



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

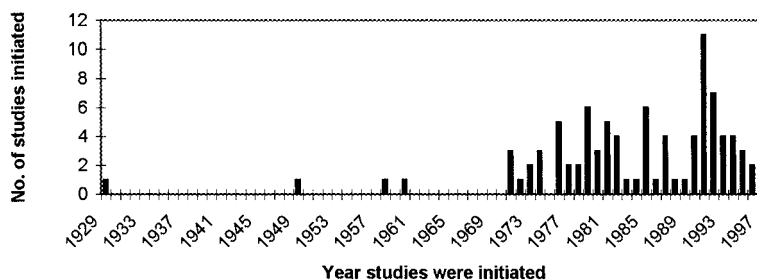


Figure 1. Mass collecting of invertebrates in the canopy of tropical rain forests: distribution of years in which the studies examined in this contribution were initiated.

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.

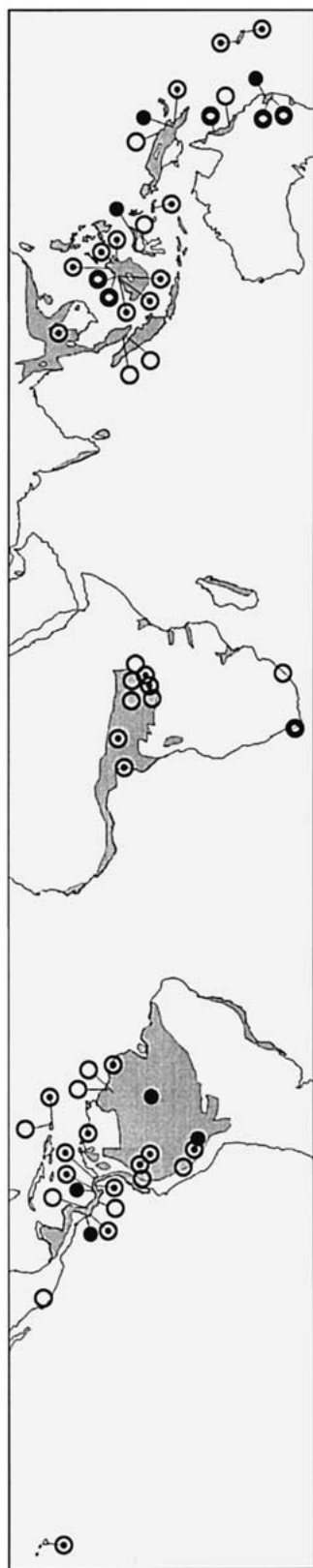


Figure 2. Location of the major sites examined in this contribution, weighted by an estimate of knowledge (see text). ● = > 10 publications, ○ = 6–10 publications, ○ = 2–5 publications, ○ = 1 publication, ○ = 1 publication (see text). ○ = 1 publication, ○ = 6–10 publications, ● = > 10 publications. A 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

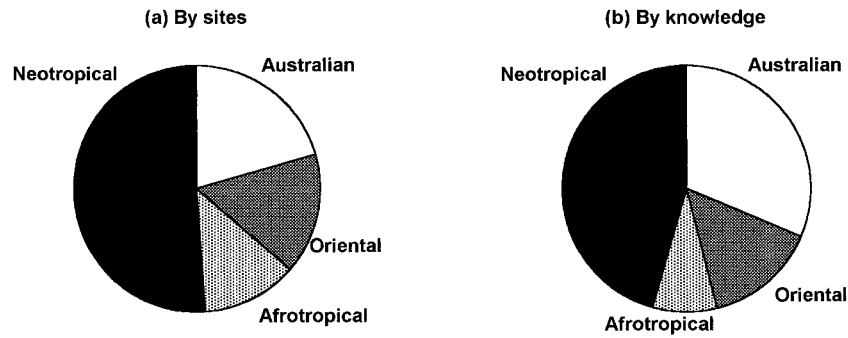


Figure 3. Distribution of studies, ordered by biogeographical regions, either by (a) sites or (b) knowledge (number of publications relevant to each site).

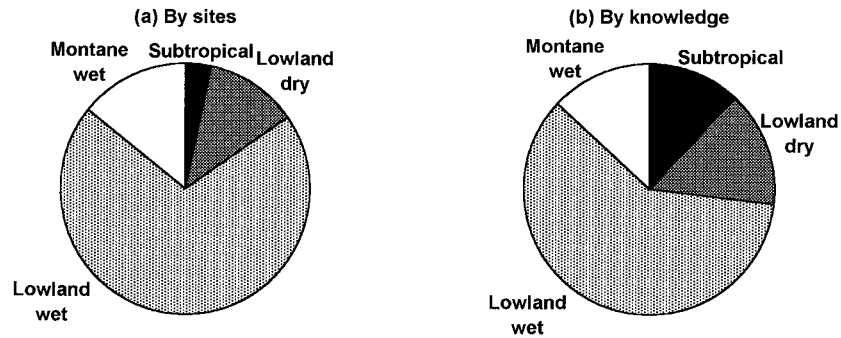


Figure 4. Distribution of studies, ordered by forest type, either by (a) sites or (b) knowledge (number of publications relevant to each site).

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.,

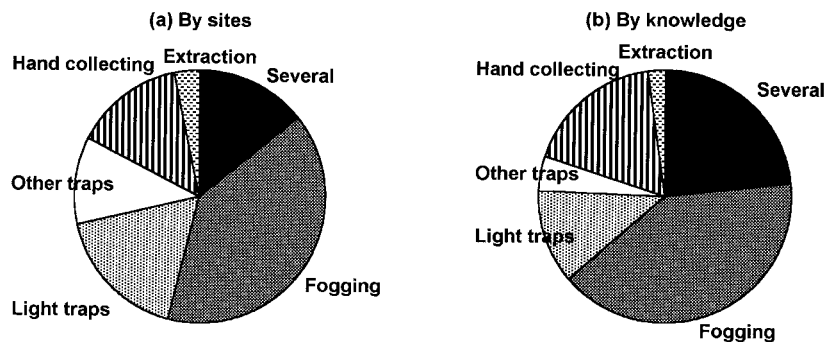


Figure 5. Distribution of studies, ordered by collecting method, either by (a) sites or (b) knowledge (number of publications relevant to each site).

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

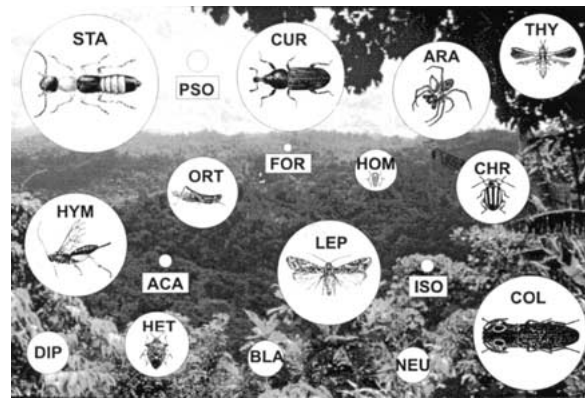


Figure 6. Species-scape in the canopy of a fictitious rain forest. The size of the circles are proportional to the putative species richness (measured as average species \times individuals⁻²) of the taxa, which are abbreviated as follows: STA: Staphylinidae (19.70); COL: other Coleoptera (15.96); CUR: 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

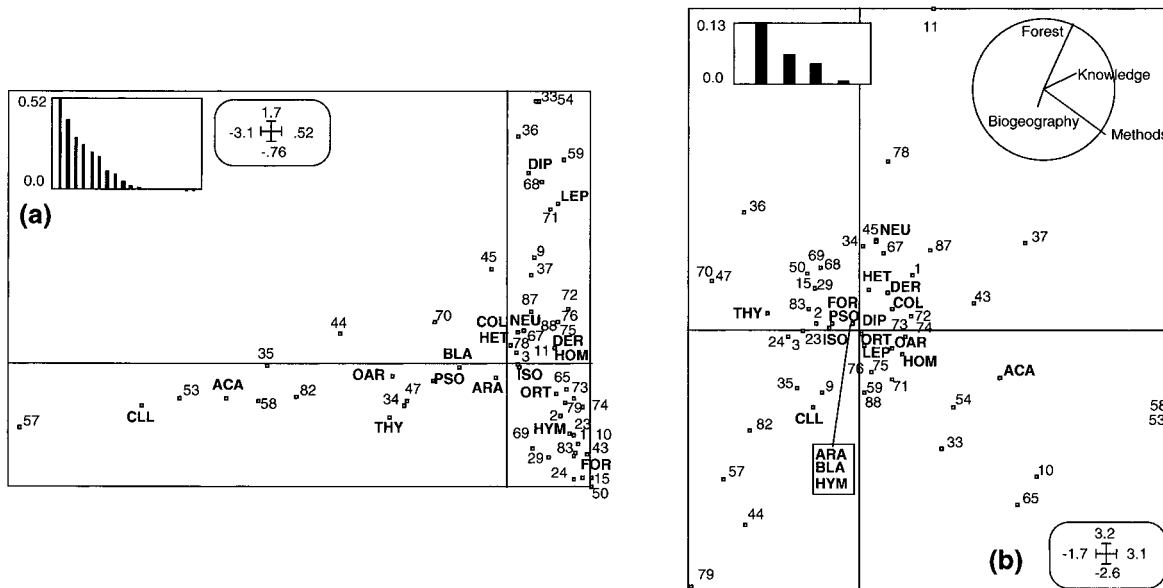


Figure 7. Ordinations of 18 higher insect taxa across 42 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Studies are coded with numbers 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.

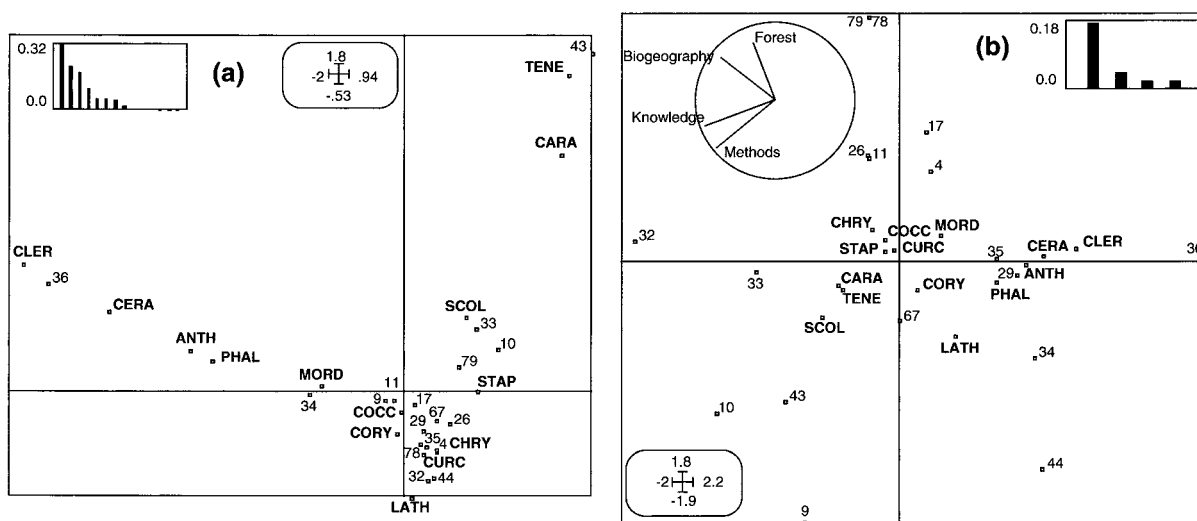


Figure 8. Ordinations of 14 beetle families across 17 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Studies are coded with numbers 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.

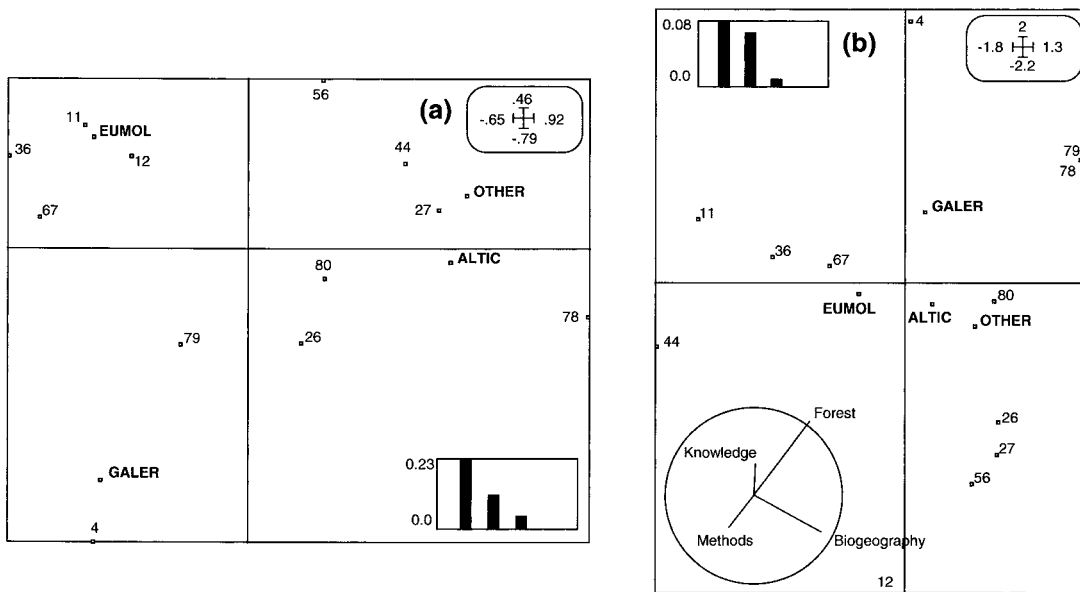


Figure 9. Ordinations of 4 chrysomelid taxa across 12 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) CA and (b) CCA. Inset boxes detail the graphs of eigenvalues and the circle the vectors representing the constraining variables. Studies are coded with numbers 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.

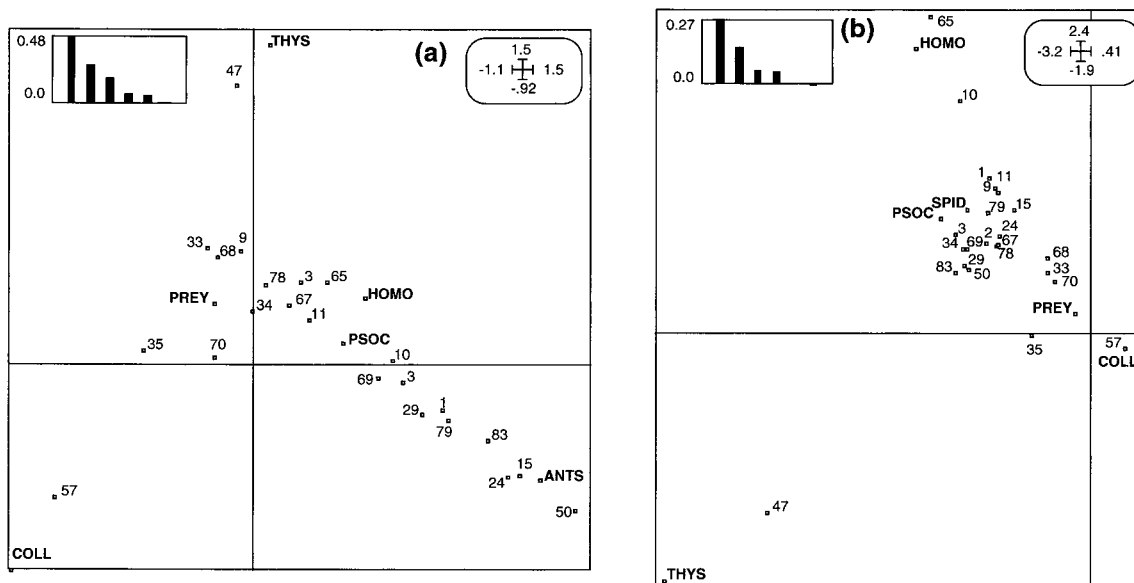


Figure 10. Correspondence analyses of prey-predator ratios across 23 canopy studies amenable to analysis. Plots of the species into axes 1 and 2 of the (a) prey-spider ratios and (b) arthropod-ant ratios. Studies are coded with numbers as in Appendix 1. Ratio codes: ANTS = Formicidae; COLL = Collembola;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