How many species are there?

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'How many species are there' is a question receiving more attention from biologists and reasons for this are suggested. Different methods of answering this question are examined and include: counting all species; extrapolations from known faunas and regions; extrapolations from samples; methods using ecological models; censusing taxonomists' views. Most of these methods indicate that global totals of 5 to 15 million species are reasonable. The implications of much higher estimates of 30 million species or more are examined, particularly the question of where these millions of species might be found.

Keywords: global species estimates; insects; species richness

Introduction

Although we now have an excellent understanding of many aspects of the living world, we have only a limited idea of how many different species or forms of life share the planet Earth with us. This is all the more surprising since Man has a fascination for nature above almost all things. For hundreds of years natural historians have been exploring, inventorying and mapping the world's fauna and flora. Linnaeus laid down a formalized system for describing organisms that has formed the basis for such for more than 230 years. Few, however, paid attention to the full extent of diversity of life on Earth. In recent years, one particular question, 'How many species are there?', has become more scientifically important (Erwin, 1982; May, 1988, 1990, 1992a; Stork, 1988; Gaston, 1991; Hodkinson and Casson, 1991). In this paper reasons why this question now has a more elevated position on the scientific agenda are suggested. Also examined are recent attempts to answer this fundamental question, focussing on arthropods, and in particular insects, since the largest proportion of described and possibly undescribed species are of these groups. Finally, issues are addressed such as, where are the estimated large numbers of undescribed species to be found and how long it will take to describe all species.

Why do we need to know?

The political arena

The term 'biodiversity', coined by Wilson (1988) as a contraction of 'biological diversity', represents the diversity of life at all levels including genetic, species and ecosystem diversity. Biodiversity as a field of scientific and common interest has rapidly become

commonplace in the literature, particularly over the last 12 months. Attention has focussed on the Biodiversity Convention agreed at the UNCED meeting in Rio de Janeiro in June 1992 and signed by 156 countries. Many conservationists, biologists and politicians have seemed surprised that it is not known how many species there are, particularly as such information would seem important in estimating rates of extinction of species. Some have suggested that unless current trends are reversed, from one quarter to one half of the Earth's species will become extinct in the next 30 to 50 years (Lovejoy 1980; Ehrlich and Ehrlich 1981; several authors in Whitmore and Sayer, 1992).

Biodiversity as a human resource

Of the many millions of species on the Earth, humans utilize only a small fraction to any great extent. Most of the Earth's food is provided by just 20 species of plant and the total diversity of plants eaten worldwide is probably less than 5000 species (Reid and Miller, 1989). Pharmaceutical companies are prospecting for chemicals in a wide range of groups as diverse as insects and fungi. To many people in both developing and developed countries, biodiversity is viewed like any other resource, with ownership belonging to the country in which it is found. Also, like any other resource, it is finite and needs to be managed in a sustainable manner. Recently, INBio (Instituto de Biodiversidad) in Costa Rica made an important collaborative two year agreement with one of the world's largest pharmaceutical companies, Merck & Co., to prospect for useful chemicals among the fauna and flora of Costa Rica. In this agreement, royalties resulting from the successful development of chemicals from organisms will be shared between Merck & Co. and Costa Rica.

Such issues are increasingly relevant as the Earth's human population rapidly increases. Biodiversity is under threat as more of natural ecosystems are converted to crop production or are destroyed for timber. Myers (1989) suggests that it is the many shifting cultivators – the displaced, small scale farmers in developing countries, trying to eke out an existence – which account for more deforestation than the two other major factors (commercial logging and cattle ranching) combined.

Biodiversity as an applied discipline

Recently, some have questioned the role of biodiversity in ecosystem functioning (di Castri and Younes 1990). Essentially, there are two schools of thought. First, that all species are essential to the continued existence of an ecosystem. Second, that many species could be lost without much damage to the ecosystem or in other words, there is built in functional redundancy. If the former is true then restoration of complex ecosystems should be either a very long process or impossible. Knowing the number of species and group composition of an ecosystem or region is seen by some (e.g. Janzen, 1993) as part of the information required for its conservation and sustainable utilization.

At a more mundane level those who administer funding of taxonomy need to know what level of financial resources are required. Linnaeus set in motion the process of describing all species. This process has very gradually increased in speed but after over 200 years still has no clear completion date. No timescale or resource requirement has ever been defined for this task, not even for any one region of the world such as the British Isles or USA. Against pre-1980 global estimates of 2–3 million species (for all organisms) such parameters seemed hardly worth consideration, but against post-1980 estimates, as much as 10 times this figure, the task seems less feasible and timescale and

resource requirements, such as taxonomic manpower, much more important. In most taxonomic institutions, the kinds of studies being undertaken, the organisms being studied and the resource implications, are being considered more carefully than ever before.

Species extinctions

Finally, with increasing concern about environmental change through pollution, landscape change, forest destruction and global warming, it is important to know how many species there are and how their distributions are changing, if only to know how many are being lost and how to slow down the rate of extinctions. Recent studies of the effects of global warming on species distributions have largely focussed on single species of agricultural or medical importance. Many are now asking on what scale will biodiversity be altered by environmental change. If rates of species extinctions are 17 500–35 000 a year (Holloway and Stork, 1991) this would indicate that a species is almost twice as likely to become extinct than to be described!

Against this background it is important to examine both progress in the process of describing all species and the likelihood of this process revealing the extent of global diversity.

How many species?

A number of different methods have been used to predict how many species there are and these are reviewed below. First, the process of discovery and description of all species. This now appears unlikely to resolve the question in the near future, if at all, for a variety of reasons such as the slow rate of description of new species, the high level of synonymy for most groups and the uneven distribution of taxonomic effort which results in low taxonomists/number of species for species-rich groups. Second, simple extrapolations from known faunas and floras of regions are reviewed. Third, extrapolations from samples of biodiversity are examined. These have received most attention in recent years and some methods have created considerable controversy. Finally, other models and surveys of taxonomists' views on this question, are examined. One not particularly useful method of species estimation, that of using description rates, is not discussed here but is considered elsewhere (Hammond, 1992).

DESCRIPTION OF ALL SPECIES

The number of all described species is imprecisely known but recent estimates suggest it is 1.4–1.8 million species (Stork, 1988; Barnes, 1989; Hammond, 1992). The main reason for the imprecision concerns the possibily large number of species that have been accidentally described more than once. Evidence from the rate of synonymies to new species in recent revisions suggests that the proportion of names which are synonyms is very high, averaging 20% or more for many groups (Gaston and Mound, 1992). However imprecise estimates of described species are, it is clear that invertebrates and insects in particular, represent the largest proportion. Well-known groups such as flowering plants, birds and mammals are far less speciose. How likely is it that all species will be described in the near future? Hammond (1992) showed that description rates across all taxa are remarkably low, averaging 13 078 per year for animals and fungi for the period 1978–1987. Given that descriptions of valid species of all organisms, including

embryophyte plants and algae, average 6 000–8 000 per year for the last 230 years (based on the above estimates of 1.4–1.8 million described species) this represents at best a doubling of the historical average rate. Even with the lowest estimates of global species diversity of around three million species it would take 90–120 years to describe all species at present rates. Most probably a large proportion of the more common species have been named but naming the rest should increase in difficulty as the remaining, probably less common species, become harder to find.

Wilson (1988) has suggested that it would take 25 000 taxonomist lifetimes to complete the task. However, taxonomy is not just a matter of placing a name to a species but requires consideration of the variation of individuals within a species and distinguishing variation due to environmental factors (phenotypic variation) and inherited variation (genotypic variation). Without the careful consideration of such factors many described species must be of dubious validity. Many entomologists will be familiar with the name of Francis Walker, who worked at the Natural History Museum in London and described thousands of species of Diptera, Hymenoptera and Coleoptera on a factory like taxonomic production line. Many of these species have since been synonymized and his efforts have created chaos and wasted valuable time. Still, however, too many species are described on the basis of single specimens or specimens form single localities.

In one study of beetle taxonomic revisions in a random sample of papers from *Zoological Record*, 45% of the species included (new and previously described species) were recorded from single localities and 13% from single specimens (N.E. Stork and S.J. Hine, unpublished). Not surprisingly, many taxonomists working in major museums or who have access to good collections spend much of their time repairing the damage created by poor taxonomists. Entomologists at the Natural History Museum (London) described a total of 739 new species of insect in 1984–1986 but synonomized 316 species! For some of them synonymies outnumber new species by a factor of more than 10. Very few taxonomists describe more than 100 species a year and most describe at most a few. In practice, the emphasis has broadly shifted from species description to analysis of relationships and to studies of economically important taxa. Too many taxonomists produce species descriptions based on a poor understanding of the natural variation of the species concerned. Such taxonomic problems are discussed more fully elsewhere (Gaston and Mound, 1993; Mound and Gaston, 1993).

If changes in taxonomic practices and in the presently biased distribution of taxonomists towards temperate regions take place we may see the rate of description increase but it is unlikely that this will be dramatic over the next decade (Hammond, 1992).

SIMPLE EXTRAPOLATIONS FROM KNOWN FAUNAS AND REGIONS

The simplest methods of estimating global diversity are those based on known faunas or floras. Raven (1985) noted that for mammals, birds and other large and well documented animals there are roughly twice as many tropical as temperate species. If the same ratio holds true for other organisms, he argues, then with 1.5 million species described and two-thirds of these being temperate, then the true global total would be 3 million plus. This simple but rather crude calculation does not consider differences there maybe, for example, between large and small organisms in their patterns of distribution. A similar argument was put forward by Stork and Gaston (1990) who estimated that there might be 4.9–6.6 million species of insects worldwide if the same ratio of butterflies to all insects in

Britain also holds true for the rest of world (22 000 species of insects and 67 species of butterflies in Britain, 15–20 000 species of butterflies worldwide). The flaws in this method of estimation are obvious but its simplicity is appealing.

However, how realistic are simple extrapolations based on ratios of different groups for known faunas and floras? It is generally recognized that species richness for most groups, with a few notable exceptions (Janzen 1981; Gauld 1986); increases latitudinally towards the equator. However, we still have little idea of whether the relative proportions of at least the major taxa are similar at different latitudes or on different continents (but see Gaston, 1991a). There is some evidence that for some groups at least, the relative proportions of groups in different parts of the Earth are surprisingly similar. Stork (1987, 1988) showed that the trophic guild structure at the species level for canopy arthropods, as sampled by knockdown insecticide fogging, was very similar for temperate–subtropical trees (Britain and South Africa – Moran and Southwood, 1982) and tropical trees (Borneo; Stork, 1987). One simple indication that this reflects similarity in taxonomic group composition is from comparisons of the species richness of beetle families in canopy samples from Panama (Erwin and Scott, 1982) and Borneo (Stork, 1991) (Table 1). Here the high Rank correlation coefficient for the number of species in different families or subfamilies of beetles shows how similar the beetle fauna of trees in the two regions is at this taxonomic level. In contrast, it is most unlikely that any of the species are shared between the two sites. Unfortunately, data of this kind are few and wider comparisons are not yet possible.

EXTRAPOLATION FROM SAMPLES

Erwin's estimates

The most publicized global estimate of 30 million insect species (Erwin, 1982) was derived from samples of arthropods obtained by canopy fogging with knockdown insecticide from 19 individuals of the tree, *Luehea seemannii* Triana and Planch (Tiliaceae). Erwin sorted 1200 species of beetles from the samples and allocated these to four trophic groups. He suggested that different proportions of these trophic groups might be specific to the tree species in question (20% of herbivores, 5% of predators, 10% of fungivores and 5% of scavengers). Thus, he suggested, 162 species might be said to be specific to *L. seemannii*. If an estimated 50 000 species of tropical trees each have 162 host-specific beetle species, if beetles represent 40% of the canopy arthropods, and if there are twice as many species in the canopy as on the ground, then a total of 30 million

Erwin's first assumption of the relative host-specificities of different trophic groups of beetles is weak (Stork, 1988) and as May (1990) and Thomas (1990) have shown, gives a much higher estimate of the numbers of host-specifics than one might reasonably expect from the available data in this field. The distribution of individuals of some canopy arthropod species may owe more to the vagility of those species and the importance

Table 1. Comparison of the number of species of beetles in different families in samples from canopy fogging in Brunei (Stork, 1991) and from *Luhea seemannii* trees in Panama (Erwin and Scott, 1981)

Family	P	B	Family	P	B
Aderidae(*)	11	45	Eucnemidae	11	5
Anobiidae	14	9	Helodidae	12	7
Anthicidae	15	12	Heteroceridae	1	0
Anthribidae	11	38	Histeridae	3	1
Biphyllidae	1	0	Hydraenidae	0	1
Bruchidae	6	0	Hydrophilidae	2	1
Buprestidae	14	17	Lagriidae	7	5
Byrrhidae	0	1	Lampyridae	12	3
Byturidae	1	0	Languriidae	14	6
Cantharidae	19	10	Lathridiidae	3	1
Carabidae	41	9	Limnichidae	1	2
Cerambycidae	62	18	Lycidae	9	9
Chelonariidae	0	2	Melandryidae	14	0
Chrysomelidae			Melyridae	2	7
Alticinae	66	15	Monommidae	1	0
Chalamisinae	2	0	Mordellidae	43	17
Cassidinae	11	1	Mycetophagidae	0	1
Chrysomelinae	2	0	Mycteridae	11	0
Clytrinae	2	0	Nilionidae	2	0
Cryptocephalinae	30	9	Nitidulidae	22	11
Eumolpinae	36	33	Phalacridae	28	19
Galerucinae	41	35	Platypodidae	2	1
Hispinae	9	4	Prionoceridae	0	1
Lamprosomatinae	1	0	Pselaphidae	7	25
Zeugophorinae	5	0	Ptiliidae	0	3
Ciidae	8	5	Ptilodactylidae	35	4
Clambidae	0	2	Ptinidae	0	6
Cleridae	12	10	Rhipiphoridae	1	0
Coccinellidae	36	20	Rhizophagidae	1	0
Colydiidae	5	7	Scarabaeidae	3	4
Corylophidae(**)	10	33	Scaphidiidae	8	5
Cryptophagidae	9	0	Scolytidae	10	11
Cryptophilidae	0	2	Scraptiidae	0	1
Cucujidae	18	4	Scydmaenidae	3	13
Curculionidae(***)	?	148	Silvanidae	0	2
Dermestidae	6	0	Staphylinidae	114	115
Discolomidae	0	1	Tenebrionidae	31	32
Dryopidae	0	9	Throscidae	1	0
Dytiscidae	1	1	Trogossitidae	7	0
Elateridae	12	27	Family ? 1	1	0
Endomychidae	5	8	Family ? 2	1	0
Erotylidae	9	3	Total	955	859

Rank correlation coefficient $= 0.624$, $p < 0.001$.
Note: from Erwin and Scott (1980): * = Euglenidae, ** = Orthoperidae, *** Curculionidae not sorted to species. Erwin's Cucujidae includes Silvanidae. Nilionidae = Tenebrionidae.
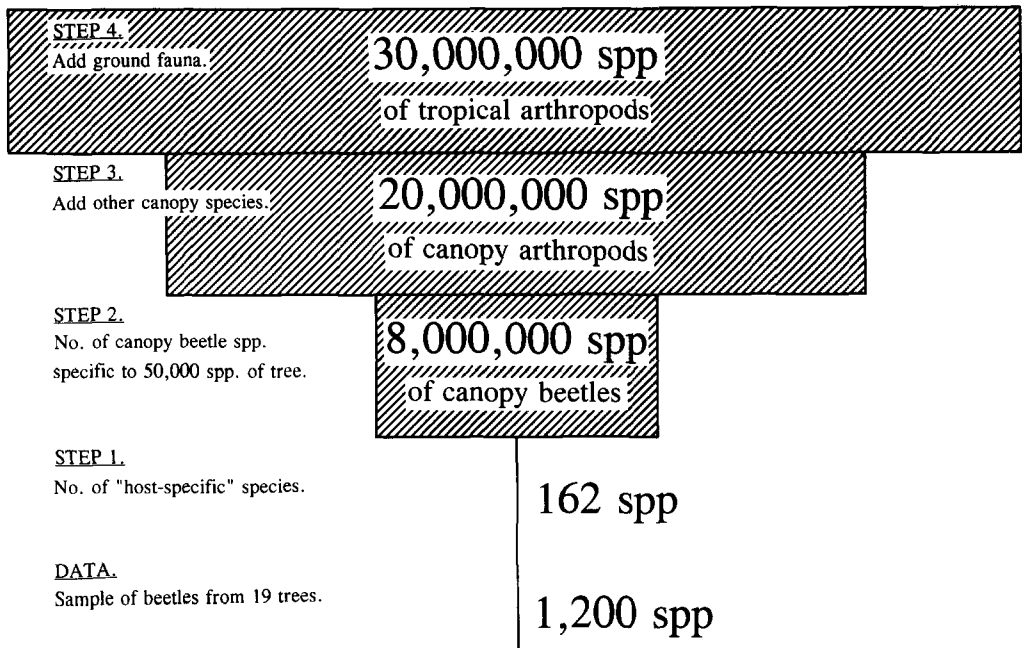
Fig. 1. Erwin's (1982) method of estimating global diversity of tropical insects. Note that on this scale the thickness of the lines for the DATA and STEP 1 levels should be 0.0016 mm and 0.012 mm thick.

of adult dispersal than to host tree specialization. Many insects therefore may be 'tourists' (*sensu* Moran and Southwood, 1982; Stork, 1987). This 'mass effect' will act to inflate measured local richness (Shmida and Wilson, 1985). In estimating the proportion of insect species specific to *L. seemannii* Erwin did not discount those herbivores, fungivores, predators or scavengers whose presence on the trees sampled may be due to chance and are therefore tourists. The high proportion of species represented by singletons in tropical canopy samples (Table 2) would suggest that a high or indeed a very high proportion of species are tourists. May (1990) has looked more closely at the theoretical distribution function $p_k(i)$, that is the fraction of canopy insects found on tree species k which utilize a total of i different tree species. Further, he examined f, the proportion of species effectively specialized to each tree species. Using reasonably accurate data on the known biologies of British beetles and their association with trees he showed that 10% were herbivores specific to the genus *Quercus*. Reminding us that this is for a single genus, May (1990) agreed with the earlier suggestion (Stork, 1988) that rather than a possible 20% of herbivorous canopy beetles being specific to the tree species, *L. seemannii* (Erwin, 1982), a figure of 5% or less (and hence a corresponding global estimate of 7 million or less) would be more likely. First estimates of tree specificity for tropical arboreal insects using May's theoretical distribution function, $p_k(i)$ and data derived from canopy fogging studies in Borneo (Stork, 1991), also support a figure of less than 5% (N.E. Stork and N. Mawdsley, unpublished).

Table 2. The diversity of Chalcidoidea collected from ten trees in Borneo using knock-down insecticide fogging (Stork, 1991) showing (a) the number of individuals of each species, and (b) the numbers of individuals and species for each family (Noyes, 1984).

(a) N(individuals)	N(spp)	(b) Family	N(individuals)	N(spp)
1	437	Agaonidae	16	14
2	160	Aphelinidae	261	146
3	54	Chalcididae	7	3
4	31	Elasmidae	10	6
5	18	Encyrtidae	299	170
6	10	Eucharitidae	7	1
7	8	Eulophidae	514	229
8	4	Eupelmidae	109	49
9	6	Eurytomidae	23	13
10	3	Mymaridae	57	36
11	2	Ormyidae	4	2
12	1	Pteromalidae	60	32
13	1	Signiphoridae	2	1
14	–	Tanaostigmatidae	5	3
15	–	Torymidae	70	24
16	–	Trichogrammatidae	11	10
17	1			
18	–			
19	1	Total	1455	739

These chalcids were sorted to species by John Noyes at the National History Museum (London, UK).

What proportion of the canopy species are beetles? Erwin suggested 40% based on the proportion beetles represent of described insect species. In the Bornean fogging samples beetles comprized about 20% of all species and this figure was used in the earlier appraisal of Erwin's estimates (Stork, 1988). Hammond (1992) suggests that beetles represent 33% of insects in tropical forests. For the ratio of canopy to ground species Erwin (1982) suggested a ratio of 2:1 whereas in contrast, Hammond suggested a ratio of 1:4 the other way round. Hammond arrives at this figure from preliminary analysis of data from the extensive programme of sampling in Sulawesi discussed below. He suggests that one in five of canopy beetle species belongs to the canopy fauna proper and illustrates this with cumulation curves for 10 and 50 canopy beetle species. A full cumulation curve for all 1277 beetle species (representing 10000 individuals collected on 900 m^2 collecting trays) from the Sulawesi lowland forest sites is shown for the first time in Fig. 2 and does not support Hammond's view. It has been suggested that the canopy to ground ratio for species might be 1:2 (Stork, 1988), midway between those of Erwin and Hammond. There is no apparent evidence to alter this view, although it may lean more to increasing the ground component. Detailed statistical analysis of the Sulawesi data should prove informative (P.M. Hammond, N.E. Stork and M.J.D. Brendell, in preparation).

In summary, reasoned alternatives to Erwin's figures would considerably reduce the number of tree-specific species, but increase the ground arthropod and the non-beetle
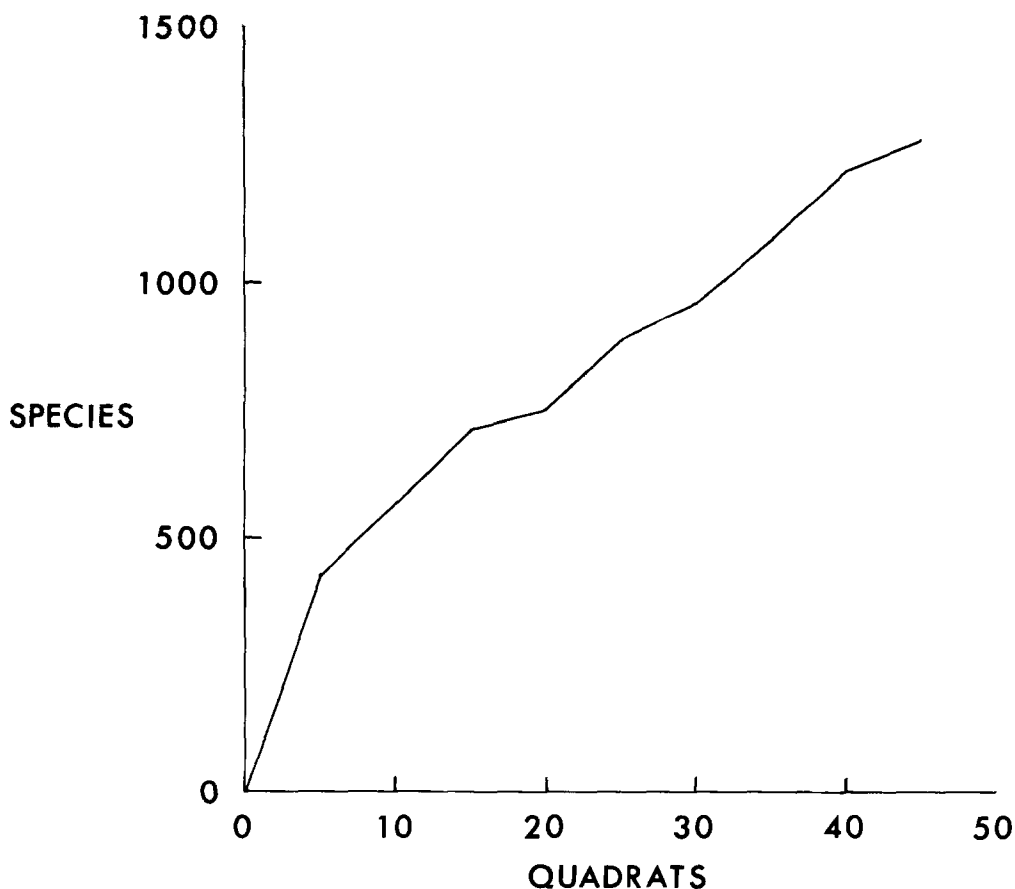
Fig. 2. Species cumulative curve for beetles in samples from canopy fogging lowland forest in N. Sulawesi. These include sampling six times during the year at one set of sites and twice at two other sites. The data used in this plot were derived from a randomised selection of quadrats (groups of 20 × 1 m^2 collecting trays) used throughout the sampling programme (Stork and Brendell, 1990).

components. These would suggest that conservative estimates of below 10 milion species of insects are more likely than higher estimates (Stork, 1988). What is so particularly compelling about this method of species estimation, even though it involves gross extrapolation, is that it is derived from first principles using real data from field samples.

Hodkinson and Casson's estimates

Analysis of samples from a year-long entomological expedition to Sulawesi in 1985, 'Project Wallace', has produced some of the best data available on arthropod diversity for a single tropical region (Noyes, 1987; Hammond, 1990; Stork and Brendell 1990; Hodkinson and Casson, 1991). Hodkinson and Casson (1991) used their data on the diversity of Hemiptera for this region in two ways to predict how many species there are. They examined the 1690 species of Hemiptera collected and, after consultation with specialists for different families, they estimated that 62.5% were new to science. They

found a significant correlation between the number of described species worldwide and the number of species from Sulawesi for different families of bugs and suggested therefore that their sample was perhaps a representative subset of the world fauna. If the same proportion of undescribed species was found worldwide then the world total for bugs would be 184 000–193 000. Applying figures of 7.5% (Southwood, 1978) and 10% (derived from Bornean canopy samples; Stork, 1988) for the proportion bugs comprise of the world's described insects produces estimates of 1.84–2.57 million for the total number of insect species. Their second line of argument is as follows; in the region sampled there were about 500 tree species and that if these had produced 1056 new species of Hemiptera then the 50 000 tree species worldwide would produce 105 600 new species. Adding on the described species would give 187 300 species and a global estimate for all insects of 1.84–2.57 million.

There are several possible problems with Hodkinson and Casson's arguments. First, they assume that their collection is representative of the area. However, they produce no evidence to show that this is the case, such as a cumulative curve for species. Their total of 1690 species is indeed impressive but they have not shown that they have collected all species in the area. The canopy samples which have been collected (Stork and Brendell 1990), for example, and from which a large proportion of the Hemiptera species derive, were far from extensive. The total area of forest sampled by canopy fogging was less than 0.20 ha (1700 1 m^2 tray samples) and included parts of the canopy of about 250 trees (number of tree species is unknown but is probably less than 100 judging by limited tree inventories in the area). Further canopy fogging might have doubled or trebled the number of species of Hemiptera, with similar multiplications for global estimates. Without species cumulation curves it is difficult to predict.

Second, although they show that the Sulawesi samples are reasonably representative of the Earth's fauna they do not demonstrate that the proportion of described to undescribed species is also representative. Third, many Hemiptera are economically important or are relatively large insects (i.e. above 2 mm long) and therefore may be better known taxonomically (Gaston, 1991b) than many other groups of insects such as the more species-rich groups Coleoptera, Diptera, Hymenoptera and Lepidoptera. This would suggest that figures of 7.5%–10.0% for the proportion of insect species that are Hemiptera are overestimates. Such assertions could easily be tested by examining the relative proportions of described to undescribed species for several groups (Hymenoptera, Coleoptera, Hemiptera and Leipdoptera) in the same samples. Such a study of the Sulawesi canopy beetles is underway (N.E. Stork and M.J.D. Brendell unpublished). These arguments would suggest that although Hodkinson and Casson's two sets of estimates are very similar, they may well be too low. Examination of the beetles from the Sulawesi samples may provide some measure of how low their estimates are.

Revised Hodkinson and Casson estimates using beetle data

The most extensive entomological survey of the Sulawesi project was that carried out by a combined team of 12 Natural History Museum (London) entomologists. Sampling was carried out throughout the year using an extensive range of methods (Malaise traps, flight interception trap, baited and non-baited pitfall traps, yellow pan traps, hand-collecting, light traps and leaf litter sampling) and with many temporal and spatial replicates for each method (Noyes, 1989; Hammond, 1990; Stork and Brendell, 1990).

The canopy was sampled by canopy fogging (Stork and Brendell, 1990). Separate voucher collections of the beetles have been prepared for the canopy fogging samples and for the other beetle samples and these are at present being combined.

The number of specimens from fogging (ca 350 000) represented only about 10% of the total arthropods sampled. With the exception of a few taxonomically intractable families, the number of beetle species collected by all sampling methods totals approximately 6000 species, some 2000 of which were collected by canopy fogging. If we assume that further collecting over other years (one year's sample is inadequate to examine the fauna of any region) and in other biotopes and from other species of trees within the region would have produced more species, then a working figure of 10 000 beetle species for the region would probably be reasonable. Again, species accumulation curves against sampling effort might give an indication as to the total fauna.

Using the same arguments as Hodkinson and Casson (*loc cit.*) concerning the ratio of tree species in the Sulawesi sampling area to that worldwide, and using estimates of the proportion of the Earth's insect fauna represented by beetles as 15% of the British beetle fauna and 20% of the Bornean canopy fauna one can estimate the world insect fauna as 3.0–4.0 million simply based on the 6000 species of beetle already collected or 5.0–6.7 million species based on a guess of 10 000 beetle species from the area. What this clearly demonstrates is that species estimates derived from samples are only as good as the sampling. If only 50% of the species are sampled then clearly such estimates will be 50% under the true figure.

Inevitably, for such an intensive listing of species for a site it is necessary to question how much sampling is required to determine the number of species that utilise a particular area. In practice the number of species utilizing an area is constantly fluctuating and cumulative curves for species will never asymptote. As a result there are well-documented temperate examples of long-term sampling resulting in much higher numbers of species being collected from areas than might be expected (e.g. Owen, 1992).

OTHER MODELS FOR SPECIES ESTIMATION

If there are consistent ecological rules that underly the distribution and community structure of organisms then it should be possible to determine the local, regional or global number of species by examination of real populations. Several models show promise in this regard.

May (1988) discussed the possibility that an understanding of food web structure might prove useful and examined the principles revealed by Cohen (1978) and Briand (1983). May noted that on average a species directly interacts with three to five other species. Similarly, Hawkins and Lawton (1987) found that typically herbivorous species of British insects were attacked by 5 to 10 species of parasitoid. Theoretically, therefore, knowing the mean number of herbivores per plant species, and hence number of parasitoid species might lead to estimates of at least a major part of the insect fauna.

One interesting model examined by May (1978, 1988, 1990) is based on species abundance and body size. May (1978, 1988) produced plots for well-known groups showing that number of species increases with diminishing size classes. This relationship appears to work well for all organisms down to about 1 mm. Fractal arguments would suggest that in the relationship, $S \sim L^{-x}$, where S is number of species and L is body length, the factor x should be between 1.5 and 3.0. Using these figures and extrapolating down to 1 mm, May (1988) suggested global estimates of from 10 million to 50 million

species. May's (1990) later extrapolation to 0.2 mm resulted in a global estimate of 10 million species, on the basis of an approximate empirical rule that species number increases 100 fold for a tenfold reduction in length. In practice, groups of smaller organisms are less well catalogued than larger organisms and this would tend to raise estimates. Having recently discovered a complex and species-rich fauna of species (largely mites and Collembola) below 1 mm in sandy soils in France and Belgium, André *et al.* (H.M. André, M.I. Noti and P. Lebrun, unpublished) suggest that extrapolation should be down to 136–65 μm which would add another 10 million to the May's total. Addition of even smaller soil organisms (Protozoa, Nematoda, Enchytraeidae and Tardigrada) they suggest would further increase the total. However, they do not consider that small species 'turnover' more rapidly than larger species and that such beta diversity is scale dependent (Brown and Maurer, 1989). Thus although André *et al.* may find many more species of mites and Collembola and Coleoptera in 100 cc of soil, the reverse is almost certainly true for soil from a hectare of forest (Fig. 2). The questions of scale, size of species and species turnover are not considered here but are elements that have not been considered sufficiently in gross extrapolations such as that by André *et al.* for soil microorganisms or by Grassle and Maciolek (1992) for deep-sea invertebrates (see comments by May 1992b).

TAXONOMISTS' VIEWS

Expert taxonomists should have a good sense of the ratio of undescribed to described species. In a survey of the views of taxonomists on this subject, Gaston (1991) found that all respondents believed that global estimates for their particular specialist group were less then ten-fold the number of described species and only a few gave predictions of more than five times the number of described species of their group. His analysis would suggest a global estimates for all insects of around five million. Erwin (1991) criticized Gaston's study, saying that it was non-scientific. However, our understanding of what species there are on the Earth and what actually constitutes a species depends on the information and understanding available to taxonomists at that point in time. It is easy to produce earlier global estimates such as those of the early 18th and 19th Century natural historians, Ray (global estimate for insects of 20 000 species; Westwood, 1833) and Kirby and Spence (global estimate for insects of 400–600 000 species; Westwood, 1833) and suggest that their low estimates are evidence that taxonomists are poor judges of species estimates. Ray, Kirby and Spence based their estimates on the information and understanding of species concepts of that time. In the same way, present day taxonomists base their predictions of their understanding of the fauna and flora as they see it through collections of specimens.

Adis (1990) supported Erwin's claims for 30 million or more arthropod species suggesting that many species were possibly comprised of a number of sibling species. His evidence for this was based largely on studies of Meinertillidae from the Amazon flood plains. These indicated that one well known species was really two sibling species occurring in two different habitats no more than 50 m apart (Wolf and Adis, 1993). Clearly, more information is required on the distribution of sibling species in other groups.

Where are the new species?

What is perhaps most surprising is that the implications of, and questions raised by, global estimates of 30 million species or more have largely been left unanswered and unwritten. For example, in which parts of the world and in what biotopes are these purported vast numbers of new species to be found, and to what groups do they belong? As Gaston (1991) noted, most insect species are members of four of the 28 recognized insect orders (Parker, 1982) and approximately half are in one, Coleoptera (approximately 400 000 described species; Hammond, 1992). Similarly, within these orders a few families are dominant in species terms. Of the 150 plus recognized families of beetles some eight families represent 70% of the described species. If one million insect species have been described and if there are 30 million species of insects then on average there must be 30 undescribed species for each described species. It is known that some groups of insects have been much better catalogued than others and therefore this would suggest that there must be some groups with more than 30 undescribed species for each described species. Furthermore, these higher ratios must be found in some of the larger orders of insects such as those listed above and in some of the larger families. Effectively we need to look for *vast* increases in the number of species for about 10–20 of the most species rich families of insects. Nowhere is there evidence of ratios of ⩽30:1 undescribed to described species for any major group of organisms. On this basis alone, it would be difficult to accept estimates of 30 million or more species of insects.

If such evidence is not available then perhaps there are regions and habitats, rich in undescribed species, that have been inadequately sampled. Myers (1988) lists 10 so-called hotspots of endemism and suggests that destruction of these would result in the loss of some 34 000 plant species, representing about 13% of all plant species. If there are 25 endemic insect species for each of these plants and they too are lost this would still only account for 850 000 species. Erwin's estimates infer that there are over 100 insect species for each described vascular plant species worldwide. Gaston (1992) found that the highest ratios of herbivorous insect species to plant species was 25:1 and for most regions of the world he examined it was considerably less. At this ratio a global estimate of 6.88–8.75 million species of insects would be derived (Gaston, 1992). One other possibility not discussed further here but requiring examination, is that many yet undiscovered species have very small distributions or occur at extremely low abundances.

Erwin (1988, 1991) found that in beetle samples produced by canopy fogging in Amazonian forests, only 1% of species were shared between all four different forest types in the same area and 2.6% shared between two regions 1500 km apart. He suggested that this was evidence for high local endemicity for insects. However, Erwin did not consider variation in his samples due to pseudo-turnover (Nilsson and Nilsson, 1985) and other sampling effects. As can be seen in Table 2, the low abundance of most species means that the chance of a species being found in two forest types (or trees in the case of Table 2) is extremely low. If there are 1 200 000 insects in tropical South America (Table 3), if 300 000 of these are beetles and if half of these are widespread throughout tropical South America, then the regional beetle fauna of the Manaus area where Erwin carried out his studies may well be up to 100 000 beetle species or more. If this is the case then his sample of 1080 beetle species from the four forest types in Manaus is very small and the value of 1% shared for all four forests would be hardly surprising. The guesses

for regional species richness presented here may prove to be over-estimates but they demonstrate the sampling dilemma that those working with super-diverse groups, such as insects in tropical forests, face.

Epilogue: where do we go from here?

Estimates of global diversity range from about 2 to 50 million. For insects those at the lower end of the scale have been questioned largely on the basis of inadequate sampling (Hodkinson and Casson, 1991). At the top end (Erwin, 1982, 1988) estimates of 30 million species or more are questionable because of the assumptions made and the lack of real evidence for vast numbers of undescribed species. The majority of estimates seem to fall within a range of 5–15 million species. Hammond (1992) has taken the bold step of trying to estimate the numbers of species for all organisms and his figures are reproduced here (Fig. 3). He regards his estimate of approximately 12.5 million species as a working figure to be adjusted in the light of new data. His figures for groups, such as bacteria, viruses and protozoa, are little more than guesses partly because of the problem of determining what is a species for these groups (but see also Hawksworth, 1991, 1992; and *Biodiv. Conserv.* **1**, 221–348 (1992)).

One way of estimating global species numbers that has received little attention is through the compilation of regional estimates (Gaston, 1991; Hammond, 1992). This method may increase in relevance through national and international biodiversity efforts. In Table 3 regional estimates are compiled for the number of species of insects based partly on my understanding of insect diversity through familiarity with major museum collections, through field work in different parts of the world, partly through discussion and partly through published regional estimates. These estimates are put forward to be tested and revised by others who may be in a better position to do so.

Table 3. Guestimates of the number of species of insects in different parts of the world

Region	No in thousands
N. America (USA and Canada)	200
Europe and former USSR	200
China and Japan	200
Asia	200
S.E. Asia	500
Australia and New Zealand	400
Africa	1000
Madagascar	300
Central America	500
Tropical South America	1200
Temperate South America	300
Pacific Islands	300
Total	5300

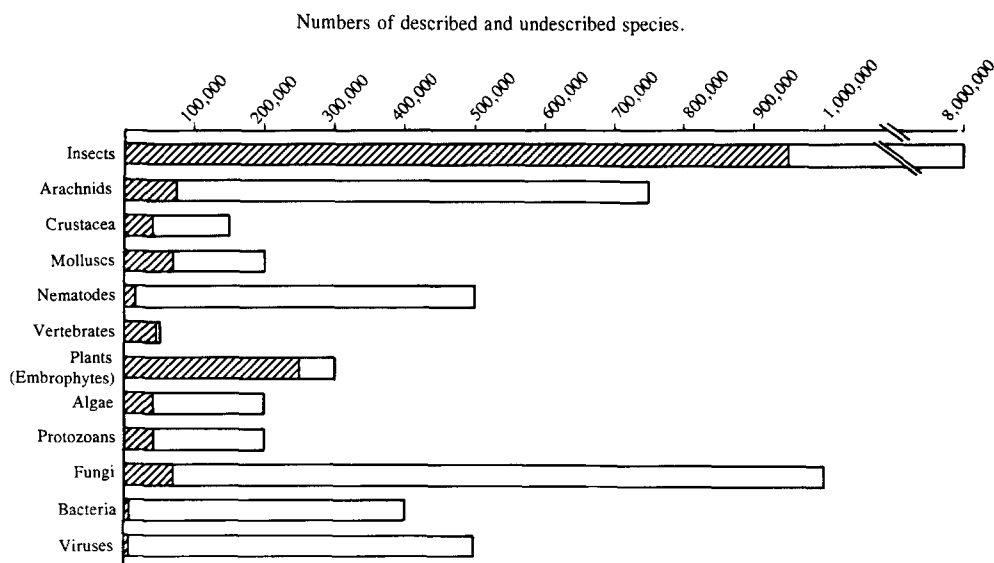Numbers of described and undescribed species.

Fig. 3. Numbers of described and undescribed species in the world for the major taxa (Hammond, 1992).

If an increase in the rate of describing the Earth's fauna and flora is to be seen and compiling of inventories then an improvement in patterns and practices of taxonomy needs to be seen. More taxonomists need to be trained in tropical countries. Taxonomic journals should accept fewer papers describing single species but should promote taxonomic works revising important groups and including keys. The process of compiling inventories on a wide scale is being addressed by international and national organizations following the signing of the Biodiversity Convention in Rio de Janeiro this year (di Castri, Robertson Vernhes and Younès, 1992; Stork, 1993) and this should result in increased funding for documenting life on the Earth and for increased coordination between organizations and countries. One result of this should be a better understanding of the number and distribution of species in different parts of the Earth and perhaps of the Earth as a whole.

Finally, it should be emphasized that solving the question 'how many species are there?' should not only lead to improved understanding of the distribution of biodiversity but should lead to improved predictions as to its fate.

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