.78)
	1.90 (0.50)	2.30 (0.40)	3.50 (0.69)	2.70 (0.37)
	3.40 (0.73)	1.40 (0.43)	2.20 (0.59)	6.60 (1.65)
	0 / 3 / 5	1 / 4 / 20	4 / 3 / 0	0 / 1 / 5
15	5.90 (1.54)	4.40 (0.85)	3.70 (0.63)	14.10 (2.45)
	1.20 (0.39)	3.50 (0.76)	2.50 (0.64)	5.90 (0.85)
	4.70 (1.32)	0.90 (0.38)	1.20 (0.33)	8.20 (2.05)
	0 / 2 / 0	0 / 2 / 60	0 / 2 / 0	3 / 4 / 5

TABLE 4. Results of two-way ANOVAs testing the effects of individual trees (trees 1–15) and of sampling periods (December 1992, January, February and March 1993) on the abundance of all insect herbivores, chewing insects and sap-sucking insects (data $\log(x+1)$ transformed for analysis).

Variable	Interaction	MS	F-ratio	p
Herbivores	Tree	1.420	3.94	0.000
	Period	11.350	31.466	0.000
	Tree * Period	1.694	4.695	0.000
	Error	0.361		
Chewing insects	Tree	1.052	3.353	0.000
	Period	3.777	12.038	0.000
	Tree * Period	1.113	3.548	0.000
	Error	0.314		
Sap-sucking insects	Tree	1.388	3.350	0.000
	Period	31.352	75.685	0.000
	Tree * Period	1.634	3.944	0.000
	Error	0.414		

herbivores, chewing and sap-sucking insects (Table 4). In particular, more variance in the abundance of herbivores, chewing and sap-sucking insects was explained by sampling period than by individual trees. Herbivores and sap-sucking insects were most abundant in December 1992 and March 1993, whereas chewing insects were most abundant in January and March 1993, the periods with highest leaf flush. Herbivores and sap-sucking insects were most abundant on trees 11, 15, 6 and 4, whereas chewing insects were most abundant on trees 15, 11, 13, 10 and 9. Interestingly, trees with high herbivore loads were not necessarily species rich: the most speciose trees were trees 11, 5 and 6 for specialist leaf-chewing beetles and trees 9, 13, 14, 12 and 1 for all leaf-chewing beetles. In the long-term, no significant correlation existed between the abundance of chewing insects and beetle species richness ($r = 0.30$, $p = 0.28$). These results suggest that on *C. acuminatissima* patterns of distribution among trees and sampling periods may be different between chewing and sap-sucking insects, and, in the long-term, patterns of insect abundance may not parallel those relevant to insect species richness.

A more precise analysis of distribution of insect herbivores on young versus mature foliage was also possible using branch clipping samples obtained from other *C. acuminatissima* trees and at different times of the year. These samples showed that the number of young leaves recorded in samples was correlated with the abundance of insect herbivores, chewing and sap-sucking insects in the samples (Spearman's rank correlation coefficient, $r_s = 0.686$, 0.640 and 0.429 , respectively, $p < 0.01$ at least in all cases, $n = 55$). Further, the abundance of insect herbivores, chewing and sap-sucking insects was significantly higher in samples including some young leaves than in samples devoid of young leaves (Mann-Whitney $U = 113.0$, 143.0 and 203.0 , $p < 0.01$ in all cases). Both the branch clipping and beating samples suggest that the abundance of insect herbivores on the foliage of *C. acuminatissima* is dependent on patterns of leaf production.

Species richness of leaf-chewing beetles and surrounding vegetation

The cumulative frequency of beetle species collected on the 15 study trees during the four sampling periods is detailed in Fig. 2. In December, the cumulative rate of discovery of beetle species was best correlated with cumulative species richness of surrounding trees and shrubs ($r = 0.970$, $p < 0.001$; Fig. 2a). In January, the sampling period with highest leaf flush, cumulative species richness of beetles was best correlated with cumulative leaf flush ($r = 0.973$, $p < 0.001$; Fig. 2b). In February, it was best correlated with cumulative species richness of trees ($r = 0.974$, $p < 0.001$; Fig. 2c) and, in March, with cumulative species richness of trees and shrubs ($r = 0.980$, $p < 0.001$; Fig. 2d). These results suggest that the species richness of the surrounding vegetation, both trees and shrubs, may influence the species richness of leaf-chewing beetles collected on particular study trees. However, during periods of high leaf flush, the influence of leaf flush on beetle species richness may exceed that of variables accounting for the species richness of the surrounding vegetation.

The dendrograms reflecting faunal and vegetational similarities of study trees are shown in Fig. 3. The grouping of the trees was quite different in the two dendrograms. No significant rank correlation existed between the distances computed for each tree in the faunal and vegetational matrices ($r_s = 0.296$, $p > 0.20$). Further, the faunal similarity of trees did not reflect precisely the location of the trees (compare Fig. 1 with the grouping of the trees in Fig. 3a). This suggests that the influence of the surrounding vegetation is but one of the many factors influencing the distribution of species of leaf-chewing beetles.

"Long-term" and "short-term" analyses of abundance and species richness

When the "long-term" data matrices were examined, none of the correlations between dependent and independent variables were statistically significant. The correlation closest to significance was between the number of species of leaf-chewing beetles and the number of species of trees and shrubs recorded within the surrounding vege-

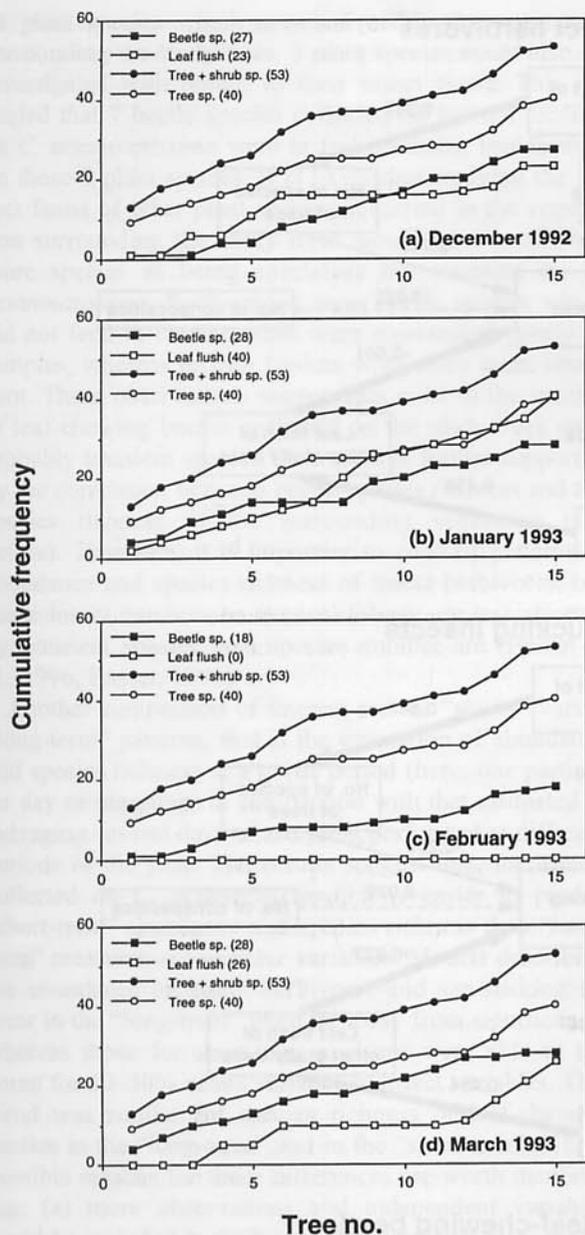


Fig. 2. Cumulative frequency of the number of species of leaf-chewing beetles (filled squares); of the number of species of trees and shrubs (filled circles) and of trees exceeding 6 m in height (open circles) within the surrounding vegetation; and of percentage of leaf flush (open squares) recorded for the 15 tree species during (a) December 1992, (b) January 1993, (c) February 1993, and (d) March 1993. Numbers in brackets denote the final value attained after sampling tree 15. For the sake of clarity, data for leaf flush were divided by a factor of 10 in January 1993.

tation ($r = 0.416$, $p = 0.122$). Consequently, path analysis was not attempted for "long-term" data.

The analysis of "short-term" data matrices was more straightforward. Rainfall was the variable best correlated with the number of herbivores, sap-sucking insects and species of leaf-chewing beetles ($r = 0.485$, 0.555 and 0.376 , $p < 0.001$, $p < 0.001$ and $p < 0.01$, respectively). None of the independent variables was correlated significantly with the number of chewing insects and of beetles considered as proven-feeders, the path analyses for these

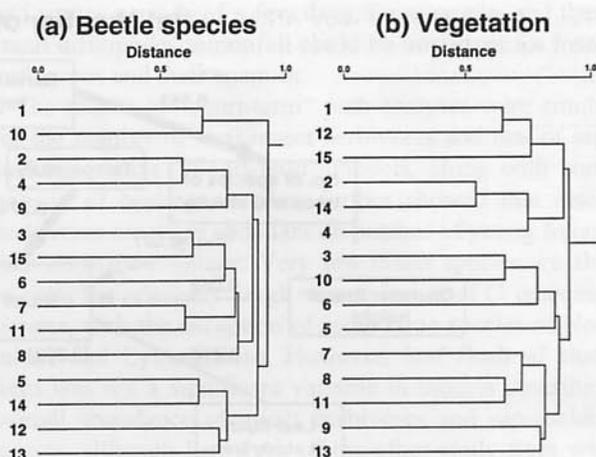


Fig. 3. Cluster analysis (UPGMA) of the study trees (1–15) with regard to (a) the abundance of 59 species of leaf-chewing beetles (i.e., faunal similarity); and (b) the abundance of 53 species of trees and shrubs within the surrounding vegetation (i.e., vegetational similarity).

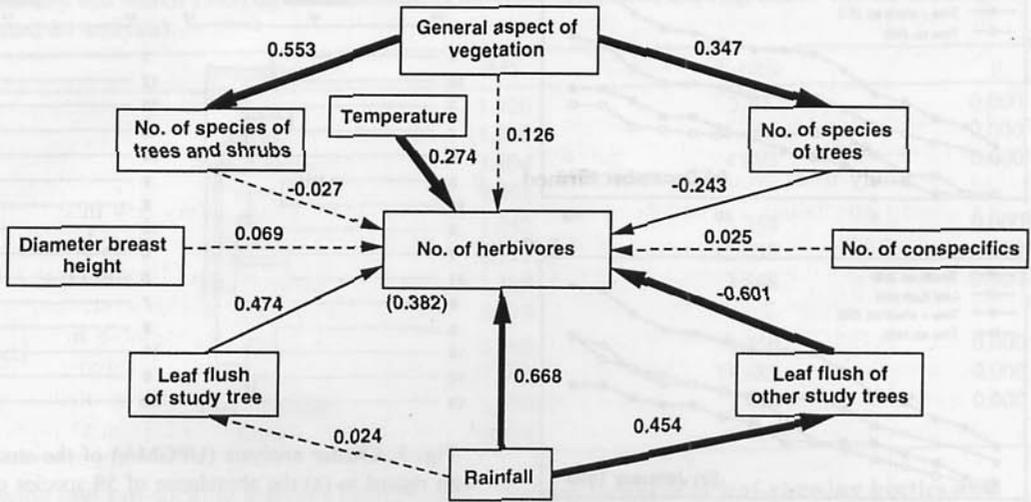
dependent variables explained little variance, and were overall not significant. The models for the other three dependent variables were all significant ($p < 0.01$, $p < 0.001$ and $p < 0.05$, respectively) and are presented in Fig. 4. For all insect herbivores, about 38% of the variance in abundance could be explained (Fig. 4a). The strongest direct paths were from rainfall (positive path), leaf flush of other study trees (negative path) and from air temperature (positive path). For the abundance of sap-sucking insects, these trends were similar, with a higher proportion of variance explained (54%; Fig. 4b). These models suggest that insect abundance on particular trees at a particular time depends on climatic parameters and host leaf flush.

However, the model was quite different for the number of species of leaf-chewing beetles (Fig. 4c). In this instance, only the global species richness of the surrounding vegetation (trees and shrubs) contributed significantly through a positive path to the dependent variable. This suggests that species of leaf-chewing beetles collected on particular trees at a particular time are influenced by the surrounding vegetation, although the total percentage explained by the model was low (28%).

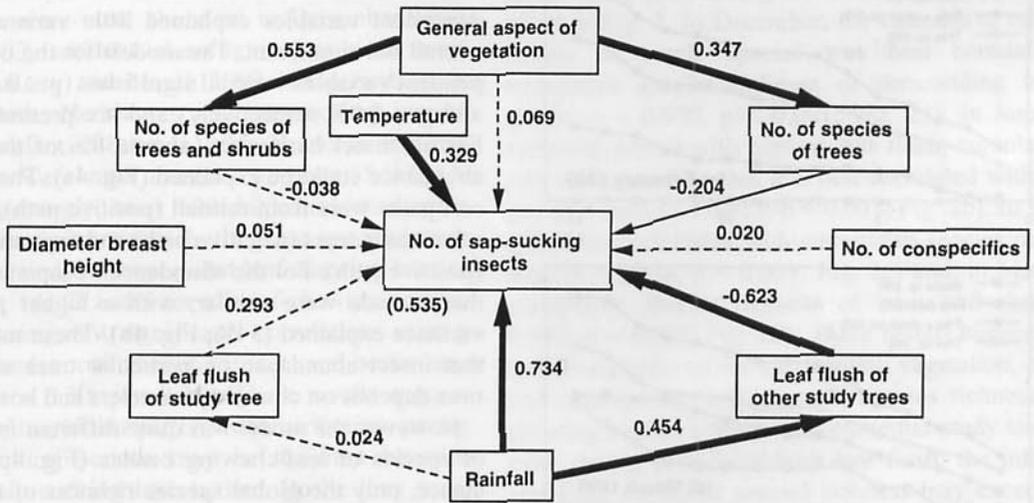
DISCUSSION

At Wau, the rich herbivore fauna feeding on *C. acuminatissima* consists mostly of caterpillars. Leaf-chewing beetles feeding on this tree species are neither particularly speciose nor abundant (see Basset et al., 1996; this conclusion is based on the results obtained with four different sampling methods). However, beating samples revealed a rich fauna of leaf-chewing beetles, more than six times as rich (59 species) as the number of species which accepted to feed on *C. acuminatissima* in captivity (9 species). It is possible that some beetle species, particularly among weevils, may feed on flowers and fruits rather than on leaves and that some other species, not tested in feeding trials, may regularly or occasionally feed on *C. acuminatissima*. However, evidence points elsewhere. Among the

(a) Number of insect herbivores



(b) Number of sap-sucking insects



(c) Number of species of leaf-chewing beetles

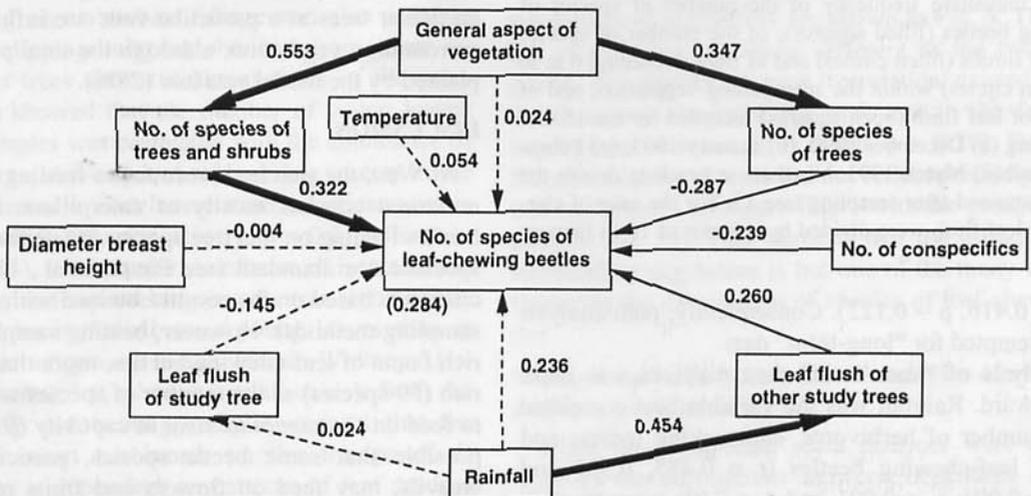


Fig. 4. Summary of path analysis models for the number of (a) herbivores; (b) of sap-sucking insects; and (c) of species of leaf-chewing beetles collected in each of the study tree and during each of the four sampling periods ("short-term" analysis). Path coefficients (direct effects) are indicated for each interaction, along with coefficients of determination (in brackets) of the model. Probabilities of path coefficients are as follows: thick line, $p < 0.05$; normal line, $p < 0.10$; broken line, $p > 0.10$.

53 plant species which occurred within the vegetation surrounding the study trees, 3 plant species could also be investigated with regard to their insect fauna. This revealed that 7 beetle species collected on but not feeding on *C. acuminatissima* were in fact specialist leaf-feeders on these 3 plant species. It is likely that studying the insect fauna of other plant species occurring in the vegetation surrounding the study trees would have confirmed more species as being specialists but transient on *C. acuminatissima*. Furthermore, most beetle species which did not feed in feeding trials were represented poorly in samples, whereas proven feeders were often more abundant. These observations suggest that most of the species of leaf-chewing beetles collected on the study trees were probably transient species. This view is further supported by the correlation between beetle species richness and the species richness of the surrounding vegetation (see below). Therefore, it is important to contrast patterns in abundance and species richness of insect herbivores, because insect numbers on tropical foliage are less affected by transient species than species number are (Basset et al., 1996; Basset, 1997).

Another comparison of interest are the "short-" versus "long-term" patterns, that is the estimation of abundance and species richness at a given period (here, one particular day of sampling) in comparison with that estimated in averaging several days of sampling performed at different periods of the year. The results suggest that, for insects collected on *C. acuminatissima*, it is easier to predict "short-term" abundance and species richness than "long-term" measurement of these variables. Models describing the abundance of insect herbivores and sap-sucking insects in the "long-term" were far away from significance, whereas those for short-term analyses were able to account for 40–50% of the variance in insect variables. This trend was similar for species richness of leaf-chewing beetles in the "long-term" and in the "short-term". Three possible reasons for these differences are worth mentioning: (a) more observations and independent variables could be included in the "short-term" models (note that if we consider sampling events as being independent, the models accounted for 60 observations, but "true" degrees of freedom are certainly much lower); (b) individual trees may present different characteristics at different periods of the year (i.e., leaf-flush, flowering, and fruiting events) and may attract insects differently at different periods of the year; and (c) other factors, which influence the insect-tree system indirectly and which may vary during the course of the year, such as rainfall, may be important. It is most likely that these explanations are not mutually exclusive. With regard to explanation (a), variables which were not measured in this study and which could be important include intraspecific differences in the biochemistry, the illumination and the enemy load of host-trees. With regard to (b), variables not measured include flowering phenology and phenology of surrounding vegetation. With regard to (c), although rainfall patterns are relatively constant throughout the year in Wau (Allison et al., 1993b), this does not prevent the occurrence of drier

and wetter periods of a few days, for example, and these small differences in rainfall could be important for insect herbivores and their enemies.

The results of "short-term" path analyses were similar for the number of total insect herbivores and that of sap-sucking insects. "Short-term" models, along with comparison of beating samples, further showed that insect herbivores are more abundant on patches of young foliage than on mature foliage. Very few insect species are able to chew the relatively tough mature leaves of *C. acuminatissima*, with the exception of some large species of Noctuidae and Lymantriidae. However, leaf flush of study trees was not a significant variable in models describing overall abundance of insect herbivores and sap-sucking insects, although leaf flush of the other study trees was, with a negative contribution. This, along with the strong positive path of rainfall, which influenced directly the leaf flush of all study trees, suggests that the general phenological state of trees in the study area was more important than the phenological state of the particular tree sampled. Further, the negative contribution suggests that relative differences in leaf flush among study trees may also be important, with isolated patches of young foliage in an overall matrix of mature foliage sustaining a high number of insect herbivores. This situation could result from different timing of bud-break among individual trees, a factor known to be important for insect herbivores feeding on temperate Fagaceae, such as *Quercus robur* (e.g., Hunter, 1992). Air temperature was also a variable of some importance in the "short-term" model, presumably because it may have increased the efficiency of the beating procedure (i.e. at high temperatures, insects may be more active, more likely to wander off their sheltering sites and to be dislodged by beating). With the available data, it was not possible to comprehend the differences between the prediction of the abundance of leaf-chewing insects and that of sap-sucking insects. It may be that entirely different sets of variables, such as illumination, are required to predict the abundance of leaf-chewing insects (see Basset, 1991).

Moreover, it is possible that patterns of abundance may be quite different from those related to species richness, but this is difficult to discuss with the present data, as models describing the abundance of leaf-chewing beetles were not significant (and therefore not comparable with the corresponding model for species richness).

In the "short-term" path analysis for the number of species of leaf-chewing beetles, species richness of the surrounding vegetation was an important factor. However, the variance explained by the model was low, and thus many other factors undoubtedly influence beetle species richness. This was reflected in the cluster analyses, which did not show a good correspondence between faunal similarity, vegetational similarity and location of study trees. Obvious differences in faunal similarity between trees close to each other, suggest that factors varying within a distance of a few meters could be important (see for example Allison et al., 1997). Illumination, which can alter both foliage biochemistry, the flight activity and subse-

quent patterns of oviposition in insect herbivores (e.g. Moore et al., 1988) and, perhaps, the activity of enemies, could be one such factor.

Cumulative frequency plots of beetle species suggested that during periods of intense leaf flush leaf production could be more important than surrounding vegetation in influencing beetle species richness. One possible reason for this would be the change in foliage reflectance induced by the presence of young leaves, which could attract both resident and transient beetle species. However, the path coefficient from leaf flush of other study trees to beetle species richness was not significant and this interpretation remains speculative. Future investigations upon this aspect should target host-species supporting a rich resident fauna of leaf-feeding beetles, unlike *C. acuminatissima* at Wau.

CONCLUSION

To conclude, the resource concentration hypothesis of Root (1973) appears not to be straightforward for the prediction of the abundance of insect herbivores foraging on the foliage of *C. acuminatissima* (i.e., the number of conspecific trees was not important in models of insect abundance, neither was the leaf flush of the tree sampled). In this instance, a subtle balance between the leaf flush of conspecific trees in the study area and that of the particular tree sampled, appears more likely. This study also presented evidence that vegetational background in the tropics can sometimes be an important predictor of the species richness of mobile insect herbivores, such as leaf-chewing beetles, collected on particular individual trees. Therefore, strict rules need to be defined to delimit the boundaries of particular insect communities associated with tropical trees. One must concur with Moran et al. (1994) (and see Basset, 1997 for further data) that transient species should be recognized and removed from data sets describing species collected from the foliage of tropical trees, at the risk of analyzing species richness patterns derived from loosely defined "assemblages" of species, with little interesting biological meaning to be gained. To achieve this, information, even at the crudest level, about the ecology of insect species collected is foremost.

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