



Invertebrates in the canopy of tropical rain forests How much do we really know?

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Abstract

The current state of knowledge of canopy invertebrates in tropical rain forests is reviewed using data drawn, without bias toward taxon, collecting method or biogeographical region, from 89 studies concerned with mass-collecting (>1000 individuals). The review is intended to identify the most serious gaps and biases in the distribution of higher taxa among forest types and biogeographical regions. With respect to knowledge, biogeographical regions can be ranked as Neotropical > Australian > Oriental > Afrotropical. The canopy of lowland wet and subtropical forests has been studied in greater detail, whereas the canopy of lowland dry and montane forests is much less well known. Collecting techniques influence greatly the present knowledge of canopy invertebrates. Invertebrates other than arthropods, often abundant in epiphytic habitats, phytotelmata and perched litter, are virtually unknown. The abundance of several groups, such as Acari, Collembola and Isoptera, is almost certainly seriously underestimated. Densities of invertebrate individuals in the canopy of tropical rain forests appear to be lower than in temperate forests, although invertebrate abundance is dissipated by the high standing-biomass of rain forests. Coleoptera, particularly Staphylinidae, Curculionidae and Chrysomelidae, along with Hymenoptera, Lepidoptera and Araneae appear to be the most speciose taxa in the canopy, and it is probable that this reflects their range of feeding habits and exploitation of rain forests habitats. The distribution of individuals among the major arthropod orders and across the studies examined is complex and depends on many factors. The amount of variance that can be directly explained by biogeography, forest types (subtropical, wet, dry or montane), or collecting methods appears to be about 11%. The explained variance increases when considering major families of Coleoptera (28%) or subfamilies of Chrysomelidae (40%). In all cases, the variance explained by the type of forest is much higher than by that explained by biogeography. These conclusions are similar when considering various prey-predator relationships in the canopy. This suggests that, at the higher taxa level, the composition of the invertebrate fauna in the canopy may vary comparatively more across forest types than across biogeographical regions and this is discussed briefly from a conservation viewpoint.

Introduction

Several reviews focusing on the canopy of tropical rain forests have considered, more or less directly, canopy invertebrates with, for example, particular reference to canopy biology (Lowman & Wittman 1996), forest ecology (Lowman & Moffett 1993), ecosystem dynamics (Stork 1996), herbivory (e.g., Coley & Aide 1991; Lowman 1995; Coley & Barone 1996), global species richness (e.g., Stork 1988; Hammond

1992; May 1994; Erwin 1995), sampling methods (e.g., Erwin 1989; Basset et al. 1997) or canopy access (Moffett & Lowman 1995). Other detailed sources of information on canopy invertebrates can be found in thorough studies of particular tropical locations (e.g., Knight & Holloway 1990; Leigh et al. 1996; Junk 1997) or in proceedings of various meetings (e.g., Sutton et al. 1983b; Stork et al. 1997).

However, to date, there has been no attempt to bring together most of the studies on canopy invertebrates without bias as to collecting methods, taxa or biogeographical regions. The aim of this article is to identify the main biases and gaps in the knowledge of canopy invertebrates in tropical and subtropical rain forests, to review the information available in terms of composition, abundance and diversity, to identify broad patterns in the distribution of higher canopy taxa and prey-predator ratios, and to discuss future prospects in the study of canopy invertebrates.

Methods and their limitations

The literature published up to September 1998 was collated, using various sources and with additional information from colleagues. Studies were retained only if they:

- concentrated on the canopy of tropical or subtropical rain forests;
- included mass collecting of at least 1000 invertebrates (with some rare exceptions below this threshold), preferably spanning over several orders;
- included quantitative data; and
- were not concerned primarily with only one or several pest species.

This search yielded 89 studies, which are summarized in Appendix 1. For sake of brevity, only a key reference is given per study, giving access to other relevant references.

There are several obvious problems with such a compilation. First, the same data set may have been used by several workers to study different taxa and topics. These 'pseudoreplicates' (from a statistical viewpoint) can be easily identified and grouped with the original data set. Second, there is a bias against agricultural, medical and forestry entomology studies. Third, the data collated were sorted to varying levels of resolution, or concentrated only on specific taxa. The analyses consider the distribution of individuals, rather than species richness, for which data are scarce. Estimates of species richness for particular taxa were derived considering species accumulation within the number of individuals collected, or an index of 'species \times individuals⁻²' averaged over the relevant studies (the higher the index the more speciose). This crude index permitted the comparison of studies with different sampling techniques, focal taxa and sampling effort.

Lastly, the data collated were collected with different methods, over different time-span and number of habitats, etc. Even for a technique such as fogging, the application of different insecticides may result in different results (Erwin 1995). To reduce the effect of sample size (collecting for longer time or in different habitats, etc.), individuals collected of a particular taxon were expressed in % of the total catch during the study. This permitted the consideration of studies not reporting data as numbers of individuals (e.g., biomass or average no. individual per m² of fogging tray, etc.). Percentages were then averaged across all studies amenable to analysis (e.g., ordinal signatures, $n = 42$), to derive relative estimates of invertebrate abundance. These estimates were further multiplied with modal classes of insect body weight, as reported in Zug & Zug (1979), to derive corresponding percentages of biomass. In a separate analysis (see below), collecting methods were coded into a variable for each study, and the specific contribution of this variable to overall variance was estimated by canonical correspondence analysis.

Analyses to identify broad patterns in the distribution of higher taxa were performed at three taxonomic levels:

- Major invertebrate orders/groups present in the canopy: Araneae, Acari, other Arthropoda, Collembola, Blattodea, Isoptera, Dermaptera, Orthoptera, Psocoptera, Homoptera, Heteroptera, Thysanoptera, Coleoptera, Diptera, Lepidoptera, Neuroptera, Hymenoptera and Formicidae.
- Most common families of Coleoptera present in canopy samples: Anthribidae, Carabidae, Cerambycidae, Chrysomelidae, Cleridae, Coccinellidae, Corylophidae, Curculionidae, Lathridiidae, Mordellidae, Phalacridae, Scolytidae, Staphylinidae, Tenebrionidae (see recent discussion of beetle taxa in the canopy in Hammond et al. 1996).
- Major subfamilies/groups of Chrysomelidae: Eumolpinae, Galerucinae, Alticinae and 'Others'.

Formicidae were also included in the first level, as most workers readily sorted ants in their samples. The choice of beetles and chrysomelids for the other levels of analyses was dictated by the nature of the data, as most workers who sorted their samples at lower taxonomic level concentrated on beetles.

The total of ecological publications that resulted from the original data was used to estimate the amount of accessible knowledge related to each study (total number of publications considered = 266; taxonomical publications were too difficult to track with an equal

MASS-COLLECTING 1929 - 1997

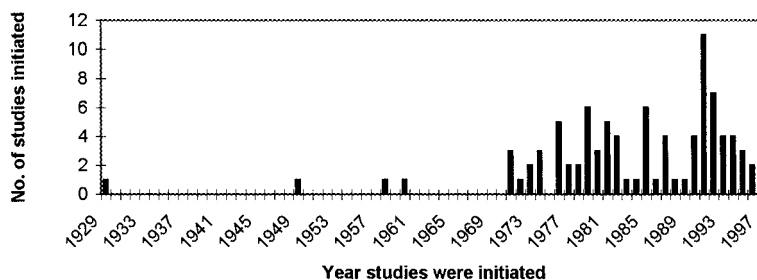


Figure 1. Mass collecting of invertebrates in the canopy of tropical rain forests: distribution of years in which the studies examined in this contribution were initiated.

accuracy for each study). To partition the respective effects of sampling methods, biogeographical effects and forest types on the data, a correspondence analysis (CA) and a canonical correspondence analysis (CCA) were performed with ADE 3.4 (Chessel & Dolédec 1992) for each level of analysis, above, with relevant data sets. The variables for the CCA included:

- sampling methods: these were ordered along a gradient from more systematic methods to those targeting particular taxa or habitats, using Basset et al. (1997) as a guide; methods were ordered as follows: several methods used; fogging; light traps; other traps; hand collecting and related; and litter extraction;
- biogeographical regions, ordered from east to west: Australian, Oriental, Afrotropical and Neotropical;
- forest types, ordered according to a climatic gradient: subtropical forest; lowland (seasonal) dry forest; lowland wet forest; montane wet forest;
- knowledge, number of publications related to canopy invertebrates at each site; this tested for independence between the data and the effort applied to study the material collected at each site.

In order to investigate prey-predator ratios in the canopy and the relationships between ants, spiders and several taxa, similar CA and CCA were also performed. However, in this case, the taxa matrix was filled with 'prey'-predator ratios (expressed as number of 'prey' available to a particular individual of predator), instead of the number of individuals. Two separate analyses were performed, one with spiders and one with ants. Both included the following taxa as 'prey': Collembola, Thysanoptera, Psocoptera, Homoptera and all arthropod prey (minus spiders and ants).

Results and discussion

A recent field of investigation

Mass-collecting of invertebrates in the canopy of tropical rain forests is a recent field of investigation (Figure 1). The oldest attempt to collect quantitatively invertebrates in the canopy of tropical rain forests appears to be the pioneering efforts lead by O. W. Richards, who hoisted light traps up in the canopy in 1929, during the Oxford University expedition in Guyana (Hingston 1932; Sutton 2001). With the exception of the erection of towers and sporadic insect collection from these late in the 50's, insect mass-collecting from the canopy did not progress notably until the development of fogging (e.g., studies by H. R. Roberts, W. C. Gagné, T. L. Erwin) and light-trapping techniques (e.g., N. Smythe, H. Wolda), in the early 1970s. The field of research is becoming increasingly popular (Figure 1) as new methods of access in the canopy (cranes, rafts, single rope techniques, etc.) permit the experimentation with a variety of collecting methods (Basset et al. 1997; Sutton 2001). It should be noted that, since a lag of 4.6 years (on average) is observed between the initiation of the collecting and the date of the first publication studies of canopy arthropods (Erwin 1995), the trends in number of studies being initiated cannot be interpreted safely past 1993.

Biogeographical biases and biases by forest types

The sites of mass-collecting of invertebrates in the canopy are mapped in Figure 2, weighted by an estimate of knowledge (number of ecological publications relevant to each study site). The areas best studied appear to be Panama, Costa Rica, Manaus and Sulawesi (included in the 'Australian' region for the present analysis). If we compare with the actual distribution of

Table 1. Taxonomic distribution of the major phyla, classes and orders of invertebrates in the canopy of tropical rain forests, with estimates of the number of species described worldwide and of relative abundance and biomass in the canopy (average % of individuals/biomass collected, see Methods).

| Taxa | No. species ^a | Abund. | Biomass | Notes | Examples |
|------------------------|--------------------------|--------------------|---------|---|---|
| Platyhelminthes | 20000 | ? | ? | Parasites of canopy animals | Bakarr et al. 1991 |
| Nematoda | 25000 | ? | ? | Various habitats | Chabaud & Bain 1990, Stoner 1996 |
| Arthropoda | 1085000 | | | | |
| <i>Arachnida</i> | 100000 | | | | |
| Araneae | 37000 | 2.85 | 3.47 | | |
| Pseudoscorpiones | 3200 | <0.30 | <0.45 | TRU, EPI | Morais et al. 1997; Guilbert 1997; Cotgreave et al. 1993 |
| Opiliones | 5000 | <0.30 | <0.45 | TRU, EPI | Paoletti et al. 1991; Cotgreave et al. 1993; Nicolai 1989 |
| Acari | 45000 | 2.71 | 0.21 | Various habitats, UND | Walter et al. 1994; Walter & Behan-Pelletier 1999; Franklin et al. 1997 |
| Crustacea | 40000 | | | | |
| Isopoda | 4000 | <0.30 | <0.45 | LIT, EPI, UND | Nadkarni & Longino 1990; Nicolai 1989; Kitching et al. 1997 |
| Amphipoda | 6000 | <0.30 | <0.45 | LIT, EPI, UND | Nadkarni & Longino 1990; Guilbert 1997 |
| <i>Chilopoda</i> | 3000 | <0.30 | <0.45 | LIT, TRU, EPI | Paoletti et al. 1991; Guilbert 1997; Kitching et al. 1997 |
| <i>Symphyla</i> | 120 | <0.30 | <0.45 | LIT, TRU, EPI | Adis et al. 1997b; Nadkarni & Longino 1990 |
| <i>Diplopoda</i> | 10000 | <0.30 | <0.45 | LIT, TRU, EPI | Paoletti et al. 1991; Hopkin & Read 1992; Kitching et al. 1997 |
| Hexapoda | | | | | |
| Collembola | 8000 | 6.35 | 0.97 | Various habitats, UND | Kitching et al. 1993, 1997; Guilbert 1997; Palacios-Vargas et al. 1998 |
| Insecta | 950000 | 88.89 | 94.90 | | |
| Blattodea | 4000 | 5.32 | 24.29 | | |
| Isoptera | 2300 | 6.20 | 0.47 | UND | Martius 1994; Eggleton et al. 1996 |
| Dermoptera | 1800 | 0.36 | 0.14 | | |
| Orthoptera | 20000 | 1.14 | 2.17 | | |
| Psocoptera | 3000 | 2.80 | 1.28 | | |
| Hemiptera | 50000 | 10.44 ² | 8.23 | ² Homoptera = 8.61, Heteroptera = 1.83 | |
| Thysanoptera | 5000 | 2.83 | 0.86 | | |
| Neuroptera | 5000 | 0.50 | 0.69 | | |
| Coleoptera | 300000 | 12.36 | 18.82 | | |
| Diptera | 250000 | 15.42 | 9.39 | | |
| Lepidoptera | 140000 | 4.44 | 8.78 | | |
| Hymenoptera | 100000 | 25.99 ³ | 19.79 | ³ Formicidae = 16.36 | |
| Mollusca | | | | | |
| Gastropoda | 70000 | Low | Low | UND | Schowalter 1994; Guilbert 1997 |
| Annelida | 12000 | | | | |
| Oligochaeta | 3000 | Low | ? | LIT, EPI, UND | Paoletti et al. 1991; Nadkarni & Longino 1990; Adis & Righi 1989 |
| Hirudinea | 500 | Low | Low | LIT, EPI, UND | Paoletti et al. 1991 |

^aWells et al. 1983; Hammond 1995; J. Adis, pers. comm. UND = abundance/biomass underestimated; TRU = on trunks and limbs; LIT = in perched litter; EPI = in epiphytes.

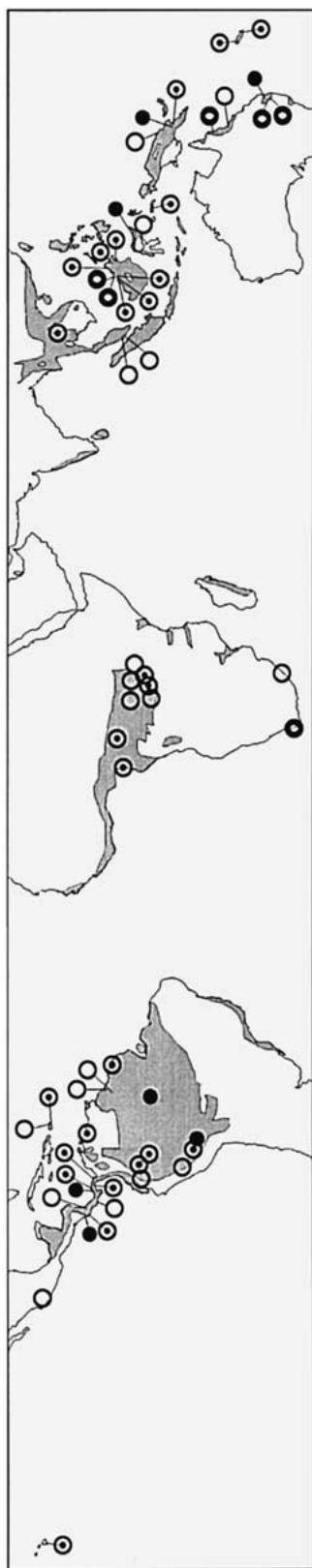


Figure 2. Location of the major sites examined in this contribution, weighted by an estimate of knowledge (see text). ● = > 10 publications, ○ = 6–10 publications, ○ = 2–5 publications, ○ = 1 publication, ○ = 1 publication (see text). ○ = 1 publication, ○ = 6–10 publications, ● = > 10 publications. A schematic distribution of rain forests is indicated in grey (after Lieth & Werger 1989).

tropical and subtropical rain forests, where the area in km^2 of rain forests can be classified as Neotropical > Oriental > Afrotropical > Australian, there are some discrepancies with regard to the location of the major studies of canopy invertebrates. If the distribution of studies is considered either by sites or by knowledge (Figures 3a and 3b), biogeographical regions can be ranked as Neotropical > Australian > Oriental > Afrotropical. Although the Neotropical area overall appears to be the best studied, when we take account of the area of rain forests available there, it becomes apparent that about 40% of the information originates from Central America – from Panama and Costa Rica. The forests of the Amazon basin are comparatively less known. The contribution of the Australian region appears disproportionately high, with regard to the area covered by rain forests there. This results from the expedition of the Royal Entomological Society in 1985 in Sulawesi. In contrast, knowledge of the canopy fauna of the Afrotropical region (André et al. 1992) and of mainland SE Asia is fragmentary.

Unsurprisingly, the canopy of lowland wet forests has been studied in greater detail, whereas the canopy of lowland dry and montane forests is much less well known (Figure 4). Ten years ago, Janzen (1988a) stressed that tropical lowland dry forests represented the most endangered tropical ecosystem and that the conservation and study of this ecosystem should be given priority. To date, this plea seems to have been only partly followed by canopy entomologists. Knowledge of subtropical forests is disproportionately high, perhaps since logistics and resources, such as insect collections, in countries such as Australia are very good and permit efficient studies of canopy habitats and of the material collected.

Methodological biases

Fogging is the most popular technique among the studies surveyed, followed by combinations involving several collecting methods, light traps and hand collecting (Figure 5). Since each of these methods has biases with regard to particular taxa (e.g., Adis et al. 1984; Basset et al. 1997), it is difficult to compare the data without accounting specifically for these effects in the analyses (see below). Interestingly, if the number of publications related to each study is compared by collecting method, ratios of number of publications per study are 4.9, 3.7, 3.0 and 2.0 for several methods, hand collecting, fogging and light traps, respectively. The high score of studies relying on several methods to

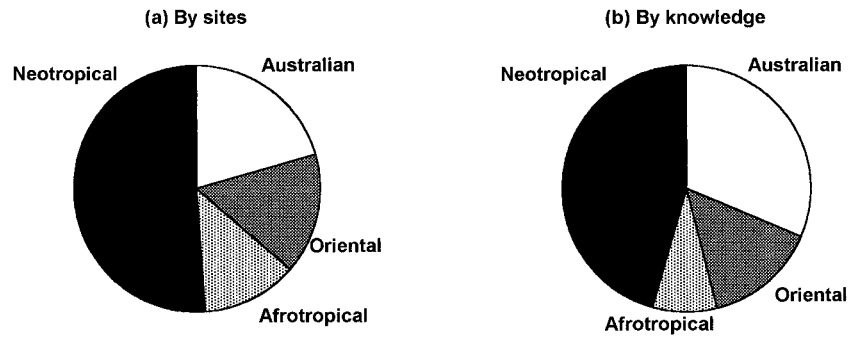


Figure 3. Distribution of studies, ordered by biogeographical regions, either by (a) sites or (b) knowledge (number of publications relevant to each site).

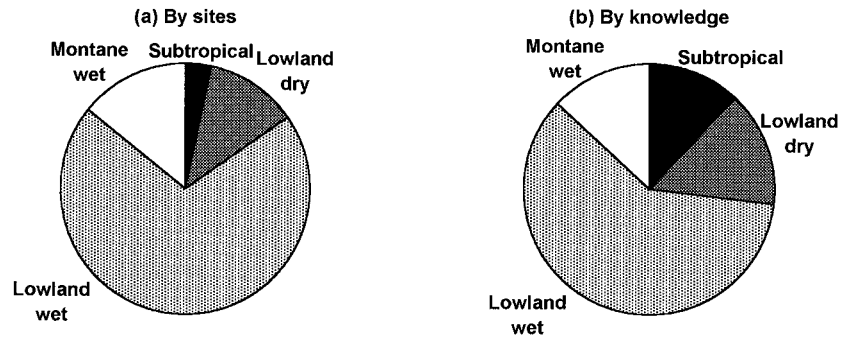


Figure 4. Distribution of studies, ordered by forest type, either by (a) sites or (b) knowledge (number of publications relevant to each site).

collects invertebrates may suggest that this strategy is also more likely to result in data directly interpretable and/or that teamwork resulted in a better knowledge of the material collected. The high score for hand collecting may result from the targeting of a particular habitat in the canopy (foliage) and particular taxa (usually insect herbivores), a strategy more amenable to analysis and publication of results than general arthropod mass-collecting.

The current knowledge of the taxonomic distribution of higher taxa in the canopy greatly depends on data collected by fogging, and of biases inherent to this and other methods commonly used by canopy workers (Figure 5). For example, inhabitants of arboreal phytotelmata (e.g., water-filled tree holes, bromeliads, ferns, etc.) represent diverse taxa which are often dominated by Diptera (e.g., Lounibos 1981; Louton et al. 1996) but cannot be sampled efficiently with fogging. Common inhabitants of bromeliads may include Oligochaeta, Opiliones and Pseudoscorpiones (e.g., Paoletti et al. 1991; Cotgreave et al. 1993; Fragoso & Rojas-Fernandes 1996). Other phytotelmata may also include some Rotifera, Polychaeta, Ostracoda or Copepoda (Kitching 1987; in press). Although crabs

may be common in mangrove canopies, an endemic Jamaican crab, *Metopaulias depressus* Rathbun, is only found in arboreal bromeliads above 300 m asl (Hartnoll 1964). Similarly, the suspended litter in the canopy is often rich in Acari, Collembola, Isopoda, Myriapoda, etc. (e.g., Kitching et al. 1997; Behan-Pelletier et al. 1993) that can be best surveyed with litter extraction or related techniques. Epiphytes in the canopy often support more insects than those closer to the ground (e.g., Paoletti et al. 1991; Kitching et al. 1997; but see counter-example in Nadkarni & Longino 1990). Another important habitat in the canopy that has rarely been studied and is difficult to sample by fogging is that provided by bryophytes (e.g., Young 1986). A rich fauna of Rotifera, Tardigrada, Copepoda, Acari, Collembola, Diptera, to cite a few taxa, may be associated with arboreal mosses.

Further, some invertebrate taxa may only be present temporarily in the canopy and a fogging snapshot is unlikely to detect their presence and reveal their true abundance and interactions with other organisms in the canopy. For example, many soil taxa migrate up in the canopy of Central Amazonian inundation forests, as a response to flooding (e.g.,

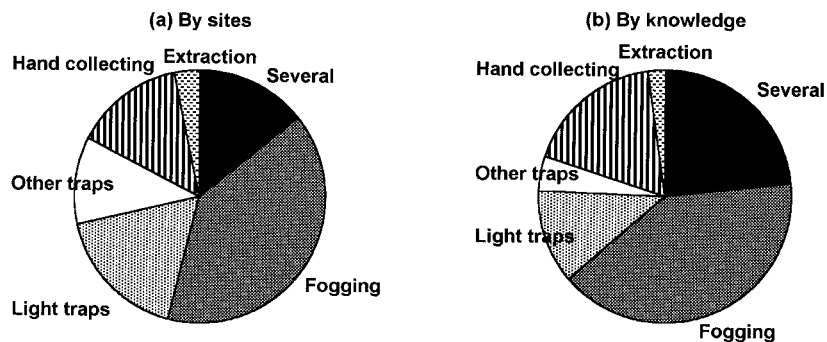


Figure 5. Distribution of studies, ordered by collecting method, either by (a) sites or (b) knowledge (number of publications relevant to each site).

Adis 1997). This may include taxa not often seen in the canopy, such as Annelida (e.g., Adis & Righi 1989), Pseudoscorpiones (e.g., Morais et al. 1997), Symphyla, Chilopoda (Adis 1997) or Scorpiones (Lourenço 1988).

Taxonomic distribution and abundance of canopy invertebrates

Current knowledge of canopy invertebrates suggests that the most abundant taxa may be Hymenoptera (mostly represented by Formicidae), Diptera, Coleoptera, Hemiptera (mostly Homoptera) and Lepidoptera (Table 1). The abundance of ants in the canopy has been reported by many studies and appears to be a characteristic of tropical rain forest canopies (review in Davidson 1997). Although often neglected in taxonomic studies, Diptera play a much more important role in arboreal community interactions than implied by their traditional designation as 'tourists' in the canopy (Didham 1997). However, a critical reading of the data presented in Table 1 is needed.

There are virtually no data about the abundance and diversity of Platyhelminthes and Nematoda in the canopy, with the exception of scattered records. These invertebrates cannot be sampled with the methods commonly used in the canopy, with the exception of litter extraction for free-living nematodes. Plants and animals in the canopy have their loads of parasitic worms (see, for example, references in Table 1). Judging by the worldwide diversity of these groups, and by the variety of life-histories of nematodes, it would be reasonable to assume that these groups must be relatively abundant in the canopy, particularly nematodes. Further, canopy animals, either vertebrates or invertebrates (e.g., Clastrier & Delecolle 1997), may also

support a rich fauna of ectoparasites (Siphonaptera, Mallophaga, Anoplura, etc.).

The abundance in the canopy of other non-arthropod groups, such as Gastropoda and Annelida, may also be underestimated. Both groups are more or less confined to epiphytes, suspended soils and accumulations of litter in the canopy. The proper estimation of their abundance may require sampling their preferred habitats selectively. Further, land snails are particularly diverse on islands, partly due to the absence or low abundance of vertebrate predators there (Wells et al. 1983), and many species are truly arboreal (see, for example, Cowie 1992, on Partulidae and Achatinellidae). Studies of forest canopies on tropical islands, such as in Puerto Rico or New Caledonia, even when performed with fogging, suggest that arboreal snails may be more abundant there (e.g., Garrison & Willig 1996; Guilbert 1997).

As for non-insect arthropods, there is no *a priori* reason why the relative abundance of spiders should be greatly underestimated, since they are often of similar or larger body size than many foliage insects, and can be readily collected with a variety of methods. Although Pseudoscorpiones, Opiliones, Chilopoda, Symphyla and Diplopoda may be more or less restricted to cryptic habitats in the canopy, they are, with the exception of the first order, rather large. If their abundance in the canopy is underestimated, it should not be by a high factor. The abundance of terrestrial crustaceans (mainly Isopoda and Amphipoda), often found in epigeal and humid habitats, may well prove to be more seriously underestimated.

However, the most serious biases are likely to be related to microarthropods which exploit a variety of canopy habitats, such as, particularly, Acari and Collembola (see references in Table 1). Most techniques used by canopy workers are inadequate for

sampling these organisms, which often represent a distinct fauna from that at ground level (e.g., Behan-Pelletier et al. 1993; Walter et al. 1994 & 1998; Wunderle 1992; Rodgers & Kitching 1998; Palacios-Vargas et al. 1998). For example, Walter and O'Dowd (1995) estimate that an individual rain forest tree in Australia may easily contain about 380 000 mites.

Numerous other insect orders other than those listed in Table 1 are present in the canopy but they are not likely to be abundant (this is also true of many other invertebrate taxa). The relative importance of the major insect orders as listed in Table 1 should be reasonably close to current knowledge, with some exceptions. Isoptera may be the second most important insect group to ants in tropical rain forests (e.g., Beebe 1925). Many species have arboreal nests and their sampling in the canopy is difficult, particularly with conventional methods (Martius 1994; Eggleton et al. 1996). Termites collected in the canopy often include alates caught by traps, not workers representing the bulk of populations and which rarely circulate beyond their galleries. The abundance of photophobe Blattodea and minute Thysanoptera may also be questioned. Thrips may be very seasonal, often associated with flowers, and the precise estimation of their abundance will require long-term surveys.

Incidentally, one common feature of many of the compiled studies is the low incidence of Apoidea in the canopy, which may appear to be surprising. Although there has been claims that good fliers such as bees may escape the fog of insecticide in the canopy, recent studies on bee stratification (e.g., Roubik 1993) suggest that relatively few species forage preferentially in the canopy.

The remainder of this contribution discusses mainly arthropods since non-arthropod data are very limited.

Biomass and density of canopy invertebrates

Blattodea, Hymenoptera (particularly ants), Coleoptera and Diptera appear to represent most of the invertebrate biomass in the canopy (Table 1). Still, estimates of percentage biomass reported in Table 1 might be imprecise and as good as those of invertebrate body weights. Although these figures may be far from reality, they draw attention to the biomass of certain taxa, such as Blattodea, which may be non-negligible in the canopy. The contribution of other groups in terms of biomass (particularly Annelida) in perched lit-

ter/epiphytes, and Isoptera in arboreal nests, may well be underestimated and needs further investigation.

Invertebrate densities in the canopy have been quantified either as number of individuals or biomass per ha of forest (e.g., Stork 1988, 1996), or as number of individuals per leaf area, particularly for insect herbivores (e.g., Basset et al. 1992). In both cases data are rare and await refinement. For example, Stork (1988) estimated that more than 42 million arthropods, equivalent to 30 kg of dry weight, were present in one ha of forest in Seram, but admitted subsequently that these figures may be too low (Stork 1996). The canopy habitat contributed more than a quarter of the individuals present and more than one third of the biomass present. Diplopoda represented most of the biomass in the soil. These calculations were derived from the numbers of arthropods collected in fogging trays of 1 m² and were summed over 1 ha of forest. It is not clear whether this, and other attempts to compare densities of invertebrates per m² of fogging trays among different sites, represent valid procedures, as the number of arthropods in the trays may be influenced greatly by the amount of leaf area in the column of foliage above the trays. Reporting data as volume of foliage suffers from the same deficiency, as it says little about leaf area, which often varies from one tree species to another. Fogging data reported as number of specimens per trays may be difficult to compare unless, for the purpose of extrapolation to a whole site, a certain number of tree species representative of the plot have been fogged (see Adis et al. 1998, for recent guidelines as to how to standardize the technique).

The data collected in Seram (Stork 1988) sparked a lively debate as to the relative contributions, either in terms of individuals, biomass or species richness of the canopy versus the soil/litter fauna in tropical rain forests (e.g., Stork 1988; Hammond 1990; André et al. 1992). Intensive fogging by T. L. Erwin in the late 1970s (e.g., Erwin 1982) revealed a rich canopy fauna and led to speculations that this fauna may be more diverse than in the soil. To date, the evidence seems to be contrary to these views (e.g., Hammond 1990, 1995; André et al. 1992; Walter et al. 1998). However, caution is required since most methods used in the canopy are inadequate to sample Acari and Collembola, which represent the dominant groups in the soil of rain forests (e.g., Stork 1988).

Invertebrate densities obtained from foliage samples in the canopy appear low, but higher than in the understorey. For example, a conservative 24 arthropod individuals in the canopy against 7 individuals in the

understorey for a sample size of 0.85 m² of foliage were reported from a rain forest in Cameroon (Basset et al. 1992). In a nutrient-poor forest with monodominant stands in Guyana, 2.1 and 3.2 insect herbivores per sample of 1.5 m² of leaf area were obtained in the understorey and canopy, respectively (Basset et al. 1999). Preliminary analyses of material collected in French Guiana also suggest that insects are more abundant in the canopy than in the understorey (Lowman et al. 1998). About 1025 insect individuals per g of dry foliage were reported from a canopy in Puerto Rico (Schowalter 1994). These densities, with the exception of the data from Puerto Rico, appear to be lower than comparable data from temperate forests (Basset et al. 1992) and this confirms the suggestion that invertebrates are scarce in tropical rain forests (e.g., Elton 1975). Note that these low densities do not imply that sampling the tropical canopy for arthropods is necessarily going to be a frustrating exercise, but rather, that the abundance of arthropods is diluted into the vast standing biomass of the rain forest. Many invertebrate herbivores have specific food requirements that render most rain forest foliage unsuitable for them, being not the proper host, tissue or proper developmental stage. Hence, herbivores tend to aggregate on certain food resources and this complicates the proper estimation of their abundance, unless sampling schemes are comprehensive enough to account for such variance, using high numbers of spatial and temporal replicates.

Species richness in the canopy

Current knowledge of the species richness of canopy invertebrates would tend to indicate that Coleoptera, particularly Staphylinidae, Curculionidae and Chrysomelidae, along with Hymenoptera, Lepidoptera and Araneae, are the most speciose taxa in the canopy (Figure 6). Since in none of the studies compiled were all invertebrates sorted to species or morphospecies (Stork 1991, represented probably the highest taxonomic effort overall), one must be cautious with these figures. Further, they refer to species accumulation in samples of individuals, not to the actual number of species. Taxa that are relatively rare, such as Heteroptera, may have a steep accumulation of species in collection, but overall may not be substantially more diverse than other taxa. Species accumulation rates for Araneae and Orthoptera may also be inflated because typically many juveniles are also collected from the canopy and these are difficult to

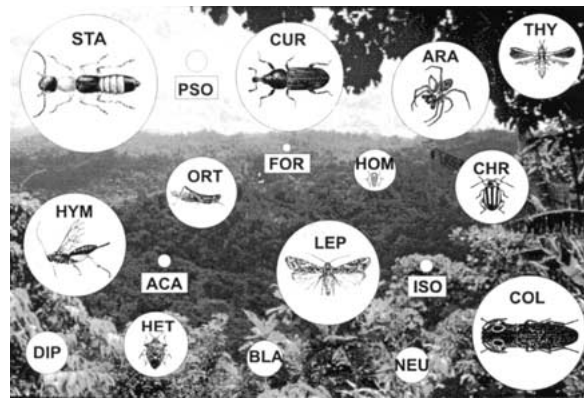


Figure 6. Species-scape in the canopy of a fictitious rain forest. The size of the circles are proportional to the putative species richness (measured as average species \times individuals⁻²) of the taxa, which are abbreviated as follows: STA: Staphylinidae (19.70); COL: other Coleoptera (15.96); CUR: Curculionidae (15.15); LEP: Lepidoptera (14.94); HYM: Hymenoptera (14.22); ARA: Araneae (13.45); THY: Thysanoptera (11.88); CHR: Chrysomelidae (10.60); ORT: Orthoptera (10.18); HET: Heteroptera (9.31); DIP: Diptera (5.66); HOM: Homoptera (5.60); NEU: Neuroptera (5.12); BLA: Blattodea (4.78); PSO: Psocoptera (3.40); ISO: Isoptera (2.27); ACA: Acari (1.80); FOR: Formicidae (1.56).

incorporate in taxonomic studies (and, therefore, in species accumulation).

Since knowledge of Hymenoptera and Diptera in the canopy certainly do not compare with that of Coleoptera or Lepidoptera, estimates of species richness for the former two groups are suspect at best. Close to 20% of the studies compiled targeted Coleoptera so that strict comparisons with other taxa should assume a level of knowledge similar to that of the Coleoptera, if this is possible at all. The Acari, for example, are likely to contribute significantly to animal diversity in the canopy since they have various life-histories and functional roles in ecosystems and, globally, represent a diverse taxon, despite being often neglected (e.g., André et al. 1992). Walter and O'Dowd (1995) suggested that mites may be the most diverse and abundant canopy arthropods.

Massive sampling in several strata of a rain forest in Sulawesi with 1.1 million of specimens collected showed that, overall, Staphylinidae, Curculionidae and Tenebrionidae were the most species-rich families of beetles (Hammond 1990). In the canopy, Chrysomelidae seems also to be diverse, as attested by many of the compiled studies. The fact that, overall, Staphylinidae and Curculionidae may be more diverse in the canopy than Chrysomelidae is interesting. This may reflect their range of feeding habits and exploitation of rain forest habitats, since in this regard

these groups can be ranked as follows: Staphylinidae (predators, fungal feeders, scavengers) > Curculionidae (wood-eaters, herbivores on roots, foliage and seeds) > Chrysomelidae (mainly herbivores on roots and foliage). Further, the species richness of these groups may also be a result from their intrinsic evolutionary dynamics, as these groups are often diverse in a variety of habitats not limited to the canopy.

The relative steep accumulation of species of Thysanoptera warrants further research, as many of them may be associated with flowers and potential pollinators. Conversely, ants seem not to be particularly diverse as their species accumulation rates are decreased by the enormous populations sustained by colonies. Wilson (1987) commented on the species-richness of ants using Peruvian data, although the species richness of other taxa within the same samples could not be compared. Indeed, the most species-rich insect families sorted from samples obtained in Borneo by Stork (1991) and collaborators included, in order of decreasing importance, Eulophidae, Encyrtidae, Aphelinidae, Curculionidae, Staphylinidae, Chrysomelidae, Formicidae, Phlaeothripidae, Cicadellidae, Chloropidae, Ceratopogonidae and Theridiidae.

Patterns of distribution of higher taxa in the canopy

The distribution of individuals among the major arthropod orders and across the studies examined was complex and depended on many factors (graph of eigenvalues of the CA, Figure 7a). Taxa of small body size, such as Collembola, Acari and Thysanoptera, scored highly on the first axis of the CA (Figure 7a). This suggests that the formation of this axis was induced by collecting methods, as well as by the specific habitat that was targeted in the canopy (e.g., epiphytes, perched litter). Interpretation of the other axes is difficult. Collectively, the variables constraining the CCA explained only 11% of the total variance (ratio of inertia of the CCA to the CA = 0.2436/2.2121). In the CCA (Figure 7b) the first axis, which explained 53% of the (explained) variance, was best correlated with collecting methods ($r = 0.862$, $p < 0.001$). The second canonical axis which explained 26% of the variance was best correlated with forest type ($r = 0.594$, $p < 0.05$), whereas biogeography loaded best on the third axis ($r = 0.936$, $p < 0.001$), which explained 18% of the variance. These analyses confirm that current knowledge of canopy invertebrates is strongly influenced by collecting methods. However, the pro-

portion of variance explained by the type of forest is higher than that explained by biogeography. Collembola seem to be particularly sensitive to forest type (Figure 7b) and this may be related to the high accumulation of organic matter in the canopy or slower decomposition rates, as discussed by Kitching et al. (1997) or Palacios-Vargas et al. (1998). For example, Kitching et al. (1997) reported higher abundances of Collembola and Acari in subtropical than in tropical forests in Australia.

The situation was similar when analyses considered only particular beetle families (Figure 8). The constraining variables included in the CCA explained 26% of the overall variance (ratio of inertia = 0.2536/0.9919). The formation of the first axis of the CA was difficult to interpret. The formation of the second axis of the CA appeared to be induced by either corticolous and wood-related families (upper part of Figure 8a) vs rather folivorous or floricolous families (lower part of Figure 8a). This may result from different amounts of wood or corticolous habitats being available in different forest types, as suggested by the results of the CCA. Of the explained variance in the CCA, the first axis represented 68% of the variance and was best related to methods ($r = 0.702$, $p < 0.01$), whereas the second axis, which explained 17% of the variance, was best correlated with forest type ($r = 0.795$, $p < 0.001$). Beetle families particularly sensitive to the effect of forest type included Lathridiidae, Scolytidae, Tenebrionidae and Carabidae (Figure 8). Several authors, such as Hammond (1990), Stork and Brendell (1990) or Wagner (1997), reported differences in the occurrence of beetle families in different forest types.

More variance (40%) was explained by the constraining variables in the analyses considering subfamilies of Chrysomelidae (ratio of inertia of CCA to CA = 0.1552/0.3840; Figure 9). The higher amount of variance explained with analyses at the lower taxonomic rank probably results from related taxa responding in a similar way to the variables considered in the analyses than is the case with higher taxa. The significance of the first axis of the CA for chrysomelid subfamilies was obscure, with no obvious influence of either biogeography, forest type, methods or knowledge. Most (52%) of the variance explained in the CCA was best related to forest type ($r = 0.779$, $p < 0.001$), which loaded highly on the first axis. The second canonical axis contributed to 43% of the variance and was best correlated with collecting methods ($r = -0.660$, $p < 0.05$). Galerucinae appeared to

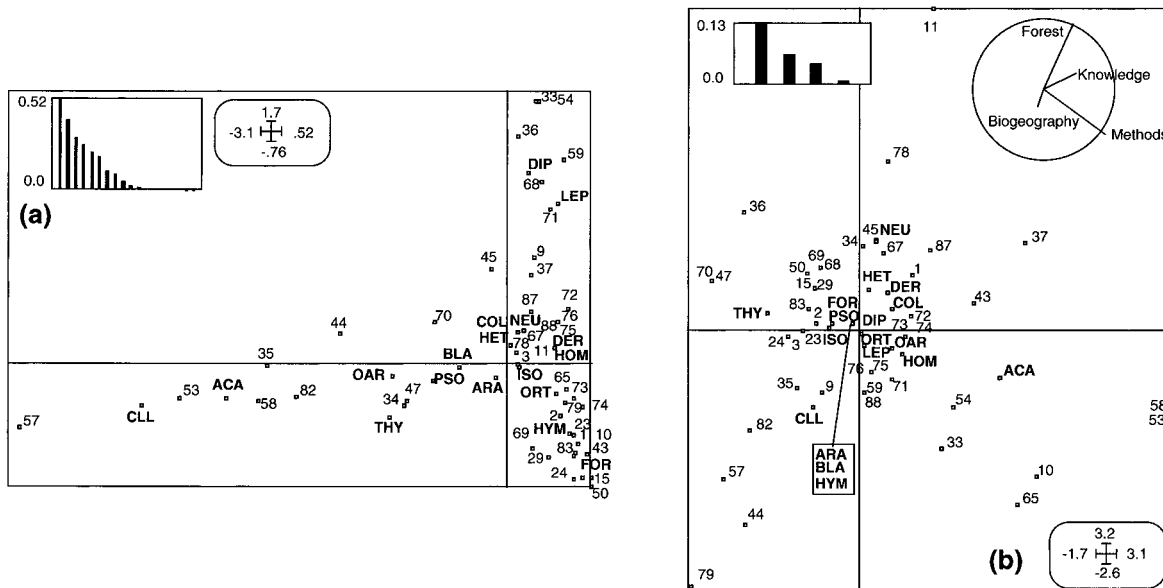


Figure 7. Ordinations of 18 higher insect taxa across 42 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Studies are coded with numbers as in Appendix 1. Taxa codes: ACA = Acari, ARA = Araneae, BLA = Blattodea, CLL = Collembola, COL = Coleoptera, DER = Dermaptera, DIP = Diptera, FOR = Formicidae, HET = Heteroptera, HOM = Homoptera, HYM = Hymenoptera, ISO = Isoptera, LEP = Lepidoptera, NEU = Neuroptera, OAR = Other arthropods, ORT = Orthoptera, PSO = Psocoptera, THY = Thysanoptera.

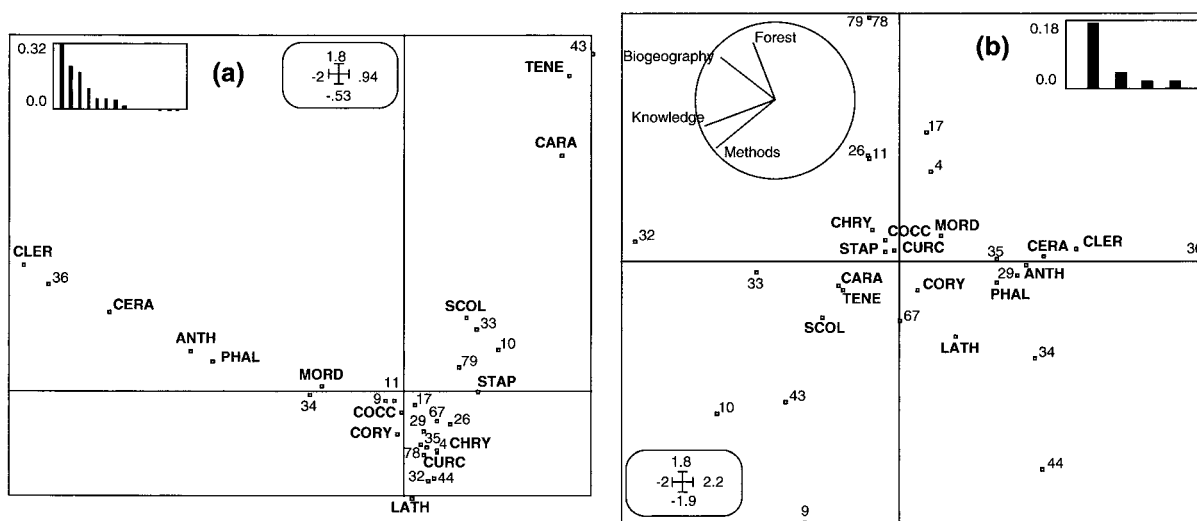


Figure 8. Ordinations of 14 beetle families across 17 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Studies are coded with numbers as in Appendix 1. Taxa codes: ANTH = Anthribidae, CARA = Carabidae, CERA = Cerambycidae, CHRY = Chrysomelidae, CLER = Cleridae, COCC = Coccinellidae, CORY = Corylophidae, CURC = Curculionidae, LATH = Lathridiidae, MORD = Mordellidae, PHAL = Phalacridae, SCOL = Scolytidae, STAP = Staphylinidae, TENE = Tenebrionidae.

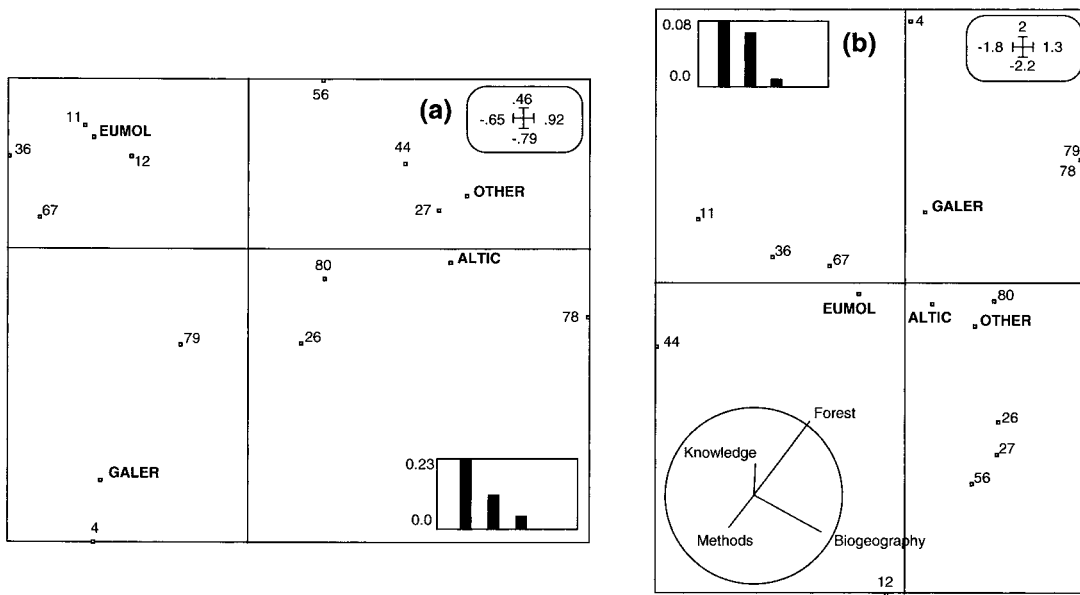


Figure 9. Ordinations of 4 chrysomelid taxa across 12 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Studies are coded with numbers as in Appendix 1. Taxa codes: ALTIC = Alticinae, EUMOL = Eumolpinae, GALER = Galerucinae, OTHER = other Chrysomelidae.

be more sensitive to the effect of forest type than were other chrysomelid subfamilies, but the biological interpretation of this observation is difficult.

Prey-predator ratios and relationships between ants and invertebrates in the canopy

There were significant regressions between spiders and several taxa most likely to be their potential prey (Collembola, Thysanoptera, Psocoptera, arthropod prey, Homoptera, etc., all with $p < 0.05$). The relationships between spiders and their potential prey in the canopy appeared to be most influenced by forest type (Figure 10a, CCA plot not presented for sake of brevity). The constraining variables explained 35% of the total variance (ratio of inertia of CCA to CA = 0.3648/1.0509) and most of the explained variance (74%) was related to forest type (correlation with canonical axis 1, $r = -0.951$, $p < 0.001$). Subtropical and, particularly, dry forest canopies appeared to support high ratios of spiders to Collembola (expressed in numbers of Collembola available to each spider individual), and of spiders to arthropod prey. In contrast, in lowland wet forests, the proportion of ants to spiders tended to be higher (Figure 10a).

In contrast, most of regressions calculated between ants and potential prey were not significant. This con-

firms that ants have a variety of feeding habits and ecological roles in the canopy, which are not restricted to predatory activities (e.g., Tobin 1991). The relationships between ants and several taxa appear to be influenced mostly by forest type (Fig 10b, CCA plot not presented). The constraining variables explained 46% of the total variance (ratio of inertia of CCA to CA 0.2471/0.5404), and 61% of the explained variance was related to forest type (correlation with canonical axis 1, $r = -0.748$, $p < 0.001$). Ratio of ants to other taxa seemed to decrease from the montane forests to lowland wet forests (cf., Stork & Brendell 1990). Montane rain forest may be too cold to allow ants to forage efficiently or for their larvae to develop fast enough (Brown 1973), or the resource base may be too low to allow large populations of their homopteran associates to exist. In lowland forests, high ratios of ants to Homoptera are more common and this may be partly related to mutualism and the tending of homopterans in the canopy in favourable situations. This is consistent with the recent views (e.g., Tobin 1991; Davidson 1997) that most arboreal ants in tropical forests, particularly the dominant forms, are not predators, but obtain their carbohydrates mainly from plant and homopteran exudates.

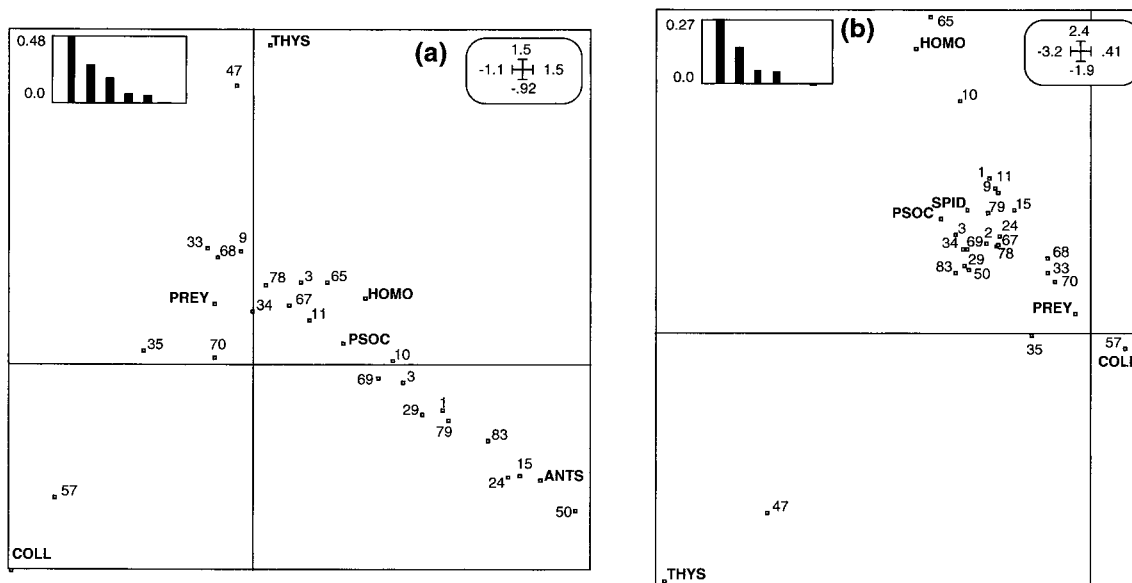


Figure 10. Correspondence analyses of prey-predator ratios across 23 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) prey-spider ratios and (b) arthropod-ant ratios. Studies are coded with numbers as in Appendix 1. Ratio codes: ANTS = Formicidae; COLL = Collembola; HOMO = Homoptera; PREY = all arthropod prey; PSOC = Psocoptera; SPID = Araneae; THYS = Thysanoptera.

Conclusions: prospects in the study of canopy invertebrates

The overall picture of the canopy as habitat for invertebrates is strongly influenced by collecting methods, a common situation in entomology. For general surveys of the canopy, it would be preferable to use a panoply of techniques rather than a particular method (Basset et al. 1997), and to standardize samples obtained with these methods (e.g., 'sampling package': Gadagkar et al. 1990; Stork 1994). Although this is common knowledge in entomology, time and financial constraints often result in only one method being applied, often fogging. The studies of Hammond (1990) and Noyes (1989) in Sulawesi, who collected Coleoptera and Hymenoptera respectively, with several complimentary methods, are exemplary and show how much can be accomplished with this strategy.

Whether the canopy should be studied on its own or conjointly with other forest habitats, such as soil and litter, is debatable. Many insect herbivores, such as some chrysomelids and curculionids, feed on roots as larvae and later migrate in the canopy to feed as adults on leaves. Although it is relatively easy to report differences in the occurrence of particular species of beetles in the adult stage either in the soil or in the canopy, our understanding of the relationships between the canopy and soil should also proceed by

assessing how many insect species depend on the soil/litter habitat during their juvenile stages and on the canopy during their adult phase. Understanding the distribution of adult insects in the canopy may require solid data on their distribution as larvae in the soil (Basset & Samuelson 1996). Further, comparison between the litter and canopy faunas may emphasize specific adaptations of arboreal invertebrates which may be important from a conservation viewpoint.

For studies of specific taxa and/or topics, many specific methods have been devised and as the study of canopy invertebrates progress, new methods are likely to surface, as entomologists represent a rather ingenious breed. Recently, arboreal bait traps have been used to study dung beetles in the canopy (Davis & Sutton 1998), selective fogging with a cotton roof to study recolonization dynamics and disturbance (Floren & Linsenmair 1997; Floren & Linsenmair 2001), and bioacoustic monitoring to study sound-producing arthropods (Riede 1997), to cite a few examples.

Studies such as these, at a finer scale in the canopy, are imperative to understand better insect distribution patterns within and between tree crowns, or movements of invertebrates between different canopy habitats. Ultimately, distribution data are important to estimate the diversity, host specificity and endemism of canopy invertebrates and how these taxa are affected by forest fragmentation and destruction. In

the 1980s there have been formidable claims that the tropical canopy may harbour most of the arthropod species on Earth and that these species are highly host-specific (Erwin 1982). To date, these claims have not been substantiated as either the soil fauna appears as rich or richer than the canopy fauna (e.g., Stork 1988; Hammond 1990), or canopy insects appear much less specialised than originally thought (Basset et al. 1996a; Kitching et al. 1997). If anything, more data are needed to substantiate this. Killing insects during a series of fogging snapshots may represent a first step towards this direction, but may not, in the end, resolve the debate. Mass-rearing of live insects, obtained from various rain forest habitats, appears much more promising toward this goal.

The study of insect host specificity in tropical rain forests and in their canopy appears to be related to at least three critical issues: (1) sample size, (2) number of singleton and rare species and (3) aggregation patterns of arthropods. Since the vegetation is highly diverse in rain forests, the sample size needed to estimate the true range of a species of herbivorous insect must be high, although no guidelines exist at the moment. Sufficient spatial and temporal replicates need to be combined with natural history data, rather than analysing the distribution of dead arthropods within a few snapshot samples, even with robust mathematics. Insufficient sampling and the mass effect described by Shmida and Wilson (1985) partly explain why so many species are represented by singletons in canopy samples (e.g., Morse et al. 1988; Allison et al. 1997; Basset 1997). In tropical rain forests, the distribution of many insect herbivores is aggregated on the foliage, even for generalist species (Novotny & Basset 2000; Basset 2000). This is reflected in their apparent host specificity and rarity at low sample size (Novotny & Basset 2000). These spatial and temporal considerations are not trivial in canopy science, since canopy access is often difficult, partial and constrained. With regard to invertebrate samples obtained *in situ*, seasonal aggregation may be better studied with construction cranes (e.g., Wright 1995; Ødegaard 1999; H. Barrios pers. comm.), whereas spatial aggregation may be better studied with mobile devices such as the canopy raft or the canopy sledge (e.g., Ebersolt 1990; see Basset et al. 1992; 1997).

That the higher taxonomic composition of the invertebrate fauna and various prey-predator relationships in the canopy vary more in particular forest types than across different biogeographical regions is interesting both from the ecological and conservationist

viewpoints. From the former, this suggests that similar forces act on canopy invertebrates in different biogeographical regions to result in predictable communities of canopy invertebrates, but that these forces are different across forest types. Both the nutrient status and weather conditions are likely to contribute much to higher taxonomic differences in the fauna across forest types.

From the conservation viewpoint, this suggests that canopy invertebrates inhabiting certain types of rain forests may be particularly at risk, depending on the selection pressures at work in these forests. The relationships between soil and canopy may be important in shaping these selection pressures. In dry (seasonal) rain forests, many tree species are deciduous or partly deciduous and it is probable that nutrient cycling there is quicker than in wet rain forests, where the foliage turnover of evergreen trees is slower. Canopy arthropods may present a variety of adaptations to cope with gradual or sudden leaf exchange and increase in irradiance and water stress, or they may migrate to other locations, as it is known for a variety of moths (e.g., Janzen 1988b). As such, resilience to natural or man-made disturbance may be greater in wet rain forests than in dry forests (see Janzen 1988a) and the inhabitants of the former may be particularly at risk from disturbance.

In montane rain forests, the trunks of trees often bear a thick cover of mosses and epiphytes and the canopy is often lower than in lowland rain forests. Thus, the continuity between the soil/litter and canopy in montane forests may be greater than in lowland forests, and this could explain the higher occurrence in the former of taxa well-represented in the soil/litter habitat, such as Collembola, Acari and Arachnida (e.g., Stork & Brendell 1990). It is possible that the resilience of a rain forest after disturbance may depend in part on the continuity between the soil/litter and canopy habitats and the ecological processes that occur there. If this is the case, the resilience after disturbance of lowland rain forests may be greater than in montane rain forests. Testing this (and the previous proposition) would be challenging, but it may provide powerful indications of which taxa in the canopy may be particularly at risk from man-induced disturbance and how best to slow down the extinction of species in these habitats.

A long-term comparative study of invertebrates in the canopy of two different forest types would represent an excellent unifying study theme, as well as a fascinating challenge, for entomologists interested

in the canopy of tropical forests. Ideally, the protocol should collect invertebrates with a wide array of collecting methods in most canopy habitats (targeting soil/litter habitats less extensively but appropriately), at locations offering good canopy access and infrastructure. The taxonomic study of the material collected in such conditions is likely to be a formidable challenge, but at least the initial burden of collecting, preparing and pre-sorting this material could be greatly facilitated by working with local parataxonomists specifically trained for this purpose (e.g., Janzen 1993; Novotny et al. 1997; Basset et al. 2000). Although Lawton et al. (1998) noted the huge scale of the biological effort required to provide inventories of tropical diversity, their view was over-pessimistic as they did not conceive recourse to local parataxonomists. Further, recent advances in digital photography and computing power are likely to help greatly in this task (Novotny et al. 1997; Basset et al. 2000). As far as possible, this collaborative effort should be planned with other zoologists and botanists, perhaps taking advantage of permanent botanical plots (Godfray et al. 1999).

The present recommendation rallies earlier pleas for local, long-term and extensive inventories of biodiversity (e.g., André et al. 1992; Janzen 1993; Stork 1994), which have been only partly implemented by the scientific community due to lack of funding and truly international enthusiasm and cooperation among scientists. To date, only three arthropod inventories in tropical forests are on-going and extensive (in terms of scope, time and methods), but they are all situated in the Neotropics and do not target specifically the canopy (Guanacaste area: Janzen 1998; La Selva: Longino & Colwell 1997; Manaus: Fonseca et al. 1998). Two of these inventories result from routine work of local parataxonomists. This type of study is not currently fashionable and may often be neglected by funding agencies, in comparison with reductionist studies of a handful of organisms (e.g., Lawton 1991). However, it appears to be one good strategy of research – if not the only one – towards a better understanding and conservation of the myriad animal and plant interactions in tropical rain forests.

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References

- Adis, J. 1997. Terrestrial invertebrates: survival strategies, group spectrum, dominance and activity patterns. Pp. 318–330. In: Junk, W. J. (ed.), *The Central Amazon Floodplain. Ecological studies*, Vol. 126. Springer-Verlag, Berlin.
- Adis, J., Basset, Y., Floren, A., Hammond, P. M. & Linsenmair, K. E. 1998. Canopy fogging of an overstorey tree – Recommendations for standardization. *Ecotropica* 4: 93–97.
- Adis, J., Lubin, Y. D. & Montgomery, G. G. 1984. Arthropods from the canopy of inundated and Terra firme forest near Manaus, Brazil, with critical consideration on the Pyrethrum-fogging technique. *Stud. Neotrop. Fauna Environ.* 19: 223–236.
- Adis, J., Paarmann, W., da Fonseca, C. R. V. & Rafael, J. A. 1997a. Knockdown efficiency of natural pyrethrum and survival rate of living arthropods obtained by canopy fogging in Central Amazonia. Pp. 67–81. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Adis, J. & Righi, G. 1989. Mass migration and life cycle adaptation – a survival strategy of terrestrial earthworms in Central Amazonian inundation forests. *Amazonia* 11: 23–30.
- Adis, J., Scheller, U., Wellington, J. de M., Rochus, C., Gomes Rodrigues, J. M. 1997b. Symphyla from Amazonian non-flooded upland forests and their adaptations to inundation forests. *Ent. Scand. Suppl.* 51: 307–317.
- Allison, A., Samuelson, G. A. & Miller, S. E. 1997. Patterns of beetles species diversity in *Castanopsis acuminatissima* (Fagaceae) trees studied with canopy fogging techniques in mid-montane New Guinea rain forest. Pp. 224–236. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Amedegnato, C. 1997. Diversity of an Amazonian canopy grasshopper community in relation to resource partitioning and phylogeny. Pp. 281–319. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy Arthropods*. Chapman & Hall, London.
- André, H. M., Lebrun, P. & Noti, M.-I. 1992. Biodiversity in Africa: a plea for more data. *J. Afr. Zool.* 106: 3–15.
- Bakarr, M. I., Gbakima, A. A., Bah, Z. 1991. Intestinal helminth parasites in free-living monkeys from a west African rain forest. *Afr. J. Ecol.* 29: 170–172.
- Barrios, H. 1997. Fluctuacion poblacional de curculionidos (Coleoptera: Curculionidae) capturados en trampa de luz en la isla Barro Colorado. *Scientia* 12: 55–68.

- Basset, Y. 1991. The taxonomic composition of the arthropod fauna associated with an Australian rain forest tree. *Aust. J. Zool.* 39: 171–190.
- Basset, Y. 1997. Species – abundance and body size relationships in insect herbivores associated with New Guinea forest trees, with particular reference to insect host-specificity. Pp. 237–264. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Basset, Y. 2000. Insect herbivores foraging on seedlings in an unlogged rain forest in Guyana: spatial and temporal considerations. *Stud. Neotrop. Fauna Environ.*, 35: 115–129.
- Basset, Y., Aberlenc, H.-P. & Delvare, G. 1992. Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecol. Entomol.* 17: 310–318.
- Basset, Y., Charles, E. C. & Novotny, V. 1999. Insect herbivores on parent trees and conspecific seedlings in a rain forest in Guyana. *Selbyana* 20: 146–158.
- Basset, Y., Novotny, V., Miller, S. E. & Pyle, R. 2000. Quantifying biodiversity: Experience with parataxonomists and digital photography in New Guinea and Guyana. *BioScience* 50: 899–908.
- Basset, Y. & Samuelson, G. A. 1996. Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. Pp. 243–262. In: Jolivet, P. H. A. & Cox, M. L. (eds), *Chrysomelidae Biology. Volume 2: Ecological studies*. SPB Academic Publishing, Amsterdam.
- Basset, Y., Samuelson, G. A., Allison, A. & Miller, S. E. 1996a. How many host-specific insect species feed on a species of tropical tree? *Biol. J. Linn. Soc.* 59: 201–216.
- Basset, Y., Samuelson, G. A. & Miller, S. E. 1996b. Similarities and contrasts in the local insect faunas associated with ten forest tree species of New Guinea. *Pac. Sci.* 50: 157–183.
- Basset, Y., Springate, N. D., Aberlenc, H.-P. & Delvare, G. 1997. A review of methods for sampling arthropods in tree canopies. Pp. 27–52. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Beebe, W. 1925. Studies of a tropical jungle; one quarter of a square mile of jungle at Kartabo, British Guiana. *Zoologica* 6: 4–193.
- Behan-Pelletier, V. M., Paoletti, M. G., Bissett, B. & Stinner, B. R. 1993. Oribatid mites of forest habitats in northern Venezuela. *Trop. Zool.*, Special Issue 1: 39–54.
- Broadhead, E. & Wolda, H. 1985. The diversity of Psocoptera in two tropical forests in Panama. *J. Anim. Ecol.* 54: 739–754.
- Brown, W. L. Jr. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas. Pp. 161–185. In: Meggers, B. J., Ayensu, E. S. & Duckworth, W. D. (eds), *Tropical forest ecosystems in Africa and South America: a comparative review*. Smithsonian Institution Press, Washington.
- Casson, D. S. & Hodkinson, I. D. 1991. The Hemiptera (Insecta) communities of tropical rain forest in Sulawesi. *Zool. J. Linnol. Soc.* 102: 253–275.
- Chabaud, A. G. & Bain, O. 1990. Three new filariae from African rain forest birds. *Bull. Mus. Nat. Hist. Nat. A* 12: 9–18.
- Chessel D. & Dolédec, S. 1992. ADE Version 3.4. HyperCard stacks and quick basic Microsoft programme library for the analysis of environmental data, user's manual, modules graphiques, fiches pratiques, URA CNRS 1451, Université Lyon 1, Villeurbanne, France.
- Chey, V. K., Holloway, J. D., Hambler, C. & Speight, M. R. 1998. Canopy knockdown of arthropods in exotic plantations and natural forest in Sabah, north-east Borneo, using insecticidal mist-blowing. *Bull. Ent. Res.* 88: 15–24.
- Clastrier, J. & Delecolle, J. C. 1997. Description de *Forcipomya (Trichohelea) roubaudi* n. sp., ectoparasite d'un Hétéroptère Reduviidae capturé dans la canopée de la forêt guyanaise (Diptera, Ceratopogonidae). *Bull. Soc. Ent. France* 102: 379–383.
- Coley, P. D. & Aide, T. M. 1991. Comparison of herbivory and plant defense in temperate and tropical broad-leaved forests. Pp. 25–49. In: Price P. W., Lewinsohn, T. M., Fernandes, G. W. & Benson, W. W. (eds), *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, New York.
- Coley, P. D. & Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol.* 27: 305–335.
- Corbet, P. S. 1961. Entomological studies from a high tower in Mpanga Forest, Uganda. VI. Nocturnal flight activity of Culiidae and Tabanidae as indicated by light traps. *Trans. Roy. Ent. Soc. Lond.* 113: 301–314.
- Cotgreave, P., Hill, M. J. & Middleton, D. A. J. 1993. The relationship between body size and population size in bromeliad tank faunas. *Biol. J. Linn. Soc.* 49: 367–380.
- Cowie, R. H. 1992. Evolution and extinction of Partulidae, endemic Pacific island land snails. *Phil. Trans. Roy. Soc. Lond. B* 335: 167–191.
- Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.* 61: 153–181.
- Davies, J. G., Stork, N. E., Brendell, M. J. D. & Hine, S. J. 1997. Beetle species diversity and faunal similarity in Venezuelan rain forest tree canopies. Pp. 85–103. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Davis, A. J. & Sutton, S. L. 1998. The effects of rain forest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. *Diversity Distrib.* 4: 167–173.
- Dejean, A., Belin, M. & McKey, D. 1992. Les relations plantes-fourmis dans la canopée. Pp. 76–80. In: Hallé, F. & Pascal, O. (eds) *Biologie d'une canopée de forêt équatoriale – II. Rapport de Mission: radeau des cimes octobre novembre 1991, Réserve de Campo, Cameroun*. Fondation Elf, Paris.
- Dejean, A., Orivel, J., Corbara, B., Delabie, J. & Teillier, L. 1998. La mosaïque des fourmis arboricoles. Pp. 140–153. 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*. Pro-Natura International & Opération Canopée, Paris.
- DeVries, P. J., Murray, D. & Lande, R. 1997. Species diversity in vertical, horizontal and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rain forest. *Biol. J. Linn. Soc.* 62: 343–364.
- Dial, R. & Roughgarden, J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* 76: 1821–1834.
- Didham, R. K. 1997. Dipteran tree-crown assemblages in a diverse southern temperate rain forest. Pp. 320–343. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Ebersolt, G. 1990. Bilan technique partie radeau. Pp. 15–26. In: Hallé, F. & Blanc, P. (eds), *Biologie d'une canopée de forêt équatoriale. Rapport de Mission. Radeau des Cimes Octobre-Novembre 1989, Guyane Française*. Montpellier II and CNRS-Paris VI, Montpellier/Paris.
- Eggleton, P., Bignell, D. E., Sands, W. A., Mawdsley, N. A., Lawton, J. H., Wood, T. G. & Bignell, N. C. 1996. The diversity, abundance and biomass of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Phil. Trans. Roy. Soc. Lond. B* 351: 51–68.

- Elton, C. S. 1975. Conservation and the low population density of invertebrates inside neotropical rain forests. *Biol. Cons.* 7: 3–15.
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Col. Bull.* 36: 74–75.
- Erwin, T. L. 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. Pp. 59–76. In: Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds), *Tropical rain forest: ecology and management*. Oxford, Blackwell.
- Erwin, T. L. 1989. Canopy arthropod biodiversity: a chronology of sampling techniques and results. *Rev. Per. Ent.* 32: 71–77.
- Erwin, T. L. 1995. Measuring arthropod biodiversity in the tropical forest canopy. Pp. 109–127. In: Lowman, M. D. & Nadkarni, N. M. (eds), *Forest canopies*. Academic Press, San Diego.
- Erwin, T. L. & Scott, J. C. 1980. Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. *Col. Bull.* 34: 305–322.
- Farrell, B. D. & Erwin, T. L. 1988. Leaf-beetle community structure in an amazonian rain forest canopy. Pp. 73–90. In: Jolivet, P., Petitpierre, E. & Hsiao, T. H. (eds), *Biology of chrysomelidae*. Kluwer Academic Publishers, Dordrecht.
- Fisk, F. W. 1983. Abundance and diversity of arboreal Blattaria in moist tropical forests in the Panama Canal area and Costa Rica. *Trans. Am. Ent. Soc.* 108: 479–490.
- Floren, A. & Linsenmair, K. E. 1997. Diversity and recolonization dynamics of selected arthropod groups on different tree species in a lowland rain forest in Sabah, Malaysia with special reference to Formicidae. Pp. 344–381. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Floren, A. & Linsenmair, K. E. 2001. Changes in arboreal arthropod communities along a disturbance gradient. *Plant Ecol.* 153: 153–167 (this volume).
- Fonseca, C. R. V. da, Adis, J. & Martius, C. 1998. Mechanisms that maintain tropical diversity – a project of Teuton-Brazilian cooperation 1991–1996. *Acta Amazon.* 28: 205–215.
- Fragoso, C. & Rojas-Fernandez, P. 1996. Earthworms inhabiting bromeliads in Mexican tropical rain forests: ecological and historical determinants. *J. Trop. Ecol.* 12: 729–734.
- Franklin, E., Adis, J., Woas, S. 1997. The oribatid mites. Pp. 331–349. In: Junk, W. J. (ed.), *The Central Amazon floodplain*. Ecological Studies, Vol. 126. Springer-Verlag, Berlin.
- Gadagkar, R., Chandrashekhara, K. & Nair, P. 1990. Insect species diversity in the tropics: sampling methods and a case study. *J. Bombay Nat. Hist. Soc.* 87: 337–353.
- Gagné, W. C. 1979. Canopy-associated arthropods in *Acacia Koa* and *Metrosideros* trees communities along an altitudinal transect on Hawaii Island. *Pac. Ins.* 21: 56–82.
- Galindo, P., Trapido, H., Carpenter, S. J., Blanton, F. S. 1956. The abundance cycles of arboreal mosquitoes during six years at a sylvan yellow fever locality in Panama. *Ann. Ent. Soc. Am.* 49: 543–547.
- García, M. N. J. 1999. Estructura y dinámica de los insectos del orden Coleoptera en la copa del árbol *Luehea seemannii* Triana y Planch 1862 (Tiliaceae), en el dosel del bosque del Parque Metropolitano, Panamá. Tesis de Maestría en Ecología y Conservación, Universidad Santa María La Antigua, Panamá.
- Garrison, R. W. & Willig, M. R. 1996. Arboreal invertebrates. Pp. 183–245. In: Reagan, D. P. & Waide, R. B. (eds), *The food web of a tropical rain forest*. The University of Chicago Press, Chicago.
- Godfray, H. C., Lewis, O. T. & Memmott, J. 1999. Studying insect diversity in the tropics. *Phil. Trans. Roy. Soc. Biol. Sci.* 354: 1811–1824.
- Guilbert, E. 1997. Arthropod biodiversity in the canopy of New Caledonian forests. Pp. 265–277. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Hammond, P. M. 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. Pp. 197–254. In: Knight, W. J. & Holloway, J. D. (eds), *Insects and the rain forests of South East Asia (Wallacea)*. The Royal Entomological Society of London, London.
- Hammond, P. M. 1992. Species inventory. Pp. 17–39. In: Groombridge, B. (ed.), *Global biodiversity, status of the earth's living resources*. Chapman & Hall, London.
- Hammond, P. M. 1995. Magnitude and distribution of biodiversity. Pp. 113–138. In: Heywood, V. T. & Watson, R. T. (eds), *Global biodiversity assessment*. Cambridge University Press, Cambridge.
- Hammond, P. M., R. L. Kitching & N. E. Stork 1996. The composition and richness of the tree-crown Coleoptera assemblage in an Australian subtropical forest. *Ecotropica* 2: 99–108.
- Hartnoll, R. G. 1964. The freshwater grasspidd crabs of Jamaica. *Proceedings of the Linnean Society of London* 175: 145–169.
- Hill, C. J. & Cermak, M. 1997. A new design and some preliminary results for a flight intercept trap to sample forest canopy arthropods. *Aust. J. Ent.* 36: 51–55.
- Hingston, R. W. G. 1932. *A naturalist in the Guiana forest*. Edward Arnold & Co., London.
- Höfer, H., Brescovit, A. D. Adis, J. & Paarman, W. 1994. The spider fauna of neotropical tree canopies in Central Amazonia: first results. *Stud. Neotrop. Fauna Environm.* 29: 23–32.
- Holloway, J. D. 1987. Macrolepidoptera diversity in the Indo-Australian tropics: geographic, biotopic and taxonomic variations. *Biol. J. Linnol. Soc.* 30: 325–341.
- Hopkin, S. P. & Read, H. J. 1992. *The biology of millipedes*. Oxford Science Publications, Oxford.
- Janzen, D. H. 1988a. Tropical dry forests. The most endangered major tropical ecosystem. Pp. 130–137. In: Wilson, E. O. (ed), *Biodiversity*. National Academy Press, Washington.
- Janzen, D. H. 1988b. Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica* 20: 120–135.
- Janzen D. H. 1993. Taxonomy: Universal and essential infrastructure for development and management of tropical wildland biodiversity. Pp. 100–113. In: Sandlund, O. T. & Schei, P. J. (eds), *Proceedings of the Norway/UNEP expert conference on biodiversity*. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim.
- Janzen, D. H. 1998. How to grow a wildland: the gardenification of nature. *Ins. Sci. Appl.* 17: 269–276.
- Junk, W. J. 1997. *The Central Amazon Floodplain. Ecology of a pulsing system*. Springer-Verlag, Berlin.
- Kato, M., Inoue, T. Hamid, A. A. Nagamitsu, T. Merdek, M. B. Nona, A. R. Itino, T., Yamane, S., Yumoto, T. 1995. Seasonality and vertical structure of light-attracted insect communities in a Dipterocarp forest in Sarawak. *Res. Popul. Ecol.* 37: 59–79.
- Kitching, R. L. 1987. A preliminary account of the metazoan food webs in phytotelmata from Sulawesi. *Malay. Nat. J.* 41: 1–12.
- Kitching, R. L. In press. *Container Habitats and Foodwebs*. Kluwer, Amsterdam.
- Kitching, R. L., Bergelson, J. M., Lowman, M. D., McIntyre, S. & Carruthers, G. 1993. The biodiversity of arthropods from Australian rain forest canopies: general introduction, methods, sites and ordinal results. *Aust. J. Ecol.* 18: 181–191.
- Kitching, R. L., Mitchell, H., Morse, G. & Thebaud, C. 1997. Determinants of species richness in assemblages of canopy arthropods

- in rain forests. Pp. 131–150. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Knight, W. J. & Holloway, J. D. 1990. Insects and the Rain Forests of South East Asia (Wallacea). Royal Entomological Society of London, London.
- Lawton, J. H. 1991. Species richness, population abundances, and body sizes in insect communities: tropical versus temperate comparisons. Pp. 209–225. In: Price, P. W., Lewinsohn, T. M., Fernandes, G. W. & Benson, W. W. (eds), *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley, New York.
- Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleston, P., Hammond, P. M., Hodda, M., Holt, R. D., Larsen, T. B., Mawdsley, N. A., Stork, N. E., Srivastava, D. S. & Watt, A. D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72–76.
- Leigh, E. G., Rand, A. S. & Windsor, D. M. 1996. The ecology of a tropical forest: seasonal rhythms and long-term changes. Second edition. Smithsonian Institution Press, Washington.
- Lieth, H. & Werger, M. J. A. 1989. *Tropical rain forest ecosystems. Biogeographical and ecological studies*. Elsevier, Amsterdam.
- Longino, J. T. & Colwell, R. C. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecol. Appl.* 7: 1263–1277.
- Lounibos, L. P. 1981. Habitat segregation among African treehole mosquitoes. *Ecol. Entomol.* 6: 129–154.
- Lourenço, W. R. 1988. Synopsis de la faune scorpionne de la région de Manaus, Etat d' Amazonas, Brésil, avec description de deux nouvelles espèces. *Amazonia* 10: 327–337.
- Louton, J., Gelhaus, J. & Bouchard, R. 1996. The aquatic macrofauna of water-filled bamboo (Poaceae: Bambusoideae: *Guadua*) internodes in a Peruvian lowland tropical forest. *Biotropica* 28: 228–242.
- Lowman, M. D. 1995. Herbivory as a canopy process in rain forest trees. Pp. 431–455. In: Lowman, M. D. & Nadkarni, N. M. (eds), *Forest canopies*. Academic Press, San Diego.
- Lowman, M. D., Foster, R., Wittman, P. & Rinker, H. B. 1998. Herbivory and insect loads on epiphytes, vines and host trees in the rain forest canopy of French Guiana. Pp. 116–128. In: Hallé, F. (ed), *Biologie d'une canopée de forêt équatoriale – III. Rapport de la mission d'exploration scientifique de la Canopée de Guyane, Octobre–Décembre 1996*. Pro-Natura International & Opération Canopée, Paris.
- Lowman, M. D. & Moffett, M. 1993. The ecology of tropical rain forest canopies. *T.R.E.E.* 8: 104–107.
- Lowman, M. D. & Wittman, P. K. 1996. Forest canopies: methods, hypotheses, and future directions. *Annu. Rev. Ecol. Syst.* 27: 55–81.
- Malcolm, J. R. 1997. Insect biomass in Amazonian forest fragments. Pp. 510–533. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Martius, C. 1994. Diversity and ecology of termites in Amazonian forests. *Pedobiologia* 38: 407–428.
- May, R. M. 1994. Past efforts and future prospects towards understanding how many species there are. Pp. 71–84. In: Sollbrig, O. T., van Emden, H. M. & van Oordt, P. G. W. J. (eds), *Biodiversity and global change*. C.A.B. International, Wallingford.
- McClure, H. E. 1978. Some arthropods of the dipterocarp forest canopy in Malaya. *Malay. Nat. J.* 32: 31–51.
- Missa, O. 1999. Diversity and spatial heterogeneity of a weevil fauna living in the canopy of a tropical lowland rain forest in Papua New Guinea. Thèse, Université Libre de Bruxelles, Bruxelles.
- Moffett, M. W. & Lowman, M. D. 1995. Canopy access techniques. Pp. 3–26. In: Lowman, M. D. & Nadkarni, N. M. (eds), *Forest canopies*. Academic Press, San Diego.
- Morais, J. W., Adis, J., Manhart, V., Berti-Filho, E. 1997. Abundance and phenology of Pseudoscorpiones (Arachnida) from a mixedwater inundation forest in Central Amazonia, Brazil. *Rev. Suisse Zool.* 104: 475–483.
- Moran, C. V. & Southwood, T. R. E. 1982. The guild composition of arthropod communities in trees. *J. Anim. Ecol.* 51: 289–306.
- Moran, C. V., Hoffmann, J. H., Impson, F. A. C. & Jenkins, J. F. G. 1994. Herbivorous insect species in the tree canopy of a relict South African forest. *Ecol. Entomol.* 19: 147–154.
- Morse, D. R., Stork, N. E. & Lawton, J. H. 1988. Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. *Ecol. Entomol.* 13: 25–37.
- Nadkarni, N. M. & Longino, J. T. 1990. Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. *Biotropica* 22: 286–289.
- Ng, R. 1978. The vertical distribution of aerial insects in Pasoh Forest Reserve. *Malay. Nat. J.* 30: 299–305.
- Nicolai, V. 1989. Thermal properties and fauna of the bark of trees in two different African ecosystems. *Oecologia* 80: 421–430.
- Novotny, V. & Basset, Y. 2000. Ecological characteristics of rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89: 564–572.
- Novotny, V., Basset, Y., Miller, S. E., Allison, A., Samuelson, G. A. & Orsak, L. J. 1997. The diversity of tropical insect herbivores: an approach to collaborative international research in Papua New Guinea. Pp. 112–125. In: Lee, B. H., Choe, J. C. & Han, H. Y. (eds), *Proceedings of the International Conference on Taxonomy and Biodiversity Conservation in the East Asia*. Korean Institute for Biodiversity Research of Chonbuk National University, Chonju.
- Noyes, J. S. 1989. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecol. Entomol.* 14: 197–207.
- Ødegaard, F. 1999. Host specificity as a parameter in estimates of arthropod species richness. PhD thesis, Norwegian University of Science and Technology, Trondheim.
- Palacios-Vargas, J. G., Castaño Meneses, G. & Gómez-Anaya, J. A. 1998. Collembola from the canopy of a Mexican tropical deciduous forest. *Pan-Pac. Ent.* 74: 47–54.
- Paoletti, M. G., Taylor, R. A. J., Stinner, B. R., Stinner, D. H., & Benzing, D. H. 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *J. Trop. Ecol.* 7: 373–383.
- Penny, A. D. & Arias, J. R. 1982. *Insects of an Amazon forest*. New York, Columbia University Press.
- Rees, C. J. C. 1983. Microclimate and the flying Hemiptera fauna of a primary lowland rain forest in Sulawesi. Pp. 121–138. In: Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds), *Tropical rain forest: ecology and management*. Oxford, Blackwell.
- Riede, K. 1997. Bioacoustic monitoring of insect communities in a Bornean rain-forest canopy. Pp. 442–452. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Roberts, H. R. 1973. Arboreal Orthoptera in the rain forests of Costa Rica collected with insecticide: a report on the grasshoppers (Acrididae), including new species. *Proc. Acad. Nat. Sci. Phil.* 125: 46–66.
- Rodgers, D. J. & Kiching, R. L. 1998. Vertical stratification of rain forest collembolan (Collembola: Insecta) assemblages: de-

- scription of ecological patterns and hypotheses concerning their generation. *Ecography* 21: 392–400.
- Roubik, D. W. 1993. Tropical pollinators in the canopy and understory: field data and theory for stratum 'preferences'. *J. Ins. Behav.* 6: 659–673.
- Russell-Smith, A. & Stork, N. E. 1994. Abundance and diversity of spiders from the canopy of tropical rain forests with particular reference to Sulawesi, Indonesia. *J. Trop. Ecol.* 10: 545–558.
- Russell-Smith, A. & Stork, N. E. 1995. Composition of spider communities in the canopies of rain forest trees in Borneo. *J. Trop. Ecol.* 11: 223–235.
- Schowalter, T. D. 1994. Invertebrate community structure and herbivory in a tropical rain forest canopy in Puerto Rico following hurricane Hugo. *Biotropica* 26: 312–319.
- Shmida, A. & Wilson, M. V. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12: 1–20.
- Smythe, N. 1982. The seasonal abundance of night-flying insects in a Neotropical forest. Pp. 309–318. In: Leigh, E. G. jr., Rand, A. S. & Windsor, D. M. (eds), *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington.
- Stoner, K. E. 1996. Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: implications for conservation biology. *Cons. Biol.* 10: 539–546.
- Stork, N. E. 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* 35: 321–337.
- Stork, N. E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *J. Trop. Ecol.* 7: 161–180.
- Stork, N. E. 1994. Inventories of biodiversity: more than a question of numbers. Pp. 81–100. In: Forey, P. I., Humphries, C. J. & Vane-Wright, R. I. (eds), *Systematics and conservation evaluation*. Clarendon Press, Oxford.
- Stork, N. E. 1996. Tropical forest dynamics: the faunal components. Pp. 1–20. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds), *Tropical rain forest research – current issues*. Kluwer Academic Publishers, Amsterdam.
- Stork, N. E., Adis, J. & Didham, R. K. 1997. *Canopy arthropods*. Chapman & Hall, London.
- Stork, N. E. & Brendell, M. J. D. 1990. Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. Pp. 173–190. In: Knight, W. J. & Holloway, J. D. (eds), *Insects and the rain forests of South East Asia (Wallacea)*. The Royal Entomological Society of London, London.
- Stork, N. E. & Brendell, M. J. D. 1993. Arthropod abundance in lowland rain forest of Seram. Pp. 115–130. In: Edwards, I. D., MacDonald, A. A. & Proctor, J. (eds), *Natural History of Seram, Maluku, Indonesia*. Intercept, Andover.
- Stuntz, S., Simon, U. & Zotz, G. 1999. Assessing potential influence of vascular epiphytes on arthropod diversity in tropical tree crowns: hypotheses, approaches, and preliminary data. *Selbyana* 20: 276–283.
- Sutton, S. L. 2001. Alice grows up: canopy science in transition from Wonderland to reality. *Plant Ecol.* 153: 13–21 (this volume).
- Sutton, S. L. & Hudson, P. J. 1980. The vertical distribution of small flying insects in the lowland rain forest Zaire. *Zool. J. Linnol. Soc.* 68: 111–123.
- Sutton, S. L., Ash, C. P. & Grundy, A. 1983a. The vertical distribution of flying insects in the lowland rain forest of Panama, Papua New Guinea and Brunei. *Zool. J. Linn. Soc.* 78: 287–297.
- Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. 1983b. *Tropical rain forest: ecology and management*. Oxford, Blackwell.
- Tobin, J. E. 1991. A neotropical rain forest canopy, ant community: some ecological considerations. Pp. 536–538. In: Huxley, C. R. & Cutler, D. F. (eds), *Ant-Plant Interactions*. University Press, Oxford.
- Wagner, T. 1997. The beetle fauna of different tree species in forest of Rwanda and East Zaire. Pp. 169–183. In: Stork, N. E., Adis, J. & Didham, R. K. (eds), *Canopy arthropods*. Chapman & Hall, London.
- Wagner, T. 1998. Influence of tree species and forest type on the chrysomelid community in the canopy of an Ugandan tropical forest. *Mus. Reg. Sci. Nat. Torino* 1998: 253–269.
- Walter, D. E. & Behan-Pelletier, V. 1999. Mites in forest canopies: filling the size distribution shortfall. *Annu. Rev. Entomol.* 44: 1–19.
- Walter, D. E. & O'Dowd, D. J. 1995. Life on the forest phylloplane: hairs, little houses, and myriad mites. Pp. 325–351. In: Lowman, M. D. & Nadkarni, N. M. (eds), *Forest canopies*. Academic Press, San Diego.
- Walter, D. E., O'Dowd, D. & Barnes, V. 1994. The forgotten arthropods: foliar mites in the forest canopy. *Mem. Qld Mus.* 36: 221–226.
- Walter, D. E., Seeman, O., Rodgers, D. & Kitching, R. L. 1998. Mites in the mist: how unique is a rain forest canopy-knockdown fauna? *Aust. J. Ecol.* 23: 501–508.
- Watanabe, H. & Ruaysoongnern, S. 1989. Estimation of arboreal arthropod density in a dry evergreen forest in Northeastern Thailand. *J. Trop. Ecol.* 5: 151–158.
- Watt, A. D., Stork, N. E., McBeath, C. & Lawson, G. L. 1997. Impact of forest management on insect abundance and damage in a lowland tropical forest in southern Cameroon. *J. Appl. Ecol.* 34: 985–998.
- Wells, S. M., Pyle, R. M. & Collins, N. M. 1983. *The IUCN invertebrate red data book*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- Wilson, E. O. 1987. The arboreal ant fauna of Peruvian Amazon Forests: a first assessment. *Biotropica* 19: 245–251.
- Wolda, H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecol. Entomol.* 4: 181–190.
- Wolda, H., O'Brien, C. W. & Stockwell, H. P. 1998. Weevil diversity and seasonality in tropical Panama as deduced from light-trap catches (Coleoptera: Curculionoidea). *Smiths. Contr. Zool.* 590: 1–79.
- Wright, J. S. 1995. The canopy crane. p. 15. In: Lowman, M. D. & Nadkarni, N. M. (eds), *Forest canopies*. Academic Press, San Diego.
- Wunderle, I. 1992. Die Baum- und Bodenbewohnenden Oribatiden (Acari) im Tief-landregenwald von Panguana, Peru. *Amazonia* 12: 119–142.
- Young, A. M. 1986. Occurrence of Diptera on tree-trunk mosses in a Costa Rican tropical rain forest. *Pan-Pac. Ent.* 62: 203–208.
- Zug, G. R. & Zug, P. B. 1979. The marine toad, *Bufo marinus*: A natural history resumé of native populations. *Smiths. Contr. Zool.* 284: 1–58.

Appendix I

Mass-collecting of canopy invertebrates examined in this contribution, listed by alphabetical order of the key reference. Collecting methods: EXT = litter extraction; FOG = fogging; HDC = hand collecting, beating and related; LIT = light traps; OTT = other traps; SEV = several methods. Numbers refers to the codes used in the ordinations.

| Key reference | Locality | Focal taxa | Method | No. ind. |
|-------------------------------|--------------------------------|---------------|--------|----------|
| 1. Adis et al. 1984 | Manaus, Brazil | Arthropoda | FOG | 9639 |
| 2. Adis et al. 1997a | Manaus, Brazil | Arthropoda | FOG | 3685 |
| 3. Adis 1997 | Manaus, Brazil | Arthropoda | FOG | 23689 |
| 4. Allison et al. 1997* | Wau, Papua New Guinea | Arthropoda | FOG | 45464 |
| 5. Amedegnato 1997* | Ampiacu, Peru | Acridoidea | HDC | 9177 |
| 6. Amedegnato 1997* | Yubineto, Peru | Acridoidea | HDC | 1156 |
| 7. Barrios 1997 | Barro Colorado Is, Panama | Curculionidae | LIT | 11843 |
| 8. H. Barrios* | Parque Metropolitan, Panama | Insecta | OTT | 77430 |
| 9. Basset 1991 | Mt Glorious, Australia | Arthropoda | SEV | 51600 |
| 10. Basset et al. 1992 | Kribi, Cameroon | Arthropoda | HDC | 2271 |
| 11. Basset et al. 1996b | Wau, Papua New Guinea | Arthropoda | SEV | 78500 |
| 12. Basset et al. 1999 | Mabura Hill, Guyana | Insect herb. | HDC | 1659 |
| 13. Broadhead & Wolda 1985 | Barro Colorado Is, Panama | Psocoptera | LIT | 14393 |
| 14. Casson & Hodkinson 1991 | Dumoga-Bone NP, Sulawesi | Hemiptera | SEV | 25000 |
| 15. Chey et al. 1998 | Brumas, Sabah | Arthropoda | FOG | 1640 |
| 16. Corbet 1961 | Mpanga, Uganda | Diptera | LIT | 2010 |
| 17. Davies et al. 1997 | Henri Pittier NP, Venezuela | Coleoptera | FOG | 6132 |
| 18. Davis & Sutton 1998 | Danum Valley, Sabah | Scarabaeidae | OTT | 2378 |
| 19. Dejean et al. 1992 | Kribi, Cameroon | Formicidae | HDC | na |
| 20. Dejean et al. 1998 | Paracou, French Guiana | Formicidae | HDC | na |
| 21. DeVries et al. 1997 | Jatun Sacha, Ecuador | Nymphalidae | OTT | 6690 |
| 22. Dial & Roughgarden 1995 | Bishley Watershed, Puerto Rico | Arthropoda | SEV | 21200 |
| 23. Erwin 1983 | Manaus, Brazil | Arthropoda | FOG | 24350 |
| 24. Erwin 1989 | Pakitza, Peru | Arthropoda | FOG | 82391 |
| 25. Erwin 1995 | Tambopata, Peru | Insecta | FOG | 42641 |
| 26. Erwin & Scott 1980 | Pipeline Road, Panama | Coleoptera | FOG | 7712 |
| 27. Farrell & Erwin 1988 | Tambopata, Peru | Chrysomelidae | FOG | 2864 |
| 28. Fisk 1983 | Barro Colorado Is, Panama | Blattodea | SEV | 2542 |
| 29. Floren & Linsenmair 1997* | Kinabalu NP, Sabah | Arthropoda | FOG | 155000 |
| 30. Gagné 1979 | Mauna Loa, Hawaii | Arthropoda | FOG | na |
| 31. Galindo et al. 1956 | La Victoria, Panama | Culicidae | HDC | na |
| 32. Garcia 1999* | Parque Metropolitan, Panama | Coleoptera | HDC | 3585 |
| 33. Garrison & Willing 1996 | El Verde, Puerto Rico | Invertebrates | OTT | 4506 |
| 34. Guilbert 1997 | Pindai, New Caledonia | Invertebrates | FOG | 110173 |
| 35. Guilbert 1997 | Riviere Bleue, New Caledonia | Invertebrates | FOG | 63930 |
| 36. Hammond 1990 | Dumoga-Bone NP, Sulawesi | Coleoptera | SEV | 19000 |
| 37. Hill & Cermak 1997 | Paluma Range, Australia | Arthropoda | OTT | 553 |
| 38. Hingston 1932 | Moraballi Creek, Guyana | Arthropoda | OTT | 88 |
| 39. Höfer et al. 1994 | Manaus, Brazil | Araneae | FOG | 235 |
| 40. Holloway 1987 | Gunung Mulu NP, Sarawak | Lepidoptera | LIT | 6066 |
| 41. Holloway 1987 | Gunung Mulu NP, Sarawak | Lepidoptera | LIT | 4834 |
| 42. Janzen 1988b | Santa Rosa NP, Costa Rica | Lepidoptera | HDC | 54000 |

Appendix I continued.

| Key reference | Locality | Focal taxa | Method | No. ind. |
|-----------------------------------|--------------------------------|----------------|--------|----------|
| 43. Kato et al. 1995 | Lambir Hills NP, Sarawak | Insecta | LIT | 1023008 |
| 44. Kitching et al. 1993 | Green Mountains, Australia | Arthropoda | FOG | 22984 |
| 45. Kitching et al. 1993 | Cape Tribulation, Australia | Arthropoda | FOG | 9967 |
| 46. Longino & Colwell 1997 | La Selva, Costa Rica | Formicidae | SEV | 6000 |
| 47. Lowman et al. 1998 | Paracou, French Guiana | Arthropoda | SEV | 1941 |
| 48. Malcolm 1997 | Manaus, Brazil | Insecta | OTT | 59795 |
| 49. McClure 1978 | Genting Sempah, Malaysia | Arthropoda | OTT | na |
| 50. Missa 1999* | Baiteta, Papua New Guinea | Arthropoda | SEV | 234743 |
| 51. Moran et al. 1994 | Pondoland Centre, South Africa | Insect herb. | HDC | na |
| 52. Moran & Southwood 1982 | The Cape, South Africa | Arthropoda | FOG | 6847 |
| 53. Nadkarni & Longino 1990 | Monteverde Forest, Costa Rica | Invertebrates | EXT | na |
| 54. Ng 1978 | Pasoh Forest Reserve, Malaysia | Insecta | OTT | 37198 |
| 55. Noyes 1989 | Dumoga-Bone NP, Sulawesi | Hymenoptera | SEV | 59100 |
| 56. Ødegaard 1999* | Parque Metropolitan, Panama | Beetle herb. | HDC | 33746 |
| 57. Palacios-Vargas et al. 1998 | Chamela, Mexico | Arthropoda | FOG | 1098248 |
| 58. Paolletti et al. 1991 | Henri Pittier NP, Venezuela | Invertebrates | EXT | 4960 |
| 59. Penny & Arias 1982 | Manaus, Brazil | Insecta | LIT | na |
| 60. Rees 1983 | Morolawi, Sulawesi | Insecta | LIT | 3500 |
| 61. Roberts 1973 | Barro Colorado Is, Panama | Acridoidea | FOG | na |
| 62. Roubik 1993 | Parque Metropolitan, Panama | Apoidea | OTT | 2356 |
| 63. Russell-Smith & Stork 1994 | Dumoga-Bone NP, Sulawesi | Araneae | FOG | 1649 |
| 64. Russell-Smith & Stork 1995 | Bukit Sulang, Brunei | Araneae | FOG | 945 |
| 65. Schowalter 1994 | El Verde, Puerto Rico | Invertebrates | HDC | 9143 |
| 66. Smythe 1982 | Barro Colorado Is, Panama | Insecta | LIT | 60000 |
| 67. Stork 1991 | Bukit Sulang, Brunei | Arthropoda | FOG | 23874 |
| 68. Stork & Brendell 1990 | Dumoga-Bone NP, Sulawesi | Arthropoda | FOG | 9158 |
| 69. Stork & Brendell 1993 | Manusela NP, Seram | Arthropoda | FOG | 12006 |
| 70. Stuntz et al. 1999 | Barro Colorado Is, Panama | Arthropoda | SEV | 36875 |
| 71. Sutton et al. 1983a | San Blas, Panama | Insecta | LIT | 4194 |
| 72. Sutton et al. 1983a | Buso, Papua New Guinea | Insecta | LIT | 7013 |
| 73. Sutton et al. 1983a | Temburong, Brunei | Insecta | LIT | 8225 |
| 74. Sutton et al. 1983a | Labi Safari, Brunei | Insecta | LIT | 25151 |
| 75. Sutton & Hudson 1980 | Scierie, Zaire | Insecta | SEV | 32474 |
| 76. Sutton & Hudson 1980 | Weko, Zaire | Insecta | SEV | 33580 |
| 77. Tobin 1991 | Pakitza, Peru | Formicidae | FOG | 19710 |
| 78. Wagner 1997 | East Rwanda | Coleoptera | FOG | 23711 |
| 79. Wagner 1997 | Kivu, Zaire | Coleoptera | FOG | 6279 |
| 80. Wagner 1998* | Budongo, Uganda | Coleoptera | FOG | 29736 |
| 81. Walter et al. 1994* | SE Queensland, Australia | Acari | HDC | 15000 |
| 82. Watanabe & Ruaysoongnern 1989 | Nam Phrom, Thailand | Invertebrates | FOG | na |
| 83. Watt et al. 1997* | Mbalmayo, Cameroon | Arthropoda | FOG | 87000 |
| 84. Wilson 1987 | Tambopata, Peru | Formicidae | FOG | 100000 |
| 85. Wolda 1979 | Barro Colorado Is, Panama | Homoptera | SEV | 6363 |
| 86. Wolda et al. 1998 | Barro Colorado Is, Panama | Curculionoidea | LIT | 95333 |
| 87. Wolda et al. 1998* | Fortuna, Panama | Insecta | LIT | 29467 |
| 88. H. Wolda* | Barro Colorado Is, Panama | Insecta | LIT | 1247264 |
| 89. Wunderle 1992 | Panguana, Peru | Oribatei | EXT | 17382 |

* = supplemented by pers. comm. of the author(s).

na = not available, data not expressed in total no. of individuals collected.

herb. = herbivores