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Stratification and diel activity of arthropods in a lowland rainforest in Gabon

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The abundance, activity and species richness of arthropods, particularly of insect herbivores, were investigated in the upper canopy and understorey of a lowland rainforest at La Makandé, Gabon. In total 14 161 arthropods were collected with beating, flight interception and sticky traps, from six canopy sites, during the day and at night, from mid-January to mid-March 1999. The effects of stratum were most important, representing between 40 and 70% of the explained variance in arthropod distribution. Site effects represented between 20 and 40% of the variance and emphasized the need for replication of sampling among canopy sites. Time effects (diel activity) explained a much lower percentage of variance (6–9%). The density and abundance of many arthropod taxa and species were significantly higher in the upper canopy than in the understorey. Arthropod activity was also higher during the day than at night. In particular, insect herbivores were 2.5 times more abundant and twice as speciose in the upper canopy than in the understorey, a probable response to the greater and more diverse food resources in the former stratum. Faunal overlap between the upper canopy and understorey was low. The most dissimilar herbivore communities foraged in the understorey at night and the upper canopy during the day. Further, a taxonomic study of a species-rich genus of herbivore collected there (*Agrilus*, Coleoptera Buprestidae) confirmed that the fauna of the upper canopy was different, diverse and very poorly known in comparison to that of the understorey. Herbivore turnover between day and night was rather high in the upper canopy and no strong influx of insect herbivores from lower foliage to the upper canopy was detected at night. This suggests that insect herbivores of the upper canopy may be resident and well adapted to environmental conditions there.

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ADDITIONAL KEY WORDS: *Agrilus* – insect herbivores – species richness – understorey – upper canopy.

INTRODUCTION

Although the magnitude of biodiversity present on Earth is largely unknown and its estimates remain highly controversial (e.g. Erwin, 1982; May, 1990), most workers agree that much, if not most, of biodiversity is represented by arthropod inhabitants of tropical rainforests (e.g. Wilson, 1988; Godfray, Lewis & Memmott, 1999). For conservation purposes, it may be argued that the study of patterns of distribution and use of resources by arthropods in rainforests is as

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pressing as the survey and description of the arthropod fauna there. For example, if most insect herbivores are highly host-specific, then loss of species will be directly dependent on the loss of host-trees, for example by logging. These issues demand integrated eco-taxonomical studies to elucidate patterns of arthropod distribution in tropical rainforests that remain only partially understood (e.g. Basset, 2001).

A high proportion of arthropods in tropical rainforests is represented by insect herbivores (e.g. Wilson, 1988; Godfray *et al.*, 1999). It is probable that most of the variance in the distribution of insect herbivores is accounted for by the following: (1) host plant effect (i.e. the presence or absence of a particular host); (2) local and regional effects, including historical factors; (3) successional gradients; (4) altitudinal gradients; (5) rainfall gradients; (6) vertical gradients (i.e. from the understorey to upper canopy); (7) seasonal gradients; and (8) diel activity. These effects and gradients are often related to each other. For example, host plant effects are strongly related to successional, altitudinal and rainfall gradients. In this paper, data relevant to two unrelated effects, vertical gradients and diel activity, are examined in a rainforest in Gabon, with particular reference to insect herbivores.

With reference to vertical gradients of arthropod distribution in tropical rainforests, the literature is replete with studies analysing samples obtained from the 'canopy', often meaning samples obtained 15 m or higher above the ground. More precisely, the 'canopy' is defined as the aggregate of every tree crown in the forest, including foliage, twigs, fine branches and epiphytes (Nadkarni, 1995; Parker 1995). In botany, the '*canopée*' or 'canopy surface' is also defined as the interface between the uppermost leaf layer and the atmosphere (Hallé & Blanc, 1990; Bell, Bell & Dines, 1999). Because entomological samples are difficult to obtain from such vegetation surface which, further, has no depth by definition, the term 'upper canopy' is used hereafter to denote the uppermost leaf layer, which is often 1–2 m deep in closed tropical rainforests (Hallé & Blanc, 1990).

The arthropod fauna of the upper canopy has been rarely sampled and studied. Most entomological studies, either with insecticidal fogging (e.g. Erwin, 1983), light traps (e.g. Wolda, 1979; Sutton, 1983) or by felling trees (Amedegnato, 1997; Basset, Charles & Novotny, 1999) cannot sample the upper canopy selectively. The origin of the material collected by fogging cannot be ascertained with precision (but see Floren & Linsenmair, 1997, for selective fogging of trees lower than 30 m) and it is probable that specimens from the canopy and upper canopy are mixed in the samples. Whether fogging performed at ground level is able to kill the fauna of the upper canopy efficiently and whether this fauna eventually falls in the collecting trays at ground level is also doubtful. Further, short-term temporal replicates are difficult to obtain. The range of attraction of light traps is uncertain, depending on lunar phase, differing between insect taxa, so that selective sampling of the fauna from the upper canopy is not straightforward. In addition, predominantly diurnal taxa are not collected. Insect material collected from felled trees may be contaminated by understorey insects (Basset *et al.*, 1999) and the procedure is highly destructive.

Studies of the arthropod fauna foraging within the upper canopy must proceed with samples obtained *in situ* by, for example, hand collecting or beating, or with a variety of trapping devices with limited power of attraction (e.g. Malaise, flight-interception and sticky traps). In practice, this has been achieved rarely due to the difficulty of reaching the upper canopy. Early studies focusing on medical entomology used metallic towers to sample mosquitoes (e.g. Corbet, 1961), whilst more ecologically-orientated studies concerned with replication relayed on hoisting sticky traps above or within the canopy (e.g. Sutton & Hudson, 1980; Koike *et al.*, 1988). Recently, entomologists have also been able to sample selectively from the upper canopy either with fixed canopy cranes (Wright & Colley, 1994) or mobile canopy raft and sledge (Hallé & Blanc, 1990). These studies targeted bees (Roubik, 1993), herbivorous beetles (Ødegaard, 1999), weevils (H. Barrios, unpubl. data), ants (e.g. Dejean, Corbara & Orivel, 1999) or arthropods in general (Delvare & Aberlenc, 1990; Basset, Aberlenc & Delvare, 1992; Lowman *et al.*, 1998). In particular, arthropod densities were about three times higher in the upper canopy of a rainforest in Cameroon than in the understorey, suggesting that food resources are higher in the former than in the latter (Basset *et al.*, 1992).

Many abiotic and biotic characteristics of the upper canopy of closed tropical rainforests are different from other forest layers below, especially from the understorey. For example, in a rainforest in Cameroon, the canopy surface characteristics are more akin to chaparral shrub vegetation than to familiar rainforest understorey vegetation (Bell *et al.*, 1999). Whereas the upper canopy receives close to 100% of the solar energy, less than 1% of this energy reaches the understorey (Parker, 1995). Average light availability decreases up to two orders of magnitude over short distances from the external surface to a few centimeters inside the canopy (e.g. Mulkey, Kitajima & Wright, 1996). Levels of ultraviolet, fluctuation of relative humidity and air temperature, and wind speed are notably higher in the upper canopy than in the understorey (e.g. Blanc, 1990; Parker, 1995; Barker, 1996). Water condensation at night is frequent within the upper canopy, whereas being absent in the understorey (e.g. Blanc, 1990). The leaf area

density and the abundance of young leaves, flowers and seeds are also usually higher in the upper canopy than below (Parker, 1995; Hallé, 1998). The leaf buds of the upper canopy appear to be extremely well protected against desiccation and herbivory (Bell *et al.*, 1999). Further, levels of secondary metabolites biologically active within individuals trees are much higher in leaves of the upper canopy as compared to similar levels in leaves situated at the base of the crown (Hallé, 1998; Downum *et al.*, in press).

The implications for the distribution of insect herbivores along vertical gradients in tropical rainforests may be significant. Insect herbivores foraging and feeding in the upper canopy encounter a serious hygrothermal stress during the day, and water condensation at night. Further, the high level of plant defences in the upper canopy may force them to specialize on leaves from the upper canopy of particular tree species. Conversely, the supply of young leaves available to them is greater in the upper canopy than in the understorey. This suggests several strategies in order to overcome this apparently conflicting situation: (1) a specialized, distinct and well-adapted fauna to the extreme microclimatic conditions of the upper canopy; (2) interchanges of fauna between the upper canopy and lower layers, such as individuals resting in lower layers at day and moving up in the upper canopy to feed at night, perhaps taking advantage of air movements (e.g. Haddow & Corbet, 1961; Sutton, 1989); or (3) both of the above.

Given the formidable species richness of canopy insects but their poor taxonomic knowledge (e.g. Erwin, 1995), the rather low densities of insect populations per unit leaf area diluted within the rainforest vegetation (Basset, 2001), and the difficulty to sample selectively the upper canopy, testing the above hypotheses will be challenging. As a first examination of this issue, an attempt was made to answer the following questions, using various collecting methods:

(1) Whether the density, activity and species richness of arthropods, particularly of insect herbivores, are higher in the upper canopy than in the understorey;
(2) Whether the density, activity and species richness of arthropods are higher during the day than during the night; and
(3) Whether the relative differences in diel activity of arthropods are of comparable magnitude in the upper canopy and in the understorey.

Question 3 is of particular relevance in order to assess whether faunal interchanges between the upper canopy and the understorey are commonplace (hypothesis 2, above). This contribution discusses the results of three sampling programmes that were performed to assess questions 1–3 during the Canopy Raft expedition in Gabon in 1999 (Hallé, 2000).

MATERIAL AND METHODS

STUDY SITES AND CANOPY ACCESS

Arthropod samples were obtained from a lowland tropical rainforest in the Forêt des Abeilles, near the station of La Makandé, Gabon (0°40′39″S, 11°54′35″E, 200–700 m asl). Annual rainfall and air temperature at the site amount to 1600–1800 mm and 24°C, respectively (Fréty & Dewynter, 1998). The height of the upper canopy often oscillates between 35 and 45 m. In general, the topography at La Makandé is relatively flat and thus the upper canopy is clearly distinct from the understorey. The main features of the forest are described in Doucet (1996), Fréty & Dewynter (1998) and Hallé (2000).

Canopy access was made possible with the assistance of 'Océan Vert' at La Makandé during mid-January to mid-March 1999. This included the use of the 'Radeau des Cimes' (Canopy Raft), the 'Luge' (Sledge), and the 'Bulle des Cimes' (Treetop Bubble). The Canopy Raft is a 580 m^2 platform of hexagonal shape, consisting of air-inflated beams and Aramide netting. An air-inflated dirigible of 7500 m^3 raises the raft and sets it upon the canopy. The raft is positioned on particular sites within the canopy and moved every fortnight by the dirigible. Access to the raft is provided by single rope techniques (Hallé & Blanc 1990; Ebersolt, 1990). The Sledge is a triangular platform of about 16 m^2 which is suspended below the dirigible and which 'glides' over the canopy at low speed (Ebersolt, 1990; Lowman, Moffett & Rinker, 1993). The Treetop Bubble is an individual 180 m^3 helium balloon of 6 m in diameter which runs along a fixed line set up in the upper canopy by the dirigible (Hallé, 2000).

During this period, five sites (coded A to E), separated by a minimum of 100 m (two Bubble sites) and a maximum of 4 km, were sampled for arthropods. For collection purposes, a site included the portion of foliage directly accessible in the upper canopy from either the Raft or the Bubble, and the projected area of the Raft (580 m^2) or transect of the Bubble (*c.* 100 m) below in the understorey. In addition, samples were also obtained from the Sledge at various locations in the upper canopy early in the morning and equivalent samples were obtained at various locations in the understorey for direct comparison ('site' coded L). Table 1 summarizes the main characteristics of the sites and collections of arthropods performed there.

SAMPLING METHODS

The sampling methods assessed the following at all sites: (a) the density of arthropods per area of foliage

Table 1. Summary of sites and arthropod collections obtained at La Makandé (Und = understorey, Ucn = upper canopy)

Site	Canopy access	Canopy height (m)	Dates of sampling	Beating samples	Flight-interception traps	Sticky traps	Major support trees on site
A	Raft	38	23–28/I/99	Day: $n=26$ Ucn Day: $n=24$ Und Night: $n=20$ Ucn Night: $n=20$ Und	Transect for 4 days, day and night	Day: $n=21$ Ucn Day: $n=21$ Und Night: $n=20$ Ucn Night: $n=21$ Und	*Leptoderris* sp. *Dialium ?pachyphyllum* Harms *Dacryodes normandii* Aubreville & Pellegrin *Paraberlinia bifoliolata* Pellegrin *Gilbertiodendron brachystegioides* (Harms)
B	Raft	*ca* 45	1–4/II/99	Day: $n=25$ Ucn Day: $n=25$ Und Night: $n=20$ Ucn Night: $n=20$ Und	Transect for 3 days, day and night	Day: $n=20$ Ucn Day: $n=21$ Und Night: $n=16$ Ucn Night: $n=21$ Und	*Cylicodiscus gabunensis* Harms Other indetermined species
C	Bubble	35	19–25/II/99	None	Transect for 3 days, day and night	Day: $n=19$ Ucn Day: $n=21$ Und Night: $n=15$ Ucn Night: $n=12$ Und	*Paraberlinia bifoliolata* Pellegrin *Aucoumea klaineana* L. Pierre *Tetraberlinia* sp. *Papillionaceae* indetermined
D	Raft	47	26/II–8/III/99	Day: $n=16$ Ucn Day: $n=20$ Und Night: $n=10$ Ucn Night: $n=20$ Und	Transect for 3 days, day and night	Day: $n=20$ Ucn Day: $n=21$ Und Night: $n=21$ Ucn Night: $n=21$ Und	*Paraberlinia bifoliolata* Pellegrin *Desbordesia glaucescens* (Engler) van Tiegh *Marquesia excelsa* R. E. Fries *Dialium* sp.
E	Bubble	35	9–10/III/99	None	None	Day: $n=20$ Ucn Day: $n=20$ Und Night: $n=20$ Ucn Night: $n=21$ Und	*Dialium* sp. *Aucoumea kleineana* Pierre *Paraberlinia bifoliolata* Pellegrin
L	Sledge	35–45	25/I–9/III/99	Day: $n=78$ Ucn Day: $n=39$ Und	— —	— —	Various

with beating samples; (b) the density activity of arthropods along a transect of three flight-interception traps situated at ground level, in the canopy and in the upper canopy and (c) the density activity of arthropods collected with traps with moderate attraction, i.e. sticky traps. These methods were intended to be complementary and to provide a better assessment of the overall arthropod fauna present than a specific method (see discussion in e.g. Basset *et al.*, 1997). The sampling methods employed were intended to collect macroarthorpods, specifically insect herbivores.

Arthropods were collected on squared beating sheets of 0.397 m^2 in area, of conical shape (slopes of 45°), ending in a circular aperture (7 cm in diameter), which was fitted with a removable plastic bag. Sheets were inserted below the foliage so that one layer of leaves above occupied approximately the entire area of the sheet. Arthropods were dislodged from the foliage with three good strokes, and gently brushed inside the plastic bag, which was then closed and replaced by a new one. At each site, 20 samples were obtained per stratum (upper canopy or understorey), either during the day (between 13:00 and 16:00) or at night (between 21:00 and 24:00). Upper canopy samples were taken from the periphery of the Raft, or with the Sledge, whereas understorey samples were collected below a height of 2 m and originating from either immediately below the projected area of the Raft, or from sampling at random in the understorey, for comparison with samples obtained with the Sledge. No beating samples were obtained from Bubble sites, as the relative instability of the Bubble precluded sampling.

Since the area of understorey leaves is often greater than that of canopy leaves (e.g. Bongers & Popma, 1988), the leaf area of samples obtained by beating in the understorey may be different from that in the canopy, and this may complicate comparisons of arthropod densities between the two layers. For 40 samples obtained from different sites (30 in the understorey and 10 in the upper canopy), the leaf area sampled was estimated by cutting the leaves present in the samples and measuring their leaf area with a transparent grid (accuracy of measurements to 5 cm^2; total leaf area one-sided). The total leaf area of understorey samples was significantly higher (mean $\pm$ SE = 3445 ± 136 cm^2) than that of canopy samples (mean = 2492 ± 267 cm^2; *t*-test, $t = 3.393$, $P<0.01$). Thus, the leaf area of understorey samples was on average 28% larger than that of canopy samples. Correcting arthropod densities accordingly was not feasible, but this important aspect will be discussed below.

Non-attractive flight-interception traps, combining features of Malaise- and window-traps, were also used at the Raft and Bubble sites. The main body of the trap consisted of a rectangular cross-panel of black netting (mesh width of 0.5 mm, double-sided collecting surface of $1.2\,m \times 1.4\,m \times 4 = 6.7\,m^2$) with a roof of the same black netting connected to vertical duct and collecting jar. A clear plastic funnel was attached below the main body of the trap (upper diameter of 1.12 m) and connected to a large collecting jar. A plastic grid with a wide mesh (2 cm) covered the plastic funnel, to prevent larger debris from falling into the lower collecting jar, but not arthropods. A grid in the middle of the lower jar permitted overflow of water during heavy rainfall. Collecting fluids were 70% alcohol in the upper jar and water saturated with salt in the lower jar. A similar trap model is described elsewhere (Springate & Basset, 1996).

At each site, one vertical transect of three flight interception traps was operated for at least 3 days (Table 1). The traps were set on a rope, with a pulley system that allowed convenient survey and re-setting of the traps in the same position. On the transect, the third trap was set immediately below the Canopy Raft or within the upper canopy at Bubble sites (upper canopy trap), the second one 6 m below (canopy trap) and the first at 2 m above ground (understorey trap). Day and night catches were segregated by surveying the three traps at 18:00 and 06:00, respectively. A fifth transect (site F) was operated for 3 days with the Bubble but is not included in Table 1 as no other samples were obtained from this site. A sample represented the pooled catches of the upper and lower collecting jars of one trap during 12 hours.

At each site, 21 sticky traps (Temmen GmbH, Ankerstrasse 74,65795 Hattersheim, Germany) were set up in the upper canopy and 21 in the understorey. Each trap was yellow, with glue (Tangle foot) coated on both faces, and 29×12.5 cm in dimension (total collecting area per trap = 725 cm^2). In the upper canopy, traps were set up in the foliage along the periphery of the Canopy Raft (maximum distance available 84 m) or along the transect of the Bubble (*c.* 100 m). In the understorey, traps were set up along a transect line of 80 m situated below the Raft or below the transect of the Bubble, at a height of 1.5 m.

At each Raft site and for each stratum, traps were run 3 hours in the afternoon (13:00–16:00), then replaced by fresh and inactive traps (protection sheet in place) at the same location, which were later operated at night for 3 hours (21:00–24:00). Due to the different topography of the Canopy Raft at night, a few traps were lost in the process (see Results and Table 1). A similar protocol was used at the Bubble sites (C and E), but, for logistical reasons, traps had to be surveyed at 7:00 and 17:00, both in the understorey and upper canopy. Thus, traps at sites C and E ran for 10 hours during the day and 14 hours during the night. A sticky

trap sample represented the corrected catches (see below) of one trap during 3 hours.

PROCESSING OF ARTHROPOD MATERIAL

Arthropods were counted and sorted to family level or higher taxonomic level. Adults of insect herbivores (*s.l.*: leaf-chewing, sap-sucking and wood-eating insects) were mounted, sorted by morphospecies (hereafter species for sake of simplicity) in beating and flight-interception trap samples, and identified with a code. The poor quality of the material collected with sticky traps did not justify this approach for these collections.

Arthropods were assigned to the arboreal guilds proposed by Moran & Southwood (1982) and Stork (1987): leaf-chewers, sap-suckers, pollinators, epiphyte grazers, fungal-feeders, insect predators, other predators, parasitoids, wood-eaters, scavengers, ants, tourists and unknown. Tourists were considered to be non-feeding residents that might have been attracted to trees for shelter, sun-basking or sexual display. Further, leaf-chewing and sap-sucking insects were merged into the 'leaf-feeder' category, which together with wood-eaters constituted the 'herbivore' guild. Since the feeding ecology of many Curculionidae had to be examined at the specific level, they were assigned to the 'unknown' category when not sorted to species (i.e. all Curculionidae collected with sticky traps).

Since one of us (GC) is a specialist working on African *Agrilus* (Coleoptera, Buprestidae; e.g. Curletti, 1993, 1994, 1996, 1997), representatives of this genus occurring in the material collected at La Makandé were named or described (Curletti, 2000). *Agrilus*, with more than 2500 described species, represents one of the most speciose genera of the Animal Kingdom. About 600 species are known from Africa (Curletti, 1993; Obenberger, 1936). Most larvae are xylophagous and primary invaders of a variety of plant species, often legumes and Rosaceae in Africa. They rarely feed at the adult stage, being heliophilous and thermophilous, and are often extremely active and difficult to catch. The *Agrilus* material collected in the understorey and upper canopy provided the opportunity to discuss the data with identified specimens.

Arthropod data were managed using the software Biota (Colwell, 1997a). Collections of insect herbivores were deposited at the Laboratoire Entotrop (Faunistique-Taxonomie) of the Centre de Coopération Internationale en Recherche Agronomique pour le Dévelopment (CIRAD-Amis), Montpellier, France.

STATISTICAL METHODS

To account for the longer exposure of sticky traps at sites C and E, arthropod catches at these sites were corrected by a factor of 0.3 for daytime catches ($10\,h \times 0.3 = 3\,h$) and a factor of 0.214 for night-time catches ($14\,h \times 0.214 = 3\,h$). Analyses were performed on these corrected data. Since many samples of either beating, flight interception or sticky traps were empty or collected only a few specimens, the data were grossly non-normal, even after various transformations. Thus, data were analysed with non-parametric methods. However, for ease of comparison between uneven number of samples obtained in various situations, means are reported without their standard errors. Since many sweat bees (Apidae: Meliponinae) harassed the collectors, some analyses were performed without this taxon, to account for this potential bias.

The effect of site was examined with Kruskal–Wallis tests and that of forest stratum with Mann–Whitney tests. The effects of time (day or night) were tested by Mann–Whitney (beating data) and Wilcoxon signed ranks tests (flight interception and sticky traps data). For the latter, only pairs of traps situated at the same location and which were safely recovered both during day and night were considered. These tests were applied to the most common guild, taxa and species encountered in the collections. The latter were only tested if they represented at least 5% of total catches with a particular sampling method. To account for the multiplicity of tests performed, Bonferroni's correction was considered (but see Discussion).

Whilst analysing beating and flight interception trap data, special attention was paid to density of insect herbivores, species richness, evenness, species-abundance distribution and faunal similarities of herbivore communities in the four following situations: understorey during day; upper canopy during day; understorey during night; and upper canopy during night (for flight interception trap data, six different situations were analysed, accounting for the traps set up at canopy level). The Chao1 statistic was calculated to estimate the total number of species present, as it is relatively insensitive to sample size and performs well in the presence of large numbers of singletons (e.g. Colwell & Coddington, 1994). The rarefied number of species present in a sample of n individuals was computed with Coleman's curve (e.g. Colwell & Coddington, 1994), whereas the evenness of communities was calculated with the index of evenness E, proposed by Bulla (1994). Similarities in herbivore communities were calculated with the Morisita–Horn index (Magurran, 1988). The Chao1, Coleman and Morisita–Horn statistics were calculated with 50 randomizations computed by the program EstimateS (Colwell, 1997b). Differences in the structure of communities were tested further between pairs of species-abundance distributions (species ranked by abundance) with the Kolmogorov–Smirnov two sample test (Tokeshi, 1993).

More robust and informative analyses were performed to partition the respective effects of site

location, forest stratum and time of day on either the beating, flight-interception or sticky trap data. This included computing a detrended correspondence analysis (DCA) and a canonical correspondence analysis (CCA) on a matrix of the most common insect taxa × samples, with the programme CANOCO (ter Braak & Smilauer, 1998). The CCA was constrained by the site location (sites A–L, ordered in chronological order of sampling), the height at which samples were obtained and a categorical variable coding for either day or night. Partialling out the total variance in the system from that accounted by the variables measured follows Borcard, Legendre & Drapeau (1992). For beating samples, analyses were performed with species collected with five or more individuals (19 species, matrix 363 lines × 19 columns). For flight interception trap samples, analyses were performed with species collected with six or more individuals (16 species, matrix 84 lines × 16 columns). For sticky trap samples, analyses were performed with taxa collected with 50 or more individuals (17 taxa, matrix 392 lines × 17 columns).

RESULTS

BEATING SAMPLES

A total of 363 samples was obtained by beating from four sites, including 195 collected in the upper canopy obtained from >40 plant species (78 collected with the Sledge), and 168 from the understorey; 253 were collected during the day and 110 at night. The total leaf area sampled amounted to 106.5 m^2, from which 2469 arthropods were collected. On average, 6.80 ± 0.536 (SE) arthropods were collected per sample, which averaged 0.321 ± 0.014 m^2 of leaf area. The arthropod material included 112 families, from which 70, 62 and 22 species of leaf-chewing, sap-sucking and wood-eating insects, respectively, were sorted. The most abundant or species-rich families were Formicidae (ants), Chrysomelidae, Curculionidae (mostly leaf-chewers), Psyllidae, Cicadellidae, Phlaeothripidae (sap-suckers), Apidae (pollinators), Staphylinidae, Tenebrionidae (scavengers) and Cucujidae (fungal-feeders).

Overall, the abundance of arthropods did not vary significantly between sites, strata or time of day, after applying Bonferroni's correction (Table 2). Site effects were significant for many guilds and taxa (Fig. 1 and Table 2), notably ants, sap-suckers and leaf-chewers, fungal-feeders, Psylloidea, Curculionidae, etc. The effects of stratum were more evident and significant when lower taxa were considered. In particular, ants, scavengers, Isopoda and Opiliones were more abundant in the understorey than in the upper canopy, and leaf-feeders, sap-suckers, pollinators, Thysanoptera, Psylloidea and Apidae showed the reverse trend. Time effects were significant only for pollinators and Apidae, which were more abundant during the day than at night. Of the nine species in beating samples that were amenable to statistical analysis, three did not show any significant trend, five were more abundant in the upper canopy than the understorey and one showed the reverse trend. However, only two species were more abundant in the upper canopy than in the understorey and one showed the reverse trend after considering Bonferroni's correction.

The average number of species collected within beating samples differed significantly between sites (Table 2), but not between time of day. Samples were also more species-rich in the upper canopy than in the understorey, but this comparison was not significant after considering Bonferroni's correction. Herbivores were significantly more abundant in the upper canopy than in the understorey (Mann–Whitney $U = 12\,399.0$, $P<0.0001$), by a factor of about 2.5 (Table 3). In contrast, herbivores were not significantly more abundant during the day than at night ($U = 150\,215.0$, $P = 0.205$). More species of insect herbivores were collected in the samples obtained from the upper canopy during the day, and the Chao1 estimate confirmed that, overall, this situation was probably the most species-rich (Table 3). However, rarefied estimates of species number and evenness of communities were higher for the understorey during the day, in comparison with the upper canopy during the day. Both Morisita–Horn indices and Kolmogorov–Smirnov two sample tests confirmed that the most similar communities, either in terms of faunal composition or community structure, were those of the understorey, during the day and at night. In contrast, the most dissimilar were those of the upper canopy during the day and in the understorey at night (Table 4). Neither the density (Table 2), species richness of herbivores (Table 3), nor the overlap of the herbivore community with similar communities of lower strata (Table 4) increased notably in the upper canopy at night, suggesting that no strong influx of insect herbivores occurred from lower strata at night.

The total inertia of the DCA amounted to 11.132, with Figure 2A representing 18% of the total variance in the system. It isolated two species from the others along Axis 1, 'CURC001' (Anthonominae) and 'PLAS007' (Plataspidae), which were only collected in the upper canopy during the day. The CCA grouped the arthropod species in a similar way than the DCA did for the first two axes. Correlations between the scores of the taxa of the DCA and of those of the CCA were significant for the first two axes but not for the third ($r = 0.92$, and $r = 0.57$ for axis 1 and 2, $P<0.05$ in both cases; $r = 0.37$ for axis 3, n.s.). The total sum of eigenvalues in the CCA was 1.089, indicating that the constraining variables (site, height and time of day) explained about 10% of the total variance in the system.

Table 2. The most common arthropod taxa collected in beating samples, detailed per site, stratum (Und = understorey, Ucn = upper canopy) and time of day (D = day, N = night). Entries are means of individuals collected per sample. T site, T stratum, T time are results of tests (probabilities) for the effect of site, stratum and time of day (see methods). Italicized probabilities are significant following Bonferroni's correction

Taxa		Site A		Site B		Site D		Site L		T site	T stratum	T time
	D/N	Und	Ucn	Und	Ucn	Und	Ucn	Und	Ucn			
All arthropods	D	6.083	6.269	5.640	5.720	2.450	5.733	12.820	7.924	0.011	0.313	0.057
	N	5.100	3.700	5.150	2.100	13.150	3.100	—	—			
Leaf-feeders	D	1.458	3.462	0.960	0.640	0.500	2.467	0.512	3.139	*0.001*	*0.001*	0.270
	N	0.650	2.150	0.200	0.650	2.200	1.400	—	—			
No. sp. herb.	D[1]	1.167	1.538	0.320	0.400	0.650	1.267	0.410	1.607	*0.001*	0.003	0.483
	N	0.750	1.500	0.150	0.550	1.300	0.300	—	—			
Isopoda	D	0.125	0	0.200	0	0	0	0.385	0.012	0.386	*0.001*	0.988
	N	0.100	0	0.050	0	0.250	0	—	—			
Opiliones	D	0.583	0	0.240	0	0	0	0.256	0	0.021	*0.001*	0.021
	N	0.200	0	0.300	0	0	0	—	—			
Araneae	D	0.916	1.269	0.840	1.520	0.300	0.867	1.436	0.886	0.534	0.375	0.205
	N	1.000	0.700	1.050	0.900	2.950	0.500	—	—			
Blattodea	D	0.042	0.115	0.240	0.040	0	0.200	0.179	0.202	0.081	0.554	0.073
	N	0.100	0.100	0.150	0.200	0.850	0.100	—	—			
Thysanoptera	D	0	0.616	0	0.320	0	0.467	0.026	0.076	0.862	*0.001*	0.026
	N	0	0	0	0	0	0.400	—	—			
PHLA001[2]	D	0	0.346	0	0.080	0	0	0	0.038	0.365	0.005	0.045
	N	0	0	0	0	0	0	—	—			
Psylloidea	D	0.125	1.307	0	0	0	0.400	0.026	1.063	*0.001*	*0.001*	0.025
	N	0.050	0.250	0	0	0	0	—	—			
PSYL001[3]	D	0.083	0.884	0	0	0	0.200	0	0.456	*0.001*	*0.001*	0.117
	N	0.050	0.200	0	0	0	0	—	—			
PSYL002[3]	D	0	0.346	0	0	0	0	0	0.367	0.017	*0.001*	0.020
	N	0	0	0	0	0	0	—	—			
Cicadellidae	D	0.083	0.115	0.480	0.040	0	0.333	0.103	0.291	0.020	0.005	0.117
	N	0.050	0.450	0	0	0	0	—	—			
CICA034	D	0	0	0	0	0	0.133	0	0.063	0.386	0.022	0.298
	N	0	0.200	0	0	0	0	—	—			
Staphylinidae	D	0.083	0	0	0	0.150	0.067	0.076	0.253	0.058	0.894	0.733
	N	0.250	0.250	0.050	0	0.050	0	—	—			
Chrysomelidae	D	0.583	0.384	0.080	0.080	0.250	0.333	0.102	0.633	0.045	0.008	0.289
	N	0.200	1.050	0	0.350	0.350	0.900	—	—			
CHRY010[4]	D	0	0.077	0	0	0	0	0	0.077	0.048	0.005	0.348
	N	0	0.350	0	0	0	0	—	—			
CHRY022[5]	D	0.167	0	0	0	0	0.067	0	0.063	0.668	0.135	0.394
	N	0	0.050	0	0.200	0	0	—	—			
CHRY027[5]	D	0.125	0.038	0	0.040	0.050	0	0.026	0.038	0.182	0.294	0.047
	N	0.100	0.200	0	0.150	0	0.200	—	—			
Curculionidae	D	0.333	0.269	0.120	0.040	0.350	0.400	0.154	0.456	*0.001*	0.093	0.497
	N	0.200	0.050	0.100	0	1.250	0	—	—			
CURC005[6]	D	0	0.038	0	0	0	0	0	0.177	0.481	0.107	0.252
	N	0	0	0	0	0	0	—	—			
CURC011[7]	D	0.167	0	0.040	0	0.150	0	0.103	0	*0.001*	*0.001*	0.278
	N	0.050	0	0	0	0.900	0	—	—			
Lepidoptera[8]	D	0.083	0.154	0.120	0	0	0	0.025	0.089	0.674	0.738	0.501
	N	0	0.050	0.050	0.050	0.100	0	—	—			
Apidae	D	0	0.846	0.440	2.920	0	0.200	0.051	0.633	0.011	*0.001*	*0.001*
	N	0	0.100	0	0.050	0	0	—	—			

[1] No. of species of herbivores per sample; [2] Phlaeothripidae; [3] Psyllidae; [4] Eumolpinae; [5] Galerucinae; [6] Anthonominae; [7] Entiminae; [8] Juveniles only.

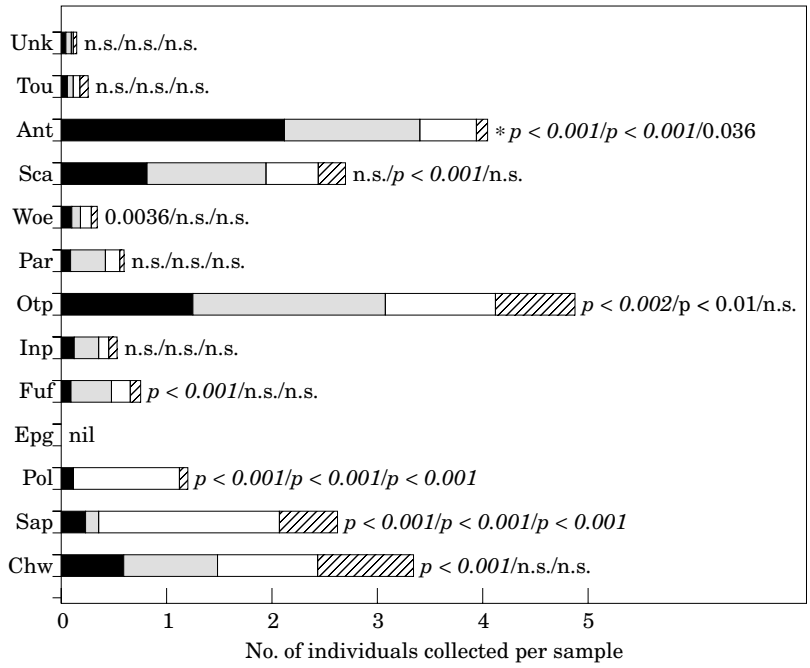

Figure 1. Distribution of arthropod guilds, as indicated by the mean number of individuals collected per beating samples, in the following situations: understorey during the day (■, Und-D); understorey during the night (▤, Und-N); upper canopy during the day (□, Ucn-D); and upper canopy during the night (▨, Ucn-N). Results (probabilities) of Kruskal–Wallis and Mann–Whitney tests testing for the effects of site, stratum and time of day, respectively, are indicated on the left of bars. Italicized probabilities are significant after applying Bonferroni's correction. Abbreviations of arthropod guilds: Unk = unknown, Tou = tourists, Ant = ants, Sca = scavengers, Woe = wood-eaters, Par = parasitoids, Otp = other predators, Inp = insect predators, Fuf = fungal-feeders, Epg = Epiphyte grazers, Pol = pollinators, Sap = sap-suckers and Chw = leaf-chewers. (*) For sake of clarity, values for ants were scaled down by a factor 2.

The first canonical axis accounted for 73% of the variance explained by the CCA, the second 19% and the third 8%. Figure 2B explains 92% of variance in the constrained system and 9% of variance in the real matrix of observations. The best explanatory variables for the formation of axes 1, 2 and 3 were stratum, site and time, respectively (Table 5). The relation between the taxa and the environmental variables was highly significant (Monte Carlo, 199 permutations, $F = 3.80$, $P < 0.001$).

FLIGHT-INTERCEPTION TRAP SAMPLES

During the 16 trapping days at the five sites, the flight interception traps provided 84 samples, including 24 samples each in the understorey, canopy and upper canopy, and 39 and 42 samples obtained during day and night, respectively. In total, 6450 arthropods were collected and, overall, catch rate amounted to 76.8 ± 12.8 (SE) arthropods per sample or about 0.5 arthropods $\times$ 500 cm^{-2} $\times$ hour^{-1}. The arthropod material included 118 families, from which 41, 92 and 76 species of leaf-chewing, sap-sucking and wood-eating insects were sorted. The most abundant or species-rich families included Apidae (pollinators), Cecidomyiidae, Chironomidae, Ceratopogonidae, Sciaridae, Phoridae, Psychodidae (tourists), Formicidae (ants), Scolytinae (wood-eaters), Staphylinidae (scavengers), Cicadellidae (sap-suckers), Silvanidae (fungal-feeders) and Chrysomelidae (leaf-chewers).

Overall, the density activity of arthropods did not differ significantly between sites, strata or time of day (Table 6). The effects of site were significant for some guilds and taxa (Fig. 3 and Table 6), notably for tourists (Cecidomyiidae, Sciaridae), sap-suckers, parasitoids, Apidae and Silvanidae. The effects of stratum were only significant for scavengers and Staphylinidae, which were more active in the understorey than in upper strata. The effects of time were significant for adult Lepidoptera, more active at night, and Apidae, more active during day. Of the seven herbivore species in trap samples that were amenable to statistical analysis, four did not show any significant trend, one was more active in the canopy than the understorey and two showed the reverse trend. However, no species showed any significant response after considering Bonferroni's correction.

The average number of species within trap samples

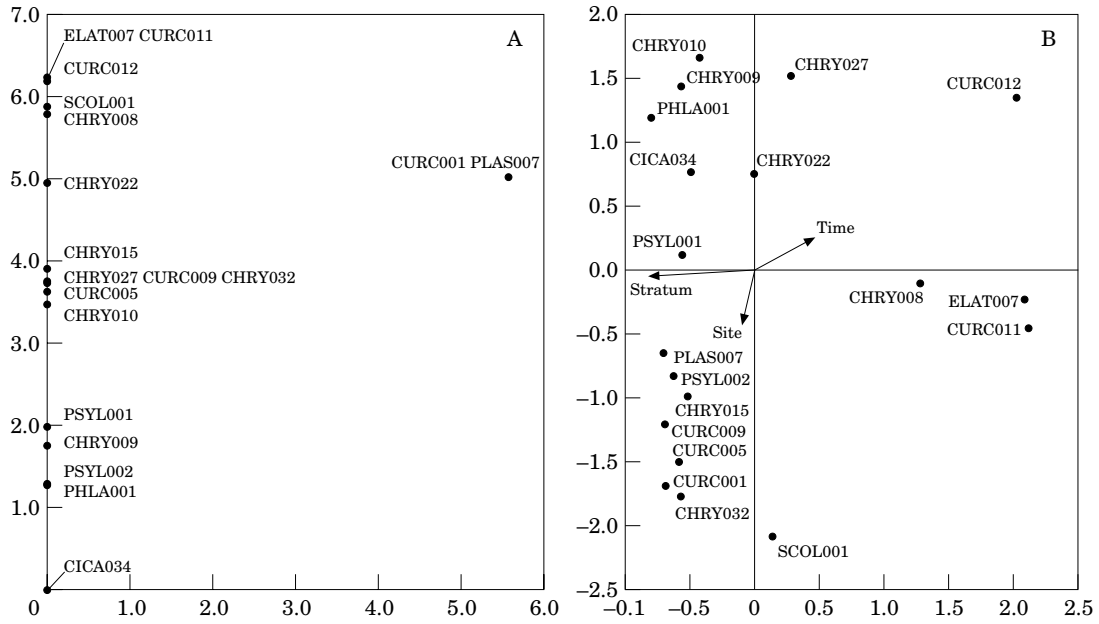

Figure 2. Ordinations of 19 species of herbivores across 363 beating samples. Plots of the taxa into axes 1 and 2 of the (A) DCA and (B) CCA. The 4 first digits of taxa codes refer to their families, as follows: CHRY = Chrysomelidae, CICA = Cicadellidae, CURC = Curculionidae, ELAT = Elateridae, PHLA = Phlaeothripidae, PLAS = Plataspidae, PSYL = Psyllidae, SCOL = Curculionidae Scolytinae.

differed significantly between sites and time of day, more species being present in night-time samples (Table 6). However, these comparisons were not significant after considering Bonferroni's correction. The activity of herbivores did not differ significantly between strata (Kruskal–Wallis = 0.470, $P = 0.790$; Table 7). The outcome of this comparison was similar when considering only the understorey and the upper canopy. Similarly, herbivore activity did not differ significantly between day and night ($U = 721.5$, $P = 0.355$). Trapping in the understorey at night yielded high numbers of species of herbivores, particularly of wood-eaters (Table 7). However, total estimates of species richness (Chao1) were highest for samples obtained from the upper canopy during day and rarefied estimates (Coleman) were highest for those obtained from the canopy during the day. The most uneven community was sampled in the understorey at night, whereas the most even was sampled in the canopy during the day, although differences were slight, as judged by the confidence limits of E (Table 7).

The lowest similarity was between the communities sampled in the understorey during the day and in the upper canopy at night, whereas the highest similarity occurred between the communities in the canopy and in the upper canopy during the day (Table 8). In terms of community structure, the most dissimilar communities were those sampled in the understorey at night and in the canopy during the day (Kolmogorov–Smirnov two sample tests, Table 8). Neither the density activity (Tables 6, 7), species richness of herbivores (Table 7), nor the overlap of the herbivore community

Table 3. Density (mean no. individual per sample), species richness estimators and evenness of communities of insect herbivores collected by beating in the understorey during the day (Und-D), the upper canopy during the day (Ucn-D), the understorey during the night (Und-N) and the upper canopy during the night (Ucn-N). The rarefaction with Coleman's curve is calculated for 50 individuals

Situation	Density ± SE	No. species	No. singletons	Chao1 ± SD	Coleman ± SD	Evenness E (c.l.)
Und-D	0.926 ± 0.141	37	26	93 ± 33	30 ± 3	0.794 (0.868, 0.719)
Ucn-D	2.793 ± 0.374	102	65	219 ± 42	27 ± 4	0.628 (0.667, 0.588)
Und-N	1.116 ± 0.250	26	19	116 ± 77	23 ± 2	0.696 (0.781, 0.610)
Ucn-N	1.440 ± 0.241	25	19	194 ± 187	25 ± 1	0.733 (0.822, 0.644)

Table 4. Community-level comparisons of insect herbivores obtained by beating between the understorey during the day (Und-D), the upper canopy during the day (Ucn-D), the understorey during the night (Und-N) and the upper canopy during the night (Ucn-N): (a) upper matrix similarities of herbivore species as measured by the Morisita–Horn index; (b) upper matrix of Kolmogorov–Smirnov two sample test for differences in the pairs of species-abundance distributions (probability in brackets)

Situation	Ucn-D	Und-N	Ucn-N
(a)			
Und-D	0.146	0.750	0.307
Ucn-D	—	0.044	0.375
Und-N	—	—	0.069
(b)			
Und-D	0.703	0.213	0.242
	(*0.001*)	(0.440)	(0.329)
Ucn-D	—	0.535	0.564
		(*0.001*)	(*0.001*)
Und-N	—	—	0.085
			(0.999)

with similar communities of lower strata (Table 8) increased notably in the upper canopy at night, suggesting that no strong influx of insect herbivores occurred from lower strata at night.

The total inertia of the DCA amounted to 5.776, with Figure 4A representing 23% of the total variance in the system. The CCA grouped the arthropod species in a similar way than the DCA did for the first two axes. Correlations between the scores of the taxa of the DCA and of those of the CCA were significant for the first two axes but not for the third ($r=0.83$, and $r=0.72$ for axis 1 and 2, $P<0.05$ in both cases; $r=0.35$ for axis 3, n.s.). The total sum of eigenvalues in the CCA was 0.835, indicating that the constraining variables explained about 14% of the total variance in the system. The first canonical axis accounted for 53% of the variance explained by the CCA, the second 41% and the third 6%. Figure 4B explains 94% of variance in the constrained system and 14% of variance in the real matrix of observations. The best explanatory variables for the formation of axes 1, 2 and 3 were site, stratum and time, respectively (Table 5). The relation between the taxa and the environmental variables was highly significant (Monte Carlo test, 199 permutations, $F=3.83$, $P<0.001$).

STICKY TRAP SAMPLES

A total of 392 sticky traps was recovered from five sites: 192 and 200 in the upper canopy and in the understorey, respectively, with 204 operating during the day and 188 at night (Table 1). A total of 5242 arthropods was collected and, on average and correcting for longer exposure at sites C and E, 7.60 ± 0.48 arthropods were caught per trap during 3 hours of exposure. This corresponded to catching rates of about 2.5 arthropods $\times$ trap^{-1} $\times$ hour^{-1} or of 1.7 arthropods $\times$ 500 cm^{-2} $\times$ hour^{-1}.

The material included at least 118 arthropod families, the most common being Chrysomelidae (leaf-chewers), Psylloidea, Cicadellidae, Thysanoptera, Membracidae (sap-suckers), Cecidomyiidae, Phoridae, Ceratopogonidae, various acalypterate and calypterate families (tourists), Scelionidae, Platygastridae, Aphelinidae, Braconidae and Encyrtidae (parasitoids). The traps also collected many sweat bees harassing the observers in the canopy during day.

Site effects were important for most taxa and guilds, but not for Chrysomelidae and parasitoids (Fig. 5,

Table 5. Canonical coefficients and intraset correlations for the different environmental variables included in the CCAs for (a) beating samples, (b) flight interception trap samples and (c) sticky trap samples

Variable	Canonical coefficients			Correlation coefficients		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
(a)						
Site	0.232	−0.396	0.176	−0.098	−0.908	0.407
Stratum (height)	−0.829	0.155	0.156	−0.957	−0.103	0.271
Time of day	0.216	0.199	0.303	0.550	0.581	0.601
(b)						
Site	0.626	0.067	−0.0863	0.966	−0.293	−0.257
Stratum (height)	−0.057	0.5646	−0.095	−0.151	0.986	−0.071
Time of day	−0.182	−0.067	−0.224	−0.309	−0.406	−0.860
(c)						
Site	0.139	−0.292	0.175	0.231	−0.743	0.628
Stratum (height)	−0.399	0.157	0.174	−0.797	0.292	0.529
Time of day	0.357	0.268	0.136	0.721	0.584	0.373

Table 6. The most common arthropod taxa collected with flight interception traps, pooled for all sites, and detailed by stratum and time of day. Entries are means of individuals collected per sample. T site, T stratum, T time are results of tests (probabilities) for the effect of site, stratum and time of day (see methods). Italicized probabilities are significant following Bonferroni's correction

Taxa	Understorey		Canopy		Upper Canopy		T site	T stratum	T time
	Day	Night	Day	Night	Day	Night			
All arthropods	144.00	58.93	70.23	43.50	99.38	52.79	0.139	0.459	0.045
Leaf-feeders	2.85	4.14	3.38	2.57	3.15	2.50	*0.001*	0.502	0.851
No. sp. herbivores[1]	3.15	7.07	3.69	4.71	4.69	4.50	0.009	0.539	0.017
Araneae	0.77	0.86	1.00	1.14	0.85	1.14	0.016	0.429	0.496
Dermaptera	0.38	2.57	0	0.14	0.15	0	0.147	0.165	0.236
PSYL001[2]	0	0.14	0.15	0.36	0.08	0.07	0.079	0.156	0.366
Cicadellidae	1.31	1.36	0.85	0.64	0.69	0.93	0.05	0.284	0.893
CICA034	0	0.14	0.08	0.14	0.15	0.36	0.596	0.625	0.096
CICA053	0.54	0.43	0	0	0.08	0	0.158	0.020	0.336
Staphylinidae	3.00	4.79	0.69	0.50	0.23	0.57	0.117	*0.001*	0.777
Silvanidae	0.54	1.14	0.46	1.50	0.15	0.29	*0.001*	0.163	0.051
MELA002[3]	0	0.07	0.15	0.07	0.23	0.29	0.027	0.171	0.914
Chrysomelidae	0.31	0.57	0.38	0.14	0.77	0.50	0.260	0.375	0.953
ANTB004[4]	0	1.07	0	0.14	0	0	0.810	0.023	0.068
Scolytinae	1.69	3.21	2.54	2.36	4.31	2.21	0.048	0.666	0.876
SCOL001	1.08	2.14	1.08	1.21	2.15	0.93	0.005	0.613	0.909
SCOL020	0	0	0.69	0.21	0.85	0.29	0.327	0.006	0.159
Cecidomyiidae	9.38	8.71	3.77	9.00	3.54	10.36	*0.001*	0.294	0.289
Sciaridae	0.85	0.79	0.77	3.00	0.38	1.07	*0.001*	0.229	0.290
Ceratopogonidae	2.54	1.93	0.54	1.07	0.15	1.14	0.035	0.156	0.239
Chironomidae	1.54	0.50	1.08	2.14	0.85	1.00	0.025	0.397	0.791
Phoridae	2.69	1.86	0.62	0.71	0.23	0.43	0.101	0.058	0.716
Lepidoptera[5]	0.46	3.79	0.62	1.79	0.38	1.93	0.868	0.479	*0.001*
Apidae	101.69	6.21	42.85	7.21	73.08	18.07	*0.001*	0.871	*0.001*

[1] No. of species of herbivores per sample; [2] Psyllidae; [3] Melandryidae; [4] Anthribidae; [5] Adults.

Table 9). In particular, Meliponinae were prominent at site B. Most taxa and guilds showed a significant preference, being more active in the upper canopy than in the understorey (Fig. 5, Table 9). Removing Meliponinae did not alter these trends (Table 9). No taxa were significantly more active in the understorey than in the upper canopy. However, Cicadellidae, Scelionidae, Formicidae, Nematocera and Curculionidae were not significantly more active within either forest strata (Fig. 9, Table 9). Twice as many Chrysomelidae and sap-sucking insects (mostly Psylloidea, Thysanoptera and Membracidae) were collected in the upper canopy than in the understorey (Fig. 5, Table 9). During the day, Brachycera, Meliponinae, Platygastridae, Scelionidae were also well collected by the traps set up in the canopy. At night, arthropod catches were also significantly higher in the upper canopy than in the understorey (Mann–Whitney $U=3399.0$, $P<0.01$).

All arthropods, as well as most taxa and guilds, were more abundant during the day than at night (Table 9). Many Nematocera (particularly Cecidomyiidae) and ants were collected at night, but these differences were not significant (Table 9). Pollinators, parasitoids and insect predators were notably less active nocturnally than diurnally (Fig. 5). The proportion of tourists in the samples also increased at night (Fig. 5). Insect herbivores were more abundant in the upper canopy during the day than at night (Mann–Whitney test, $U=8775.0$, $P<0.001$). Catches of herbivores did not increase notably in the upper canopy at night, suggesting no strong influx of herbivores from lower strata at night (Table 9).

The total inertia of the DCA amounted to 4.049, with Figure 6A representing 29% of the total variance in the system. The CCA grouped the arthropod taxa in a similar way than the DCA did for the first two axes. Correlations between the scores of the taxa of the DCA and of those of the CCA were significant for the first two axes but not for the third ($r=0.82$, and $r=0.65$ for axis 1 and 2, $P<0.05$ in both cases; $r=0.43$ for axis 3, n.s.). The total sum of eigenvalues in the CCA

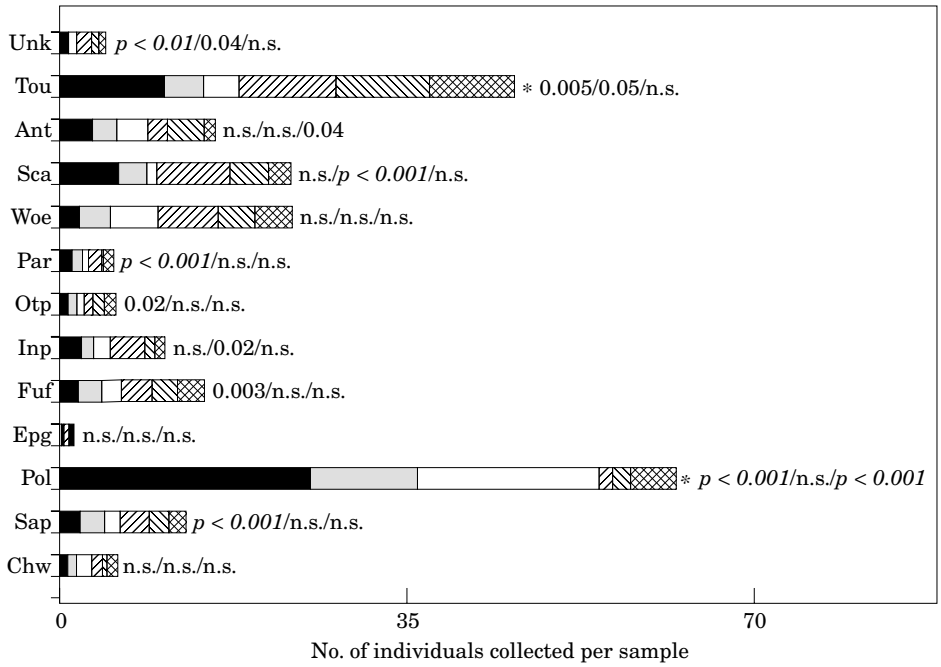

Figure 3. Distribution of arthropod guilds, as indicated by the mean number of individuals collected per flight interception trap samples, in the following situations: understorey during the day (■, Und-D); canopy during the day (▤, Can-D); upper canopy during the day (□, Ucn-D); understorey during the night (▨, Und-N); canopy during the night (▧, Can-N) and upper canopy during the night (▩, Ucn-N). Results (probabilities) of Kruskal–Wallis and Mann–Whitney tests testing for the effects of site, stratum and time of day, respectively, are indicated on the left of bars. Italicized probabilities are significant after applying Bonferroni's correction. Abbreviations of arthropod guilds as in Fig. 1. (*) For sake of clarity, values for pollinators and tourists were scaled down by a factor 4 and 2, respectively.

Table 7. Density (mean no. individual per sample), species richness estimators and evenness of communities of insect herbivores collected by flight interception traps in the understorey, canopy and upper canopy, during day and night. The rarefaction with Coleman's curve is calculated for 50 individuals. Abbreviations as per Table 3, plus canopy during the day (Can-D) and during the night (Can-N)

Situation	Density ± SE	No. species	No. singletons	Chao1 ± SD	Coleman ± SD	Evenness E (c.l.)
Und-D	4.846 ± 0.853	32	28	424 ± 419	30 ± 1	0.772 (0.854, 0.690)
Und-N	10.571 ± 1.847	64	51	498 ± 279	137 ± 91	0.689 (0.744, 0.634)
Can-D	6.538 ± 1.071	40	34	185 ± 88	208 ± 147	0.794 (0.868, 0.721)
Can-N	6.143 ± 1.113	43	32	145 ± 59	128 ± 78	0.781 (0.851, 0.711)
Ucn-D	8.077 ± 1.766	47	39	807 ± 799	182 ± 151	0.703 (0.769, 0.638)
Ucn-N	6.000 ± 0.949	44	33	180 ± 84	120 ± 67	0.783 (0.853, 0.714)

was 0.604, indicating that the constraining variables explained about 15% of the total variance in the system. The first canonical axis accounted for 60% of the variance explained by the CCA, the second 29% and the third 11%. Figure 6B explains 89% of variance in the constrained system and 13% of variance in the real matrix of observations. The best explanatory variables for the formation of axes 1 and 2 were stratum and site, whereas site again best explained the third axis (Table 5). The relationship between the taxa and the environmental variables was highly significant (Monte Carlo test, 199 permutations, $F = 20.79$, $P < 0.001$).

DIVERSITY AND ABUNDANCE OF *AGRILUS* IN THE UNDERSTOREY AND UPPER CANOPY AT LA MAKANDÉ

Specimens of *Agrilus* were collected by beating, flight interception, sticky traps, hand collecting, window, yellow pan and Malaise traps. Since the last four methods were only used in the understorey, sampling

Table 8. Community-level comparisons of insect herbivores collected with flight interception traps between the understorey, canopy and upper canopy during day and night. Abbreviations as per Tables 3 and 7. (a) Upper matrix of similarities of herbivore species as measured by the Morisita–Horn index; (b) upper matrix of Kolmogorov–Smirnov two sample test for differences in the pairs of species-abundance distributions (probability in brackets)

Situation	Und-N	Can-D	Can-N	Ucn-D	Ucn-N
(a)					
Und-D	0.748	0.649	0.700	0.758	0.586
Und-N	—	0.630	0.742	0.699	0.601
Can-D	—	—	0.780	0.870	0.724
Can-N	—	—	—	0.794	0.755
Ucn-D	—	—	—	—	0.752
Ucn-N	—	—	—	—	—
(b)					
Und-D	0.281	0.062	0.219	0.125	0.219
	(0.130)	(0.999)	(0.373)	(0.937)	(0.373)
Und-N	—	0.375	0.328	0.266	0.313
		(*0.001*)	(*0.002*)	(*0.022*)	(*0.004*)
Can-D	—	—	0.078	0.109	0.078
			(0.989)	(0.839)	(0.989)
Can-N	—	—	—	0.062	0.047
				(0.999)	(1.000)
Ucn-D	—	—	—	—	0.047
					(1.000)
Ucn-N	—	—	—	—	—

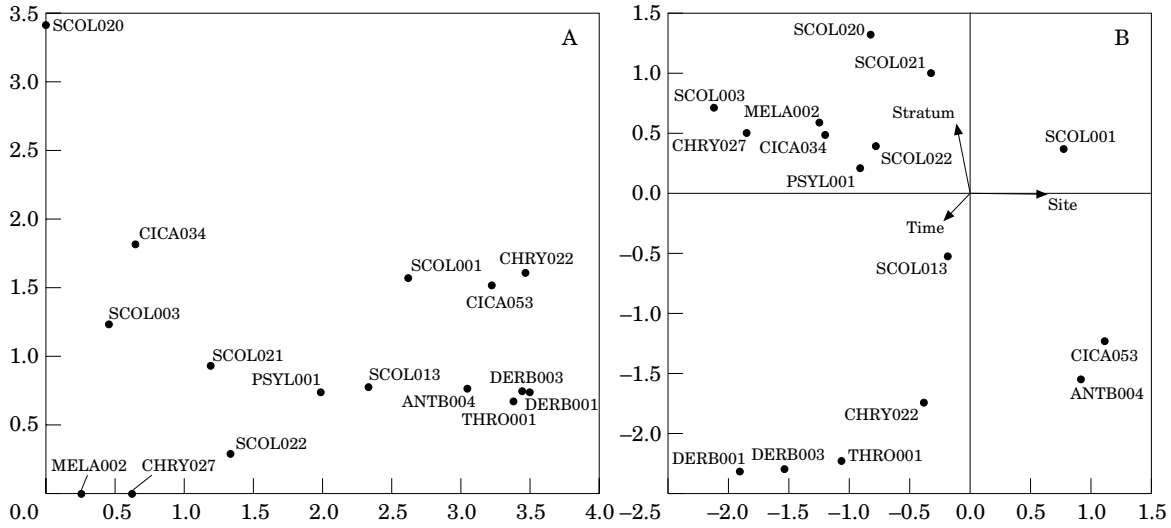

Figure 4. Ordinations of 16 species of herbivores across 84 flight interception trap samples. Plots of the taxa into axes 1 and 2 of the (A) DCA and (B) CCA. The four first digits of taxa codes refer to their families, as follows: ANTB = Anthribidae, CHRY = Chrysomelidae, CICA = Cicadellidae, DERB = Derbidae, MELA = Melandryidae, PSYL = Psyllidae, SCOL = Curculionidae Scolytinae, THRO = Throscidae.

effort was much higher in this stratum than in the upper canopy. In total, 68 specimens were collected, representing 26 species (Table 10), all new for Gabon (previously only seven species were known from this country), including 12 new species, which will be described elsewhere (Curletti, 2000). Twelve species were collected only from the upper canopy, 11 only from the understorey, and three species were collected from

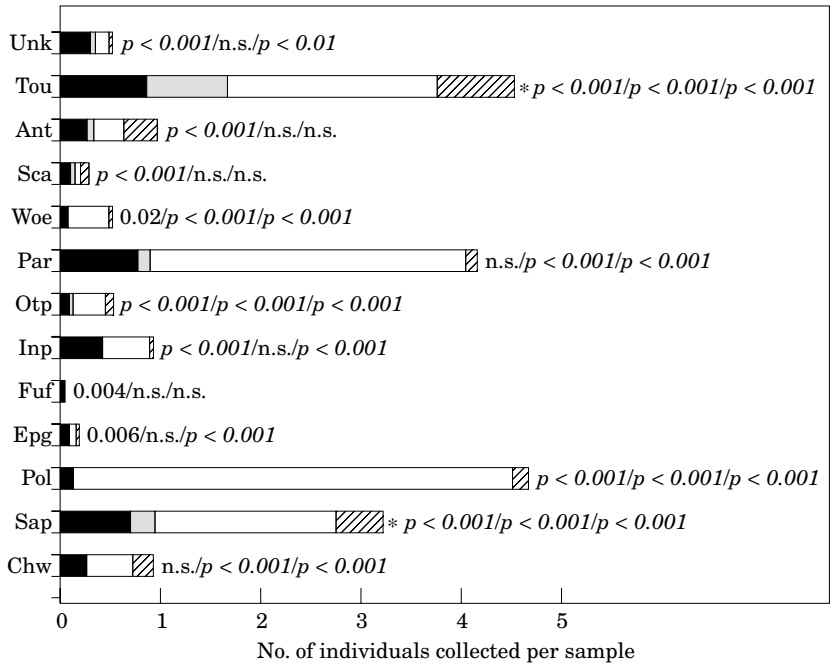

Figure 5. Distribution of arthropod guilds, as indicated by the mean number of individuals collected per sticky trap samples, in the following situations: understorey during the day (■, Und-D); understorey during the night (▤, Und-N); upper canopy during the day (□, Ucn-D); and upper canopy during the night (▨, Ucn-N). Results (probabilities) of Kruskal–Wallis and Mann–Whitney tests testing for the effects of site, stratum and time of day, respectively, are indicated on the left of bars. Italicized probabilities are significant after applying Bonferroni's correction. Abbreviations of arthropod guilds as in Fig. 1. (*) For sake of clarity, values for pollinators and tourists were scaled down by a factor 2.

both strata, suggesting a low faunal overlap between the two strata. Despite the much higher sampling effort in the understorey, more specimens and species were collected from the upper canopy, suggesting that the latter may support more species of *Agrilus* at La Makandé (upper canopy: Chao1 $\pm$ SD = 75.5 $\pm$ 71.1; understorey: 18.5 $\pm$ 4.8).

DISCUSSION

METHODOLOGICAL REMARKS

As anticipated, the fauna collected with each of the three sampling methods was rather different. Beating reflected the density of sedentary arthropods, particularly many species of herbivores, whereas flight interception and sticky traps reflected the density activity of airborne arthropods of larger and smaller body weight, respectively (e.g. Robinson & Robinson, 1973; Fürst & Duelli, 1988). Beating may not be as discriminatory as the two other methods to examine differences in diel activity of arthropods: species may well be present at night on the foliage, but not being active. These important distinctions, as well as other factors discussed below, should be kept in mind when examining the results of the present study.

The present estimates of 6.8 arthropods per 0.32 m^2 of leaf area (or 21 arthropods per m^2 of leaf area) obtained with beating are within the range of values reported for rainforests, and close to data reported from a lowland rainforest in Cameroon (maximum 28 arthropods per m^2 of leaf area: Basset, 2001; Basset *et al.*, 1992). Similarly, the present estimates of 1.7 arthropods $\times$ 500 $cm^{-2} \times hour^{-1}$ collected with sticky traps lie within the range of values reported from rainforests (e.g. Robinson & Robinson, 1973; Sutton & Hudson, 1980; Shelly, 1988). However, estimates of 0.5 arthropods $\times$ 500 $cm^{-2} \times hour^{-1}$ collected with flight interception traps are lower by a factor of about 3 than estimates obtained with sticky traps. This confirms that sticky traps are more efficient at collecting numerous and small airborne arthropods, but also that their yellow colour may further enhance their efficiency, in comparison with passive flight interception traps.

The reflectance of the sticky traps and their efficiency may be higher during the day than at night and higher in the canopy than in the understorey. The yellow colour is well known to be a mild attractant for certain Thysanoptera, Homoptera, Diptera and Hymenoptera (e.g. Wolf, Gaspar & Verstraeten, 1968). Yellow appears to be a better attractant for non-grass-feeding herbi-

Table 9. The most common arthropod taxa and guilds collected with sticky traps, detailed per site, stratum (Und = understorey, Ucn = upper canopy) and time of day (D = day, N = night). Entries are means of individuals collected per sample. T site, T stratum, T time are results of tests (probabilities) for the effect of site, stratum and time of day (see methods). Italicized probabilities are significant following Bonferroni's correction

Taxa/Guild		Site A		Site B		Site C		Site D		Site E		T site	T stratum	T time
	D/N	Und	Ucn	Und	Ucn	Und	Ucn	Und	Ucn	Und	Ucn			
All arthropods	D	4.71	22.38	6.81	27.65	4.61	8.78	5.43	14.25	5.67	14.61	*0.001*	*0.001*	*0.001*
	N	4.33	3.95	3.38	3.63	2.02	4.08	0	2.05	2.74	3.61			
All arthropods[1]	D	4.71	21.48	6.33	9.15	4.61	8.65	5.43	12.20	5.67	14.49	*0.001*	*0.001*	*0.001*
	N	4.33	3.90	3.33	3.13	2.02	4.02	0	2.00	2.74	3.56			
Leaf-feeders	D	1.57	8.24	2.24	1.05	1.71	1.91	1.48	3.20	1.20	5.98	*0.001*	*0.001*	*0.001*
	N	0.05	1.30	0.14	0.75	1.27	1.44	0	0.95	1.28	1.01			
Araneae	D	0	0.53	0.19	0.45	0.19	0.17	0	0.20	0.03	0.29	*0.001*	*0.001*	*0.001*
	N	0	0.10	0.10	0.13	0.02	0.01	0	0.10	0.06	0.05			
Thysanoptera	D	0	3.76	0.24	0.25	0.90	0.68	0	0.15	0.12	1.08	*0.001*	*0.001*	*0.001*
	N	0	0.10	0	0.06	0	0.04	0	0.05	0.04	0.04			
Psylloidea	D	0	2.62	0.05	0.15	0.01	0.36	0.05	2.20	0.24	2.39	*0.001*	*0.001*	*0.001*
	N	0	0.80	0.05	0.06	0	0.51	0	0.19	0.04	0.35			
Cicadellidae	D	1.10	0.24	1.71	0.15	0.39	0.17	0.57	0.20	0.45	1.02	*0.001*	0.069	*0.001*
	N	0	0.20	0	0.19	1.23	0.58	0	0.43	1.06	0.43			
Membracidae	D	0.10	0.14	0	0.15	0.17	0.35	0.38	0.10	0.02	0.87	*0.001*	*0.001*	*0.001*
	N	0	0	0	0	0	0.14	0	0	0	0.09			
Chrysomelidae	D	0.33	1.29	0.19	0.20	0.13	0.16	0.24	0.35	0.24	0.27	0.141	*0.001*	*0.001*
	N	0	0.15	0	0.38	0.04	0.11	0	0.14	0.02	0.07			
Curculionidae	D	0	0	0.05	0.05	0.63	0.08	0	0	0.74	0.20	*0.001*	0.164	*0.001*
	N	0	0	0	0	0.02	0	0	0	0.01	0.01			
Nematocera	D	0.29	0.19	0.76	1.85	0.13	1.69	1.62	0.65	0.27	1.04	*0.001*	0.003	0.002
	N	3.76	2.05	1.86	1.43	0.12	0.97	0	0.65	0.68	0.88			
Brachycera	D	1.00	3.57	1.14	1.75	0.69	1.84	0.71	3.70	1.73	4.26	*0.001*	*0.001*	*0.001*
	N	0.10	0.15	0.71	0.19	0.12	0.41	0	0.10	0.24	0.59			
Scelionidae	D	0.09	3.29	0	0	0.03	0.05	0.10	0.10	0.11	0.18	*0.001*	0.002	*0.001*
	N	0	0	0	0	0	0.01	0	0	0.04	0.03			
Apidae	D	0	0.95	0.48	18.50	0	0.14	0	2.05	0	0.14	*0.001*	*0.001*	*0.001*
	N	0	0.05	0.05	0.50	0	0.06	0	0.05	0	0.04			

[1] Without Meliponinae.

vores, rather than red, brown or black which is preferred by wood-eaters (Kirk, 1984). However, sticky traps may also be more efficient for insect herbivores in the understorey. There, insects may be more sensitive to small amounts of light, in comparison with near-saturation of light in the upper canopy. Since many insect herbivores are efficient at locating and using the smallest gaps in the understorey (e.g. Charles, 1998), this warrants further investigation.

Other factors may also complicate the interpretation of arthropod density activity as measured by flight interception and sticky traps. Stronger winds in the upper canopy may increase catches of airborne insects in comparison with more still air in the understorey, particularly for passive insect fliers (e.g. Sutton & Hudson, 1980). Further, increases in air temperature may also improve trap catches. For example, on 25 January 1999 at site A, at 15:00, the air temperature was 29.9°C in the understorey and 40.0°C in the upper canopy. In these conditions, arthropods may well be more active in the upper canopy and trap catches may increase (e.g. Basset, 1991).

The distribution of spatial and temporal replicates obtained with the three sampling methods also requires attention. Although the true degree of freedom cannot be assessed for these samples, the maximum number of spatial replicates available was 363,204 and 15 (five sites × three traps) for beating, sticky and flight

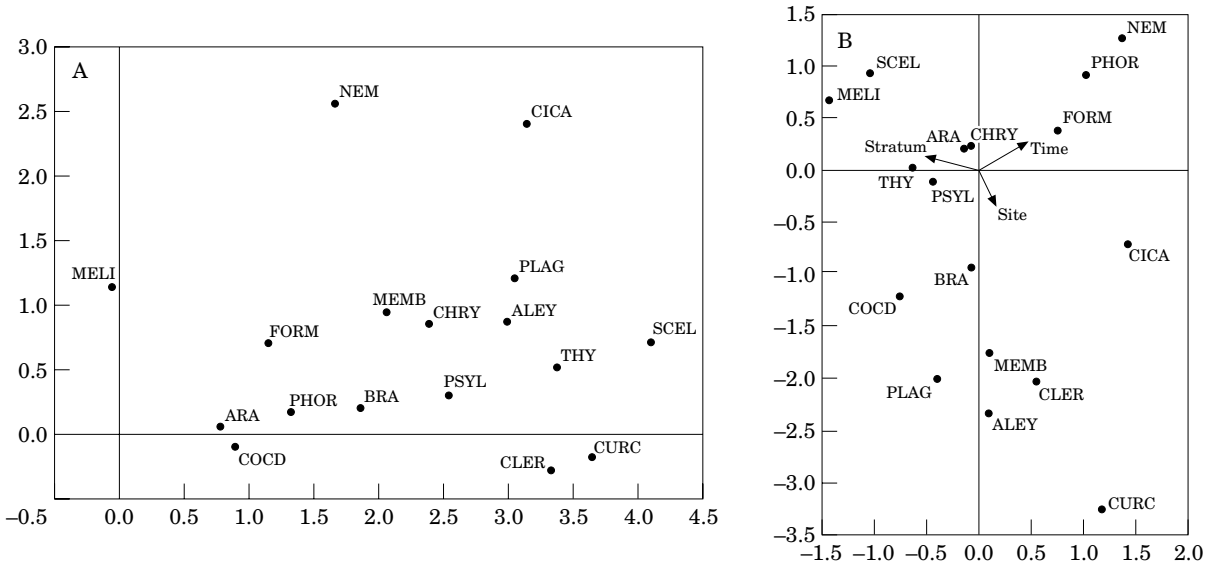

Figure 6. Ordinations of 17 higher insect taxa across 392 sticky traps. Plots of the taxa into axes 1 and 2 of the (A) DCA and (B) CCA. Taxa codes: ALEY = Aleyrodidae, ARA = Araneae, BRA = Brachycera, CHRY = Chrysomelidae, CLER = Cleridae, CICA = Cicadellidae, COCD = Coccinellidae, CURC = Curculionidae, FORM = Formicidae, MELI = Meliponinae, MEMB = Membracidae, NEM = Nematocera, PHOR = Phoridae, PLAG = Platygastridae, PSYL = Psylloidea, SCEL = Scelionidae, THY = Thysanoptera.

interception trap samples, respectively. Conversely, temporal replicates are lacking for beating data, represent 6 hours for sticky traps, and about 72 hours for flight interception traps.

Overall, beating data may indicate real differences between the spatial occurrence of sedentary taxa, but may be less suitable for temporal analyses. Flight interception trap data reflect the flight activity of larger arthropods and may be suitable for temporal analyses and less so for those spatial. Sticky trap data reflect the flight activity of smaller arthropods within certain areas at certain times, perhaps increasing the magnitude of differences observed, although to which extent is not clear.

SPATIAL HETEROGENEITY IN RAINFORESTS

Site effects were significant for many arthropod taxa and guilds. Sticky traps showed these effects best, followed by beating and flight interception traps. Site effects represented 19, 41 and 29% of the variance explained by environmental variables for beating, flight interception and sticky trap data, respectively. In absence of replication, site effects could mislead the overall interpretation of the results. For example, the density of leaf-feeders as measured by beating was not higher in the upper canopy than in the understorey at site B, an observation differing from the overall results. Further, the presence of arboreal nests of Meliponinae in the vicinity of site B greatly increased the catches of this taxon in sticky and flight interception traps positioned at this site, particularly in the upper canopy where they might also have been attracted to perspiring observers.

Site effects represent the accumulative effects of many factors, including canopy structure (e.g. Koike *et al.*, 1998), the presence of particular host-plants in particular phenological states, micro climatic conditions constraining the flight or distribution of arthropods, arboreal ant mosaics (e.g. Dejean *et al.*, 1999), etc. They are considerable for insect herbivores in highly heterogeneous environments, such as tropical rainforests (e.g. DeVries, Murray & Lande, 1997; Basset, 2000; Willott, 1999). However, in the present study, the categorical variable accounting for site effects was too crude to account for a large part of the total variance in arthropod distribution. The environmental variables included in the ordinations, site, stratum and time, accounted only for between 10 and 15% of the total variance, depending on the sampling method. This confirms that arthropod distribution in rainforests is complex and each taxon may favor optimal and specific conditions, making any generalization difficult, particularly in absence of spatial replicates.

This emphasizes the need for spatial replicates, but also the problems of obtaining them in the upper canopy. Fixed structures such as canopy cranes (e.g. Wright & Colley, 1994) may generate interesting data with regard to temporal replication, but they cannot

Table 10. Species of *Agrilus* and number of individuals collected in the understorey and upper canopy at La Makandé, during January–March 1999

Species	Understorey	Upper canopy
Agrilus (Agrilus) isabellae Obenberger, 1921	0	1
Agrilus (Agrilus) n. sp. *6*	0	5
Agrilus (Agrilus) n. sp. *8*	0	1
Agrilus (Agrilus) n. sp. *10*	3	1
Agrilus (Bubagrilus) n. sp. *2*	0	2
Agrilus (Melagrilus) africanus Kerremans, 1899	1	1
Agrilus (Melagrilus) escalerai Obenberger, 1921	2	0
Agrilus (Melagrilus) teocchii Curletti, 1999	2	0
Agrilus (Nigritius) torpedo Curletti, 1995	1	0
Agrilus (Nigritius) n. sp. *1*	0	1
Agrilus (Robertius) aberlenci Curletti, 1997	1	0
Agrilus (Robertius) gibbosus Kerremans, 1899	7	0
Agrilus (Robertius) marcens Obenberger, 1935	2	13
Agrilus (Robertius) motoinus Obenberger, 1935	4	0
Agrilus (Robertius) mundanus Obenberger, 1935	3	0
Agrilus (Robertius) pelops Obenberger, 1935	2	0
Agrilus (Robertius) zebratus Curletti, 1999	0	6
Agrilus (Robertius) n. sp. *3*	0	1
Agrilus (Robertius) n. sp. *4*	0	1
Agrilus (Robertius) n. sp. *5*	0	1
Agrilus (Robertius) n. sp. *7*	1	0
Agrilus (Robertius) n. sp. *9*	0	1
Agrilus (Robertius) n. sp. *11*	1	0
Agrilus (Robertius) n. sp. *12*	1	0
Species indet. 1, damaged	0	1
Species indet. 2, damaged	0	1
TOTAL	31	37

be used easily to study the important aspects of spatial variability of arthropod distribution in highly heterogeneous rainforests. Mobile infrastructures, such as those used in the present study, offer different advantages and should be operated in combination with fixed structures.

THE ABUNDANCE AND ACTIVITY OF ARTHROPODS IN THE UNDERSTOREY AND UPPER CANOPY

The data producing the best spatial resolution—beating and sticky traps—are suitable for comparing arthropod abundance, species richness and activity between the understorey and the upper canopy. Overall density was not significantly higher in the upper canopy than in the understorey, but activity was, by a factor of 2.7. Both the density and activity of leaf-feeders were significantly higher in the upper canopy than in the understorey, by a factor of 2.5. Differences in arthropod density between the two strata may have been actually higher, since understorey samples were on average 28% larger than those in the upper canopy. The highest densities of insect herbivores encountered were in the upper canopy during the day, where they were about three times higher than in the understorey.

These results are in agreement with the study of Sutton & Hudson (1980) in Zaïre, who showed that the density activity of airborne insects collected with sticky and light traps at two sites was higher in the upper canopy than in the understorey. Similar results were obtained with similar traps in Brunei, Panama, Papua New Guinea, Sulawesi (review in Sutton, 1989), Sarawak (Kato *et al.*, 1995) and Kalimantan (Koike *et al.*, 1998). A study performed with a canopy raft in Cameroon further showed that arthropod densities were three times as high in the upper canopy than in the understorey during the day (Basset *et al.*, 1992). However, one important difference is evident between the two studies performed with the canopy raft in Africa. Whereas Formicidae were notably more abundant in the upper canopy than in the understorey in Cameroon, at La Makandé their abundance was actually higher in the latter stratum and their activity was not significantly different between the two strata.

This was confirmed by an independent study of ant taxa there (A. Dejean & B. Corbara, pers. comm.). At the four Cameroon sites, many herbivores in the upper canopy included ant-attended Coccoidea, which were rare at the six sites studied in Gabon. In contrast, many more Psylloidea were present in the samples from Gabon than from Cameroon.

In particular, the following guilds and taxa were either more abundant or active in the upper canopy than in the understorey: sap-suckers (Thysanoptera, Psylloidea, Membracidae), pollinators (Apidae), chewers (Chrysomelidae), tourists (Brachycera) and parasitoids (Scelionidae). However, other taxa and guilds were either more abundant or active in the understorey: scavengers (Isopoda, Staphylinidae), ants and Opiliones.

Beating data also indicated that a diverse fauna of herbivores, particularly of leaf-feeders, were present in the upper canopy and were twice as diverse than in the understorey. Although flight interception trap data were dominated by wood-eaters, which did not tend to discriminate overall between forest strata, they also showed this trend (Chao1 and Coleman estimators). The ordinations confirmed that, for beating and sticky trap data, stratum effects primed over site and time effects, explaining 73 and 60% of the explained variance, respectively. This suggests that the high abundance and activity of insect herbivores in the upper canopy may be independent from ant abundance and may rather result from the high supply and variety of food resources in this stratum.

Sixteen herbivore species were common enough to be amenable to statistical analysis. Despite low sample size, six species showed a significant preference for the upper canopy and three for the understorey, before applying Bonferroni's correction. After the correction, two species still showed a preference for the upper canopy and one for the understorey. Test results obtained with the Bonferroni correction depend not only on data relevant to the question, but also on irrelevant information such as the number of other questions studied (Stewart-Oaten, 1995). Thus, we leave to the reader to decide whether it is sound to use rigid significance levels for multiple comparisons; the biological reality exists between these two extreme results. In spite of this, the data suggest that some herbivore species were more abundant or active in either stratum, a view confirmed by the taxonomical study of the *Agrilus* material collected at La Makandé. Other arthropod taxa have been reported to show vertical stratification in rainforests, including mosquitoes in Uganda (Corbet, 1961), Scolytinae in Ivory Coast (Cachan, 1964), coprophagous Scarabaeidae in Gabon (Walter, 1983), Coleoptera in Sulawesi (Hammond, 1990; Hammond, Stork & Brendell, 1997), fruit-feeding Nymphalidae in Ecuador (DeVries *et al.*, 1997), Acridoidea in the Amazon (Amedegnato, 1997), Collembola and Acari in Australia (Rodgers & Kitching, 1998; Walter *et al.*, 1998) and arthropods in Kalimantan (Koike *et al.*, 1998). In particular, the studies of Amedegnato (1997) and Rodgers & Kitching (1998) also appear to show distinct faunal assemblages between the upper canopy and the canopy.

All but two species of *Agrilus* that were previously known to science were collected in the understorey. One of the known species also collected in the upper canopy, *Agrilus marcens*, appears to be locally the most common species of *Agrilus*. Interestingly, locally the most common species of Scolytinae and Chrysomelidae (SCOL001, near *Xyleborus* sp., and CHRY027, Galerucinae, respectively) also showed no preference for forest strata and were active both during the day and at night. These 'indifferent' species, as well as species engaged into mating swarms and dispersal, may render the boundaries between communities of the upper canopy and understorey less distinct (Sutton, 1989). However, the ecology of the 'indifferent' species and the causes leading to their local dominance would be fascinating to study.

In sum, there is little doubt that the fauna foraging in the understorey and upper canopy is rather different. The most dissimilar herbivore communities appear to be those exploiting the understorey at night and the upper canopy during the day (Table 4). Further, the fauna of the upper canopy appears to be very poorly known.

DIEL ACTIVITY OF ARTHROPODS IN RAINFORESTS

The sticky and flight interception trap provide the basis for discussion of arthropod diel activity. The former indicated that activity was much higher during the day than at night, but the significance of this observation for the latter was only marginal. Since other studies with flight interception or Malaise traps (Hammond, 1990; Springate & Basset, 1996) have also revealed significantly higher diurnal than nocturnal activity in tropical rainforests, sticky trap data may well reflect a biological reality, although the magnitude in the differences observed may be inflated.

In particular, pollinators (Apidae), sap-suckers (Thysanoptera, Psylloidea, Membracidae), chewers (Chrysomelidae), parasitoids (Scelionidae), tourists (Brachycera) and insect predators were more active during the day than at night. In contrast, adult Lepidoptera showed the reverse trend. However, for herbivore communities, the effects of time were of lesser importance as compared to those of stratum and site and represented only 9% and 6% of the explained variance in beating and flight interception trap data. It was not possible to detect the same effects where higher taxa were concerned.

Of herbivore assemblages collected in the understorey, canopy and upper canopy, the most similar assemblages between day and night appeared to be those occurring in the canopy, although differences were slight. Beating data also suggested that faunal turnover between day and night was very high in the upper canopy (Morisita–Horn index of 0.375, Table 4), in comparison with that in the understorey (0.750). Communities of insect herbivores in the upper canopy during day were species-rich, but unevenly distributed with a few species dominating the communities there. This suggests that the magnitude of changes in the microclimatic conditions between day and night in the upper canopy may be more severe than in the understorey, and that only a well-adapted fauna may cope with these changes. It is well known that many insect taxa of tropical rainforests show behavioural and physiological adaptations which result in thermal guilds, such as 'light-seeking' or 'shade-seeking' insects (e.g. Shelly, 1985). Further, Roubik (1993) argued that canopy-level pollination may require specific physiological traits among bees that forage persistently in this stratum.

CONCLUSIONS

The present study represents one of the first attempts to factor out the effects of site, stratum and time in the distribution of arthropods in a tropical rainforest. Further, the selective data obtained from the upper canopy appear to be the first data set replicated between several canopy sites (six) and sampling methods (three). The data stress the importance of replication between canopy sites and the appreciably different arthropod fauna that forages in the understorey and upper canopy, where microclimatic conditions appear to be very different for arthropods. In contrast, stratification of insect herbivores has rarely been observed in temperate forests (e.g. Fowler, 1985; Schowalter & Ganio, 1998; Le Corff & Marquis, 1999), presumably due to the less severe vertical changes in microclimatic and biotic gradients there.

With reference to questions 1–3 posed in the Introduction, the results of the three sampling methods suggest that decrease in the abundance, activity and species richness from day to night may be comparatively higher in the upper canopy than in the understorey. Since few compensatory effects occur, the data do not indicate a strong influx of insect herbivores from lower foliage to the upper canopy at night. This suggests that insect herbivores of the upper canopy may be resident and well adapted to environmental conditions there. Although not well suited for spatial analysis, the flight interception trap data suggest that the herbivore fauna of the upper canopy is more similar to that in the canopy than that in the understorey, so that the principal faunal exchanges may occur between the canopy and upper canopy.

Since faunal stratification in tropical rainforests may depend on slope (e.g. Sutton, 1983), it may be optimum and may lead to a diverse fauna in the upper canopy of closed and wet lowland forests (in contrast with montane forests), which also represent the most endangered type of rainforest. Whether the fauna collected in the upper canopy is very specialized and whether it may be different from that foraging a few metres below in the canopy constitutes the next problem to explore. Since the upper canopy may well be distinguished from the canopy only in closed and undisturbed rainforests, the implications for the conservation of tropical rainforest arthropods may also be important.

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REFERENCES

Amedegnato C. 1997. Diversity of an Amazonian canopy grasshopper community in relation to resource partitioning

and phylogeny. In: Stork NE, Adis J, Didham RK, eds. *Canopy Arthropods*. London: Chapman & Hall, 281–319.

Barker MG. 1996. Vertical profiles in a Brunei rain forest: I. Microclimate associated with a canopy tree. *Journal of Tropical Forest Science* **8:** 505–519.

Basset Y. 1991. The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecological Entomology* **16:** 265–278.

Basset Y. 2000. Insect herbivores foraging on seedlings in an unlogged rain forest in Guyana: spatial and temporal considerations. *Studies on Neotropical Fauna and Environment* **35:** 115–129.

Basset Y. 2001. Invertebrates in the canopy of tropical rain forests: how much do we really know? *Plant Ecology in press*.

Basset Y, Aberlenc H-P, Delvare G. 1992. Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology* **17:** 310–318.

Basset Y, Charles EC, Novotny V. 1999. Insect herbivores on parent trees and conspecific seedlings in a Guyana rain forest. *Selbyana* **20:** 146–158.

Basset Y, Springate ND, Aberlenc H-P, Delvare G. 1997. A review of methods for sampling arthropods in tree canopies. In: Stork NE, Adis J, Didham RK, eds. *Canopy Arthropods*. London: Chapman & Hall, 27–52.

Bell AD, Bell A, Dines TD. 1999. Branch construction and bud defence status at the canopy surface of a West African rainforest. *Biological Journal of the Linnean Society* **66:** 481–499.

Blanc P. 1990. Bioclimatologie comparée de la canopée et du sous-bois. In: Hallé F, Blanc P, eds. *Biologie d'une canopée de forêt équatoriale. Rapport de Mission Radeau des Cimes Octobre–Novembre 1989, Petit Saut – Guyane Française*. Montpellier/Paris: Montpellier II et CNRS-Paris VI, 42–43.

Bongers F, Popma J. 1988. Is exposure-related variation in leaf characteristics of tropical rain forest species adaptative? In: Werger MJA, van der Aart PJM, During JH, Verhoeven JTA, eds. *Plant Form and Vegetation Structure. Adaptation, Plasticity and Relation to Herbivory*. The Hague: SPB Academic Publishing bv, 191–200.

Borcard D, Legendre P, Drapeau P. 1992. Partialling out the spatial component of ecological variation. *Ecology* **73:** 1045–1055.

Bulla L. 1994. An index of evenness and its associated diversity measure. *Oikos* **70:** 167–171.

Cachan P. 1964. Analyse statistique des pullulations de Scolytoidea mycétophages en forêt sempervirente de Côte d'Ivoire. *Annales de la Faculté des Sciences, Université de Dakar* **14:** 5–70.

Charles E. 1998. The impact of natural gap size on the communities of insect herbivores within a rain forest of Guyana. Unpubl. MSc. Thesis, University of Guyana, Georgetown, Guyana.

Colwell RK. 1997a. *Biota: the Biodiversity Database Manager*. Sunderland: Sinauer Associates.

Colwell RK. 1997b. *EstimateS: Statistical estimation of species richness and shared species from samples. Version 5*. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Colwell RK, Coddington JA. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B)* **345:** 101–118.

Corbet PS. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda. IV. Mosquito breeding at different levels in and above the forest. *Transactions of the Royal Entomological Society of London* **113:** 275–283.

Curletti G. 1993. First contribution to the revision of the genus *Agrilus* of the Ethiopic region. *Lambillionea* **93:** 421–444.

Curletti G. 1994. Deuxième contribution à la revision des *Agrilus* de la région éthiopienne. Le subgenus *Personatus*. *Lambillionea* **94:** 477–486.

Curletti G. 1996. Quinto contributo alla revisione degli *Agrilus* della regione Etiopica. Il sottogenere *Coroebilus* Curletti, 1993. *Lambillionea* **96:** 305–310.

Curletti G. 1997. Nuove specie *Agrilus* africani (Coleoptera Buprestidae). *Bollettino Società Entomologica Italiana* **128:** 213–222.

Curletti G. 2000. Gli *Agrilus* della spedizione "Radeau des Cimes 1999" in Gabon. *Lambillionea* **100:** 459–470.

Dejean A, Corbara B, Orivel J. 1999. The arboreal ant mosaic in two Atlantic forests. *Selbyana* **20:** 133–145.

Delvare G, Aberlenc H-P. 1990. Des entomologistes sur la canopée. In: Hallé F, Blanc P, eds. *Biologie d'une canopée de forêt équatoriale. Rapport de Mission. Radeau des Cimes Octobre–Novembre 1989, Guyane Française*. Paris/Montpellier: Montpellier II et CNRS-Paris VI, 211–221.

DeVries PJ, Murray D, Lande R. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* **62:** 343–364.

Doucet JL. 1996. *Régénération Naturelle dans la Forêt des Abeilles (Gabon)*. Faculté Universitaire des Sciences agronomiques de Gembloux (Belgique), U.E.R. Sylviculture.

Downum K, Lee DW, Hallé F, Quirke M, Towers N. In press. Plant secondary compounds in the canopy and understory of a tropical rainforest in Gabon. *Tropical Ecology*.

Ebersolt G. 1990. Opération "Radeau des Cimes", Mission 1989—Guyane. Bilan technique partie radeau. In: Hallé F, Blanc P, eds. *Biologie d'une canopée de forêt équatoriale. Rapport de Mission. Radeau des Cimes Octobre–Novembre 1989, Guyane Française*. Paris/Montpellier: Montpellier II et CNRS-Paris VI, 15–26.

Erwin TL. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36:** 74–75.

Erwin TL. 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In: Sutton SL, Whitmore TC, Chadwick AC, eds. *Tropical Rain Forest: Ecology and Management*. Oxford: Blackwell, 59–76.

Erwin TL. 1995. Measuring arthropod biodiversity in the tropical forest canopy. In: Lowman MD, Nadkarni NM, eds. *Forest Canopies*. San Diego: Academic Press, 109–126.

Floren A, Linsenmair KE. 1997. Diversity and recolonisation dynamics of canopy arthropod communities in a lowland rain forest in Sabah, Malaysia. In: Ulrich H, ed. *Tropical Biodiversity and Systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn, 1994*. Bonn: Zoologisches Forschunginstitut und Museum Alexander Koenig, 245–249.

Fowler SV. 1985. Difference in insect species richness and faunal composition of birch seedlings, saplings and trees: the importance of plant architecture. *Ecological Entomology* **10:** 159–169.

Fréty T, Dewynter M. 1998. Amphibiens Anoures de la Forêt des Abeilles (Gabon). *Journal of African Zoology* **112:** 171–184.

Fürst R, Duelli P. 1988. Fensterfallen und Klebgitterfallen im Vergleich: die Flugaktive Insektenfauna einer Kiesgrube. *Mitteilungen Deutsche Allgemeine und Angewandte Entomologie* **6:** 194–199.

Godfray HC, Lewis OT, Memmott J. 1999. Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society, Biological Sciences* **354:** 1811–1824.

Haddow AJ, Corbet PS. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda. V. Swarming activity above the forest. *Transactions of the Royal Entomological Society of London* **113:** 284–300.

Hallé F. 1998. Distribution verticale des métabolites secondaires en forêt équatoriale – une hypothèse. In: Hallé F, ed. *Biologie d'une Canopée de Forét Equatoriale – III. Rapport de la Mission d'Exploration Scientifique de la Canopée de Guyane, Octobre–Décembre 1996*. Paris: Pro-Natura International, Opération Canopée, 129–138.

Hallé F, ed. 2000. *Biologie d'une canopée de forêt équatoriale – IV. Rapport de Mission: Radeau des Cimes Janvier Mars 1999, La Makandé, Gabon.* Paris: Pro-Natura International, Opération Canopée.

Hallé F, Blanc P, eds. 1990. *Biologie d'une canopée de forêt équatoriale. Rapport de Mission Radeau des Cimes Octobre–Novembre 1989, Petit Saut – Guyane Française.* Montpellier/Paris: Montpellier II et CNRS-Paris VI.

Hammond PM. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. In: Knight WJ, Holloway JD, eds. *Insects and the Rain Forests of South East Asia (Wallacea)*. London: The Royal Entomological Society of London, 197–254.

Hammond PM, Stork NE, Brendell MJD. 1997. Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. In: Stork NE, Adis J & Didham RK, eds. *Canopy Arthropods*. London: Chapman, Hall, 184–223.

Kato M, Inoue T, Hamid AA, Nagamitsu T, Merdek MB, Nona AR, Itino T, Yamane S, Yumoto T. 1995. Seasonality and vertical structure of light-attracted insect communities in a Dipterocarp forest in Sarawak. *Research in Population Ecology* **37:** 59–79.

Kirk WDJ. 1984. Ecologically selective coloured traps. *Ecological Entomology* **9:** 35–41.

Koike F, Riswan S, Partomihardjo T, Suzuki E, Hotta M. 1998. Canopy structure and insect community distribution in a tropical rain forest of West Kalimantan. *Selbyana* **19:** 147–154.

Le Corff J, Marquis RJ. 1999. Differences between understorey and canopy in herbivore community composition and leaf quality for two oak species in Missouri. *Ecological Entomology* **24:** 46–58.

Lowman M, Moffett M, Rinker HB. 1993. A new technique for taxonomic and ecological sampling in rain forest canopies. *Selbyana* **14:** 75–79.

Lowman MD, Foster R, Wittman P, Rinker HB. 1998. Herbivory and insect loads on epiphytes, vines and host trees in the rain forest canopy of French Guiana. In: Hallé F, ed. *Biologie d'une Canopée de Forêt Equatoriale – III. Rapport de la Mission d'Exploration Scientifique de la Canopée de Guyane, Octobre–Décembre 1996*. Paris: Pro-Natura International, Opération Canopée, 116–128.

Magurran AE. 1988. *Ecological Diversity and its Measurement.* London: Croom Helm.

May RM. 1990. How many species? *Philosophical Transactions of the Royal Society of London, Series B* **330:** 293–304.

Moran CV, Southwood TRE. 1982. The guild composition of arthropod communities in trees. *Journal of Animal Ecology* **51:** 289–306.

Mulkey SS, Kitajima K, Wright SJ. 1996. Plant physiological ecology of tropical forest canopies. *Trends in Ecology and Evolution* **11:** 408–412.

Nadkarni NM. 1995. Good-bye, Tarzan. *The Sciences*, January/February **1995:** 28–33.

Obenberger J. 1936. *Coleopterorum Catalogus W. Junk, Buprestidae V* (V:935–1246). Gravenhage: Schenkling ed.

Ødegaard F. 1999. Host specificity as a parameter in estimates of arthropod species richness. Unpublished PhD thesis, Norwegian University of Science and Technology, Trondheim, Norway.

Parker GG. 1995. Structure and microclimate of forest canopies. In: Lowman MD, Nadkarni NM, eds. *Forest Canopies*. San Diego: Academic Press, 431–455.

Robinson MH, Robinson B. 1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology* **149:** iv + 1–76.

Rodgers DJ, Kiching RL. 1998. Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. *Ecography* **21:** 392–400.

Roubik DW. 1993. Tropical pollinators in the canopy and understorey: field data and theory for stratum "preferences". *Journal of Insect Behavior* **6:** 659–673.

Schowalter TD, Ganio LM. 1998. Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern Washington, USA. *Bulletin of Entomological Research* **88:** 633–640.

Shelly TE. 1985. Ecological comparisons of robber fly species (Diptera: Asilidae) coexisting in a neotropical forest. *Oecologia* **67:** 57–70.

Shelly TE. 1988. Relative abundance of day-flying insects in treefall gaps vs shaded understorey in a Neotropical forest. *Biotropica* **20:** 114–119.

Springate ND, Basset Y. 1996. Diel activity of arboreal arthropods associated with Papua New Guinean trees. *Journal of Natural History* **30:** 101–112.

Stewart-Oaten A. 1995. Rules and judgments in statistics: three examples. *Ecology* **76:** 2001–2009.

Stork NE. 1987. Arthropod faunal similarity of Bornean rain forest trees. *Ecological Entomology* **12:** 219–226.

Sutton SL. 1983. The spatial distribution of flying insects in tropical rain forests. In: Sutton SL, Whitmore TC, Chadwick AC, eds. *Tropical Rain Forest: Ecology and Management*. Oxford: Blackwell, 77–92.

Sutton SL. 1989. The spatial distribution of flying insects. In: Lieth H, Werger MJA, eds. *Tropical Rain Forest Ecosystems. Bigeographical and Ecological Studies*. Amsterdam: Elsevier, 427–436.

Sutton SL, Hudson PJ. 1980. The vertical distribution of small flying insects in the lowland rain forest Zaire. *Zoological Journal of the Linnean Society* **68:** 111–123.

Ter Braak CJF, Smilauer P. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Ithaca, NY, USA: Microcomputer Power.

Tokeshi M. 1993. Species abundance patterns and community structure. *Advances in Ecological Research* **24:** 111–186.

Walter DE, Seeman O, Rodgers D, Kitching RL. 1998. Mites in the mist: how unique is a rainforest canopy-knockdown fauna? *Australian Journal of Ecology* **23:** 501–508.

Walter P. 1983. Contribution à la connaissance des Scarabaéides coprophages du Gabon (Col.). 2. Présence de populations dans la canopée de la forêt Gabonaise. *Bulletin de la Société entomologique de France* **88:** 514–521.

Willott SJ. 1999. The effects of selective logging on the distribution of moths in a Bornean rainforest. *Philosophical Transactions of the Royal Society, Biological Sciences* **354:** 1783–1790.

Wilson EO. 1988. The current state of biological diversity. In: Wilson EO, ed. *Biodiversity*. Washington: National Academy Press, 3–18.

Wolda H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecological Entomology* **4:** 181–190.

Wolf F, Gaspar G, Verstraeten C. 1968. Recherches sur l'écosystème forêt. La chênaie à Galeobdolon et à Oxalis de Mesnil-Eglise (Ferage). Hyménoptères récoltés dans des bacs d'eau. *Bulletin de la Station de Recherches Agronomiques de Gembloux* **3:** 566–579.

Wright SJ, Colley M, eds. 1994. *Accessing the Canopy. Assessment of Biological Diversity and Microclimate of the Tropical Forest Canopy: Phase I*. Nairobi, Kenya: United Nations Environment Programme.