

Preface

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Biodiversity: measurement and estimation

Preface

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SUMMARY

In introducing a series of 11 papers on the measurement and estimation of biodiversity, eight crucial questions are posed: What is 'biodiversity'? Is biodiversity just the number of species in an area? If biodiversity is more than the number of species how can it be measured? Are all species of equal weight? Should biodiversity measures include infraspecific genetic variance? Do some species contribute more than others to the biodiversity of an area? Are there useful indicators of areas where biodiversity is high? And can the extent of biodiversity in taxonomic groups be estimated by extrapolation? In addition, the modern concept of biological diversity is attributed to Elliot R. Norse and his colleagues.

1. INTRODUCTION

Within six years the word 'biodiversity' has exploded into the vocabulary of the popular press, governmental and intergovernmental reports, scientific papers and meetings. In the scientific literature the growth in usage of the term has been dramatic (figure 1).

It seems reasonable to ask of a word that is so widely used, just what is it supposed to mean. Is it just a new linguistic bottle for the wine of old ideas – a changed fashion label designed to attract funding – or does it refer to new and fundamental questions in science? Most especially, it seems sensible to ask whether 'biodiversity' is a property that can be measured and if so what is the most appropriate form that such measurement should take.

We may wish to ask such questions as: 'Does biodiversity confer stability?'; 'Does biodiversity confer productivity?'; 'Does biodiversity reflect sustain-

ability?'; 'Does biodiversity reflect the evolutionary time elapsed without major disturbance?'; alternatively, 'Does biodiversity reflect the frequency of major disturbance in ecological or evolutionary history?'.* We might reasonably expect to have some measure of this thing that we call biodiversity that we might use in a graphic plot or statistical analysis designed to answer these questions. In particular, we may wish to ask whether one species (or population, or community) is more or less diverse than another. Until we have decided how to measure 'biodiversity' we cannot begin to mobilize serious science into answering these questions and others posed in the 'research

* We might have mentioned 'ecosystem function' among those features that might be influenced by biodiversity. However, one of us finds the notion that an ecosystem might 'function' (verb) or 'have a function' (substantive) so incongruous that he has relegated the mention to this footnote (where it is even more likely to be noticed).

agenda for biodiversity' (Solbrig 1991). But, 'The need for increased objectivity through measurement is not merely a scientific quest but can contribute to issues of topical concern at all levels of society' (Lovejoy, this volume).

In particular we need such a measure as part of the justification for spending limited financial resources on protecting, conserving, studying or exploring some communities and so denying the resources to do the same to others.

Of course, the collection of papers in this volume may reveal that the word 'biodiversity' means quite different things to different people. This would be a pity but better to be revealed and acknowledged than allowed to cause confusion.

This series of papers has been commissioned to encourage the scientific analysis of biodiversity, and particularly to force the question 'How do we best measure organismal biodiversity?' We are aware that the answer might simply be 'By counting the number of species', but it is clear from various papers contributed to this theme volume that there are deeper issues involved. There is also plenty of scope for controversy.

2. WHAT IS 'BIODIVERSITY' ?

'Biological diversity' has a long history of usage in a variety of contexts, but the start of its rise in the current senses can be traced to three publications which appeared in 1980: Lovejoy (1980*a,b*) did not provide a formal definition but used it essentially in the sense of the number of species present, and Norse & McManus (1980) employed it to include 'two related concepts: genetic diversity and ecological diversity'. The latter authors equated ecological diversity with species richness, 'the number of species in a community of organisms'. There were various usages in the United States in the early 1980s, mainly in connection with conferences with which Elliot Norse or his colleagues were involved, most notably the *U.S. Strategy Conference on Biological Diversity* in November 1981 (U.S. Department of State 1982). However, it was Norse *et al.* (1986, p. 2) who expanded this usage to refer unequivocally to biological diversity at three levels: genetic (within species), species (species numbers) and ecological (community) diversity.

The contracted form 'biodiversity' was evidently coined by Walter G. Rosen in 1985 for the first planning conference of what was to be a key meeting, the 'National Forum on BioDiversity', which convened in Washington, D.C. in September 1986. The proceedings of that forum, edited by Wilson (1988*a*) under the title *Biodiversity*, launched the word into general use. The term was defined only in as far as it 'represents, as well as any term can, the vast array of topics and perspectives covered during the Washington forum' (Wilson 1988*b*, p. vi). Norse's seminal papers were not cited in any of the 57 contributions to that volume. The word 'biodiversity' first appears in the *Biological Abstracts* 'BIOSIS' database in 1988 with four references, and by the end of April 1994 that number had escalated to 888 (figure 1).

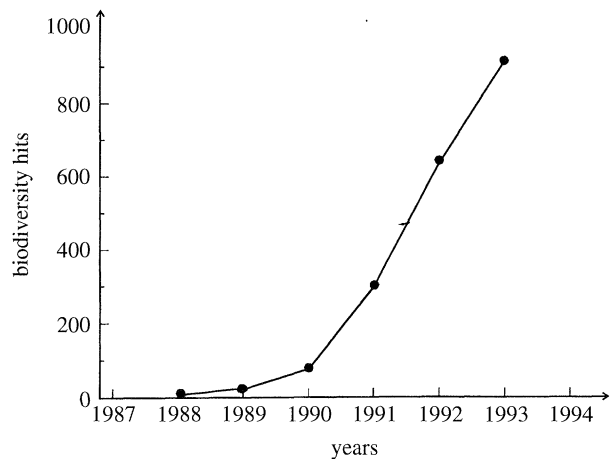


Figure 1. Growth of the number of hits for the term 'biodiversity' in the scientific literature as catalogued in BIOSIS File 5 (1969 onwards). This presentation is based on accumulating the number of hits within each year; the total of 921 at the end of April 1994 is an overestimate due to double-counting of citations with more than one year date; the actual number of single titles in the period was 888.

For practical purposes, 'biodiversity' can be considered as synonymous with 'biological diversity' as defined by Norse *et al.* (1986). This is reinforced by the official definition in Article 2 of the 'Convention on Biological Diversity', signed by 156 nations and the European Community at the United Nations Conference on the Environment and Development, 'The Earth Summit' in 1992 which closely mirrors the concept of Norse *et al.* (United Nations Environment Programme 1992, p. 27):

“*Biological diversity*” means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems [*sic*].”

These three levels are all considered in the *Global Biodiversity Assessment* currently being prepared by the United Nations Environment Programme with funding through the Global Environment Facility (GEF) administered by the United Nations Development Programme.

It is therefore essential that scientists, who use either the expanded or the contracted term in a technical sense that does not embrace all three levels, specify which level is intended. We therefore propose the use of the adjectives 'genetic', 'organismal', and 'ecological'. 'Organismal' is preferred to 'species' so as to embrace taxonomic categories above species rank. Eldredge (1992) used 'genealogical', 'phenotypic', and 'ecological' in a parallel manner, but we prefer 'organismal' to 'phenotypic' as its meaning is more transparent to a non-specialist. The usage of 'organismal' is also consistent with the need identified by Norse (1993) to view biological diversity at higher taxonomic levels.

We are unhappy with references to 'ecosystem' diversity and prefer 'community' or 'ecological'

diversity. Tansley (1935) introduced the word 'ecosystem' to refer to a community of organisms in the context of and including their physical environment. Clearly the physical environment does not have a biodiversity. Reference to 'the biodiversity of an ecosystem' devalues two useful concepts in the same phrase.

3. IS BIODIVERSITY JUST THE NUMBER OF SPECIES IN AN AREA?

Species can be counted and the number of species present at a site might seem to be a quantitative measure of its biodiversity and allow comparison with other sites. But this assumes that all species at a site, within and across systematic groups, contribute equally to its biodiversity.

This is clearly questionable as illustrated by the following hypothetical sites in all of which there are just two species present. One of the species present is a species of *Ranunculus* and the other is:

1. Another species of *Ranunculus* from the same section of the genus.
2. Another species of *Ranunculus* from a different section of the genus.
3. A species from a different genus in the same family (*Ranunculaceae*).
4. A species from a different family within the same order as the *Ranunculaceae*.
5. A species from a different family and in a different order (e.g. a grass).
6. A rabbit.
7. A fungus of the genus *Agaricus*.
8. A protozoan of the genus *Amoeba*.
9. An archaebacterium.
10. A eubacterium of the genus *Pseudomonas*.

This simple hypothetical series could easily be expanded, but is sufficient to make the point that any measure of biodiversity that described all of these sites as equal would be peculiarly uninformative. A measure of the biodiversity of a site ought ideally to say something about how different the inhabitants

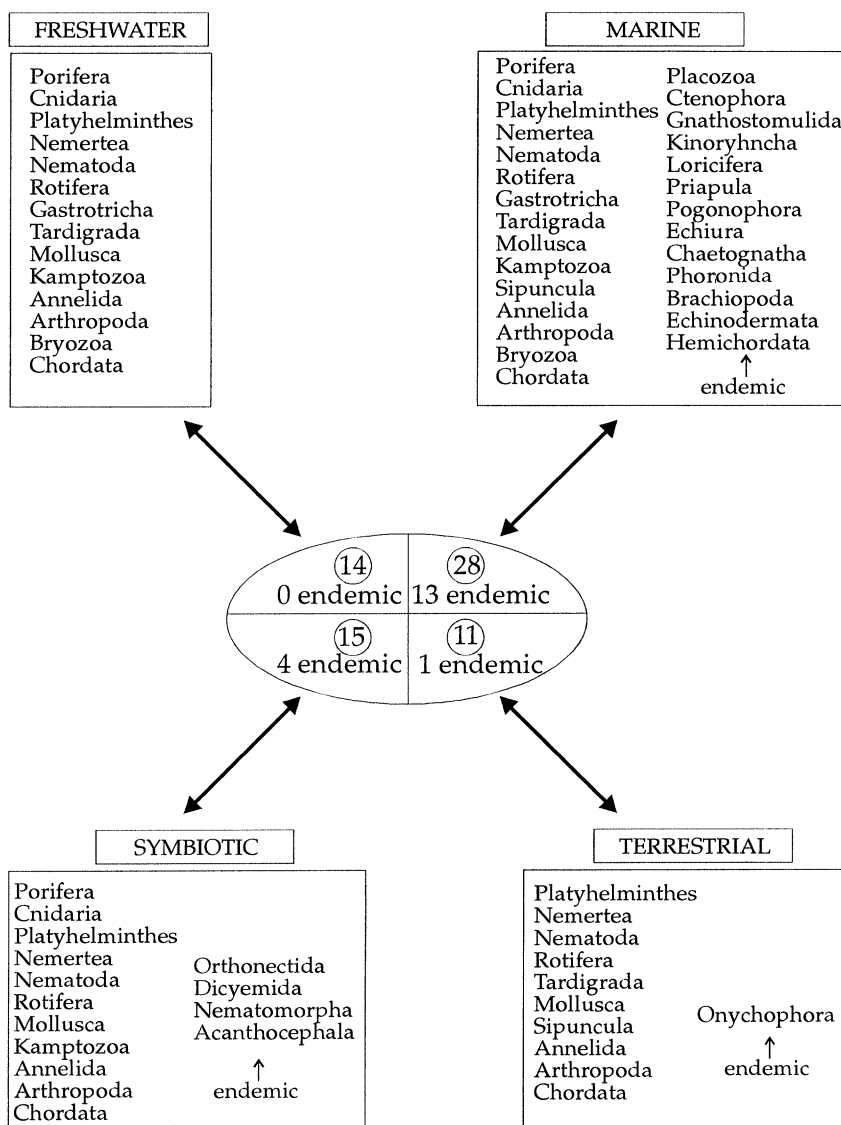


Figure 2. The distribution of phyla in the Animalia by habitat. Adapted from Grassle *et al.* (1991).

are from each other. A measure that reflects the increasing phylogenetic divergence of the organisms present at a site in the series progressing from case (1) to case (10) might be one promising possibility.

4. IF BIODIVERSITY IS MORE THAN THE NUMBER OF SPECIES HOW CAN IT BE MEASURED?

Three approaches are considered by contributors to this collection of papers:

(a) *Taxic measures*

Does the number of higher taxa, for example phyla, orders and families, provide a more appropriate measure of the biodiversity in a site than the number of species? In marine environments the number of phyla and higher taxa is substantially greater than on land (May, this volume); indeed 13 animal phyla are known only from marine environments whereas only one is exclusively terrestrial (Grassle *et al.* 1991; figure 2). For those concerned with the allocation of resources to the global conservation of life on Earth this statistic at least raises the question of whether the present balance of emphasis on terrestrial systems needs rethinking.

If the aim of conservationists is simply to conserve the maximum number of species we may ask whether the number of higher taxa present is a convenient quick estimator of the number of species in an area. Prance (this volume) finds that in the neotropics only 6.4% of the species belong to the approximately 40 exclusively or almost exclusively neotropical families. He argues that we need to focus our attention at the species level when assessing biodiversity for conservation planning. However, Williams *et al.* (1994) found a very close relationship between the number of families present in 0.1 ha plots and the number of species present (least squares regression $r^2 = 0.913$, $p < 0.001$). These authors point out that complete counts of organisms are impractical at present and that indirect solutions are needed that are both cheap and quick. They used data from families of seed plants to make world-wide maps of the regional distribution of family richness and endemism. The peak richness of families occurs in Cambodia which (if sampled first) contributes 53.67% of the total number of families. Mexico (Oaxaca), China (southern Sichuan) and Madagascar (north) add a further 11.65%, 5.82% and 4.81% respectively. The areas with peak richness of endemics are strikingly different with New Caledonia, south-west China and northern Australia contributing most.

If we planned to conserve those plant communities that could provide the richest diversity of pharmaceutical compounds, what measure of biodiversity would be the best guide? Either family richness or endemic richness might be good candidates but species richness itself could be dangerously misleading. The 242 species of *Hieracium* and 234 species of *Taraxacum* listed in the Norwegian flora (Lid 1952) are better indicators of taxonomic traditions than of

the scale of natural biological diversity. Pearson (this volume) considers the problems of using indicator taxa in the assessment of biodiversity.

In considering measurements through geological time, Niklas & Tiffney (this volume) concluded that the taxonomic level which yields statistically independent observations of sampling remained unresolved for vascular plants. They make the point that, as new evolutionarily successful characters arise within populations or species, they form the basis of radiations as the characters are incorporated in groups of increasing size and ultimately of higher rank. The community biodiversity that we are able to examine at any time may therefore contain differences between organisms that are comparable in magnitude but expressed at quite different systematic ranks. There is a frightening spectre that in some communities the relevant and comparable measure of biodiversity may be best expressed in some groups by the number of species, but in others by the number of genera or even of families.

(b) *Molecular measures*

An attractive possibility for the measurement of biodiversity is to use divergences in molecular characters, especially the percentage of either nucleic acid homology or base sequence differences. Unlike higher taxa which may be based on characters which are not necessarily directly comparable, the DNA and RNA found in all living cells can provide a basis on which to make direct comparisons between diverse organisms. There is a sense in which the biodiversity of a community is expressed as the sum of the variety of genetic information coded within the genotypes of the inhabitants. A biodiversity calculus could be envisaged for which we ask of the various species (and individuals) in a community how many new base sequences they each contribute to the genetic vocabulary of the whole. Embley *et al.* (this volume) demonstrate that the application of molecular technology to the study of biodiversity can destroy treasured icons. Some prokaryotic groups have proved so diverse at the molecular level, in comparison with eukaryotes, that new taxonomic hierarchies above the level of kingdom (e.g. 'domains') have had to be recognized properly to reflect the extent of their divergence.

(c) *Phylogenetic measures*

Cladistics can be used to give an objective measure of taxonomic distance or 'independent evolutionary history' (IEH) using methods pioneered by Vane-Wright *et al.* (1991). The technique has considerable promise (May, this volume), and is examined in depth by Faith (this volume). The approach provides information that is of especial value for the conservation of target groups (Vane-Wright *et al.* 1991) and in selecting areas appropriate for their conservation (Pressey *et al.* 1993) but it is difficult to see how sufficient phylogenetic data could be generated in the near future for this method to be used to compare the

diversity of whole countries. In the most speciose groups such as fungi and insects in which only 5–10% of the species on Earth may have been described, most of the species in an area will lack data suitable for phylogenetic analysis. Rather than progressing up from bumble-bees to Hymenoptera to Insecta and so on, an ideal index of biodiversity ought perhaps to be obtained by proceeding in the opposite direction, asking first the biggest question about diversity, ‘How many kingdoms are represented on a site?’, then ‘How many phyla are represented per kingdom?’, ‘How many orders per phylum?’, and so on. There is sufficient logic in this suggestion to elicit a wringing of hands and even apoplexy from those who might have to apply it.

5. ARE ALL SPECIES OF EQUAL WEIGHT?

The varying species concepts in different groups, and indeed often within a single group, are a major cause of uncertainty intrinsic to all aspects of biodiversity research that use the species as the ‘standard’ unit. If the unit of measurement is itself variable, conclusions based on it have necessarily to be treated with considerable caution. This applies equally to discussions of the relationship between biodiversity and community behaviour (Baskin 1994), to theoretical models (Lovelock 1992), and to indicators developed for policy makers (Reid *et al.* 1993).

The ‘biological species’ has been viewed as a comparable entity across groups as diverse as insects and fungi (Claridge & Boddy 1994), but how do such entities compare when examined by molecular or phylogenetic methods? How can biological species be recognized with confidence in the majority of organisms which are only known from preserved material? And how can a biological species concept be applied in groups that never undergo sexual reproduction or parallel exchanges of genetic material?

The species concept in bacteria is especially conservative at the molecular level in comparison with most other groups of organisms. Different strains placed within the single bacterial species *Legionella pneumophila* have DNA hybridization homologies as different as those characteristic of the genetic distance between mammals and fishes (May, this volume). Bacterial strains with 70% or more DNA–DNA relatedness are generally treated as belonging to the same species (O’Donnell *et al.*, this volume); on that basis, rather few species would be accepted in some macroorganism groups, and hominids with 98% homology would certainly be regarded as conspecific! We also wonder how many (or rather how few) ‘species’ of beetles could be sustained on the grounds that they possess less than 70% DNA homology! However, in DNA homology studies in particular, should not some allowance be made for the size of the genomes being compared?

Caution is clearly required when molecular data are used at or near the species level because of the discrepancies between DNA–DNA homology and rRNA sequence data for the same taxa (O’Donnell

et al., this volume). It would be rash to base far-reaching taxonomic decisions on a single type of molecular data at this time.

There is an urgent need for biologists working in different disciplines to move towards more comparable species concepts. Nowhere is this more important than in the treatment of apomictic ‘species’ of flowering plants in genera such as *Alchemilla*, *Hieracium*, *Taraxacum* and *Sorbus* which can grossly inflate measures of plant species richness in an area.

6. SHOULD BIODIVERSITY MEASURES INCLUDE INFRASPECIFIC GENETIC VARIANCE?

The genetic variation within species can be of major importance in identifying priorities for the conservation of crop plants and their wild relatives. These same measures can be useful in trying to judge which species have a sufficiently wide vocabulary of genetic information to allow them to respond to natural selection and evolve if the environment changes rather than become extinct.

Templeton (this volume) considers the possible ways of measuring genetic variation within species. These include the percentage of polymorphic loci, the number of alleles, heterozygosity, the average number of nucleotide differences, the number of segregating sites, and the construction of an allele or haplotype tree. Even within mammals the use of these measures shows that it is difficult to generalize about the size of the populations that might be required to maintain the genetic variation of the species.

Although it would clearly be desirable to include some measure of infraspecific biodiversity in the overall assessment of the biodiversity of a particular site, how this could be achieved for more than a handful of species in a locality at a time eludes us. However, the very act of thinking about the problem makes it clear that the concept of ‘biodiversity’ can mean all things to all people. To most geneticists it will seem absurd that any measure of ‘biodiversity’ should exclude infraspecific variance: the very stuff of the evolutionary process by which biodiversity is made.

7. DO SOME SPECIES CONTRIBUTE MORE THAN OTHERS TO THE BIODIVERSITY OF AN AREA?

The biological diversity of an area is much more than the number of species present, whether or not the species richness is discounted by measures of phylogenetic distance or relatedness. For an ecologist other dimensions of biodiversity are represented by the number of trophic levels present, the number of guilds, the variety of life cycles, and the diversity of biological resources. The presence of certain species makes a great contribution to overall species richness because, like the oak in Great Britain (Morris & Perring 1974), they provide specialist resources for a multiplicity of other species (nesting sites, gall-wasps, lepidoptera, mycorrhizal fungi, bark and leaf-

inhabiting fungi, pests and pathogens, bryophytes, lichens, other epiphytes, etc.). Trees, in general, contribute a wider range of biological resources to a site than annual or herbaceous plants. However, the role of organisms with less obvious 'keystone' roles, including pollinating insects, mutualistic symbionts and population-regulating pathogens and biocontrol agents can also have effects on the biodiversity of a site (Hawksworth *et al.* 1994; LaSalle & Gauld 1993).

Many individual species of marginal aquatic flowering plants contribute a diversity of leaf forms to a community. Batrachian species of *Ranunculus*, *Sagittaria sagittifolia*, and *Cabomba caroliniana*, bear distinct submerged and floating forms of leaf and a single species occupies two niches in a community that would commonly be occupied by two monomorphic species. In a similar vein, animal species with complex life-cycles contribute extra biological diversity to a site. Frogs, toads and other amphibians contribute to the species richness of a site as tadpoles in aquatic and as adults in terrestrial patches. In a sense each of these species contributes two doses of biological diversity to a community. Lepidoptera are also obvious examples of animal species that contribute more to the ecological diversity of a community than just a count of the species numbers would imply.

One biological measure of the diversity of a community must be the way in which it is sampled by different organisms that live in it (a worm's-, bird's-, or caterpillar's-eye view). During a single day a wood pigeon may experience the full above-soil biodiversity of a forest (fine-grained sampling) whereas the same forest, sampled by a caterpillar is experienced as the 'biomonotony' of a single leaf (coarse-grained sampling). The use of the concept of grain to describe an organism's eye view of the diversity of an environment is due to Robert MacArthur (e.g. MacArthur & Connell 1966). Even if we confine our measure of biodiversity to species richness and forget any discounting for differences in phylogenetic distances or ecological contribution there remains the fact that, *at the 'grain' of community diversity sampled by us*, some of the various species present in a community are abundant and others are very rare. This issue is especially acute for microbial groups; in most instances the largest numbers of individuals at a site will be the microorganisms which are not only unseen but often also unculturable (Embley *et al.*, this volume; O'Donnell *et al.*, this volume).

'Equitability' is therefore clearly an element of 'biodiversity' and is one aspect that has been built into formal mathematical indices, for example the Shannon Diversity Index and Simpson's Index that are defined and illustrated in ecological texts (e.g. Begon *et al.* 1990) e.g. Simpson's Index

$$D = \frac{1}{\sum_{i=1}^s P_i^2},$$

which is calculated by determining, for each species, the proportion of individuals or biomass that it contributes to the total in the sample, i.e. the

proportion is P_i . For the i th species where s is the total number of species in the community (i.e. its richness). The index suffers for some purposes because it is possible for a species-rich but inequitable community to have a lower index than one that is less species-rich but highly equitable.

Such an index, although it may be useful for a particular group (e.g. all vascular plants or all insect species at a site) is difficult to apply and perhaps largely meaningless if it were to be applied to the mixture of systematically diverse groups that forms most natural communities.

8. ARE THERE USEFUL INDICATORS OF AREAS WHERE BIODIVERSITY IS HIGH?

Although much is made of the need to focus nature conservation on areas of high biological diversity, choices are usually made on quite different grounds. Particular taxonomic groups appeal to the public and their conservation attracts political and financial support. The risk of losing a furry or feathery animal or a plant with appealing flowers will presumably continue to dominate most judgements about nature conservation rather than any formally considered scientific measures of biodiversity. This will certainly continue to be the case so long as science fails to develop appropriate measures for more rational (less emotional) decisions.

Ideally, comprehensive biological inventories of sites (ATBIS, see below), will be needed if full quantitative measures of biodiversity are to be used in making conservation decisions. However, these are unlikely to be obtained from more than a handful of sites in the foreseeable future. We need therefore to look for simpler yet objective ways of predicting where high biodiversity will occur. Are some taxa particularly good indicators of community biodiversity? Might it be that, by chance, those mammals, birds and plants (such as orchids) that appeal so strongly to the lover of wild-life happen to live in (and are therefore good predictors of) areas of particularly high biodiversity? Or are there other often unstudied yet easily observed groups such as the larger lichens that have the most potential in this regard? Pearson (this volume) considers the factors that could be used in selecting appropriate indicator taxa and Hammond (this volume) assesses the practical steps that can be taken to estimate biodiversity in the most speciose groups.

The most daunting problems arise in making any measure of biodiversity in the soil (O'Donnell *et al.*, this volume) where there may be more than 10^9 microorganisms per gram of soil, and in the sea where microscopic algae may have average densities of 10^6 cells per litre (Andersen 1992) and a 1 cm marine core may contain 4×10^{10} bacterial cells (Embley *et al.*, this volume).

Reid *et al.* (1993) discuss biodiversity indicators that may be of value to policy makers in establishing conservation priorities, but these have to be seen against the backcloth of questions raised here. The indicators so far proposed may be of value in the context of particular specified groups (e.g. wild plants

and their relatives), but are unlikely to reflect the total biodiversity in an area.

9. CAN THE EXTENT OF BIODIVERSITY IN TAXONOMIC GROUPS OR COMMUNITIES BE ESTIMATED BY EXTRAPOLATION?

A major challenge of biodiversity science is to develop firmer estimates of species numbers. May (this volume) considers the conceptual problems in current approaches to estimating the total numbers of species in different groups. The highest degree of probability exists where different approaches lead to broadly similar numbers, but insufficient data sets, especially from tropical and marine habitats are a major hindrance to progress in the development of protocols.

Theoretical aspects of the use of extrapolation to measure species richness are critically examined by Colwell & Coddington (this volume) with particular reference to the use of species accumulation curves, parametric models of relative abundance, and non-parametric methods. They also explore the problem of estimating complementarity from samples and propose a measure of this.

The companion contribution of Hammond (this volume) focuses on the practical aspects of the estimation of species diversity in speciose groups, and is based on extensive data sets from the U.K. and Indonesia. He concludes that simple ratios of species from taxon to taxon, focal group to inclusive group, site to site, sample to inventory, and across spatial scales provide the firmest base for extrapolation. The choice of both focal groups for extrapolative purposes and sampling methods to obtain reliable comparable data sets is critical, and there needs to be an awareness of, for example, the interplay between patchy distributions and sample dimensions.

A major stimulus to the improvement of the scientific base of extrapolative approaches would be the realization of Janzen's (1993) proposal to establish a series of sites which have an All-Taxon Biodiversity Inventory (ATBI). The efficacy of sampling and extrapolative procedures could be rigorously tested against known biota at such sites. The lack of a comprehensive inventory of all groups of the biota for any site in the world, even in the U.K., is a major obstacle to developing extrapolative methods. Yet it is just such methods that will have to become the norm in site assessments because of the impracticability of routinely attempting comprehensive inventories.

10. CONCLUSIONS

It will be evident from the questions we have raised and our comments on them, and also from many of the contributions to this collection of papers, that it is easier to identify the issues than to provide scientifically sound and testable answers. By openly posing basal questions, however, the challenges that need to be addressed are also brought firmly onto the scientific agenda. The issues identified need now to be confronted if the scientific foundation of the study of organismal biodiversity is to proceed on a firm basis.

There are two significant obstacles internationally to progress in the scientific study of biodiversity: (i) the inadequate size and inappropriate location of the workforce with the appropriate biosystematic skills; and (ii) the state and location of the collections and literature database (May, this volume). The mismatch between the magnitude and priority of the task and the resources available has to be addressed at the highest international levels (Janzen 1993).

We thank Professor W. G. Chaloner and Dr N. J. Stork for helpful suggestions of possible contributors, Professor V. H. Heywood for access to his correspondence with Dr E. A. Norse relating to early usages of the term 'biological diversity', and to Dr Norse for supplemental information. Mrs E. Wheeler conducted the BIOSIS database search which formed the basis of figure 1. Especial thanks are due to Julia Neary of the Society's Editorial Office for shouldering the major part of the correspondence with contributors and referees.

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