



## How many species of arthropods? Erwin's estimate revised

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Erwin's much debated estimate of 30 million species of arthropods is revised. The original estimate is based on the evaluation of host specificity of guilds in beetle samples, and subsequent hierarchical ratio extrapolations. The growing number of studies including mass sampling of arthropods have provided several data sets suitable for obtaining an empirical basis of this estimate. The structure in this modified version is somewhat changed compared to the original estimate in order to make each hierarchical step more easily testable. Plant species are separated into different growth forms, and host specificity measures are based only on phytophagous species. Effective specialization is applied as a measure of host specificity to correct for the fauna shared between plant species. A between community correction factor is applied to correct for differences in host specificity at different spatial scales. There are still great uncertainties attended with such estimates. The largest problems refer to the between community correction factor and the proportion of canopy species to total species. Further work on host specificity and the least known hyperdiverse groups are also needed. The revised version of the estimate does not support hyperestimates of 30–100 million species. Rather, it compares nicely with estimates derived from other estimation methods, indicating a global arthropod species richness of 5–10 million species.

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**ADDITIONAL KEY WORDS:**—beetles – biodiversity – Coleoptera – estimation – host specificity – species richness.

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## INTRODUCTION

Estimation of global species richness has been an important issue for more than 250 years (e.g. Linnaeus, 1758; Westwood, 1833; Metcalf, 1940; Erwin, 1982; Stork, 1993). In the 17th century, John Ray stated that “. . . in consequence of having discovered a greater number of English moths and butterflies I am induced to consider that the total number of British insects might be about 2000; and those of the whole Earth 20 000” (Westwood, 1883). Linnaeus (1758) in *Systema Naturae*, included 4400 species of animals, thinking this figure was close to the global species richness. However, as the number of described species increased by orders of magnitude during the next two centuries, biologists realized that species richness was much greater. Until the 1980s global species richness was thought to be 2 to 3 times the number of described species (i.e. 2–3 million species) (Stork, 1997).

The debate was revived when Erwin (1982) estimated 30 million species, based on the host specificity of guilds in beetle samples, and subsequent hierarchical ratio extrapolations. Such ecological estimates are derived from samples taken in association with particular substrates (e.g. plant species). The arthropod species are classified into guilds (herbivores, fungivores, predators, and scavengers), and the host specificity of each guild to the particular substrate is assessed. Combining the number of species and the host specificity for the guilds, the total number of species in the sample area can be estimated. Extrapolations from ratios are then used to estimate species richness at larger spatial scales. Erwin, for example, enumerated the beetle species harboured by one species of tropical tree (*Luehea seemannii* Tr. & Planch.). From this, he guessed percentages of host specificity of different guilds, ratios of beetles to other arthropods, canopy arthropods to ground arthropods, and finally, multiplied by the number of tree species in the world tropics (Table 1). His estimate increased global species richness by an order of magnitude. This estimate was subject to considerable debate (Stork, 1988; May, 1990; Thomas, 1990; Gaston, 1991; Hodkinson & Casson, 1991; Hammond, 1992; Basset *et al.*, 1996; Mawdsley & Stork, 1997) and created intense activity to produce alternative estimates of global species richness (May, 1988, 1990, 1992; Stork & Gaston, 1990; Thomas, 1990; Gaston, 1991, 1992; Hodkinson & Casson, 1991; Hodkinson, 1992; Hodkinson & Hodkinson, 1993; Stork, 1993, 1997; Gaston & Hudson, 1994; Hammond, 1995).

There are now several methods of estimating regional species diversity but no single one has proved better at extending knowledge of species richness. It is important to use several independent methods to overcome methodological biases (Mawdsley, 1996). Most studies extrapolate from ratios (Stork & Gaston, 1990; Hodkinson & Casson, 1991; Gaston, 1992; Hodkinson & Hodkinson, 1993). Relationships between body size and species numbers (May, 1978, 1988), species turnover or differentiation ( $\beta$ ) diversity (Erwin, 1983a, 1991; Mawdsley, 1996) are other methods used to estimate species richness.

Ecological extrapolation from samples is particularly interesting in that each step of the estimate can be formulated as a testable hypothesis. Erwin's estimate was based on subjective assumptions but the last two decades have produced several data sets for local communities of arthropod species from canopies of tropical forests

TABLE 1. Erwin's estimate (Erwin, 1982) of the number of arthropod species in the tropics

1. Number of beetle species from canopy fogging of 19 individual trees of <i>Luehea seemannii</i>			1200
2. Number of host specific species (four trophic guilds)			163
Trophic guild	# Species	Host Spec. (%)	# Host Spec.
Herbivores	682	20	136
Predators	296	5	15
Fungivores	69	10	7
Scavengers	96	5	5
Total	1200+		163
3. One hectare of tropical forest has on average 70 tree species. Number of host specific beetle species per hectare: $(70 \times 163) =$			11 410
4. Plus the remaining transient species. Number of beetle species per hectare: $(11 410 + 1038) =$			12 448
5. Beetles constitute 40% of all Arthropod species. Number of arthropod species per hectare: $(12 448 \times 100)/40 =$			31 120
6. The canopy fauna makes up 2/3 of the total. Total arthropod fauna per hectare: $(31 120 \times 3)/2 =$			41 389
7. There are an estimated 50 000 species of tropical trees. Based on the formula above, total number of tropical arthropod species			30 000 000

suitable for estimation by his method (e.g. Erwin & Scott, 1980; Stork, 1987b; Basset, 1991b; Basset *et al.*, 1996; Kitching & Zalucki, 1996; Allison, Samuelson & Miller, 1997; Davies *et al.*, 1997; Wagner, 1997). This allows revision of Erwin's estimate based on real data sets. The present survey aims to revise Erwin's estimate and overcome some of its shortcomings by using revised parameters.

#### ASSESSMENT AND MODIFICATIONS OF ERWIN'S ESTIMATE

This modified estimate is largely based on real data sets. It is not meant as a total summary of all published studies, but more as an outline of how this information can be combined for diversity estimation purposes. Some qualified guesses are still made reflecting the lack of certain types of data. The modified version is based on beetle samples in the canopy, as in Erwin, because such data are readily available. A revision of each step is necessary for adapting them to fit the existing data sets. Further important steps are added while others are made more easily testable.

#### *Host specificity*

Host specificity is a problematical parameter in estimates of species diversity. It is evolutionarily labile (Radtkey & Singer, 1995) and a species often has a greater host range than a single individual (Fox & Morrow, 1981; Mawdsley & Stork, 1997). Consequently, host specificity is relative, dependent on both temporal and spatial scales. Estimates of species richness based on host specificity have thus to be evaluated very carefully (Thomas, 1990).

Studies now indicate that the proportion of monophagous species in communities

varies considerably (Basset *et al.*, 1996). Similarly, host specificity and the relative species richness of major groups (families/subfamilies) may differ between sites. For example, Neotropical Chrysomelidae are dominated by Alticinae, whereas those from Papua New Guinea and Borneo are dominated by Eumolpinae (Basset *et al.*, 1996). Alticinae, in general, are more host specific than Eumolpinae (Jolivet, 1988), and the proportion of Chrysomelidae specialists in the Neotropics may thus be higher than in tropical Asia. However, Basset *et al.* (1996) found that at one site, the relative proportions of specialist insects and specialist beetles alone on each tree species were comparable.

Erwin estimated host specificity by the proportion of monophagous to polyphagous species associated with one tree species. Such measures of host specificity can never be wholly accurate unless all plant species in the range of the insect species are included. There are also problems with fauna shared among plant species (Basset *et al.*, 1996). Host specificity is a sliding scale, from strict monophagy to broad polyphagy (Stork, 1988). Every measurement of host specificity must, therefore, inversely weight each species against the number of its hosts a principle, termed effective specialization (May, 1990). Effective specialization ( $F_T$ ) ( $f_i$  of May (1990),  $x$  of Thomas (1990)) may be expressed as:

$$F_T = S_T / (\bar{S}_T \times T) \quad (1)$$

where  $T$  is the number of plant species,  $S_T$  is the number of insect species associated with  $T$  plant species, and  $\bar{S}_T$  is the average number of insect species associated with each plant species. It is thus the total number of plant-associated insect species divided by the number of host observations of those insects. Since  $F_T$  is a relative measure dependent on  $T$ , the real  $F_T$  for a community must be calculated indirectly (Diserud & Ødegaard, 2000). The average number of species effectively specializing on each plant species (effective number of specialized species) is given as  $\bar{S}_T \times F_T$ . Erwin (1982) apparently ignored effective specialization recognizing only monophagous and polyphagous species.

There are few studies on effective specialization of arthropods in the tropics. Mawdsley & Stork (1997) calculated effective specialization indirectly, based on material from canopy fogging of ten Bornean trees (four species). By measuring the beetle species' turnover between and within tree species, they concluded that average effective specialization was less than 5% at a species level (Stork, 1997). If we guess that the lower limit of this estimate reaches 3%, and we know that there was on average 115 beetle species per tree species, then, the effective number of species per tree species ranges from 3.5 to 5.8 species (equ. 1; Table 2, step 1a).

A similar study of insects on 10 tree species in Papua New Guinea revealed 23 to 37 monophagous leaf feeding beetles out of 391 species (Basset *et al.*, 1996). Erwin's method estimates 138 monophagous species for the same system suggesting that his estimate should be corrected down by a factor of 3.8 to 6.0, to estimate similarly host specificity at 3.3–5.2% (Basset *et al.*, 1996). On average, they found 69 species per tree species, thus the effective number of beetle species ranges from 2.3 to 3.6 per tree species (equ. 1; Table 2, step 1a).

Effective specialization of phytophagous beetles on 24 tree and 26 liana species in the canopies of a dry tropical forest in Panama ranged from 5 to 9% and 8 to 11% for trees and lianas, respectively (Ødegaard, 2000; Ødegaard *et al.*, 2000). There were 55.8 beetle species per tree species, and 47.0 species per liana species, giving the effective number of beetle species per plant species then ranges 2.8 to

TABLE 2. Erwin's estimate revised. The estimate is based on empirical data suitable for separate steps. The working figure is based on the median value of the data, and minimum and maximum estimates are calculated from quartiles

How many Species are there?	Minimum	Working figure	Maximum
1. Number of phytophagous beetles in canopy			
(a) Effective number of species specialized on life forms of plants			
2.8–5.0 species effectively specialized on trees (Ødegaard <i>et al.</i> , 2000)			
2.3–3.6 species effectively specialized on trees (Basset <i>et al.</i> , 1996)			
3.5?–5.8 species effectively specialized on trees (Mawdsley & Stork, 1997)			
Lower quartile: 3.0, Median: 3.9 Upper quartile: 4.7 (based on mean value of each range) × 37 000 (total no. trees)	111 000	144 300	173 900
3.8–5.6 species effectively specialized on lianas (Ødegaard <i>et al.</i> , 2000)			
Lower quartile: 3.8, Median: 4.7, Upper quartile: 5.6 × 18 500 (total no. lianas)	70 300	87 000	103 600
0.5 species effectively specialized on epiphytes (guess) × 20 000 (total no. epiphytes)	10 000	10 000	10 000
Total no. of species associated with trees, lianas, and epiphytes	191 300	241 300	287 500
(b) Proportion of the total phytophagous beetle fauna associated with the plant species at a given site through the geographical range of these plant species			
50% (Cassidinae, Panama)			
44% (Scolytinae, Norway)			
Lower quartile: 44%, Median: 47%, Upper quartile: 50%	383 000	513 300	652 000
(c) Between community correction factor (Thomas, 1990)			
Working figure: 2.5 (May, 1990)	153 000	205 300	261 000
2. Number of beetle species in the canopy			
The proportion of phytophagous beetles to total beetle fauna in the canopy			
37% (Davies <i>et al.</i> , 1997)			
40% (Majer <i>et al.</i> , 1994)			
41% (Wagner, 1997)			
44% (Stork, 1991)			
47% (Basset, 1991)			
47% (Erwin, 1980)			
56% (Erwin, 1983a)			
Lower quartile: 40%, Median: 44%, Upper quartile: 47%	326 000	466 600	652 000
3. Number of beetles			
The proportion of canopy beetles to the total beetle fauna			
25% (Hammond, 1997)			
33% (guess, Stork, 1993)			
50% (guess, May, 1990)			
66% (guess, Erwin, 1982)			
Lower quartile: 29%, Median: 42%, Upper quartile: 58%	561 000	1 111 000	2 249 000
4. Number of arthropods			
The proportion of beetles to the total arthropod fauna			
18% (Southwood <i>et al.</i> , 1982)			
22% (Majer <i>et al.</i> , 1994)			
23% (Stork, 1988)			
23% (Basset, 1991)			
33% (Hammond, 1992)			
Lower quartile: 22%, Median: 23%, Upper quartile: 23%	2 441 000	4 830 000	10 224 000

3.5, and 3.8 to 5.6 for trees and liana species, respectively (equ. 1; Table 2, step 1a).

By comparison, effective specialization for phytophagous beetles associated with epiphytes is unknown. Most canopy epiphytes are small sized with low structural complexity compared to trees and lianas (Benzing, 1995). Thus, a rough guess would be that on average 0.5 species are effectively specialized on each epiphyte species (Table 2, step 1a).

There are critical aspects of effective specialization that have to be considered when estimating species richness. Effective specialization is independent of taxonomic relatedness of host plants. A beetle feeding solely on two hosts within a plant genus receives the same consideration as a species feeding on two distantly related plant species, possibly leading to low observed specialization in species-rich plant families/genera. Effective specialization is also independent of insect-density per biomass of host plants. Density is important when assessing host specificity, because infrequent occurrence of insects on plants inflate the estimates of both an insect host range and a plant's range of associated insects (Futuyma & Gould, 1979).

#### *Variation between and within plant species*

The number of arthropods associated with different plant species varies both among and within plant species. The number of insect species associated with each plant species depends on the geographic range and local abundance of the plant (Neuvonen & Niemelä, 1981), and its intrinsic characteristics, such as size, structural complexity and biochemical properties (Connor *et al.*, 1980; Strong, Lawton & Southwood, 1984). Taxonomically or chemically isolated plant species generally acquire fewer insect species than close relatives (Strong *et al.*, 1984; Tahvanainen & Niemelä, 1987). Common plant species acquire more insect species than rare ones (Southwood, 1960; Strong *et al.*, 1984). Thus, it is important to investigate a wide range of tree species. A random selection of trees, for example, will always overrepresent the common tree species, thereby overestimating insect species richness. A better approach is to select plant species at random from a known species list.

Each plant does not host all insect species that feed on that species in one geographic area. Insect load depends on the size of host plant patches and host plant density (Strong *et al.*, 1984). Individual load variation pinpoints the importance of including several individual plants when producing species lists of host associations.

#### *Range of host plants*

A tree species may have different insect species in different parts of its range (May, 1990). Erwin's test tree, *Luehea seemannii*, is distributed from southern Mexico to northern Argentina (Croat, 1978). His study was restricted to an area of 5 km<sup>2</sup> in Panama. It is reasonable that *L. seemannii* has a very different beetle fauna in southern Mexico compared to that of northern Argentina, and these two faunas are also probably very different from the one in Panama. Thus, the total range of a plant species should be investigated to achieve a correct picture of its insect associates. That is a hard task; however, an assessment of the proportion of the total fauna

associated with a host plant, represented at a particular site, is possible for well-known taxa. The tortoise beetles (Cassidinae), a well-known group in the neotropics (Buzzi, 1988, Buzzi, 1994; Windsor, Riley & Stockwell, 1992), are suitable for this purpose. Fifty percent of the total number of Cassidinae species that is known to feed on 50 different plant species in Panama, were recorded on these plant species in a 0.8 ha plot (Ødegaard & Windsor, *unpublished data*). Since many of these plant species have a range outside Panama, the 50% figure is a minimum estimate. From a temperate spruce forest, 17 species of Scolytinae associated with Norway spruce (*Picea abies* (L.) Karst.) were recorded from an area of 1 km<sup>2</sup> in an intensive trapping-regime (Tømmerås *et al.*, 2000). Thirty-nine species of Scolytinae are associated with Norway spruce in the central and western Palaearctic region (Pfeffer, 1995). Accordingly, the local representation of the Scolytinae fauna on Norway spruce at this site was 44% (Table 2, step 1b).

#### *Between community correction*

Thomas (1990) has shown that for a well-known group of insects (Heliconinae), the relationship between the number of host plant species (Passifloraceae) recorded and the number of insect associates does not increase proportionally. The more plant species recorded, the relatively fewer insect species are associated with each plant species. The reason for this is that relatively specialized insects use taxonomically different (although ecologically similar) species of plants in different regions of their range (May, 1990). Thomas found that this between community relation accounted for an overestimate of species richness by a factor of 7 in Erwin's estimate. However, as pointed out by May (1990), approximately 2.5 would be a more proper factor, because some 2/3 of the plant species included in this study only grow at an elevation above the range of these insects (Gilbert & Smiley, 1978) (Table 2, step 1c).

#### *Host specificity of guilds*

Erwin evaluated host specificity for different functional feeding guilds associated with *Luehea seemannii* as different. (Only phytophagous species are discussed above.) It is extremely difficult to identify the host specificity of fungivores, scavengers, and predators in the context of one particular tree species. Host specificity of fungivores, for instance, requires assessment of host specificity of both the fungi and the insects. Fungi show only weak preferences for tree species (Gregory Gilbert, *pers. comm.*), while beetles show more or less strong associations to certain species of fungi (Lawrence, 1973; Økland, 1995; Fossli & Andersen, 1998). Thus, host specificity of fungivores (in the conventional sense) is a feature of great interest in its own right, which can be calculated in the same way as Erwin did for beetles associated with a certain tree. The host specificity of the fungi itself is not interesting when applying this approach. The evaluation of scavengers and predators could be simplified similarly by calculating host specificity to substrate and prey, respectively.

In the modified version of Erwin's estimate (Table 2), host specificity measures are given only for phytophagous beetles. The problems with other guilds are simply

overcome by assessing the proportion of phytophagous species to species of other guilds in a separate step (Table 2, step 2).

### *Major life forms of plants*

In ecological estimates of global arthropod species richness (Erwin, 1982; Thomas, 1990; Basset *et al.*, 1996) only tree species are considered as plant units. Other major life forms (i.e. lianas, shrubs, epiphytes and herbs) are virtually overlooked as hosts. In Erwin's study site in Panama, tree species make up only 26.6% of total flora (Croat, 1978). His numbers could lead to considerable underestimation of species richness if other major life forms of plants turn out to have relatively high numbers of arthropod associates. Indirect evidence of the importance of other life forms of plants was found by Stork (1987a), studying the faunal similarity of ten Bornean trees. He stated that the similarity in amount of vines and epiphytes was more important for faunal similarity than taxonomic relatedness among the trees. Furthermore, as pointed out by Wolda (1979), the leaf production of lianas may exert a greater influence on local species richness of insects than the leaf production of the tree itself. Ødegaard (2000) have shown that the total numbers of beetle species associated with trees and lianas were not significantly different in a tropical dry forest in Panama.

Life forms of plants differ in the number of microhabitats they provide for insects. Plant-size and complexity, therefore, are major determinants for the number of insect associates (Lawton & Schröder, 1977; Strong & Levin, 1979; Lawton, 1983). Thus, host specificity of each group of major life forms of plants should be calculated separately in ecological estimates of arthropod species richness. At a local scale, arthropod species richness ( $N$ ) could be calculated by:

$$N = \sum_l k(l) \times S_F(l) \quad (2)$$

where  $k(l)$  is number of plant species within the region of life form  $l$ , and  $S_F(l)$  is the average effective number of arthropods specialized on each plant of this life form. In this way, the arthropods associated with lianas, shrubs, epiphytes and herbs may be treated properly.

### *Number of plant species in the tropics*

The number of tree species in the tropics is an essential parameter in ecological estimates of global arthropod species richness (Erwin, 1982; Thomas, 1990). It is generally accepted that 50 000 tree species is a feasible working figure in estimation of arthropod species richness (Erwin, 1982; Stork, 1988; Thomas, 1990; Hodkinson & Casson, 1991). However, this figure does not pay attention to the size of the tree species. Erwin's estimate is based on calculations from canopy samples. Thus, it is incorrect to include small trees that never reach the canopy. Arthropods associated with these plants are included in the canopy to ground fauna ratio. Trees >10 cm DBH (diameter at breast height), a standard in botanical literature, should be used as a life form unit in this context. Gentry & Dodson (1987) found that trees (>10 cm DBH) made up 21% of the total flora of flowering plants in seven tropical sites. If



TABLE 3. Number of species of tropical flowering plants of major life forms in different regions

	Total	Trees	%	Shrubs <sup>a</sup>	%	Climbers <sup>b</sup>	%	Epiphytes	%	Herbs	%
Total number of species in the tropics	185 000 <sup>1</sup>	37 000*	20.0 <sup>2</sup>	18 500	10.0 <sup>2</sup>	18 500 15 000 <sup>d</sup>	10.0 <sup>2</sup>	30 000 <sup>3</sup>	16.2	65 000	42.7 <sup>4</sup>
Number of species in the neotropics	90 000 <sup>5</sup>	18 000*	20.0 <sup>6</sup>	9 000	10.0 <sup>6</sup>	9 000 <sup>7</sup>	10.0	15 000 <sup>7</sup>	16.7	39 000	43.3 <sup>6</sup>
Number of species in Panama <sup>8</sup>	7289	1952**	26.8	2311	31.9	895	12.3	197	2.7	3126	42.9
Number of species in BCT <sup>9</sup>	1212	211**	17.4	270	22.3	265	21.9	135	9.0	331	27.3

<sup>a</sup>Includes treelets (<10 m tall or <10 cm DBH) and parasitic shrubs

<sup>b</sup>Includes lianas, vines, hemiepiphytes

<sup>c</sup>Lianas

<sup>1</sup>Prance, 1995; <sup>2</sup>extrapolated from the neotropics; <sup>3</sup>Benzing, 1983; <sup>4</sup>adapted number; <sup>5</sup>Gentry, 1982; <sup>6</sup>Numbers adapted from Gentry & Dodson (1987); <sup>7</sup>Gentry, 1991; <sup>8</sup>D'Arcy, 1986 (percentages do not total 100%, because of multiple categories); <sup>9</sup>Croat, 1978.

\*Trees >10 cm DBH, \*\*trees >10 m tall,

this number is representative for the rest of the tropics, some 37 000 tree species would be a more appropriate number (Table 3).

There is no exact account of the total number of liana species, but in the Neotropics about 10% of the 90 000 species of flowering plants are climbers and half of these are lianas (Gentry, 1991). Jacobs (1976) suggests that 8% of all tropical plants are lianas. Accounting for some 185 000 species of flowering plants in the tropics (Prance, 1995), the number of tropical lianas then should be about 15 000 species. Other groups of climbers include herbaceous climbers (vines) and woody or herbaceous climbers that begin life as an epiphyte, or begin life at ground with subsequent loss of terrestrial contact after production of adventive roots (hemiepiphytes) (Gentry, 1991). Species richness of climbers is fairly constant across continents, although there are some distinct differences in taxonomic composition. The Bignoniaceae climbers, typical to the Neotropics, are replaced by Apocyanaceae in Africa and by Annonaceae in Asia (Gentry, 1991). Their pan-tropical species richness is estimated to some 18 500 species based on extrapolation from the neotropical region (Table 3). Accordingly, climbing plant species amount to scarcely half as many as the number of tree species (>10 cm DBH) in the tropics. The third life form of significance in tropical canopies, the epiphytes, make up some 20 000 species mainly occurring in the canopies (Benzing, 1995).

### *Canopy fauna*

It is crucial to have a clear definition of the canopy to be able to separate the canopy fauna from faunas at other height levels. However, the literature does not provide a clear definition. The canopy is the combination of all leaves, twigs, and all small branches in a stand of vegetation, and it is a region as well as a collection of elements (Parker, 1995). The canopy is also defined as the uppermost layer of the forest roof (e.g. Norse, 1990), which differ significantly in leaf production, abundance of flowers, temperature fluctuations, wind, and exposure to sunlight. None of these definitions are tied to height. They could, therefore, include tree gaps at ground level as well. In ecological estimates, the canopy is probably best viewed

as the tree crowns, or more precisely the total volume of the forest, which is out of reach of the ground. This view is more a description of the unexplored body of forest habitats, often referred to as the last biotic frontier (Erwin, 1983b), than it is a biological definition.

According to this somewhat arbitrary canopy definition, the *canopy fauna* could be defined as those arthropod species harbouring trees >10 cm DBH or life forms of plants interfering with these trees. Arthropods exclusively associated with seedlings or saplings of trees or lianas should not be included. Many ground dwelling arthropods also occur in the canopies. Hammond, Stork & Brendell (1997), therefore, separate canopy specialists and stratum generalists, which together constitute the canopy residents. Those ground dwelling species accidentally occurring in the canopies are the casual canopy visitors ('tourists') (Hammond *et al.*, 1997). Canopy specialists may occur at edges or in gaps of forests, because the physical conditions of these habitats are similar to those in the tree-tops. However, that does not affect their status as canopy specialists.

The canopy comprises a major volume of the tropical forests and include a wide range of habitats which are little or non-existent in the understory. Two thirds of the epiphytes are exclusively canopy plants (Benzing, 1995) and the major production and structural diversity of lianas occur in the canopy (Hegarty & Caballe, 1991). Spatial heterogeneity within trees is shown to be higher in the canopy due to the dominance of young leaves (Basset, 1991a). In total, canopy plants account for more than 90% of tropical forest leaves (Wright & Colley, 1994). Arthropod species richness correlates positively with plant species richness (Gaston, 1992) and the number of microhabitats available (May, 1978). On this background, between 1/3 and 2/3 of arthropod species in tropical forests are believed to inhabit the canopies (Erwin, 1982; May, 1990; Stork, 1993). Contrary to this, Hammond *et al.* (1997) found that only 20–30% of the beetles at a site in North Sulawesi, Indonesia were canopy residents. However, the proportion of this fauna may be underestimated without direct canopy access. Nonetheless, the canopy inevitably plays a crucial role in estimates of arthropod species richness. The modified version of the estimate (Table 2, step 3) includes some qualified guesses due to great uncertainty on this point. Only one empirical study exists (Hammond *et al.*, 1997).

#### *Proportion of beetles*

Erwin proposed that beetles constitute 40% of all arthropods. This number is certainly too high (Southwood, Moran & Kennedy, 1982; Stork, 1988; Thomas, 1990; Basset, 1991b; Hammond, 1992; Majer, Recher & Postle, 1994). The uncertainties are mainly due to large, virtually unknown taxonomic groups like mites. They certainly comprise a major proportion of species richness (Watanabe, 1997), but we know very little about their contribution to species richness, not even at which order of magnitude (Walter & O'Dowd, 1995; Walter, 1999). Without information from such groups, we can say little about total arthropod species richness (Table 2, step 4).

#### *The modified estimate*

The modified version of Erwin's estimate of tropical arthropod species richness gives an estimated 4.8 million species (minimum 2.4 million species, and maximum

10.2 million species) (Table 2). The working figure of the estimate is built upon median values of the available data sets. Maximum and minimum values are defined as the quartiles of the available data in each step as a simple method to give a relative picture of the variation in the data and weighting down the extreme values. There are still too few studies available for doing a proper statistical treatment of the data by means of analysis of variance in order to assess the limits of maximum and minimum values.

#### DISCUSSION

As Stork (1993) pointed out, species estimates derived from samples are only as good as the samples. This statement pinpoints both the importance of samples from many sites, and the needs of a satisfactory sampling effort. A reliable estimate of global species richness needs to be built up from local samples in different types of forest in each continent. For instance, lowland forests are generally more species-rich than highland forests, while wet forests are generally more species-rich than dry forests (Gentry, 1985). Tropical islands should also be treated separately, because they often have different flora than continents (Gentry, 1991).

Theoretically, as the number of empirical studies from a variety of taxa, and from different geographical regions increase, the difference between minimum and maximum values will stabilize, and the working figure becomes more reliable. If we had thousands of appropriate data sets, the difference between maximum and minimum values still would be very high due to the variation in species richness and host specificity in different taxa and in different regions. Hence, the maximum- and minimum values do not express the uncertainty in the estimate. Rather, they indicate what global diversity would look like if all regions had been similar to the most hyper-diverse or the most hypo-diverse region.

Weighting of each study in accordance with distribution range of the forest types from which the samples are obtained will further improve the estimate. Consequently, such an estimate could be subject to continuous updating and progressive improvement. The various steps may be easier to test after further modifications, and different approaches should be used concerning different taxa, strata or habitats. The working figure, however, would probably approach the real species richness if such data sets had been available.

Future work on ecological estimates should concentrate on host specificity and a better understanding of within- and between-community variation in host specificity. Furthermore, the importance (i.e. the magnitude) of the canopy fauna is still poorly understood. Also, inclusion of the least known of the hyper-diverse groups (e.g. mites) is badly needed.

A major restriction relates to the assessment of host specificity and the scale dependence of this phenomenon. It has to be emphasized that Erwin's estimate originally was adapted for a local scale whereat it undoubtedly works best (May, 1990; Hammond, 1992; Basset *et al.*, 1996; Mawdsley & Stork, 1997). The global consequences of this estimation were suggested only tentatively in the last sentence (see Erwin, 1982). Host specificity can be viewed as a property of populations rather than a species attribute, because many insect species commonly use a different selection of plant species in different parts of their distribution area (Fox & Morrow,

TABLE 4. Estimates of global species richness of arthropods based on different independent methods

Estimated no. of species (in millions)	Ref.	Estimation method
5.0–6.7	Stork, 1993	revised Hodkinson & Casson, 1991 (based on ratio extrapolations from samples)
2.75–8.75	Gaston, 1992	Ratios of insect to plant species
10.0	May, 1990	Relationship between body size and abundance
5.0	Gaston, 1991	Taxonomists' view
4.9–6.6	Stork & Gaston, 1990	Extrapolations from known fauna and regions

1981). Therefore, Mawdsley & Stork (1997) pointed out that it is unlikely that estimates of host specificity will be useful in determining global species richness. However, this phenomenon is corrected for in the 'between community correction factor' (*sensu* Thomas, 1990). It is an issue of interest in its own right to test the magnitude of this factor for different groups in different regions, and to evaluate its variation and how it should be used in diversity estimates. Furthermore, Mawdsley & Stork (1997) argued that host-specificity patterns vary between taxa. Therefore, it is important to test host specificity for other taxa than beetles. Alternatively, separate estimates should be developed for each major taxon.

This survey has shown that diversity estimation based on host specificity does not provide any new information on global species richness. Uncertainty is too high, and data sets are still too few. We certainly have a long way to go before we can obtain a reliable estimate of global species richness based on this method. At this stage, the modified version of the estimate does not support the hyper-estimates of 30–100 million species (see Erwin, 1982, 1988; Stork, 1988), not even if the maximum value is considered. Mawdsley (1996) emphasized the importance of using several independent methods to overcome methodological biases of various estimates. Interestingly, the working figure of this modified Erwin estimate (4.8 million species) lies within the range of the majority of estimates based on other methods (Table 4). Presumably, there are no reasons to believe in hyper-estimates, at least not for insects.

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