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Arthropod Abundance, Canopy Structure, and Microclimate in a Bornean Lowland Tropical Rain Forest[1]

Roman J. Dial[2]

Department of Environmental Science, Alaska Pacific University, 4101 University, Drive, Anchorage, AK 99508, U.S.A.

Martin D. F. Ellwood, Edward C. Turner, and **William A. Foster**

Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

ABSTRACT

This study applies a novel, vertically stratified fogging protocol to document arthropod abundance, density, and biomass across a vertical gradient in a primary, lowland dipterocarp forest canopy in Borneo. We fogged arthropods at 5 m vertical intervals and 20 m horizontal intervals along six full-canopy transects and measured leaf surface areas along the same transects. The results show that arthropod biomass in the aboveground regions was 23.6 kg/ha, the abundance was 23.9 million individuals/ha, and the density on leaf surfaces was 280 individuals/m^2 leaf area. All three numbers are five to ten times higher than estimated by previous surveys of tropical lowland rain forest canopies using mass-collection techniques. Arthropod abundance and biomass were analyzed in relation to canopy structure, composition, vapor pressure deficit (VPD), photosynthetic photon flux density (PPFD), and height. Using stepwise regression we found that 13 of 14 arthropod groups had significant positive relationships with one-sided leaf area, 11 had significant negative relationships with VPD, 3 had significant relationships with height, and none showed positive relationships with light. Classifying the 14 taxa based on their responses to leaf area and VPD created three groups that corresponded roughly to the biology of these taxa. This study suggests that the biomass and abundance, and perhaps therefore—by extrapolation—the biodiversity, of tropical canopy arthropods may be very much higher than previously estimated.

Key words: arthropod abundance; Borneo; canopy arthropods; canopy microclimate; canopy structure; fogging; leaf area index; lowland tropical rain forest.

LOWLAND TROPICAL RAIN FORESTS CONTAIN AN UNPARALLELED RICHNESS AND ABUNDANCE of terrestrial arthropods, but these habitats are under serious threat from human activities (Erwin 1988, Marsh & Greer 1992, Floren & Linsenmair 2001, Sodhi *et al*. 2004, Curran *et al*. 2004). Arthropods carry out a range of vital ecosystem functions (*e.g.*, Janzen 1987, Basset *et al*. 2003a), and their loss may therefore have profound ecological consequences (Raven & Wilson 1992, Ozanne *et al*. 2003). We do not at the moment have enough reliable information to understand what these consequences might be (Basset 2001). We have only limited data about the true abundance of these animals and their distribution within the forest canopy, or about how they respond to environmental gradients from the canopy surface to the forest floor (Basset *et al*. 2003b).

The most widely used method for mass-sampling these canopy arthropods is fogging with knockdown insecticide (Adis *et al*. 1998). Although fogging cannot provide a complete inventory—animals living within plant tissue, for example, are very poorly sampled (Yanoviak *et al*. 2003)—it is nevertheless an effective, flexible, and powerful technique. However, previous fogging studies have often concentrated on a specific range of taxa (Allison *et al*. 1993, Hammond *et al*. 1997, Bruhl *et al*. 1998, Floren & Linsenmair 1998), often from a discrete range of locations within the canopy (Basset *et al*. 1992, Floren & Linsenmair 2001, Ellwood *et al*. 2002, Basset *et al*. 2003a), or have used fogging protocols that were not designed to locate the precise source of the animals (Erwin 1983, Stork 1991). Furthermore, conventional fogging procedures (Adis *et al*. 1998) are unable to distinguish between fauna from different levels within the canopy. A full description of the vertical distribution of canopy arthropods using a fogging technique requires vertically stratified and replicated transects from the litter surface to the upper surface of the canopy, ideally consisting of a set of equal and adjacent volumes of habitat from which the arthropods can be extracted in a standard manner (Basset *et al*. 2003b).

Here we describe such a protocol using replicated precision fogging (Ellwood & Foster 2002), whereby small, well-defined, and vertically stratified volumes of canopy are sampled with knockdown insecticide. In precision fogging, distances between the fogger, the canopy habitat fogged, and the collecting tray are less than 10 m. Our fogging protocol enabled us to provide a detailed account of the vertical distribution of biomass and abundance for more than 25 arthropod orders in a tropical rain forest. In addition, we measured vertical density of foliage, photosynthetic photon flux density (PPFD), air temperature, and humidity along the same vertical transects. This enabled us to compare arthropod abundances with environmental variables measured within the canopy.

This study is the first step in a detailed investigation, using refined fogging techniques, of the distribution, abundance, and biodiversity of arthropods in a complex tropical rain forest. Our main objective in this paper is to obtain a reliable estimate of arthropod abundance in the canopy, in particular in terms of the number of individuals per m^2 of foliage. We also describe how arthropods in general and from particular taxa are distributed throughout the canopy. Finally, we will show how the abundance of individual arthropod taxa correlates with environmental variables, such as height above ground, canopy structure and composition, PPFD, temperature, and relative humidity.

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[2] Corresponding author; e-mail: roman@alaskapacific.edu

METHODS

STUDY SITE.—From 6 to 25 May 2002, we sampled the undisturbed canopy of a primary lowland dipterocarp rain forest in Danum Valley (described by Marsh & Greer 1992), Sabah, Malaysian Borneo (4°586′N, 117°48′E). The 160 × 70 m sample plot, located on level ground at 150 m above sea level, was chosen as representative of the Danum forest in structure and composition (Dial *et al*. 2004a, b). In this respect it was a typical dipterocarp stand with a vertical distribution of foliage density similar to that depicted in other studies from Borneo (*e.g.*, Whitmore 1984, Ashton & Hall 1992, Koike & Syabuddin 1993, Koike & Nagamitsu 2003): an unstratified upper layer and a dense lower layer covered in lianas. Within the sample plot, the upper canopy surface was 40–75 m above the ground. Eleven individual trees represented by nine species from four families (Fig. 1) were more than 40 m tall (mean = 59.5 m, SD = 10.1 m), presenting a relatively high density of large-girthed trees (Dial *et al*. 2004b) when compared to other forest plots from SE Asia (reviewed in Newberry *et al*. 1992). Diverse but unidentified species of lianas and vascular epiphytes, particularly orchids and ferns, grew abundantly in the crowns of most understory and some overstory trees (particularly at T3, T4, and T6 in Fig. 1). Overall we observed 30 percent more tree leaves than liana leaves; however, this distribution was not uniform across the vertical gradient. Above 35 m and below 15 m the most abundant foliage type was tree foliage, while from 15–35 m the most abundant foliage type was liana foliage. Understory trees (<40 m) were not identified and the only palms above 10 m in the plot were climbing rattans.

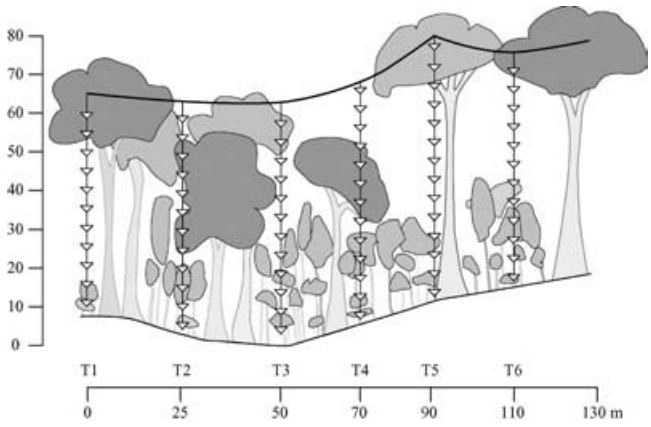

FIGURE 1. Sampling protocol for full-canopy, precision fogging. Vertical axis: meters above lowest topographic point (*not* height above ground). Horizontal axis: meters along traverse. Horizontal traverse line (bold) supports transects (T1, T2, . . . , T6). Small triangles along transects indicate position of arthropod sampling trays. Trees (>40 m tall) shown from left to right are dipterocarps *Shorea leprosula*, *Parashorea malaanonan*, *S. parvifolia*; *Pentaspodon motleyi* (Anacardiaceae); *S. johorensis; Koompassia excelsa* (Fabaceae); *P. malaanonan.* Not shown are *Parashorea tomentella, S. parvifolia, Dialium indum* (Fabaceae) and *Azadirachta excellsa* (Meliaceae).

ARTHROPOD SAMPLING.—During April 2002, a 130 m horizontal traverse of doubled 12 mm nylon ropes was established along the centerline of the sample plot between the tops of three emergents (Dial *et al*. 2004b; Fig. 1). From this traverse, we established six vertical sampling transects that reached from the upper canopy surface to the ground. We accessed these sampling transects using single rope technique on 10 mm nylon ropes attached to the horizontal traverse ropes. These transects were horizontally positioned every 20–25 m along a 110 m segment of the 130 m traverse. Each transect was sampled for arthropods using a vertical array of 1 m^2 fogging trays (circular nylon funnels equipped with alcohol bottles). These trays were positioned as near to 5 m vertical intervals as possible. During the fogging operation, neither the fogger (Swing-Fog model SN50, Phoenix Fogger, Dallas, TX, USA using 1.6% aqueous solution of the synthetic pyrethrum, Cypermethrin) nor the collection tray was more than 5 m from the foliage sampled, except in the case of transects T1 and T5 (traverse anchor trees) where the distance between the uppermost tray and canopy surface was 11 and 9 m, respectively (Fig. 1). The arrangement of 74 total locations of fogging trays provided six vertically stratified sampling cylinders, each with a cross-sectional area of 1 m^2, that stretched from near ground level to above the canopy surface.

We sampled the transects on six sunny days (1 d for each transect) between 12 and 24 May during 0700–0930 h. Trays were suspended the afternoon before fogging and removed following arthropod collection. As the fogger operator ascended to begin each fog, he brushed the trays clean and attached alcohol pots. Starting from above the uppermost tray, the operator fogged each vertical meter from 2–3 m away (except for the uppermost samples mentioned above) for approximately 6 s by rappelling down the access rope from the traverse line to the ground. No more than one full sampling cylinder was fogged per day and each fogging event was separated by 1–3 d. Each sampling cylinder was at least 20 m from adjacent cylinders. Fogging events on neighboring transects were separated by 3.2 d on average to minimize possible cross-transect contamination. The arthropods were collected from the trays 1–2 hours after fogging and preserved in 80 percent ethanol. Insects and arachnids were identified to Order, except for immature endopterygotes, which were grouped together as endopterygote larvae, and the Hymenoptera, which were split into ants (Formicidae) and non-ant Hymenoptera. Other arthropods were identified to Class. Specimens were digitally photographed and measured to the nearest 0.1 mm using computer software (photographs available at DataBank http://scidb.evergreen.edu/databank/studyCenter). We applied length-to-biomass allometry equations (Rogers *et al*. 1976, Richardson *et al*. 2000) to estimate arthropod biomass.

In addition to the stratified canopy sample, and to provide a background corroboration for the transect samples, we also collected two sets of independent fogging samples from a range of sites within 2 km of the sample traverse. These independent samples were five emergent trees (21 fogging trays per tree) and 20 low-canopy sites (4 trays per site), the latter fogged up to a height of 15 m. The emergent trees were specimens of *Parashorea tomentella* (one of the tree species in the full-canopy sample plot) and the

low-canopy sites were selected at random so that the arthropod numbers represent an unbiased estimate of the average arthropod density in the understorey of this particular forest.

CANOPY ENVIRONMENT VARIABLES.—We investigated four factors that might determine the vertical distribution of arthropods: (1) sample height; (2) canopy element and foliage density; (3) photosynthetic photo flux density (PPFD); and (4) dryness of the air measured as vapor pressure deficit (VPD). We chose to combine temperature and relative humidity as VPD because at typical tropical temperatures the principle effect of increasing temperature is most likely to dehydrate arthropods. For any given transect, all canopy variable measures were taken within 1–6 d of each other and of arthropod fogging. Height above ground was measured with a measuring tape anchored to the forest floor at the base of each transect.

CANOPY STRUCTURE AND COMPOSITION.—We constructed foliage density profiles along each transect from the ground to the canopy surface for three transects (T2, T3, T4; Fig. 1) and within 11 m of the surface for three others (T1, T5, and T6; Fig. 1). An individual observer suspended along the transect access rope used a laser range finder (Impulse 200 LR, Laser Technology Incorporated, Englewood, CO, USA) to sample horizontal distances to nearest foliage (*i.e.*, leaves, stems, trunks, epiphytes, lianas, etc.) at uniform vertical intervals (sampling methods fully described in Dial *et al.* 2004a). Along each transect (located at $x = 0$, 25, 50, 70, 90, and 110 m) we established sample locations z meters above the ground at 2 m intervals ($z = 1, 3, 5, \ldots$) from which we measured the distance to the nearest vegetation in 12 horizontal directions ($0^\circ, 30^\circ, 60^\circ, 90^\circ, \ldots, 330^\circ$) as r_i, $i = 1, 2, \ldots, 12$.

At each sample point (x, z) we characterized the structure in two ways. First, using only the distance measures that were 5 m or less to the nearest object, we classified the identity of these nearby canopy elements into one of five coarse canopy element classes: (1) tree foliage; (2) liana foliage; (3) woody; (4) epiphyte; or (5) dead. We refer to these counts as *canopy composition* at sample point (x, z). Overall, dead and epiphytic elements made up, respectively, only 5.4 and 1.8 percent of all elements identified within 5 m of the arthropod sample cylinders. Therefore we used composition counts of total elements within 5 m, tree foliage (37.0% of all elements identified), liana foliage (28.4% of all elements), and woody elements (27.4% of all elements) in correlation analysis (see below).

The second method of characterizing structure estimated leaf area (LA). Because we could differentiate between stems and leaves, which represent two very different habitats for arthropods, we were able to estimate one-sided *leaf surface area* between sample trays.

We made several assumptions. (1) LA over an interval can be calculated by multiplying the number of leaf intersections over a vertical interval by the area at the base of the interval. (2) The density of leaves near a sample point is approximately equal in both horizontal and vertical directions (MacArthur and Horn 1969). (3) If the average number of leaves intersected by a straight line at height z is given by $L(z)$ in units leaves/m, then the average distance between leaves at height z is $d(z) = 1/L(z)$ in units m/leaf. (4) Consider a sample point (x, z) at z m above ground and x horizontal m from a reference point. Then provided with j sample distances to nearest leaf from a sample point (x, z) as $r_i(x, z)$, $i = 1, \ldots j$, $j \leq 12$, the number of leaves intersected per meter at height z along the transect at x is $L(x, z) = \frac{1}{d(x,z)} = \text{mean}[\frac{1}{2r_i(x,z)}]$, since an observer can only expect to be midway between two leaves so that distance, d, between two leaves is $d = 2r$. (5) $L(x, z)$ gives the number of leaf interceptions per meter by a line above a given point at height z. Define the mean $L(x,z)$ above a given sample tray but below the next higher tray as $\bar{L}(x, z)$ with units of leaves/m. Multiplying $\bar{L}(x, z)$ by tray area (=1 m^2) and distance between sample trays, Δz (=5 m), provides an estimate of the one-sided *leaf surface area* (in units m^2) above a sample tray or leaf area [in m^2] = tray area[in m^2] $\cdot$ Δz[in m] $\cdot$ $\bar{L}(x, z)$[in per m^{-1}] = $1{\cdot}5 \cdot \bar{L}(x, z)$[in m^2]. (6) To calculate total LA, $LA(x)$, along each transect x, we summed all $L(x,z)$ as $LA(x) = \sum_{k=1}^{\max} L(x, z_k) \cdot \Delta z \cdot 1$, where the sum is taken over all heights sampled from $k = 1, 3, 5$, max meters above ground, $L(x, z_k) = \text{mean}[\frac{1}{2r_i(x,k)}]$, $\Delta z = 2$ meters (the vertical distance between successive samples of leaf density), and the total LA is measured over 1 m^2 of the forest floor. (7) This last calculation is analogous to "leaf area index" (LAI, *e.g.,* Funk & Lerdau 2004), which gives the one-sided surface area of leaves divided by the unit surface area of the forest floor below the leaves; hence, leaf area index is a unitless measure that is conceptually equivalent to the average number of leaf layers above a point on the forest floor.

PHOTOSYNTHETIC PHOTON FLUX DENSITY (PPFD).—At the same (x, z) locations (except the four uppermost heights on T5) where we measured distance to nearest canopy elements (*i.e.,* every 2 m vertically and ~20 m horizontally), we also made spot light readings of PPFD, PPFD(x, z). We used a handheld light meter (Quantum Lightmeter, Spectrum Technologies, Plainfield, IL, USA) that measures 400–700 nm radiation in μmol/m^2/s. We normalized each reading with the maximum measured light value along a given transect x, maxPPFD(x), to give PPFD transmittance:

$$\text{PPFD}(x, z)\text{transmittance} = \text{PPFD}(x, z)/\text{maxPPFD}(x).$$

MICROCLIMATE.—Every 3 m along each vertical transect we sampled temperature (T in °C) and relative humidity (RH in %) at 0.5 h intervals for 24 h using data loggers (Hobo Pro RH/Temperature Data Logger, Onset Computer Corporation, Pocassest, MA, USA). The two negatively correlated measures were combined to calculate vapor pressure deficit (VPD in kPa). VPD measures the difference between moisture content in the air and maximum possible content for a given temperature T (Read 1968). If the maximum vapor pressure of air at temperature T is e_s, then $\text{VPD} = e_s(1 - RH/100) = 0.6108 \exp(\frac{17.27T}{T+237.3})(1 - RH/100)$. VPD for each transect and height above ground was averaged over the 24 h sampling time to get VPD at each (x, z).

DATA ANALYSIS.—To test the null hypothesis of uniform distribution of arthropod biomass, abundance, and density we applied repeated-measures ANOVA with rank transformation, because of possible

nonindependence of trays within sampling cylinders. In this case, the cylinders were considered as subjects and the tray heights were considered repeated-measures factors (using the Huyn-Feldt epsilon adjustment to degrees of freedom).

To calculate overall arthropod density (individuals/m^2 of LA) we followed three procedures. The first procedure calculated the mean number of arthropods per square meter of leaf by dividing the number of arthropods in each tray by the LA above that tray. The second method used stepwise (with $P < 0.05$ an inclusion criterion for regression variables) multiple linear regression of arthropod abundance with LA as one of four canopy variables (height above ground and the mean of LA, VPD, and PPFD transmittance, each averaged over the 5 m vertical interval that was fogged); the partial regression coefficient of LA gives an average density estimate. The final method regressed the total number of arthropods in each sampling cylinder against total LA in that cylinder and considered the regression coefficient as the average density estimate. The first two methods treat each tray as an independent sample; the third method treats each sampling cylinder as an independent sample.

RESULTS

Overall arthropod abundance, biomass, and density.—Biomass and abundance in the upper and lower trays were not significantly different from those that we measured independently in other parts of this lowland rain forest (Upper canopy median abundance 250 vs. 173 ind./m^2: Mann–Whitney $U_{5,6} = 15$, two-tailed $P = 1.0$; upper canopy median biomass 152 vs. 222 mg/m^2: Mann–Whitney $U_{5,6} = 12$, two-tailed $P = 0.66$. Lower canopy median abundance 184 vs. 83 ind./m^2: Mann–Whitney $U_{20,6} = 30$, two-tailed $P = 0.07$; lower canopy median biomass 193 vs. 133 mg/m^2: Mann–Whitney $U_{20,6} = 42$, two-tailed $P = 0.30$). The similarities of these two strata with corresponding strata in other parts of the forest support the contention that the vertical transects are representative of the forest as a whole.

We collected a total of 14,355 individual arthropods representing 25 arthropod taxa, giving a total biomass of 14.15 g (dry mass) from the six vertical transects and 74 arthropod samples, which represent a total of 52.21 m^2 of LA and 6 m^2 of forest canopy projected to the forest floor. This provided an overall mean (± SE) of 196.2 ± 43 individuals per sample tray. Summing all arthropods from each sampling cylinder, the mean number of canopy arthropods per m^2 of forest floor was 2392 ± 883 (range: 632–6611; $N = 6$ cylinders), and the mean biomass was 2.36 ± 1.17 g/m^2 (range: 0.23–8.12; $N = 6$ cylinders). Taking each of the 74 samples and dividing by the estimated LA above the sample tray gave a mean density of 280.2 ± 26.43 individuals/m^2 leaf area ($N = 74$ trays). Alternatively, the stepwise linear regression procedure using samples with all canopy variables (leaf area, VPD, PPFD transmittance, height) provided a partial regression slope for LA of 114.8 individuals/m^2 (regression coefficient SE = 17.6, $P < 0.001$, df = 66, $R^2 = 0.64$). The latter method provides a substantially lower density estimate probably because of the important and significant effect of VPD on arthropod abundances (Table 1). Finally, summing the total arthropods sampled from each transect and regressing on the total LA for each transect (total arthropods = 288.1 LA – 595.9, LA = total transect leaf area in m^2) gave a density of 288.1 individuals/m^2 LA (regression coefficient SE = 61.0, $P < 0.01$, df = 5, $R^2 = 0.848$).

Arthropod abundances across vertical gradients.—Neither the horizontal nor vertical distribution of arthropods (Fig. 2) was uniform for biomass (repeated-measures ANOVA of rank-transformed biomass: Huyn-Feldt, $\varepsilon = 1.0$, height repeated-measures factor $F_{10,50} = 4.8$, $P < 0.001$, transect fixed factor $F_{1,5} = 470.4$, $P < 0.001$) or for numerical abundance (repeated measures ANOVA of rank transformed abundance: Huyn-Feldt, $\varepsilon = 0.89$, height repeated measures factor $F_{8,44} = 4.5$, $P < 0.001$, transect fixed factor $F_{1,5} = 473.4$, $P < 0.001$). The density of arthropods (arthropods/m^2 leaf area) did not vary significantly with height (repeated measures ANOVA of rank transformed density: Huyn–Feldt, $\varepsilon = 1.0$, height repeated measures factor $F_{10,50} = 0.88$, $P = 0.56$, transect fixed factor $F_{1,5} = 918.1$, $P < 0.001$). Most of the major orders appear to be present across the vertical gradient (Fig. 2), but vary in their abundance vertically.

Relationships of arthropods with canopy variables.—Overall, total arthropod abundance corresponded well to canopy composition on a transect-by-transect basis (Fig. 3). Treating trays as independent samples (and omitting one arthropod outlier that was more than 7 SD from the mean), abundance per tray was correlated positively and significantly with mean total number of elements within 5 m of each sample tray ($r = 0.751$, $P < 0.001$, $N = 73$), mean foliage counts ($r = 0.747$, $P < 0$ .001, $N = 73$), mean tree foliage count ($r = 0.588$, $P < 0.001$, $N = 73$), mean liana foliage counts ($r = 0.552$, $P < 0.001$, $N = 73$), and mean woody element count ($r = 0.381$, $P = 0.001$, $N = 73$), which were all correlated with each other as well.

We found that LA, VPD, PPFD transmittance, and height were each significantly correlated with one another and with transformed (square-root of abundance and log of biomass) arthropod measures (Pearson's correlation $|r| \geq 0.365$, two-tailed $P \leq 0.002$, $N = 68$). We used stepwise multiple linear regression to investigate the individual response of 14 arthropod groups to variation in canopy variables (Table 1). Of the four variables, LA and VPD showed the strongest responses among untransformed arthropod measures. Total arthropod abundance, ant biomass, total non-ant arthropods, and individual abundance for 10 of 14 arthropod groups had partial regression coefficients for LA significantly greater than zero *and* partial regression coefficients for VPD significantly less than zero. Only three groups had significant partial regression coefficients for PPFD transmittance (all negative) and three arthropod groups had significant partial regression coefficients for height (negative for Diptera; positive for Blattodea and Thysanoptera). The ants were the only arthropod group in which abundance had only a single significant partial regression coefficient (LA); non-ant Hymenoptera was the only group not significant for LA and significant for both VPD and PPFD transmittance.

TABLE 1. *Relationship between abundance of arthropod taxa (with % of all individuals represented by each taxa shown in parentheses in the first column) and selected environmental variable showing regression coefficients from stepwise multiple regression (P-values in parentheses) retaining predictor variables with partial regression coefficients significantly different from zero ($P < 0.05$). Dependent variable is abundance of each arthropod group in 1 m^2 sample trays: total biomass (with and without ants) is also shown. Predictor variables, all measured just above the sample tray, are: leaf area (in m^2)—one-sided leaf area;* VPD— *mean vapor pressure deficit (kPA) averaged over 24 h;.* PPFD—*mean transmittance* (%) *of photosynthetic photon flux density. Height (in m) is of sample tray above the ground. Degrees of freedom (df) give degrees of freedom from multiple regression with outliers removed, including bivariate outliers and removal of one arthropod sample that was 7.89 standard deviations from the mean in total abundance and biomass. The number of samples of each predictor variable is given by n, but only 68 samples had all five variables.*

Arthropod Group (% of all individuals)	df	R^2	Leaf area ($N = 72$)	VPD ($N = 72$)	PPFD ($N = 69$)	Height ($N = 73$)
Total arthropod abundance	66	0.64	114.8	−409.2	0	0
			(<0.001)	(<0.001)	(0.129)	(0.371)
Total non-ant abundance	66	0.63	71.6	−359.7	0	0
			(<0.001)	(<0.001)	(0.389)	(0.235)
Acari (2.90% of total)	66	0.35	2.8	−15.4	0	0
			(0.008)	(0.003)	(0.367)	(0.836)
Araneae (4.82% of total)	66	0.50	5.8	−18.6	0	0
			(<0.001)	(<0.001)	(0.759)	(0.734)
Collembola (7.79% of total)	68	0.38	8.8	−45.4	0	0
			(<0.001)	(<0.001)	(0.557)	(0.154)
Orthoptera (0.63% of total)	67	0.59	0.9	−4.6	0	0
			(<0.001)	(<0.001)	(0.738)	(0.198)
Blattodea (1.37% of total)	65	0.29	1.4	0	−0.03	0.08
			(0.011)	(0.236)	(0.006)	(0.001)
Psocoptera (1.75% of total)	65	0.57	1.4	−10.0	0	0
			(<0.001)	(<0.001)	(0.552)	(0.548)
Homoptera (4.49% of total)	67	0.38	4.0	0	−0.1	0
			(0.002))	(0.178)	(0.004)	(0.097)
Heteroptera (1.83% of total)	66	0.49	2.6	−7.4	0	0
			(<0.001)	(0.004)	(0.840)	(0.063)
Thysanoptera (12.17% of total)	67	0.38	9.6	−122.2	0	0.5
			(0.026)	(<0.001)	(0.255)	(0.020)
Endopterygote larvae (3.68% of total)	66	0.42	3.3	−12.4	0	0
			(<0.001)	(0.005)	(0.192)	(0.735)
Coleoptera (7.65% of total)	66	0.56	6.1	−53.9	0	0
			(0.001)	(<0.001)	(0.231)	(0.459)
Diptera (6.97% of total)	67	0.62	5.5	−53.8	0	−0.241
			(0.005)	(<0.001)	(0.958)	(0.020)
Non-ant Hymen (8.69% of total)	67	0.36	0	−41.7	−0.2	0
			(0.257)	(0.017)	(0.028)	(0.439)
Formicidae (33.67% of total)	66	0.53	47.1	0	0	0
			(<0.001)	(0.386)	(0.168)	(0.584)
Total biomass in mg/m^2	67	0.38	111.8	0	−1.6	0
			(<0.001)	(0.234)	(0.013)	(0.980)
Non-ant biomass (48% of total)	66	0.35	50.9	0	−0.7	0
			(<0.001)	(0.271)	(0.028)	(0.056)
Ant biomass (52% of total)	66	0.31	41.6	−165.0	0	0
			(<0.001)	(0.011)	(0.354)	(0.927)

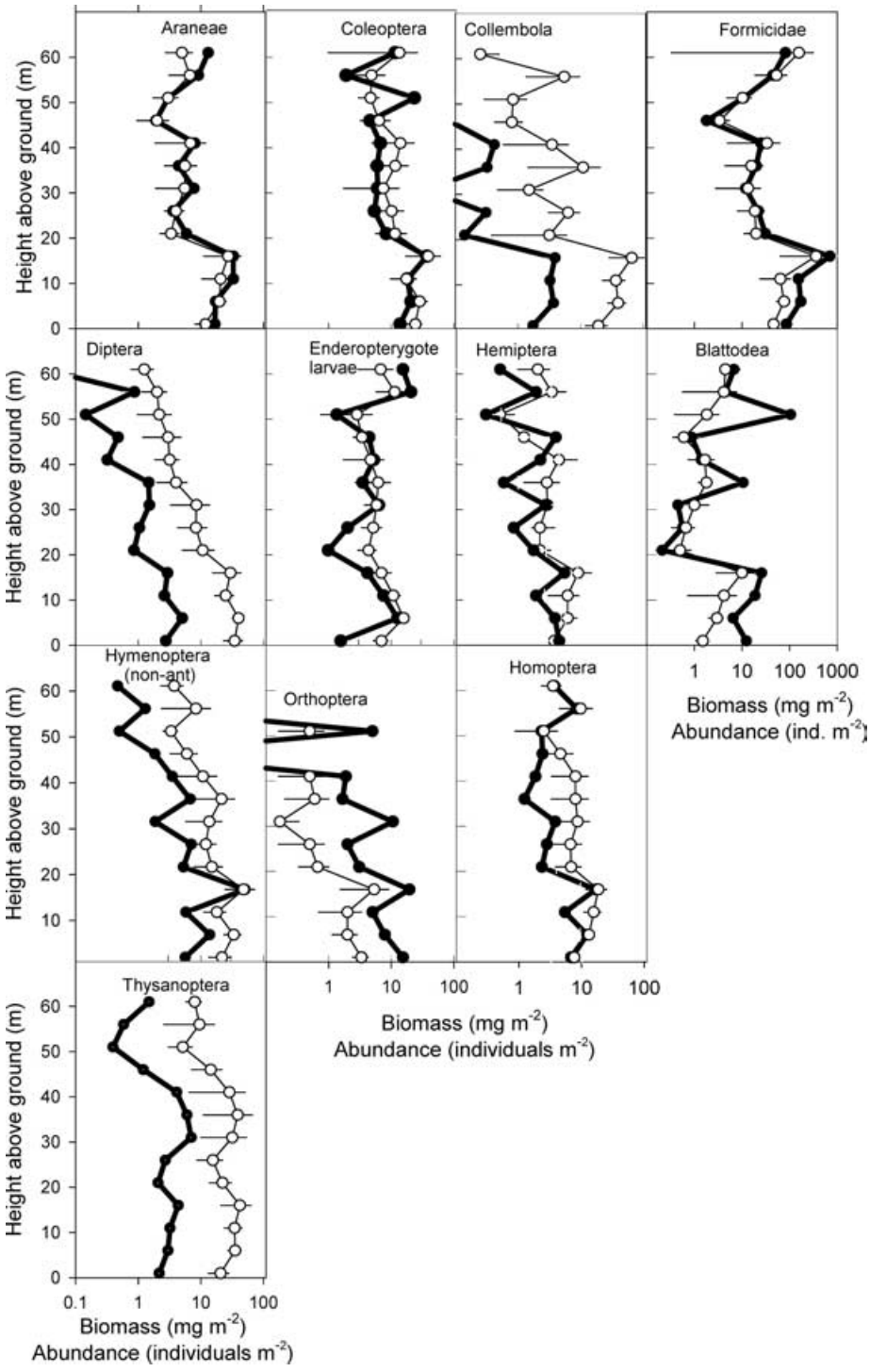

FIGURE 2. Average arthropod abundance as numbers of fogged individuals collected per square meter of sample tray (ind./m) shown as open circles (mean ± SE, $N = 6$) and as biomass per sample tray (bullets as means) by taxa across a vertical gradient of rain forest canopy. Note different scale for Formicidae and Blattodea.

PARTIAL CORRELATION ANALYSIS AND HIERARCHICAL CLASSIFICATION OF ARTHROPOD GROUPS.—We used partial correlations to determine the strength of responses shown by individual arthropod groups to variation in canopy variables. Partial correlation analysis measures the correlation between any pair of variables when other specified variables have been held constant. When controlling for LA and VPD the partial correlation coefficients for both PPFD transmittance and height were not significant ($P > 0.10$). By contrast, both

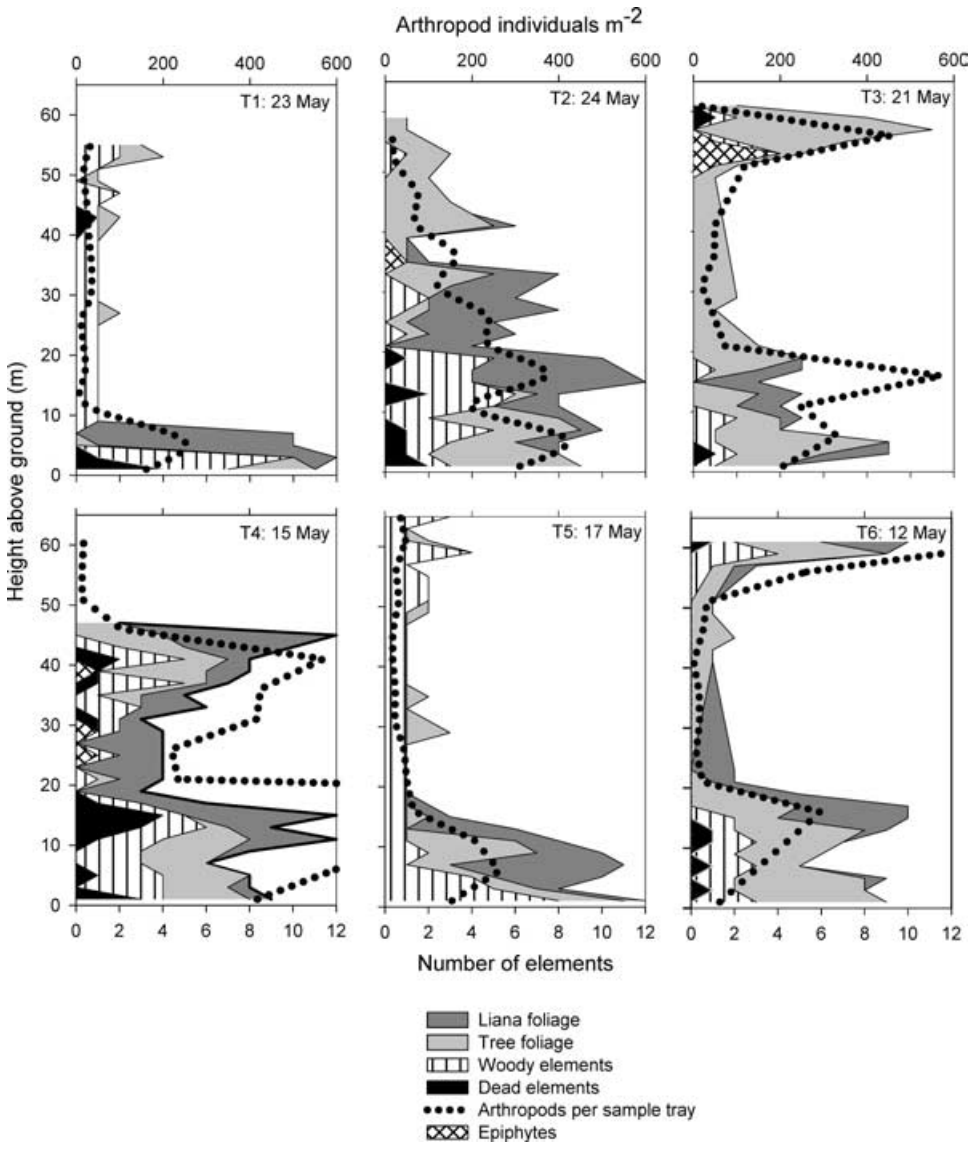

FIGURE 3. Canopy profiles from six vertical transects showing arthropod abundance as numbers of fogged individuals collected per square meter of sample tray (top axis) and the number of canopy elements (bottom axis) that were observed within 5 m of a sample point (out of 12 total observations at each point). Canopy elements were identified into one of five coarse canopy element classes: woody, tree foliage, liana foliage, epiphyte, and dead. T1, T2, etc. correspond to transects shown in Figure 1. Dates are dates of fogging.

LA and VPD had significant ($P < 0.02$, $N = 68$) partial correlations with total arthropod abundance (LA partial $r = 0.659$; VPD partial $r = -0.290$) and with arthropod biomass (LA partial $r = 0.623$; VPD partial $r = -0.297$) when holding PPFD transmittance and height constant. The nonsignificance of partial correlations between arthropod abundance measures and height and light suggested that we drop PPFD transmittance and height from further analysis of arthropod groups. We re-applied partial correlation analysis to quantify responses of the 14 arthropod groups in Table 1 to LA and VPD without PPFD and height. These 14 arthropod groups were then clustered on the basis of their partial correlation coefficients using Ward's hierarchical method with Euclidean distance. We found that the individual arthropod groups fell into three distinct clusters in their response, in terms of individual abundance, to canopy structure and VPD (Fig. 4), whether we quantified structure with one element class (total number of canopy elements within 5 m), or LA. These three clusters appear to relate to the mode of locomotion and morphology of the arthropods in the cluster: (i) a group of small, soft-bodied, flying and hopping insects (Diptera, Thysanoptera, non-ant Hymenoptera, Collembola, and Orthoptera), apparently associated with relatively moist conditions and relatively indifferent to element density; (ii) a group of nonflying arthropods (endopterygote larvae, Blattodea, and Formicidae) associated with high element density and relatively indifferent to

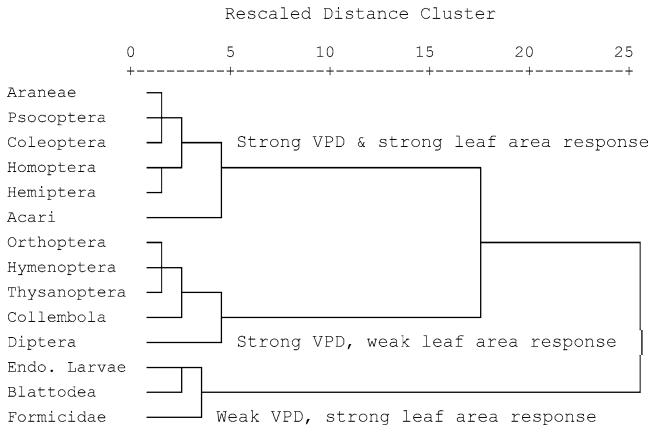

FIGURE 4. Dendrogram using Ward's method with Euclidean distance on arthropod abundance responses to total leaf area (LA) and vapor pressure deficit (VPD). Arthropod groups were classified using partial correlation coefficients for each group with respect to LA and VPD across all samples (df = 70). Endo. Larvae = Endopterygote Larvae; Hymenoptera = non-ant Hymenoptera.

VPD; and (iii) a remaining group (Araneae, Acari, Coleoptera, Psocoptera, Homoptera and Hemiptera) that respond equally to both foliage density and VPD. These analyses imply that a substantial portion of the variability in arthropod abundance seen across the vertical gradient, both in numbers and biomass, is due primarily to variability in canopy structure and microclimate.

DISCUSSION

Our estimates of arthropod biomass and abundance are very much higher than previously reported values for any tropical forest canopy arthropod sampling scheme. The values presented from the canopy sampling cylinders here are equivalent (mean ± SE) to 23.6 ± 10.2 kg/ha of arthropod biomass, 23.9 ± 8.8 million individual arthropods/ha, and 280.2 ± 26.4 individual arthropods/m^2 of leaf surface. The large standard errors reflect both the range in sample values and the small sample size. Our mean estimate of tropical canopy arthropod biomass is six times greater than and almost two standard errors distant from the previously highest replicated fogging estimate of canopy biomass (3.8 kg/ha; Ellwood & Foster 2004); our estimate of canopy arthropod abundance is five times higher than and more than two standard errors distant from the highest reported estimate of abundance (4.7 million individuals/ha; Erwin *et al.* in press); and our density estimate is 14 times higher than and almost 10 standard errors distant from the highest previously published density (20 individuals/m^2 of leaf surface, Basset *et al.* 1992). In another comparable study of canopy arthropods in Borneo, Stork (1991) fogged 10 trees 27–72 m high in Brunei and found 117 ± 15 (mean ± SE) arthropods/m^2, an estimate 20 times lower than the estimate we found here. Floren and Linsenmair (2001) reported results of fogging mid-canopy trees in a primary lowland Bornean rain forest but do not give arthropods/m^2; however their appendix 1 showed that ants contributed a larger proportion and small-bodied arthropod orders a substantially smaller proportion of total individuals than found in the data we present here (Table 1).

There are probably two main reasons why our figures are so much higher than those from previous fogging studies. First, in most previous investigations, only part of the above-ground vegetative structure in a forest was sampled. The second reason may be that, because of the large vertical gap between the fogging machine and the trays in most fogging protocols (Adis *et al.* 1998), a significant proportion of the falling animals are lost either through drift or, most likely, entanglement in intervening vegetation. Indeed, since this study sampled only those animals available to fogging—missing mites in domatia, insects embedded within leaves and stems, and arthropods in epiphytes and phytotelmata—even the figures presented here must underestimate the true numbers and biomass. However, we are unaware of published studies that quantify the loss of fogged arthropods due to habitat interference. Our results strongly support previous suspicions that biomass estimates for canopy arthropods have been grossly underestimated (Stork 1988, Basset 2001, Ellwood & Foster 2004). Since canopy abundance is greater than previously measured, it is possible that canopy arthropod species richness may also be higher.

This study demonstrates for the first time that arthropod abundances in tropical forests can be well correlated with structural measures of forest canopy. We are unaware of any other mass-collection studies that document such a clear quantitative relationship between arthropod abundances and canopy habitat characteristics such as structure, light, and microclimate. Our conclusions differ from some previous inferences of determinants of arthropod abundance and distribution (*e.g.*, Basset *et al.* 1992, Koike *et al.* 1998), which may be because of differences in sampling technique (fogging) and study scale (full-canopy samples). We found the greatest number of arthropods and highest biomass where there was the greatest amount of foliage. This result differs from sticky trap samples of another rain forest study in Borneo that found most canopy arthropods were located above a river and not in the most dense foliage (Koike *et al.* 1998). Among the six transects fogged in the present study, 85 percent of the variability in arthropod abundance was explained by variability in total LA. Because we sampled and identified canopy structure from within the canopy itself, we were able to distinguish between stems and leaves of lianas and trees and to calculate their densities separately. Indeed, by doing so we determined that total arthropod abundance was generally well correlated with foliar elements regardless of whether these were liana leaves or tree leaves, but much less so with woody elements (Fig. 3). We also found taxonomic variation (Table 1), both by total individuals and biomass, in arthropod responses to spatial gradients in LA, PPFD transmittance, VPD, and height. Importantly, the strength of arthropod responses to canopy variables allowed us to infer natural groupings (Fig. 4) based on arthropod biology, much as vegetation can be shown to vary morphologically across environmental gradients. We are unaware of any previous study that has generated hypotheses about the distribution and abundance of canopy arthropods across multiple environmental gradients and related them to arthropod biology.

Our results suggest that most arthropods, in mass and individual abundance, are not located necessarily in the highest canopy, but rather where foliage is dense and moist. Thus, upper crowns of tall dipterocarps and legumes of Borneo, which are drier than the equally foliose but more humid lower forest, may hold fewer arthropods. The fact that we found a mid-canopy peak in arthropod abundance, where foliage was dense and relatively moist, probably reflects the biology of canopy arthropods, as suggested by Figure 4.

We temper our conclusions with consideration of our techniques. First, while fogging is arguably among the least biased of mass sampling techniques (Floren & Linsenmair 1997), certain arthropod groups such as those that infest plant tissues, as well as that live in epiphytes, are not well sampled by fogging. Nor did we directly measure the LA of the canopy habitat, but rather estimated it by calculating leaf density at 2 m intervals from within the canopy; however, averaging the sum of these densities across each transect gives a stand level measure of LA index (measured in the unitless m^2/m^2) of LAI = 8.7 (SE = 1.42, $N = 6$), which compares favorably to published values of LAI for other tropical forests of unspecified locations ($7 < \text{LAI} < 12$ from Parker 1995; LAI = 6.3 from Funk & Lerdau 2004).

Contamination of any given transect from fogging another transect was probably very small, since we separated each successive fogging by at least 25 m and one full day (Fig. 3) and the foggings themselves were relatively light. While we may have under-fogged higher and over-fogged lower samples because of fog drift, we do not believe that inconsistent fogging biased our results substantially for the following reasons. If inconsistent fogging had biased our results, then the strongly bimodal distributions of arthropod abundance that parallel canopy structure would not be so apparent for each transect (Fig. 3). Contamination would have obscured the strong correlations with structure, as many more arthropods would have been captured in intermediate trays. Moreover, if inconsistent fogging and downward drift had determined the results, then the vertical distributions by taxa (Fig. 2) would show peak arthropod abundance at the lowest sample (1 m) for all taxa. In fact, no taxon had highest abundance or biomass at 1 m. Indeed, the strong parallels between vertical profiles of arthropods and foliage on a transect-by-transect basis (Fig. 3) suggest that contamination among transects was minimal. Finally, the fact that the appropriately matched vertically stratified samples were not significantly different from independent high-crown and near-ground samples taken elsewhere in the forest further supports the argument that inconsistent fogging did not bias the results. Clearly, greater spatial and temporal replication at different seasons and even times of day would establish further insights although the emotional demands of precision fogging high, tropical canopies at night are daunting.

It is important to establish whether the patterns that we report here apply to other forest types and to other parts of the world. More data from more sites and during more seasons may establish generality to the hypotheses proposed here. Precision fogging techniques together with a canopy gradient approach may help elucidate how canopy structure and microclimate influence arthropod assemblages. For example, PPFD transmittance was *not* generally correlated with arthropod abundances, perhaps because arthropods respond most strongly to abiotic variables related directly to moisture stress, as suggested by Didham and Springate (2002).

The fogging technique that we have described here is readily applicable to other sites. As a mass-collecting technique it may prove useful for describing distributions of biomass and individuals at larger spatial scales than more limited manual collections from leaf or stem surfaces. We also recommend that future studies of canopy arthropods clearly state which part of the canopy is being sampled or, if the aim is to sample the entire canopy, adopt a protocol comparable to the one described here. While we are far from understanding the complex nature of tropical rain forests, the discovery that the animals in them are more dense, more abundant, and possibly more diverse, than previously suspected further underlines the urgent need to study—and conserve—these threatened habitats.

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