PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

How Many Species? [and Discussion]

Robert M. May and R. J. H. Beverton

Phil. Trans. R. Soc. Lond. B 1990 **330**, 293-304
doi: 10.1098/rstb.1990.0200

How many species?

ROBERT M. MAY

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K., Imperial College, London, U.K.

SUMMARY

This paper begins with a survey of the patterns in discovering and recording species of animals and plants, from Linnaeus' time to the present. It then outlines various approaches to estimating what the total number of species on Earth might be: these approaches include extrapolation of past trends; direct assessments based on the overall fraction previously recorded among newly studied groups of tropical insects; indirect assessment derived from recent studies of arthropods in the canopies of tropical trees (giving special attention to the question of what fraction of the species found on a given host-tree are likely to be 'effectively specialized' on it); and estimates inferred from theoretical and empirical patterns in species–size relations or in food web structure. I conclude with some remarks on the broader implications of our ignorance about how many species there are.

1. INTRODUCTION

Earlier papers in this volume have surveyed our growing understanding of the factors that govern the population densities of individual species. Later papers have gone on to consider the dynamics of single populations in relation to the systems of interacting species in which they are embedded (Godfray & Blythe; Sugihara *et al.*), to their genetic structure (Travis), and to past (Valentine) and present (Hubbell; Lawton) patterns of relative abundance of species within communities. Ideally, this final paper should build on this foundation to arrive at an analytic understanding, as distinct from a mere compendium, of how many species of plants and animals we may expect to find in a given community or in a particular region. Ultimately, such analyses could aim to pyramid toward a fundamental understanding of why the total number of species on our planet is what it is, and not grossly more or less.

Needless to say, we are a long way from this goal. This paper, therefore, focuses on the plainly factual question of how many species of plants and animals there are on earth, a number currently uncertain to within a factor 10 or more, and does not ask about the underlying reasons. The paper thus differs from an earlier review with a similar title (May 1988), in which I dealt mainly with basic factors that may influence species diversity, both locally and globally.

My paper begins with an account of those species that have been named and recorded. Amazingly, this current total is not known, because there is no central catalogue or list of named species; a good estimate may be around 1.8 million (Stork 1988). I then discuss a variety of ways in which the total number of plant and animal species on earth today may be estimated: by extrapolating past trends of discovery within particular groups; by inferences from detailed studies of the arthropod canopy fauna in tropical trees; by direct estimates of the proportion of new species in studies of groups of tropical insects (often different from extrapolating past trends, which come predominately from temperate regions); from species–size relations; and so on. Different approaches yield global totals as small as 3 million or as large as 30 million or more. A penultimate section raises some broader questions about species diversity that are prompted by such estimates of local or global totals. I conclude with subjective thoughts on why it is important to know how many species there are.

2. HOW MANY RECORDED SPECIES?

It is noteworthy that Linnaeus' pioneering codification of biotic diversity came a century after Newton, in the mid-1700s. Whatever the reason for this lag between fundamental studies in physics and in biology, the legacy lingers. Today's catalogues of stars and galaxies are effectively more complete (by any reasonable measure), and vastly better funded, than catalogues of Earth's biota. And this certainly is not because stellar catalogues offer more opportunity for commercial application than do species catalogues.

The 1758 edition of Linnaeus' work records some 9000 species of plants and animals. Table 1 summarizes estimates of the numbers recorded since then up to 1970, for different groups. Table 1 also gives the time it took to record the second half of the total number of species (up to 1970) in each group, and the era when new species within each group were being discovered at the fastest rate (from Simon 1983). The table gives a sense of the differences in the attention paid to different groups, with half of all known bird species already recorded in the century after Linnaeus, while half the arachnid and crustacean species known in 1970 were recorded in the preceding 10 years; contrast figure 1 and figure 2.

The furries and featheries are, of course, very well

Table 1. *Taxonomic activity, from 1758 to 1970, for different animal groups, as revealed in patterns of recording new species* (*after Simon 1983*)

animal group	estimated number of species recorded up to 1970	length of time (years), prior to 1970, to record the second half of the total in the previous column	period of maximum rate of discovery of new species
Protozoa	32000	21	1897–1911
'Vermes'	41000	28	1859–1929
Arthropoda (excluding insects)	96000	10	1956–1970
Arthropoda (insects only)	790000	55	1859–1929
Coelenterata	9600	58	1899–1928
Mollusca	45000	71	1887–1899
Echinodermata	6000	63	1859–1911
Tunicata	1600	68	1900–1911
Chordata			
Pisces	21000	62	1887–1929
Amphibia	2500	60	1930–1970
Reptilia	6300	79	1859–1929
Aves	8600	125	1859–1882
Mammalia	4500	118	1859–1898

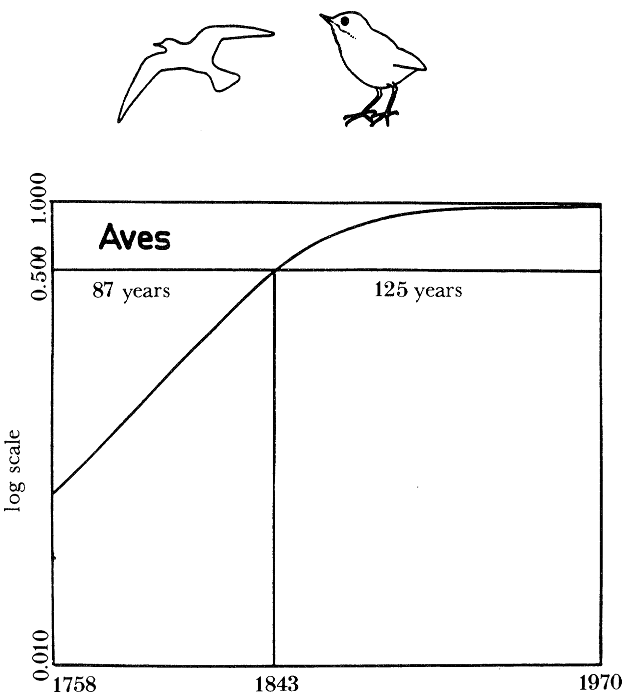

Figure 1. The curve shows the rate of discovery of bird species, from the time of Linnaeus (1758) up to 1970. Numbers of known species (expressed as a fraction of those known in 1970, on a logarithmic scale) are plotted against time. The vertical and horizontal lines show the point (1843) when half the 1970 total of species had been discovered. After Simon (1983).

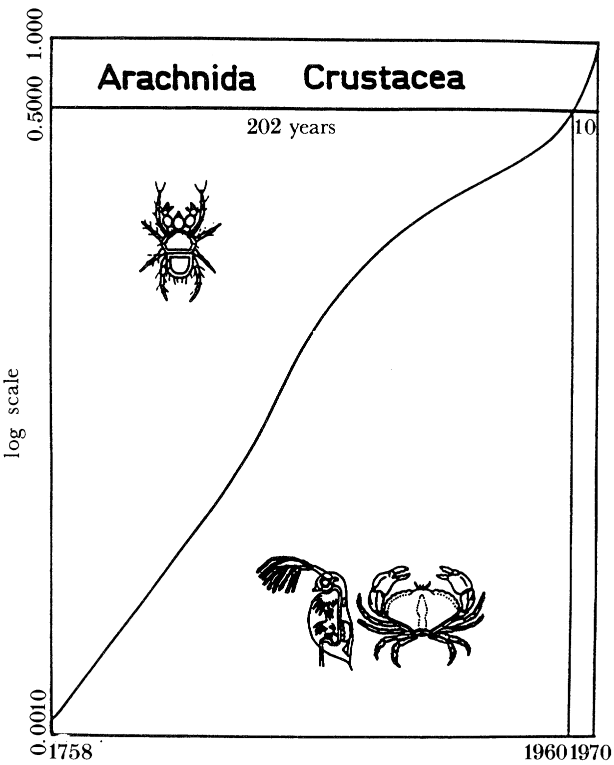

Figure 2. As for figure 1, but now showing recorded numbers of Arachnid and Crustacean species (essentially, arthropods excluding the Insecta) over time. The pattern of discovery is very different from that for bird species, with half of the total up to 1970 being recorded since 1960. After Simon (1983).

known by now. As reviewed in detail by Diamond (1985), only 134 bird species have been added to the total of just over 9000 since 1934, representing a rate of discovery of around three species per year since 1940 (most of them small, brown tropical birds). Rates of discovery are somewhat higher for mammals, with 134 of the current total of 1050 genera added since 1900, at a rate of about 1 genus per year since 1940 (most of them tropical bats, rodents or shrews, or small marsupials). As we shall see below, however, the story is altogether different for insects and other smaller creatures.

Publication rates provide another measure of the differential attention paid to different groups (see table 3, May 1988). Of papers listed in the *Zoological Record* over the past few years, mammals and birds average about 1 paper per species per year, reptiles, fish and amphibians about 0.5 papers per species per year,

Table 2. *Estimated numbers of canopy beetle species that are specific to the host tree species* Luehea seemanii, *classified into trophic groups (after Erwin 1983)*

trophic group	number of species	estimated fraction host-specific (%)	estimated number of host-specific species
herbivores	682	20	136
predators	296	5	15
fungivores	69	10	7
scavengers	96	5	5
Total	1100+	—	160

whereas insects and other groups average from 0.1 to 0.01 or fewer papers per species per year.

Even within a given class, or order, different families can show different patterns in the study they have received. Thus, looking at different families of insects, Strong *et al.* (1984) show that recorded species of whiteflies (Aleyrodidae: Hemiptera) and phytophagous thrips (Thripidae: Thysanoptera) increased dramatically this century with a peak around 1920–40; weevils (Curculionidae: Coleoptera) show a gradual rise since Linnaean times, again peaking around 1920–40; whereas the papilionoid and danaid butterflies (Papilionodea and Danainae: Lepidoptera) are more like birds, with broad peaks in recording rates in the second half of the 19th century.

Such patterns in rates of recording new species can be projected forward, group by group, by standard statistical techniques. In this way, we can obtain an estimate of the eventual global total of species of plants and animals. As mentioned earlier, however, the records of named species are scattered, so that estimates of the total number actually named by a given date are themselves insecure (three frequently cited estimates are 1.5 million (Grant 1973), 1.4 million (Southwood 1978), and the more current 1.8 million (Stork 1988)). Projected totals are correspondingly subject to wide fluctuations, depending on the views taken of trends in particular groups and the statistical procedures used. Simon (1983, table 31) surveys several estimates arrived at by these methods, which range from concluding that essentially all species have already been named(!) to Simon's own estimates of around 6–7 million animal species in total. Grant's (1973) projection of 4–5 million is often referred to, but it is essentially based on the crude procedure of multiplying the recorded total number of insect species (which he put at 0.75 million in 1973) by 5. It must be emphasized that all the estimates based on projecting rates of discovery pre-date the dramatic studies of tropical insects discussed in §3 and §4.

A cruder, but intuitively satisfying, estimate that the global total lies in the range of 3–5 million species has been provided by Raven (1985) and others. This estimate rests on two observations. First, among well-studied groups such as birds and mammals there are roughly two tropical species for each temperate or boreal species. Second, the majority of species are insects, for which temperate and boreal faunas are much better-known than tropical ones; overall, approximately two thirds of all named species are found outside the tropics. Thus if the ratio of numbers of tropical to temperate and boreal species is the same for insects as for mammals and birds, we may expect there to be something like two yet-unnamed species of tropical insects for every one named temperate or boreal species. This carries us from the recorded total of 1.4–1.8 million species to the crude estimate that the grand total may be around 3–5 million.

3. QUESTIONS RAISED BY STUDIES OF TROPICAL CANOPY FAUNAS

Recent studies of the arthropod faunas of tropical trees raise serious doubts about the validity of the above estimates, based as they are on projecting forward from past trends of discovery and recording. The essential point is that all the past trends are dominated by temperate-zone invertebrate groups, especially insects, whereas the recent work (surveyed in this section and the next two) suggests that tropical insect faunas may have very different patterns of diversity.

One frequently quoted upward revision to a global total of 30 million species or more comes from Erwin's (1982, 1983; Erwin & Scott 1980) studies of the insect fauna in the canopy of tropical trees. By using an insecticidal fog to 'knock down' the canopy arthropods, Erwin concluded that most tropical arthropod species appear to live in the treetops. This is not so surprising, because the canopy is where there is most sunshine as well as most green leaves, fruits and flowers.

Specifically, Erwin's original studies were on canopy-dwelling beetles (including weevils) collected from *Luehea seemannii* trees in Panama, over three seasons. As summarized in table 2, he found more than 1100 species of such beetles, which he partitioned among the categories of herbivore, predator, fungivore and scavenger.

To use the information in table 2 as a basis for estimating the total number of insect species in the tropics, one first needs to know what fraction of the fauna is effectively specialized to the particular tree species or genus under study. Unfortunately, there are essentially no systematic studies of this question even for temperate-zone trees, much less tropical ones. Erwin guessed 20% of the herbivorous beetles to be specific to *Luehea* (in the sense that they must use this tree species in some way for successful reproduction). As shown in table 2, his overall answer is more sensitive to this estimate than to the corresponding figures of 5%, 10%, and 5% for predator, fungivore, and scavenger beetles, respectively. In this way, Erwin arrived at an estimate of around 160 species of canopy beetles effectively specialized to a typical species of tropical tree.

Several other assumptions and guesses are needed to go from this estimate of 160 host-specific species of canopy beetles per tree to 30 million species in total. Slightly simplified, the argument runs as follows. First, Erwin noted that beetles represent 40% of all known arthropod species, leading to an estimate of around 400 canopy arthropod species per tree species. Next, Erwin suggested that for every two insect species in the canopy there may be one species elsewhere on the tree or the immediately neighbouring forest-floor, increasing the estimate to around 600 arthropod species effectively specialized to each species or genus-group of tropical tree. Finally, by using the estimate of 50000 species of tropical trees, Erwin arrived at the possibility that there are 30 million tropical arthropods in total.

As Erwin emphasizes, this chain of argument does not give an answer, but rather an agenda for research. Setting aside the question of whether *Leuhea* (along with its ensemble of associated lichens, vines, bromeliads, etc.) is a typical tropical tree, there are at least four areas of uncertainty: (i) what fraction of the beetle (or other) fauna on a given tree species are effectively specialized to it; (ii) do beetle species constitute the same fraction of insect faunas in the tropics as they do in better-studied temperate regions; (iii) for each insect species in the canopy, how many other species are found elsewhere or in or around a tree, and (iv) how do we scale up from the number of insect species associated with a given tree species in a given place to a global total? These four links in Erwin's chain of argument serve to organize the remainder of this section.

(*a*) *What fraction of the fauna is 'effectively specialized' to a given tree species?*

Suppose a given region contains 100 different tree species, and a total of 1000 different species of canopy beetles. At one extreme, all the beetles may be complete generalists, so that (setting aside sampling problems) all 1000 species could be found on any one tree species. At the opposite extreme, it could be that all beetles were complete specialists, with the total of 1000 made up by each of the 100 tree species contributing its particular 10 species of beetles. Now turn this around, and suppose that in a region where there are 100 tree species we find 100 species of canopy beetles in exhaustive sampling from just one tree species. How many beetle species are there likely to be in total? The above argument suggests that, if the studied tree is indeed representative, the total number of canopy beetle species lies somewhere between 100 (all generalists) and 10000 (all highly specialized).

Suppose we are investigating a region containing a total of M different tree species. The above issues can now be made precise by formally defining $p_k(i)$ to be the fraction of canopy beetles (or other insects) found on the tree species labelled k ($k = 1, 2, \ldots, M$), which utilize a total of i different tree species (including the one labelled k). Further, let N_k denote the total number of canopy beetles (or other insects) found on tree species k. Then, of the beetles found on tree species k, $N_k\,p_k\,(1)$ are found only there, $N_k\,p_k\,(2)$ are found on k and on only one other tree species, and so on. The total number of distinct canopy-beetle species, N, in the region is then given by the sum:

$$N = \sum_{k=1}^{M} \sum_{i=1}^{M} (1/i)\; N_k\, p_k\,(i). \qquad (1)$$

That is, we sum the numbers of beetle species over all tree species, discounting each tree by the factor $1/i$ for those of its beetle species found on i tree species.

The 'effective average' number of beetle species per tree species, or overall average number of beetles 'effectively specialized' to each tree species, is then N/M, with N given by equation (1). For the tree species labelled k, the proportion of its beetle species that are 'effectively specialized' to it, f_k, is given by

$$f_k = \sum_{i=1}^{M} (1/i)\; p_k(i). \qquad (2)$$

The corresponding overall proportion of beetle species 'effectively specialized', averaged over all tree species, is denoted by f:

$$f = N/\sum_{k} N_k. \qquad (3)$$

Here N is given by equation (1). Equation (3) says that the overall average fraction of beetle species 'effectively specialized' to each tree species, f, is given by the total number of different species divided by the sum of the totals from each tree species, without discounting for overlaps.

Unfortunately, there is to my knowledge not a single systematic study of the distribution functions $p_k(i)$ for the apportionment of any faunal group among any group of plant or tree species. At best there are some studies, essentially all for temperate communities, which distinguish among monophagous, oligophagous, and polyphagous insects (roughly, those feeding on a single species or genus, on a family, or more generally, respectively). The assumptions codified in table 2 correspond to assuming that f_k is 0.20, 0.05, 0.10, 0.05 for herbivore, predator, fungivore, scavenger beetles in the canopy of *Leucea*, respectively; but these are guesses.

Although quantitative studies are lacking, the formal definitions embodied in equations (1–3) can at least alert us to some of the pitfalls in intuitive estimates of the proportion of beetle species that are 'effectively specialized'. Suppose, for example, that for a given group of insects in a particular tree species (labelled 1) the distribution function, $p_1(i)$, has the geometric-series form $p_1(i) = c\alpha^i$ (with $\alpha < 1$). This says that the fraction of species utilizing i tree species decreases geometrically as i increases. The normalization constant, c, ensures that $\Sigma\, p_1(i) = 1$ (if the total number of tree species is large, $M \rightarrow \infty$, then $c \rightarrow (1-\alpha)/\alpha$). In this event, the fraction of the insect species on tree species 1 that are effectively specialized to it, f_1, can be seen to be given

Table 3. *A very preliminary study of the distribution of beetle species among four species of British oaks, to show ideas about the distribution function, $p_k(i)$, and definitions of 'effective specialization' (from unpublished data provided by T. R. E. Southwood)*

oak species	number of beetle species found on a given oak species, N_k	number of beetle species found on a given oak species, that are found on a total of i of the 4 oak species (proportion found on i species, $p_k(i)$)				proportion of beetle species effectively specialized on this oak species, f_k, from eqn (2)
		$i = 1$	2	3	4	
cerris	28	5 (0.18)	8 (0.29)	7 (9.25)	8 (0.29)	0.48
ilex	47	20 (0.43)	10 (0.21)	9 (0.19)	8 (0.17)	0.64
petraea	48	14 (0.29)	15 (0.31)	11 (0.23)	8 (0.17)	0.57
robur	50	15 (0.30)	15 (0.30)	12 (0.24)	8 (0.16)	0.57
totals	173	54	24	13	8	average, $f = 0.57$

(in the limit of very large M) by $f_1 \simeq [(1-\alpha)/\alpha] \ln[1/(1-\alpha)]$. But an estimate of f_1 based on biological intuition might simply ask about the 'monophagous' fraction, that are found only on that tree species or genus-group; this would lead to the estimate $f_1 \simeq p_1(1) = 1-\alpha$. Suppose that in fact $p_1(1)$, the fraction monophagous within this distribution, is 20% (that is, $\alpha = 0.8$). Then in this illustrative example the fraction 'effectively specialized' is $f_1 = 0.40$, which is twice as large as might be guessed on intuitive grounds.

What are needed, of course, are not speculative abstractions, but analytic studies of the distribution functions $p_k(i)$ for particular floral and faunal communities. By way of illustration, table 3 shows a very preliminary analysis of the distribution of beetle species among four species of oak trees, *Quercus cerris*, *Q. ilex*, *Q. petraea* and *Q. robur* in Wytham Wood, Oxford (data provided by T. R. E. Southwood). The data in table 3 represent the species 'knocked down' by insecticidal fog (specifically, from 6 foggings per tree species in the months of May and June). On this basis, the four above-mentioned oak species show totals of 28, 47, 48 and 50 beetle species, respectively, for a gross total of 173 species. But in fact only 99 distinct beetle species are present, with the pattern of overlap as shown in table 3. The table also shows that, for this example, the fraction of the beetle species that are 'effectively specialized' to a given oak species (as defined by the formulae above) is roughly around 60%. It must be emphasized that this example is presented for illustrative purposes, to make the above ideas more concrete; it is a very crude and preliminary analysis of a fragment of a much larger data set.

The definition of the distribution function $p_k(i)$ was made on biological grounds, based on the number of tree species whose resources are utilized in some way by a particular insect species. The data in table 3 are, however, surely dominated by sampling considerations. A few of the beetle species in table 3 are represented by only one individual, and many of the species that utilize these oaks are absent from the samples altogether. Moreover, the table does not distinguish between species that are known to utilize a given tree, and those that accidentally happen to be on it when the sample is collected by fogging (Moran & Southwood's (1982) 'tourist' species). In this respect the data presented in table 3 are similar to those likely to be collected in most studies of canopy and other faunas: the patterns of distribution of insect species among tree species will be a mixture of the underlying biological patterns of resource use (and of specialization and generalization), clouded or often dominated by sampling effects. I believe there is a need here both for theoretical studies (clarifying the interplay between sampling effects and the underlying distributions of resource utilization, among other things) and for empirical investigations. Such work will ultimately illuminate fundamental aspects of the structure of ecological communities, and will contribute to more reliable estimates of the global total of species. My aim in this sub-section, which obviously provides questions not answers, is to stimulate such further work.

The coarse and conventional division of phytophagous insects into monophages, oligophages and polyphages may be sharpened somewhat for the phytophagous beetles on oak trees in Southwood's study. By using standard handbooks (Fowler 1913; Joy 1931; Portevin 1935), it is possible to determine: (i) what fraction of the approximately 100 species are restricted to oaks (that is, to the genus *Quercus*); (ii) what fraction to the family Fagiacea, or (iii) the order fagaces, as opposed to (iv) those found generally on angiosperms, or (v) even more broadly. A tentative analysis of Southwood's data suggests the proportions of phytophagous beetle species in the five categories thus defined are 0.10, 0.03, 0.06, 0.77 and 0.04, respectively.

If these exceedingly rough figures were taken as representative, they would suggest that Erwin's estimate that 20% of herbivorous canopy beetles are host-specific be replaced by a figure of 10% or less (remember, the 10% above is for the oak genus, not for a particular species). This would halve the estimated global total, to 15 million species or fewer. And if tropical beetles are typically less specialized than temperate ones, as they may need to be in response to the much patchier distribution of a vastly greater diversity of tree species, then the percentage that are host-specific (and thence the estimated global species total) could be smaller yet. On essentially these grounds, Stork (1988) had suggested that the effective fraction of host-specific beetle species in tropical canopies may be closer to 5% or less than to 20% (with a corresponding global total of 7 million or fewer species); see also Beaver (1979). There is clear need both for more theory (dealing with f_k and the way sampling and other effects influence it), and for more facts.

(*b*) *In particular settings, what proportion of insect species are beetles?*

Although roughly 40% of all recorded insect species are beetles, the existing handful of detailed studies suggest that beetle species constitute a smaller fraction of insect faunas collected by fogging tropical or temperate trees.

Southwood *et al.* (1982) sampled the invertebrate fauna (essentially all of which were insects) of six tree species in both Britain and South Africa, by using pyrethrum knockdown. In Britain, the total number of invertebrate species on the different tree species varied from 176 to 465, and the beetle species constituted, on average, 7% of the total (ranging from a low of 5% on *Salix* to a high of 11% on *Quercus*; see table 1 in Southwood *et al.* (1982)). The corresponding species totals on South African trees ran from 105 to 300, of which an average of 19% were beetle species (ranging from a low of 15% on *Salix* to a high of 23% on *Erythrina* and *Quercus*). Of the roughly 2800 species represented in the 24000 arthropod individuals collected in fogging samples from 10 trees in Borneo by Stork (1988, figure 3), approximately 30% were beetles.

These numbers have led Stork to speculate that beetles may more typically constitute around 20% of the insect species found in tree canopies, rather than the 40% that is characteristic of beetles more generally. All other things being equal, such a revision to this link in Erwin's chain of argument would double the global total number of species. My view is that these different results from different studies speak to the complexity and contingent nature of the underlying questions. Until such time as we have a better understanding of why beetles (or any other group) make up such different fractions of the species totals in different trees at different places, I would be inclined to stay with the overall average figure of 40% beetle species when making global estimates by 'scaling up' local studies.

(*c*) *What is the ratio of canopy insects to all insects on a tree?*

There are no studies of all the arthropod species found on the various parts of a tropical tree, but there are some studies of how the numbers of individuals are distributed.

Stork (1988) used a range of techniques to sample the fauna from each of five parts of trees in the lowland rainforest of Seram in Indonesia: canopy; tree trunk; 'ground vegetation' (from 0 to 2 m above the forest floor); leaf litter; and soil (the first few cm). In this site, Stork estimates there were approximately 4200 individuals per square metre, distributed among the five categories listed above as 1200, 50, 10, 600 and 2400. Roughly 70% of all individuals are found in the soil and leaf litter, mostly springtails (Collembola) and mites (Acarina). In the canopy, which contains about 14% of all individuals, ants are the most abundant arthropods (constituting roughly 43% of the individuals). If numbers of species bore a direct relation to numbers of individuals, we can see that Erwin's estimate of one insect species elsewhere on the tree for every two species in the canopy would be out by almost a factor 10. But although ants tend to be more abundant than beetles in tropical canopies, they contribute significantly fewer species. The same seems likely to be true for the springtails in the soil and leaf litter. I have serious doubts, however, whether it is also true for the mites (moreover, the number of individual mites in the soil and leaf litter is typically an order-of-magnitude larger than the number of beetle individuals in the canopy).

Adis and colleagues (Adis & Schubart 1984; Adis & Albuqueque 1989) have made similar studies of the arthropod faunas of seven different types of Amazonian forests and plantations, using soil cores (0–7 cm), ground and arboreal traps of various kinds, and canopy fogging. Like Stork, they found the majority of individuals were Collembola and Acarina in the soil and leaf litter (with two thirds or more of these in the top 3.5 cm of the soil). The main difference between these Amazonian studies and the Indonesian ones is in the total numbers of individuals, which ranged as high as 30000 or more per square metre at some Amazonian sites. But the divisions of numbers of individuals among canopy, trunk, ground vegetation, leaf litter and soil are broadly similar in all the studies, as are the broad apportionments of individuals among taxonomic groups.

Understandably but unfortunately, all of these studies are of numbers of individuals in the different parts of the tree, not of the numbers of species. Until more is known, a consensus guess may be that for every insect species in the canopy there is one elsewhere in the typical tropical tree (rather than Erwin's 0.5). But this could lead to a serious underestimate of the global total, if the mites turn out to be as surprisingly diverse as the tropical canopy beetles.

(*d*) *How do we scale up from insect species per tree to a global total?*

Even if we knew how many insect species were effectively specialized to a truly representative species of tropical tree at a particular place, there remain serious difficulties in scaling this up to the roughly 50000 species of tropical trees. The reason that we cannot simply multiply the number of species per tree by the number of tree species is twofold: on the one hand, the same tree species may play host to different insects in other parts of its range (so that simple multiplication underestimates the global total); on the other hand, the same insects may be effectively specialized on other tree species in other regions (so that simple multiplication could lead to overestimation).

Ward's (1977) study of Juniper in Britain is an example of the first of these two complications. Looking at each one degree band of latitude in the range of Juniper, from 50° N to 59° N, she found the recorded numbers of species of arthropods varied from 5 to 20. The total number of species associated with Juniper in Britain in this study is 27, which is larger by a factor 1.4–5.0 than the total that might be inferred from any one regional study.

The converse phenomenon, the same species specialized to different plants in different places, is shown by Thomas's (1990) analysis of the *Passiflora–Heliconius* system in South America. For this unusually well-studied association, Thomas averages over 12 sites to find a mean of 7.2 Passifloraceae species and 9.7 Heliconiinae species per site (he uses families or subfamilies, because a few Heliconiinae are not in the genus *Heliconius*, and likewise a few Passifloraceae are not in the genus *Passiflora*). The total number of recorded Passifloraceae species in the neotropics is 360. A naive scaling up may therefore suggest 360 times $(9.7/7.2) \simeq 485$ Heliconiinae species. But this total is in fact only 66 species. The complicating factor is, of course, that these relatively specialized butterflies use taxonomically different (although ecologically similar) species of Passifloraceae in different parts of the neotropics, with the result that simple multiplicative estimates are an order-of-magnitude too high. There are further complications and caveats here. For one thing, it could be that, to some extent, systematists have tended to split the Passifloraceae and lump the Heliconiinae (Gilbert & Smiley (1978) refer to one downward revision from 70 to 7 species of *Heliconius*). For another thing, only some 100–150 species of Passifloraceae are found below 1500 m, which represents an upper limit to the range of Heliconiinae species (Gilbert & Smiley 1978), so that simple multiplication might more properly suggest 135–200 Heliconiinae species. This is still significantly larger than the 66 that exist.

The essential point is that the simple procedure of multiplying the average number of species per tree by the number of tree species can be misleading for those insect species with ranges significantly larger than that of the host-tree species in question, and conversely for tree species whose ranges exceed that of the insects in a given region. We cannot begin to resolve these problems until we have a better understanding of the patterns in the distributions of geographical ranges for plant and animal species.

Despite some pioneering efforts (Rappoport 1982; Hanski 1982; Brown 1984; Root 1988), little is yet known about range-size patterns for individual species, much less for joint distributions of, for instance, herbivorous insects and their host plants. Figure 3 summarizes one recent analysis of the distributions of range sizes for all North American mammals, showing that most species have relatively restricted ranges (the median range size is about 1% of the area of North America), but that there is considerable variability. On the whole, it seems likely that for tree species with below-average ranges, we may need to acknowledge that many of the insects that are effectively specialized to them range more widely, using other trees in other places (so that Erwin's simple multiplicative procedure may overestimate totals). Conversely, trees with above-average ranges may embrace different faunas in different places, resulting in underestimated totals if one location is treated as definitive. Ultimately, such questions of range-size and geographical distribution shade into larger questions of how we define commonness and rarity, and how patchiness and regional differentiation affect extinction probabilities (Rabinowitz *et al.* 1986; Pagel *et al.* 1990; Hubbell, this symposium).

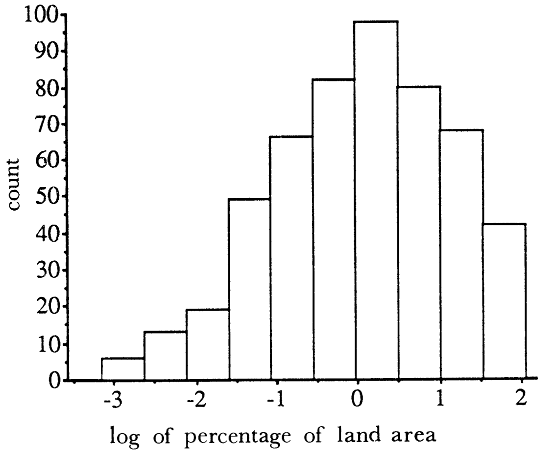

Figure 3. Histogram of the logarithms of the sizes of species's geographical ranges for 523 species of North American non-aquatic mammals. The range size is expressed as a percentage of the total land area of North America. The distribution is roughly lognormal in shape, with the proportion of species in the different (logarithmic) range-size categories falling away roughly symmetrically on either side of the median value of around 1%. After Pagel *et al.* (1990).

I end this section by circling back to Erwin's method of estimating the total number of species on Earth. Suppose we accept a total of 1200 beetle species in the canopy of a tropical tree species as typical. Further assume there are 2.5 other canopy insect species for each beetle species (40% of insects are beetles), and one species elsewhere on the tree for each one in the canopy. Suppose a fraction, f, of this fauna is effectively specialized to the tree species in question. Finally, assume we can simply multiply the effective number of insect species per tree species by the number of tropical tree species (50000) to arrive at the grand total. This total is then $(300f)$ million. If, overall, 10% of the insects are effectively specialized to a given tree, we recover Erwin's 30 million. To reduce an estimate along these lines down to the previously-conventional figure of around 3 million, we need to assume that only 1% of the insect species are effectively specialized, which seems a bit low. I return to this below.

4. DIRECT ESTIMATES OF GLOBAL TOTALS

Hodkinson & Casson (1990) have presented a very direct way of estimating species totals, based essentially on determining what fraction of a thoroughly sampled group, in a particular region, have previously been described.

Specifically, they use several methods to sample the bug (Hemiptera) fauna of a moderately large and topographically diverse region of tropical rainforest in Sulawesi, in Indonesia, over a one-year period. Hodkinson & Casson (1990) estimate that their samples represent the bug fauna on the roughly 500 tree species in their study sites in Dumoga Bone

National Park in Sulawesi. They found a total of 1690 species of terrestrial bugs, of which 63% were previously unrecorded (this proportion of undescribed species is weighted according to the number of species per family within the group).

If the bugs in Sulawesi are representative of tropical insects more generally, then we may say that the total number of recorded insect species (approximately 1 million) represents 37% of the real total, leading to an estimated 2.7 million insect species in total. Hodkinson & Casson give a somewhat more detailed argument, with several intermediate steps, to reach an estimated total of 1.8 to 2.6 million, but I believe the more direct approach outlined above contains the essentials.

Hodkinson & Casson also use their data to give a different derivation of the global total number of insects. First, if they find roughly 1700 bug species on 500 tree species, we might expect 170000 bug species on the tropical total of 50000 tree species. Second, bugs comprise approximately 7.5% of all described insects (Southwood 1978), so we can estimate a grand total of 2.3 million insects (again, Hodkinson & Casson's somewhat more detailed estimate gives a total of 1.9–2.5 million). This second estimate is surprisingly close to the first, and much more direct, estimate of 2.7 million. This rough coincidence between the two estimates is not trivial or tautological; it can be seen to arise essentially because the factor of 100 in the ratio between tree species globally and in Dumoga Bone Park is roughly cancelled by the factor of 109 in the ratio between all known bug species and the number of known species in their study (or 114 if aquatic bugs are included in the global total).

This is a brief summary of an important study. There is obviously an enormous amount of work in completely sampling and classifying any group of tropical insects, and one must always worry whether the group or site is representative of more general patterns. But I see this as the simplest and most direct route to estimates of global totals. When other taxa are added, Hodkinson & Casson's estimate of insect species totals carries us back to the previously conventional global total of 3–5 million species. On the other hand, to reconcile Hodkinson & Casson's estimate with Erwin's data, we need to assume that over 400 of his roughly 1200 beetle species in the canopy of *Leuhea* have been described and recorded, which seems unlikely to me.

5. SPECIES TOTALS FROM SPECIES–SIZE RELATIONS

An altogether different approach to estimating how many species there are derives from examining patterns in the numbers of terrestrial animal species in different body-size categories (May 1978, 1988). Very roughly, as one goes from animals whose characteristic linear dimension is a few metres down to those of around 1 cm (a range spanning many orders-of-magnitude in body weight), there is an approximate empirical rule which says that for each tenfold reduction in length (1000-fold reduction in body weight) there are 100 times the number of species.

This empirical relation begins to break down at body sizes below 1 cm in characteristic length. As the relation itself is not understood, this break-down may mean nothing. But the break-down may plausibly be ascribed to our incomplete record of smaller terrestrial animals, most of which may be unrecorded tropical insects. If the observed pattern is arbitrarily extrapolated down to animals of characteristic length around 0.2 mm, we arrive at an estimated global total of around 10 million species of terrestrial animals (May 1988).

This frankly phenomenological estimate would be more interesting if we had a better understanding of the physiological, ecological or evolutionary factors generating species-size distributions (Lawton, this symposium).

6. SOME MORE GENERAL CONSIDERATIONS

This section touches briefly on some more general questions that are prompted by the above discussion.

(*a*) *Different patterns for different groups?*

We have seen that Hodkinson & Casson's direct estimates of global species totals, based on the fraction of bug species in their Sulawesi samples that were previously known, agree with estimates of around 3 million species of insects that earlier were obtained by projecting past trends of discovery. But conservative reappraisals of Erwin's estimate, based on beetle species in tropical canopies, suggest totals of at least 7 million and possibly more. To produce a total of as little as 3 million insects from Erwin's or other similar data requires that we assume only 1% of the beetle fauna are effectively specialized to a given tree species, or that more than 400 of the beetle species found in the canopy of *Leuhea* have been previously recorded; these assumptions seem a bit extreme.

One way of squaring this circle is to recognize that very different patterns may pertain to different taxonomic groups, or in different settings. We have already seen hints of this in the canopy fauna. Tobin's preliminary analysis of data from tree canopies in Manu National Park in Amazonian Peru suggests ants constitute 70% of the individuals and beetles less than 10%, but that there are many more beetle species than ant species (May 1989). Similarly, Stork's fogging samples from 10 Bornean trees were dominated by ants (4489 individuals), but they only contributed 99 of the total of 2800 species; one family of beetles contributed 1455 individuals but 739 species. In tropical canopies generally, ants contribute many individuals, typically half or more, but relatively few species, while beetles contribute relatively few individuals but many species. It seems likely to me that patterns of 'effective specialization' will also vary greatly from group to group, so that we need a much better understanding of the ecology of specific communities of organisms, before we can draw general conclusions about species diversity from limited studies of particular groups in particular places.

(*b*) *Food web structure and species totals*

Studies of the structure of food webs are beset with many difficulties of biases and inconsistencies in the way data are assembled. Provocative generalizations are nevertheless emerging (Cohen *et al.* 1990: Yodzis 1990; Nee 1990; Lawton 1989). One of these is the suggestion by Lawton and co-workers (for example, Strong *et al.* (1984)) that there may typically be something like 10 species of phytophagous insects for each plant species. Applied globally, and given that there are at least 300000 recorded species of higher plants, this would put a lower limit of around 3 million on the number of insect species. However, Lawton's ratios come mainly from studies of temperate-zone plants, and corresponding ratios may be higher for tropical plants (which would tend to support higher estimates of the global total).

Similar arguments about food web structure suggest there could be, on average, as many as five species of parasitoids (parasitic wasps and flies that lay their eggs on or in larval or pupal stages of other insects) for each phytophagous insect species, in both tropical and temperate regions (Hawkins 1990). Applied generally, this estimate could clearly escalate the global total to very high levels (Hochberg & Lawton 1990). I think such estimates are probably too extravagant, although they do suggest that closer studies of tropical hymenopterans may produce surprises to match Erwin's work on beetles.

Such estimates of global species totals, based on the number of plant species combined with the structure of food webs, are akin to the estimates in § 5 based on species–size relations. They provide independent lines of attack upon the problem, related only obliquely to direct estimates based on counting species.

(*c*) *Microbial diversity*

Throughout this chapter, I have followed the usual practice of assuming species diversity to mean the numbers of animal species, or sometimes plant and animal species. More precisely, five kingdoms are usually recognized, distinguished by different levels of cellular organization and modes of nutrition. Two of these kingdoms, the prokaryotic monerans and the eukaryotic protists, comprise microscopic unicellular organisms, and together they account for something like 5% of recorded living species. The fungal and plant kingdoms represent roughly another 22% of species. The animal kingdom thus does comprise the majority (more than 70%) of all recorded living species. The extent to which these recorded numbers of species in the different kingdoms accurately reflect their relative diversities is, however, open to question. As one moves down the size-spectrum of organisms, from the romantic large mammals and birds, through nondescript small anthropods, on down to protozoan, bacterial and viral species, not only does concern for diversity and conservation fall away, but it even changes sign. In the Smithsonian Institution in Washington, a touching label attached to Martha, the last passenger pigeon, laments her death in 1914, but no-one mourned the passing of the last smallpox virus.

Regardless of the amount of study they have received, the microorganisms that act as decomposers in the soil and leaf litter are crucial to the functioning of ecosystems. Recent work has, moreover, revealed that the diversity in natural populations of microbial organisms is far greater than that found in conventional studies of laboratory cultures (Olsen 1990). Ward *et al.* (1990) examined the ribosomal RNA sequences from a well-studied photosynthetic microbial mat from a hot spring in Yellowstone National Park, and found eight distinct sequence types, none of which were the same as any of the 12 laboratory-cultured prokaryotes believed to be characteristic of this mat. More surprisingly, only one of the eight sequences bears any close resemblance to a recognized bacterial 'phylum'. Broadly similar results were obtained by Giovannoni *et al.* (1990) from studies of ribosomal RNA gene sequences of microorganisms from samples of ocean water. These studies of natural populations of microorganisms, as distinct from laboratory cultures, are, in their own way, even more astonishing than Erwin's and others' revelations about tropical canopy faunas. They mark the advent of a new stage in our understanding of microbial ecology and diversity. We have not yet begun to address the questions that such studies of naturally occurring microbial diversity raise, for example, for the release of genetically engineered organisms.

(*d*) *What is a species?*

Up to this point, I have deliberately avoided any definition of what is meant by a species, nor will I pursue it in detail here. But a few remarks should be made.

First, some researchers recognize more species than others, even within well-studied groups. This is particularly noticeable for asexually reproducing organisms. For examples, some taxonomists see around 200 species of the parthenogenetic British blackberry, others see only around 20 (and a 'lumping' invertebrate taxonomist may concede only two or three). Some strongly inbreeding populations are almost as bad, with 'splitters' seeing an order-of-magnitude more species than do 'lumpers'; *Erophila* and *Arabidopsis*, British plants in the mustard family, are notable examples.

Second, and more fundamentally, studies of nucleotide sequences show homologies of less than 50% (as revealed by DNA hybridization) for different strains of what is currently classified as a single bacterial species, *Legionella pneumophilia* (Selander 1985). This is as large as the characteristic genetic distance between mammals and fishes. Relatively easy exchange of genetic material among different 'species' of microorganisms could mean that basic notions about what constitutes a species are significantly different for vertebrates than for bacteria.

Third, the increasing armamentarium of techniques for exploring the genetic structure of populations is uncovering further complexities in what we mean by a species. For example, *Neomachilellus scandens*, a member of the Meinertellidae, is found in inundation forests in the Rio Negro valley (which are flooded for 5–6 months each year), and in primary and secondary dryland forests near Manaus. Ecological studies show the species to be univoltine in inundation forests, with a defined reproductive period, but polyvoltine in dryland forests. These two ecologically distinct forms of *N. scandens* are effectively indistinguishable on morphological grounds, and traditional taxonomy would at most recognize them as 'biotype-specific races'. But protein analyses by Adis (1990), using electrophoresis to test 15 enzymes, shows that there is no gene flow between the univoltine and polyvoltine populations, even when the typical spatial separation is less than 50 m. Adis (1990) proposes that on ecological and genetic grounds we should recognize two species here, and that this situation may be much commoner in the tropics than is currently recognized. If so, we could be dealing with even more species than suggested by Erwin.

(*e*) *Are some species more equal than others?*

Human activities are destroying natural habitats, and the associated biota, at rates that are probably without precedent in the history of life on Earth. In particular, the clearance and burning of an area of tropical forest roughly the size of Britain each year is surely contributing to accelerating losses of tropical arthropods and other animals. Against this background, we need to go beyond knowing how many species there are, and to use this knowledge to optimize conservation efforts (either in planning National Parks and other protected regions, or in devising strategies that reconcile sustainable exploitation of resources with preservation of an appreciable fraction of the original fauna).

Such conservation efforts will pose increasingly difficult choices. Should all species be treated as equal? Or should we take the view that, for conservation purposes, a species not closely related to other living species is more important than one with many widely distributed congeners? And if the answer to this latter question is yes, how do we quantify the relative importance of different species?

Vane-Wright *et al.* (1990) have made a beginning of this task, showing how taxonomy and systematics can build from species lists toward assessment of the relative distinctness of different species and, ultimately, communities. At one extreme, we could of course regard all species as equally important. At the opposite extreme, we could take a phylogenetic or cladistic tree, which represents the hierarchical relations among the constituent species, and measure taxonomic distinctness by weighting each group equally with respect to the summed weights of their terminal taxa. This scheme has the merit of recognizing taxonomic distinctness, but it has the fault that taxonomic rank overwhelms species numbers: on this basis, the two Tuatara species would be seen as equal to all 6000 other reptile species taken together. Vane-Wright *et al.* propose an intermediate scheme, which quantifies the amount of information contained in a given hierarchical classification. Their method gives answers that depend on the topology of the hierarchy (even for a fixed number of terminal taxa), and that recognize the importance of, for example, Tuataras without amplifying it out of all proportion (see May 1990).

My purpose here is not to dwell on the details of these pioneering efforts, but rather to emphasize that a more complete understanding of how many species there are is only a first step. More and more, conservation efforts will be faced with difficult choices. It will be helpful to be guided by quantitative measures of distinctness that are based on systematic understanding of the phylogenetic relations among species.

7. CONCLUDING REMARKS

Why should we care how many species there are? One line of argument is narrowly utilitarian. Thus, for instance, essentially all modern medicines and other pharmaceutical products have been developed from natural products, and so it would seem sensible to be looking at the other shelves in the larder rather than destroying them. The triumphs of intensive agriculture have been accompanied by progressive narrowing of the genetic diversity of the plants we exploit. The likelihood of global changes in climate gives fresh emphasis to the desirability of conserving existing gene pools and exploring the possibility of utilizing new plants.

Important though such considerations are, I think a more pressing and more basic utilitarian reason for studying and cataloguing diversity is because it is a prerequisite to understanding how biological systems work. The scale and scope of human activity are now so large that they rival the natural processes that created and maintained the biosphere as a place where life can flourish. Current rates of input of carbon dioxide, chlorofluorocarbons and other gases are beginning to disturb the balance of the biosphere. Most of our uncertainties about the long-term consequences stem from uncertainties about how physical and biological processes are coupled. We need to understand the structure and functioning of ecosystems, particularly tropical ecosystems, much better than we do. And we cannot hope to do this if we do not even know what is there, and why tropical diversity is what it is.

Beyond these practical motivations, I believe we need to understand the diversity of living things for the same reasons that compel us to reach out toward understanding the origins and eventual fate of the universe, or the structure of the elementary particles that it is built from, or the sequence of molecules within the human genome that code for our own self-assembly. Unlike these other quests, understanding and conserving biological diversity is a task with a time limit. The clock ticks faster and faster as human numbers continue to grow, and each year 1–2 % of the tropical forests are destroyed. Future generations will, I believe, find it incomprehensible that Linnaeus still lags so far behind Newton, and that we continue to devote so little money and effort to understanding and conserving the other forms of life with which we share this planet.

I have been helped by Paul Harvey, Michael Hassell, Ian Hodkinson, John Lawton, Nigel Stork, Chris Thomas and many others. I am particularly grateful to Sir Richard Southwood for letting me use his unpublished data. This work was supported, in part, by the Royal Society and by NERC (through its Interdisciplinary Research Centre at Silwood Park).

REFERENCES

Adis, J. 1990 Thirty million arthropod species – too many or too few? *J. Tropical Ecol.*, **6**, 115–118.

Adis, J. & Albuqueque, M. O. 1990 Impact of deforestation on soil invertebrates from Central Amazonian inundation forests and their survival strategies to long-term flooding. *Wat. Quality Bull.* **14**, 88–98.

Adis, J. & Schubert, H. O. R. 1984 Ecological research on arthropods in Central Amazonian forest ecosystems with recommendations for study procedures. In *Trends in ecological research in the 1980s* (ed. J. H. Cooley & F. B. Golley), pp. 111–144. New York: Plenum Press.

Beaver, R. A. 1979 Host specificity of temperate and tropical animals. *Nature, Lond.* **271**, 139–141.

Brown, J. H. 1984 On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279.

Cohen, J. E., Briand, F. & Newman, C. M. 1990 *Community food webs: data and theory*. New York: Springer–Verlag. (*Biomathematics* **20**)

Diamond, J. M. 1985 How many unknown species are yet to be discovered? *Nature, Lond.* **315**, 538–539.

Erwin, T. L. 1982 Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* **36**, 74–82.

Erwin, T. L. 1983 Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In *Tropical rain forest: ecology and management* (ed. S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 59–75. Oxford: Blackwell.

Erwin, T. L. & Scott, J. C. 1980 Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* in the Canal Zone of Panama. *Coleopt. Bull.* **34**, 305–335.

Fowler, W. W. 1913 *British Coleoptera* (6 volumes). London: Lovell, Reeve and Co.

Gilbert, L. E. & Smiley, J. T. 1978 Determinants of local diversity in phytophagous insects: host specialists in tropical environments. In *Diversity of insect faunas* (ed. L. A. Mound & N. Waloff), pp. 89–104. Oxford: Blackwell Scientific.

Giovannoni, S. J., Britschgi, T. B., Moyer, C. L. & Field, K. G. 1990 Genetic diversity in Sargasso Sea bacterioplankton. *Nature, Lond.* **345**, 60–63.

Grant, V. 1973 *The origin of adaptations*. New York: Columbia University Press.

Hanski, I. 1982 Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* **38**, 210–221.

Hawkins, B. A. 1990 Global patterns of parasitoid assemblage size. *J. Anim. Ecol.* **59**, 57–72.

Hochberg, M. E. & Lawton, J. H. 1990 Competition between kingdoms. *Trends Ecol. Evol.* (In the press.)

Hodkinson, I. D. and Casson, D. 1990 A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biol. J. Linn. Soc.* (In the press.)

Joy, N. A. 1931 *A practical handbook of British beetles*. (2 volumes.) London: Witherby.

Lawton, J. H. 1989 Food webs. In *Ecological concepts* (ed. J. M. Cherret), pp. 43–78. Oxford: Blackwell Scientific.

May, R. M. 1978 The dynamics and diversity of insect faunas. In *Diversity of insect faunas* (ed. L. A. Mound & N. Waloff), pp. 188–204. Oxford: Blackwell.

May, R. M. 1988 How many species are there on earth? *Science, Wash.* **241**, 1441–1449.

May, R. M. 1989 An inordinate fondness for ants. *Nature, Lond.* **341**, 386–387.

May, R. M. 1990 Taxonomy as destiny. *Nature, Lond.* **347**, 129–130.

Moran, V. C. & Southwood, T. R. E. 1982 The guild composition of arthropod communities in trees. *J. Anim. Ecol.* **51**, 289–306.

Nee, S. 1990 Community construction. *TREE* **5**, 337–340.

Olsen, G. J. 1990 Microbial ecology: variation among the masses. *Nature, Lond.* **345**, 20.

Pagel, M. D., May, R. M. & Collie, A. 1990 Ecological aspects of the geographical distribution and diversity of mammal species. *Am. Nat.* (In the press.)

Portevin, G. 1935 *Histoire Naturelle des Coléoptère de France* (4 volumes.) Paris: Lechavier.

Rabinowitz, D. Cairns, S. & Dillon, T. 1986 Seven forms of rarity. In *Conservation biology* (ed. M. E. Soule), pp. 182–204. Sunderland, Massachusetts: Sinauer.

Rapoport, E. H. 1982 *Areogeography: geographical strategies of species*. Oxford: Pergamon.

Raven, P. H. 1985 Disappearing species: a global tragedy. *The Futurist* **19**, 8–14.

Root, T. 1988 *Atlas of wintering North American birds*. Chicago: Chicago University Press.

Selander, R. K. 1985 Protein polymorphism and the genetic structure of natural populations of bacteria. In *Population genetics and molecular evolution* (ed. T. Ohta & K. Aoki), pp. 85–106. Berlin: Springer–Verlag.

Simon, H. R. 1983 Research and publication trends in systematic zoology. Ph.D. thesis London: The City University.

Southwood, T. R. E. 1978 The components of diversity. In *Diversity of insect faunas* (ed. L. A. Mound & N. Waloff), pp. 19–40. Oxford: Blackwell.

Southwood, T. R. E., Moran, V. C. & Kennedy, C. E. J. 1982 The richness, abundance and biomass of the arthropod communities on trees. *J. Anim. Ecol.* **51**, 635–649.

Stork, N. E. 1988 Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* **35**, 321–337.

Strong, D. R., Lawton, J. H. & Southwood, T. R. E. 1984 *Insects on plants: community patterns and mechanisms*. Oxford: Blackwell Scientific.

Thomas, C. D. 1990 Estimating the number of tropical arthropod species. *Nature, Lond.* **347**, 237.

Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. 1990 What to save? Systematics, the biodiversity crisis, and the agony of choice. *Biol. Conserv.* (In the press.)

Ward, D. M., Weller, R. & Bateson, M. M. 1990 16S rRNA sequences reveal numerous uncultured microorganisms in a natural community. *Nature, Lond.* **345**, 63–65.

Ward, L. K. 1977 The conservation of juniper: the associated fauna with special reference to Southern England. *J. appl. Ecol.* **14**, 81–120.

Yodzis, P. 1990 *Introduction to theoretical ecology*. New York: Harper and Row.

Discussion

R. J. H. Beverton (*Montana, Old Roman Road, Gwent, U.K.*). The 'target' of the total number of species is not, of course, static because species are continually being lost by natural and man-made processes and added by speciation. Could Professor May say something about these rates of change, and how they compare with the overall picture of species diversity?

R. M. May. It is true that throughout most of the recorded history of life on Earth, species have been going extinct and new species have been appearing. The next half-century or so is, however, likely to be singular in two respects. First, there is the scope and timescale of impending extinctions in relation to speciation. For most of the time, extinction rates and speciation rates have been roughly in balance, and both have been on geological timescales: something like half the species currently extant appeared over the past 50–100 million years or so. Over half are likely to become extinct over the next 50–100 years. Thus rates of disappearance or extinction and rates of appearance or speciation are likely to be out of balance by a factor of a million! This clearly is not what has been going on over most of geological time. Secondly, most past 'extinctions' see the basic lineage continued (at least since the Cambrian); likely current rates of extinction in the tropics will see lineages ended, not transformed.