Journal of Tropical Ecology (2005) **21**:329–336. Copyright © 2005 Cambridge University Press
doi:10.1017/S0266467405002300 Printed in the United Kingdom

Vertical stratification of leaf-beetle assemblages (Coleoptera: Chrysomelidae) in two forest types in Panama

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(*Accepted 17 October 2004*)

Abstract: To study vertical gradients of arthropod species richness in tropical forests, adult chrysomelids were surveyed with similar sampling effort by beating in four plots of 0.8 ha, representative of the canopy and understorey of one wet and one dry forest in Panama. Samples included in total 4615 individuals representing 253 species, and were of similar species richness at the two study sites. At both sites, chrysomelids were significantly more species-rich in the canopy than in the understorey. The proportion of species shared between the two study sites was 24%, whereas 16% and 28% of species were shared between the canopy and understorey of the wet and dry sites, respectively. Mature trees supported more and different chrysomelid species than conspecific saplings. A higher proportion of liana feeders vs. tree feeders occurred at the dry site than at the wet site. Multivariate analyses confirmed the faunal differences between the wet and dry sites and that stratification was more marked at the wet site than at the dry site. The latter observation may relate to differences in forest physiognomy (a tall and closed canopy at the wet site) and to the high interconnectivity via lianas between the understorey and canopy at the dry site.

Key Words: canopy, dry forest, rain forest, resource availability, species richness, understorey

INTRODUCTION

Which habitat supports the largest bulk of arthropod biodiversity on Earth? This question has been at the centre of previous investigations in the tropics and many studies pointed at tropical forest canopies as being a repository of very high biodiversity (Erwin 1982). This habitat continues to promote scientific interest, as evidenced by recent studies worldwide (summarized in Basset *et al.* 2003, Stork *et al.* 1997). The canopy is defined as the aggregate of every tree crown in the forest, including foliage, twigs, fine branches and epiphytes (Nadkarni 1995). The lower part of the canopy, the 'understorey' may be defined as the vegetation immediately above the forest floor and reachable by the observer. Hereafter, for sake of simplicity, we will use the term 'canopy' to denote the mid- and upper canopy *sensu* Nadkarni (1995).

In tropical rain forests, the understorey may support different habitats for arthropods than those in the canopy above, particularly in the upper canopy. At any one time, the canopy receives more illumination than the understorey, thus promoting an abundant productivity in the upper forest layer (Parker 1995). The greater occurrence of young and dense foliage, flowers and seeds in the canopy in turn attracts more insect herbivores than in the understorey (Basset 2001).

In tropical rain forests, arthropod use of different food resources and habitats along the vertical forest profile may generate complex vertical gradients of arthropod diversity. Studying these gradients appears crucial in refining global estimates of species richness (May 1988) and to evaluate the conservation implications of altering habitats by breaking the canopy surface of tall wet forests. Such studies may also be critical in comparing distribution patterns of species richness in tropical and temperate forests. For example, tropical herbivores may be less specialized with regard to resource use (i.e. use of different host-plants), but more specialized with regard to habitat use (i.e. use of host-plants in different forest strata) than temperate herbivores (Basset *et al.* 2003, Novotny *et al.* 2002).

Testing vertical gradients of arthropod diversity in tropical forests may be frustrating. Since canopy access

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is constrained, often the understorey is more thoroughly surveyed than the canopy. Comparable sample units for lower/higher strata are frequently lacking. Popular methods such as insecticide knockdown or light traps cannot readily and selectively sample the fauna at different forest heights. Further, with material collected dead, it is difficult to ascertain ecological relationships, such as feeding observations on a putative host plant, and to delineate the boundaries of the community under study. A promising approach in the discipline may involve quantitative collections of live arthropods *in situ*, relying on improved methods of canopy access (Basset *et al.* 2003).

Herbivores such as leaf beetles (Chrysomelidae) represent suitable test organisms to study vertical gradients in tropical forests, since they are dependent on the presence of young foliage with high protein content (Ohmart *et al.* 1985). Thus, their feeding preferences and occurrence on young foliage in different forest strata can be compared with the actual distribution of young leaves in the forest (Novotny *et al.* 1999). Although several indirect lines of evidence suggest that leaf beetles may be diverse in the canopies of tropical forests (Basset & Samuelson 1996, Farrell & Erwin 1988, Ødegaard 2000, Wagner 2000), to date there has been no quantitative comparison with standardized techniques of chrysomelid assemblages in the canopy and understorey of any tropical forest (Furth *et al.* 2003 attempted a comparison of the vertical overlap of Alticinae using different methods and sampling effort).

The main objective of this study was to test for differences in the faunal composition, abundance and diversity of chrysomelid assemblages foraging in the understorey and canopy of one dry forest and one wet forest in Panama, taking advantage of the canopy crane system of the Smithsonian Tropical Research Institute (STRI; see methods). This system allowed us to collect quantitatively specimens alive and to ascertain their feeding relationships with putative host plants within each forest stratum. To evaluate leaf beetle use of similar food resources in the understorey and canopy, we also compared chrysomelid assemblages feeding on mature trees and conspecific saplings.

METHODS

Study sites and canopy access

Fieldwork was performed at the two sites of the crane canopy access system of STRI in Panama (Wright 2002). These sites, 80 km distant from each other, are located in a wet tropical forest near Fort Sherman (FTS) and in a dry tropical forest in the Parque Natural Metropolitano (PNM) (details in Table 1). The FTS site is part of the San Lorenzo Protected Area, Colon Province (9°17′N, 79°58′W, *c.* 150 m asl). At this site, a 6-ha plot includes 228 species of tree and shrub with dbh ≥ 1 cm (S. Lao, *pers. comm.*). PNM represents a 270-ha reserve near Panama City (8°58′N, 79°33′W, 10–138 m asl), which is connected to a larger complex of national parks to the north. About 85% of the rainfall falls between May and November at PNM.

At both sites a tower crane provided access to the canopy (Wright 2002). E.C. collected chrysomelids from a

Table 1. Characteristics of the two study sites, Fort Sherman (FTS) and Parque Natural Metropolitano (PNM).

Parameter	FTS	PNM
Forest type	wet tropical	dry tropical
Average annual temperature (°C)	25.5	28
Average temperature 1999 (°C)	24.9	25.6
Average annual rainfall (mm)	2700–3000	1740
Annual rainfall 1999 (mm)	3419.1	1893.9
Not disturbed since (y)	~ 200	~ 80
Average canopy height (m)	25–35	20–30
Crane height; arm length (m)	54; 55	44; 52
Projected area of the crane perimeter (m^2)	9000	8100
Range of height of canopy samples (m)	16–35	15–33
No. of plant species/families sampled in the canopy	34/22	24/16
No. of plant species/families sampled in the understorey	51/30	38/24
No. of plant species sampled both in the understorey and canopy	5	3
Common plant species in the canopy	*Brosimum utile* (Kunth) Oken ex J. Presl, *Manilkara bidentata* (A. DC.) A. Chev., *Dussia munda* C.H. Stirt., *Guatteria dumetorum* R.E. Fr.	*Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels, *Astronium graveolens* Jacq., *Castilla elastica* Sessé ex Cerv., *Annona spraguei* Saff.
Common plant species in the understorey	*Tovomita stylosa* Hemsl., *Socratea exorrhiza* (Mart.) H. Wendl., *Geonoma* spp., *Cyathea petiolata* (Hook.) R. M. Tryon	*Heliconia latispatha* Benth., *Piper reticulatum* L., *Hirtella racemosa* Lam., *Psychotria* spp.

range of plant species in four habitats: the understorey and canopy at FTS, and, similarly, the understorey and canopy at PNM. Each habitat consisted of the projected ground area of the smallest crane perimeter (PNM, *c.* 0.8 ha, Table 1), for ease of comparison. Thus, canopy habitats were defined as the vegetation within the crane perimeter above 15 m at PNM and, similarly, the vegetation within the equivalent crane perimeter above 15 m at FTS. Understorey habitats were defined as the vegetation below 3 m in marked plots of similar area, partly overlapping with the adjacent crane perimeter. In short, the sampling strategy aimed at collecting leaf beetles with similar sampling effort (see below) within equivalent areas of forest, representative of the canopy and understorey. Only one plant species was shared between both study sites, *Cecropia longipes* Pitt. (Cecropiaceae). In the canopy, a crane operator controlled the position of the crane gondola, from which collections were made. In the understorey, only plants that were within the reachable height of the collector were sampled.

Chrysomelid collections

In each habitat, adult Chrysomelidae (not including seed-eating Bruchinae) were collected with a beating sheet of 3970 cm^2 area, which was fitted with a removable plastic bag. Beetles were dislodged from the foliage with 3–4 strokes, brushed inside the plastic bag, which was then closed and replaced by another bag for a new sample. One beating sample included only the foliage of one plant species. As far as possible, beating samples in the canopy and understorey were collected the same or following day, often between 08h00 and 14h00. A survey in one habitat (either stratum of either study site) consisted of 40 such beating samples. Twenty-five beating surveys were conducted from April to November, 1999. Thus, sampling effort in each habitat consisted of 1000 beating samples, spread among available plant species (24–51 species per habitat, Table 1).

All plant species included in beating samples were identified with the help of botanists at STRI. Further, the following variables, likely to influence the distribution of leaf-beetles, were scored for each beating sample:

- occurrence of young foliage: absent (coded as 0); covering less than 50% of the sample (1); covering over 50% of the sample (2);
- absence (0) or presence (1) of flowers within the samples;
- whether the sample was collected during the drier or wetter part of 1999 (variable 'season': at both study sites during 1999, near twice as much rainfall fell during August–November [wet] as opposed to April–July [dry]).

Every beetle collected was placed in a plastic vial in a laboratory with a portion of young leaf, mature leaf or flower from the plant it was collected from. Evidence of feeding or frass was recorded for a period of up to 3–5 d and each specimen was eventually classified as 'feeding' or 'not feeding'. All leaf-beetles collected were mounted and sorted to morphospecies (hereafter, 'species'). As far as possible, leaf-beetles were then identified by comparing voucher specimens in the collections of STRI and of the University of Panama, and by sending representative collections to taxonomists. The specimens were deposited at the University of Panama, STRI and at the National Museum of Natural History, Washington.

Statistical analyses

The analyses focused on comparing the canopy and understorey of each forest type. To evaluate the degree of partitioning of chrysomelids per strata, we used a randomization method based on the algorithm of Patefield (1981). For this analysis, 25 000 random matrices (the default number from the algorithm) were generated with the same row and column totals as the original matrix, detailing the sum of individuals for each chrysomelid species collected either in the understorey or canopy. A test statistic, T, was calculated for all matrices (details from Blüthgen *et al.* 2000). Highly structured matrices (implying a high degree of partitioning among species) result in higher values of T, while overdispersed matrices yield lower T values. The statistics of our empirical data (T_{obs}) were then compared with the distribution of statistics of all random matrices (T_{ran}). The significance level P of the differences between T_{obs} and the random sample was calculated as

$$P = \min(P_L, P_U)$$

where P_L is the proportion of all T_{ran} being equal to or smaller than T_{obs}, and P_U is the proportion of all T_{ran} being equal or higher than T_{obs} (Manley 1997). These calculations were performed with the computer program described in Blüthgen *et al.* (2000) and available at http://itb.biologie.hu-berlin.de/~nils/stat/. We also used a more conventional method (but not necessarily more adequate, see Hurlbert & Lombardi 2003) to test for differences in chrysomelid abundance between the two strata. We performed Mann–Whitney tests adjusted with Bonferroni correction for multiple comparisons, for higher taxa (subfamilies) and common species (total individual collected $n \geq 10$; 67 species).

Comparisons of the species richness and diversity among habitats were assessed with the following indices: species observed, Chao1, Coleman rarefaction and alpha of the log-series. These statistics, as well as the number of unique and singleton species in the samples and

Morisita–Horn similarity indices among habitats, were computed with EstimateS (Colwell 1997).

We used multivariate analyses to (1) evaluate the distribution of the most common chrysomelid species collected (total individuals $n \geq 10$), (2) to relate this distribution to simple features of the habitat and (3) to estimate the fraction of variance so explained. In order to remove the many empty samples, we pooled the 40 samples obtained from a particular habitat in each survey (4 habitats and 25 survey = 100 pooled samples). First, a detrended correspondence analysis (DCA) was performed (67 species × 100 pooled samples) to evaluate graphically any pattern in the grouping of the samples. Second, a canonical correspondence analysis (CCA) was performed on the same data set using as constraining variables the three following categories: forest type (dry or wet), stratum (canopy or understorey) and season (dry or wet). Analyses were performed with CANOCO (ter Braak & Smilauer 1998) and partialling out the total variance in the system from that accounted by the environmental variables followed Borcard *et al.* (1992).

RESULTS

Faunal composition and species richness

A total of 4615 leaf beetles were collected, and they were significantly more abundant at the dry site (PNM) than at the wet site (FTS; Mann–Whitney tests, $U = 16.5$, $P < 0.001$). They were also significantly more abundant in the canopy than in the understorey at FTS, but not so at PNM ($U = 35.3$, $P < 0.001$ and $U = 0.06$, $P = 0.061$, respectively; Table 2). Thirteen subfamilies were represented in the collections and their abundance often differed significantly between the two strata (data not presented here). The three most abundant species in each habitat belonged to the following genera: FTS, canopy: *Rhinotmetus, Dinaltica* and *Antitypona*; FTS, understorey: *Dinaltica, Phylacticus* and *Phanaeta*; PNM, canopy: *Rhinotmetus, Antitypona* and *Caryonoda*; PNM, understorey: *Margaridisa*, *Allocolapsis* and *Rhabdopterus*.

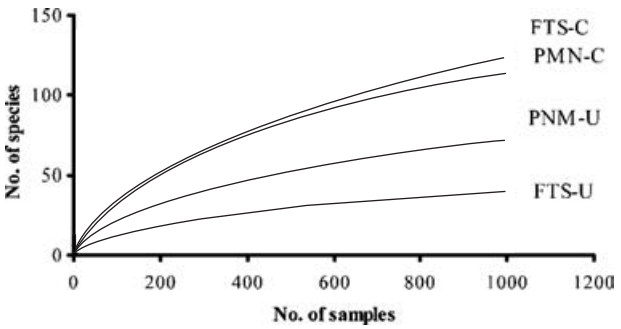

Figure 1. Species accumulation curves of chrysomelid species for the four habitats surveyed, canopy (C) and understorey (U) of FTS and PNM.

In total, 253 species of leaf beetle were collected, including 147 and 152 species at FTS and PNM, respectively. At each study site, more species were collected from the canopy than from the understorey (Table 2). At both study sites, singletons contributed to more than one third of the total species (38%). The proportion of singletons at the wet site was also higher than at the dry site (Table 2; FTS: 45%, PNM: 36%). As in other tropical studies, species accumulation curves failed to reach an asymptote in the four habitats surveyed (Figure 1). PNM had a significantly faster rate of species accumulation than did FTS (Kolmogorov–Smirnov two-sample test, $KS = 8.57$, $P < 0.05$). The canopies of FTS and PNM had a significantly higher rate of species accumulation than did their respective understorey (Kolmogorov–Smirnov two-sample tests all significant; Figure 1). Although slightly more chrysomelid species were collected at PNM than at FTS, the Chao1 and Coleman estimators suggested that FTS was more species-rich than PNM (Table 2). At both sites, the number of species observed, Chao1, Coleman and alpha indices all indicated that the canopy was more species-rich and diverse than the understorey (Table 2).

Faunal similarity and distribution of species between strata

Sixty-one species, representing 24% of the total number of species collected, were shared between the two

Table 2. Species richness and diversity statistics (SD = standard deviation) of leaf beetles collected by beating in the canopy (C) and understorey (U) of the two study sites, FTS and PNM. Species obs. = species observed; N Coleman = common sample size (no. of individuals) for the Coleman rarefaction. See Methods for the description of the statistics.

Variable	FTS-C	FTS-U	PNM-C	PNM-U	∑ FTS	∑ PNM
Samples	1000	1000	1000	1000	2000	2000
Individuals	1443	436	1818	918	1879	2736
Species obs.	129	41	118	76	147	152
Uniques	78	13	51	30	101	106
Singletons	59	17	50	30	66	55
Chao1 ± SD	274.0 ± 57.7	69.9 ± 19.8	256.9 ± 61.9	110.6 ± 16.9	314.5 ± 63.5	236.0 ± 31.5
Coleman ± SD	71.8 ± 4.6	39.5 ± 1.2	63.4 ± 4.2	52.8 ± 3.5	144.4 ± 1.6	130.1 ± 3.9
N Coleman	400	400	400	400	1800	1800
Alpha ± SD	34.3 ± 1.7	11.1 ± 1.0	28.2 ± 1.4	19.7 ± 1.3	37.3 ± 1.7	34.7 ± 1.4

Table 3. Upper matrix of similarity (Morisita–Horn index) calculated between the canopy (C) and understorey (U) of the two study sites, FTS and PNM, for (a) chrysomelid species collected by beating; (b) chrysomelid species collected by beating and feeding; and (c) plant species surveyed during beating.

Method/habitat	FTS-U	PNM-C	PNM-U
(a) Beating			
FTS-C	0.14	0.10	0.02
FTS-U	–	0.03	0.03
PNM-C	–	–	0.17
(b) Feeding			
FTS-C	0.02	0.05	0.002
FTS-U	–	0.008	0.007
PNM-C	–	–	0.084
(c) Plants			
FTS-C	0.003	0.004	0
FTS-U	–	0	0
PNM-C	–	–	0.019

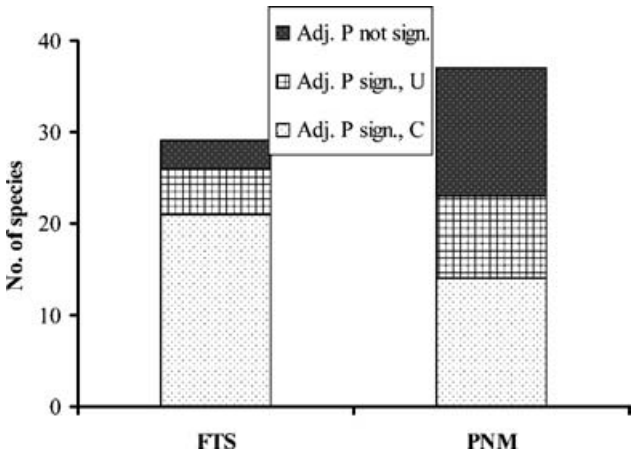

Figure 2. Results of Mann–Whitney tests comparing the abundance of the most common species ($n \geq 10$ individuals) in the canopy and understorey of each study site (FTS and PNM). Adj. P sign., C = number of species significantly more abundant in the canopy after Bonferroni correction; Adj. P sign., U = number of species significantly more abundant in the understorey after Bonferroni correction; Adj. P not sign. = number of species not significantly different between the two strata.

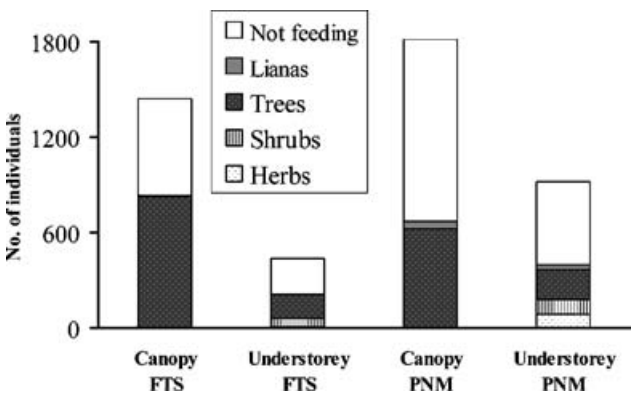

Figure 3. Number of individuals either feeding on different plant categories or not feeding, in the canopy and understorey of the two study sites, FTS and PNM.

study sites. Most of these species were Eumolpinae and often recorded as singletons (56% of the number of shared species). When considering the sum of individuals collected for each chrysomelid species in the understorey and canopy, chrysomelids were significantly partitioned between strata. At both sites, the observed matrices were significantly different from the mean of random matrices (FTS: $T_{obs} = 8410$, mean $T_{ran} = 7720 \pm 7.6$ SD; PNM: $T_{obs} = 14\,200$, mean $T_{ran} = 13\,100 \pm 8.1$, $P < 0.001$ in both cases). These results did not differ when including either common chrysomelid species (total individuals $n \geq 10$) or only feeding individuals in the observed matrices.

Similarity values were low between habitats but higher between strata of the same study site (Table 3). About 69% and 70% of species at FTS and PNM, respectively, were collected from the canopy exclusively (uniques, Table 2). Further, 16% and 28% of species were shared between the canopy and understorey at FTS and PNM, respectively. These trends were similar when considering only chrysomelid species which fed in feeding tests (Table 3). To some extent, chrysomelid similarities among habitats paralleled similarities among habitats calculated with plant species, with the higher similarity between plants surveyed in the understorey and canopy occurring at the dry site (PNM, Table 3). At each study site, more species preferred the canopy than the understorey, after adjustment for multiple testing (Figure 2). The highest proportion of species preferring the canopy was observed at FTS, whilst the highest proportion of species preferring the understorey was observed at PNM (Figure 2).

Feeding tests and community analysis

Out of 4613 leaf beetles tested, 2115 fed on the plant species from which they were collected. In general, species which fed were also numerically dominant in the samples. A significantly higher proportion of beetles fed in the wet forest (FTS, 55%) than in the dry forest (PNM, 39%; Figure 3; Fisher's exact test, $P < 0.001$). Although the majority of specimens fed on tree foliage, a higher proportion of liana feeders vs. tree feeders occurred at PNM than at FTS (Figure 3, Fisher's exact test, $P < 0.001$). Only three individuals fed on epiphytes, in the canopy of FTS.

Five and three plant species were sampled both in the understorey and canopy of FTS and PNM, respectively. However, sample sizes differed greatly between strata for a sound comparison of these data and only three plant species were investigated in this regard (Table 4). This comparison, which could be extended to two plant species surveyed extensively at the same locations by different authors (Table 4), emphasized the low similarities of

Table 4. Comparison of chrysomelid assemblages supported by saplings (understorey) and conspecific mature trees (canopy) at the two study sites, PNM and FTS. Sample size refers to the number of samples obtained by beating in the understorey and canopy, respectively, and are broadly similar among studies. Number of species (in parentheses: no. of species confirmed to feed on that plant species) collected in the understorey, canopy and shared between these two strata.

Host and location	Sample size	Understorey	Canopy	Shared	Source
Castilla elastica Sessé ex Cerv. (Moraceae), PNM	64, 58	9 (1)	14 (2)	1 (0)	This study
C. elastica, PNM	1000, 1000	(5)	(8)	(1)	Barrios (2003)
Pourouma bicolor Mart. (Cecropiaceae), FTS	4, 16	1 (0)	6 (3)	0	This study
P. bicolor, FTS	1000, 1000	(1)	(5)	(1)	Basset (2001)
Socratea exorrhiza (Mart.) H. Wendl. (Arecaceae), FTS	11, 8	2 (0)	5 (0)	0	This study

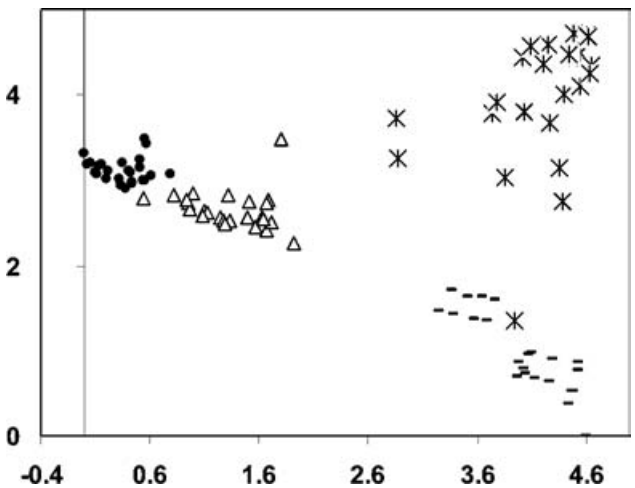

Figure 4. Ordination of 67 common chrysomelid species among 25 surveys of beating samples of the canopy (dashes) and understorey (stars) of FTS and in the canopy (open triangles) and understorey (closed circles) of PNM (total 100 surveys). Plot of the samples in the plane formed by axes 1 and 2 of the DCA.

chrysomelid assemblages on saplings and conspecific mature trees (e.g. Morisita–Horn index of 0.079 for *Castilla elastica*).

At both sites, the occurrences of young foliage and flowers in the samples were significantly higher in the canopy than in the understorey (Mann–Whitney tests all with $P < 0.001$). Further, the occurrence of lianas within the samples of PNM was significantly higher than in samples from FTS ($U = 51.8$, $P < 0.001$).

The total inertia of the DCA was 8.46 and its two first axes explained 19% of the variance in the system. In the plane formed by these two axes, surveys performed at the two study sites were clearly isolated. Further, surveys performed within the canopy and understorey of FTS were also clearly distinct, whereas those performed in the canopy and understorey of PNM were not so (Figure 4). The total inertia of the CCA (graphical display not presented here) was 1.79, indicating that the environmental variables measured explained 21% of the total variance in the system (Borcard *et al.* 1992). Monte Carlo permutation tests ($n = 199$) were significant ($P < 0.001$) for the first axis and for the overall analysis. The first two axes explained 85% of the variance explained by the environmental variables (47% and 38% for axis 1 and 2, respectively). The first axis was best explained by forest type ($r = 0.98$, $P < 0.05$), whereas the second axis was best explained by stratum ($r = 0.95$, $P < 0.05$).

DISCUSSION

It is unlikely that all leaf-beetle species were collected in each habitat surveyed, as suggested by Chao1 indices. However, the most common species occurring within the four habitats surveyed were probably collected, particularly in the understorey (Figure 1). Although beating samples were only obtained during daytime, the majority of chrysomelids are active during daytime in tropical forests (Basset *et al.* 2001). Thus, we do not believe that problems related to beetle diel activity or seasonality (which did not influence significantly the variance explained in the CCA) might affect the interpretation of our data significantly. Other methodological problems in this study may include the taxonomic study of singletons, since morphospecies assignment is easier with long series of specimens. For example, many of the species shared between the two forest types were singletons, so there could be some uncertainty in this figure.

Even our crude scoring system was able to detect significant differences in the abundance of young foliage and flowers between the canopy and understorey of the two forest types. These two variables are known to affect the distribution of adult leaf-beetles in tropical rain forests (Basset & Samuelson 1996) and may in part explain the higher abundance and diversity of leaf beetles in the canopy, especially at the wet site. This pattern occurred despite more species of plant being surveyed in the understorey than in the canopy (Table 1). Chrysomelid assemblages were 1.5–3 times more species-rich in the canopy than in the understorey, depending on forest type, and included 33–53% of species unique to the canopy. The canopy of the wet forest was confirmed as being a distinct habitat for adult leaf beetles, in comparison with the other habitats surveyed (Figure 4).

It was difficult to survey conspecific plants in the canopy and understorey (Table 1), but in this regard our study plots were not unrepresentative of the two

forest types. Since most plant species reach their optimum growth in either the canopy or the understorey as herbs, shrubs or mature trees, it is difficult to find at any time similar volumes of conspecific foliage to sample in both strata. Nevertheless, available data confirmed that mature trees supported a rich and distinct chrysomelid fauna as compared to that of conspecific saplings. These observations suggest that the occurrence of different plant species in the understorey and canopy is only partly responsible for the faunal differences observed between the two strata. Other important factors in this regard include microclimatic conditions, the complexity of the foliage, the physiological state of the host plant and enemy-free space (Basset 2001, Tanabe 2002).

The CCA indicated that forest type was the most important factor influencing leaf beetle distribution (Wagner 2000), followed by the effects of stratum. The proportion of non-feeding individuals was highest at the dry site. This may be related to adult diapause and the cessation of feeding activity during the driest period of the year (Rockwood 1974). Of greater importance, our data indicated that chrysomelid assemblages were stratified in the wet forest, but less so in the dry forest (Figure 4). Many factors may influence the vertical stratification of chrysomelids. First, the canopy at the wet site was on average taller and more closed than at the dry site. Illumination levels may thus differ between the two forest types and indirectly affect the availability of resources for leaf beetles (young foliage, flowers). Second, the higher occurrence of lianas at the dry site than at the wet site may have promoted interconnectivity between the understorey and the canopy at the dry site (*cf.* plant similarity, Table 3).

Three implications are obvious from the present study. First, the low faunal similarity observed between the understorey and the canopy suggests that different food-webs may occur in these two strata, with likely consequences on a variety of forest processes. Second, our data suggest that different rainfall regimes may indirectly, via the more important factors of illumination and resource availability, influence the intensity of vertical stratification and species packing, as observed in the two types of forest studied. This contention is important with regards to the ongoing debate about estimates of global richness. Last, many leaf-beetle species appear to be unique to the canopy, particularly in wet tropical forests. Since indiscriminate removal of canopy habitats by logging is rampant in these forests, these diverse beetle assemblages may be particularly at risk.

ACKNOWLEDGEMENTS

We thank the Smithsonian Canopy Crane Team: S. J. Wright, V. Horlyck, M. Samaniego, J. Herrera, E. Andrade and O. Saldaña, and H. Barrios, R. Chang, V. Novotny, C. Costa, E. Medianero and A. Valderrama who assisted with fieldwork. The wife of the first author, Shevon, supported him in almost every area of his field and laboratory work. D. M. Winsdor, D. G. Furth, M. Samaniego and O. Calderón helped with the taxonomic analyses of beetles and plants. C. M. P. Ozanne and two referees commented helpfully on the manuscript. Laboratory space was provided by the University of Panama. The study was funded by a fellowship from the Government of Denmark through UNEP and STRI to E. C., and by a Tupper fellowship and the NERC-sponsored Visitor Programme at the Centre for Population Biology, Imperial College London, to Y. B.

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