

An Offprint from

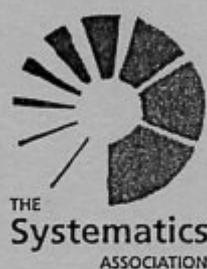
The Systematics Association
Special Volume No. 50

Systematics
and
Conservation Evaluation

Edited by

P. L. FOREY,
C. J. HUMPHRIES, and
R. I. VANE-WRIGHT

*The Natural History Museum,
London*



Published for THE SYSTEMATICS ASSOCIATION by
CLARENDON PRESS · OXFORD

1994

25. Taxonomy and functional biotic measurement, or, will the Ark work?

STEVEN H. COUSINS

*International Ecotechnology Research Centre, Cranfield Institute of Technology,
Cranfield, Bedfordshire MK43 0AL, UK*

Abstract

Biodiversity is represented differently in systematics and in ecology. This chapter uses hierarchy theory to relate the two approaches. Modifications, based on functional attributes, are made to representations of ecological biodiversity. Taxonomic uniqueness measures are scale independent whereas the functional evaluation tools proposed are different for local, ecosystem, and global scales. Higher taxonomic categories are functionally important for ecosystem analysis and may indicate a shift in the role of taxonomy in ecology. The quantity of life in contrast to the number of types is seen as important at the global scale. The measurement of human interaction strength with the existing biological environment is necessary for conservation evaluation. UK data for birds and mammals are used to exemplify the above points.

Introduction

The two indices of diversity—indeed, the very meaning(s) of the word diversity—are different in ecology and systematics. The mechanisms of extinction may lie squarely in the province of ecology, but we measure extinction taxonomically, squarely within the realm of systematics (Eldredge 1992).

The role of systematics in providing solutions to the global biodiversity crisis has been substantially strengthened by recent work which offers new priorities for conservation (Vane-Wright *et al.* 1991; Faith 1992; Williams and Humphries and others in this volume). This paper integrates these important new developments within a wider framework. As may be inferred

from the quotation above, a different set of priorities may arise from the 'province' of ecology. Given these two views there is a need to explore the relationship between ecology and systematics to see if complementary methodologies for conservation evaluation can be derived. It is suggested here that certain steps towards this are provided by establishing a basis in ecological theory for linking taxonomic and functional ecological measurement derived from Cousins (1985, 1987, 1988), and by making functional measures of biodiversity as it is understood in ecology (Cousins 1991). In spite of improvements to biodiversity measurement in both ecology and systematics, biodiversity itself may not be sufficient to provide a satisfactory basis for conservation evaluation; the quantity of life as well as number of types is important.

Ultimately it is human action which is driving the current extinction process. It is suggested that some independent measure of the strength of human interaction with ecosystems is necessary in order to judge the success or failure of conservation measures which are undertaken, on whatever basis. All these taxonomic and functional measures are relatively new, and require extensive research and testing if these and other solutions are to be realistic and effective in meeting the truly overwhelming task of global biodiversity conservation.

Systematics and ecology

The valuable potential of the new systematics approach is that, by very carefully choosing which parts of the land surface are conserved, a very substantial amount of the world's biodiversity can be contained on a relatively small area, at least in the short term (the principle of efficiency; Pressey and Nicholls 1989). The degree to which this can be achieved depends, in part, on re-assessing the traditional view that all species are equal, and instead prioritising areas according to the uniqueness of biological form that are represented there as well as the absolute number of species found. The rest is achieved by selecting a priority sequence (Williams and Humphries, this volume) or set of reserves (Rebello, this volume), which contain these species with a minimum of duplication (by application of the complementarity principle of Vane-Wright *et al.* 1991). However, this selection of the most highly complementary pieces of the global biotic landscape does not tell us how to conserve species they include. We cannot presume that a reserve will protect a species for ever and questions of a functional nature immediately arise. How big does the reserve have to be and what would happen if the climate changes, or if a new disease or predator arrives in the reserve? These questions require an ability to understand the functional relationships between species in a strongly biased sample of species-rich ecosystems.

As Eldredge (1992) notes, the process of extinction, or to paraphrase him, of persistence, is an ecological one arising out of the population dynamics and feeding-interactions of locally dispersing and interacting organisms. In contrast, the description of species, and of their relative position vis-a-vis all other species, is a matter for systematics and is achieved by making taxonomic trees showing historical and genealogical relationships.

There are several aspects to this current dichotomy between ecology and systematics. Species diversity in ecology is measured as an index or count of the species found at a particular place or area. More precisely (Eldredge 1992) species diversity, as it is used in ecology, relates to a count of those species represented by at least one organism at a particular location. This concept is spatial and is quantitatively determined by the scale of observation to the extent that the species area curve is fundamental to ecological species diversity measurement. In systematics, species diversity is essentially relational rather than spatial and concerns the number of species within a particular taxon and how those species are related by assumed evolutionary descent. However, because each species tends to be reasonably cohesive in its distribution, we can speak of a spatial distribution of a species as its 'range', the spatial area it occupies on the Earth's surface at any one time. Ecological species diversity measurement is thus concerned with all species at one point, whereas systematic species diversity is concerned with all locations of single or related groups of species. The range of the species is all important here; just one reserve on earth will 'preserve' a species, whereas the range of each species determines how many species are found at each point. From here we can ask what kind of biodiversity does the Rio Convention want: big ranges or little ranges? The result will considerably affect the local biodiversity experienced by the world's human population.

Vane-Wright *et al.* (1991) show how the perceived dichotomy of ecology and systematics carries through into different conservation strategies:

McNaughton (1989) has observed that we have to 'determine what should be conserved and how it is to be conserved. A critical places strategy . . . could accomplish this objective'. McNaughton is an ecologist, and his 'critical places' refer to representative ecosystems. As systematists we think instead of areas of endemism, or critical faunas and floras for particular taxonomic groups.

However, critical flora and fauna also translate into a critical places strategy, although Vane-Wright's *et al.* set priorities via taxonomic assessment and then require the conservation of all organisms in the preferred location, i.e. the local ecosystem, because the biotic environment in which the critical fauna sits is also necessary to support that fauna.

A theoretical justification for these separate ecological and systematic approaches is provided by Eldredge and others (Greene 1987; Eldredge and Salthe 1984; Vrba 1984; Damuth 1985), who have adopted a model of

evolution based on the interactions of a 'dual hierarchy'. This is the hierarchy of systematics 'going from kingdoms down through taxonomic categories to species, individual genotype to chromosomes and DNA; and the 'economic' or ecological hierarchy of energy and matter transfer which passes from biosphere to ecosystem, down to individual phenotype, cells and subcellular organelles, and so on. These two hierarchies are seen as hierarchies of real objects that can 'do things' and not abstract classes which cannot do anything in the world in their own right.

Taxonomic ecology

One way of establishing a theoretical basis for linking the systematic and ecological hierarchies would be to establish that there is only one hierarchy of objects (that can do things) above the individual organism, and that the other relationships were those of classes, not objects. Although I have put forward such a single hierarchy (Cousins 1988, 1990) I do not propose to reiterate the arguments regarding classes and objects, but instead, I will to try to demonstrate the benefits that accrue from viewing biological systems in this way.

First, we may say that organisms interact to form ecosystems, principally by eating each other or avoiding being eaten. If organisms were all of the same type, that is of the same species, and were of the same size, then feeding interactions would be difficult to sustain. It is the difference between organisms which is at the heart of interactions which form ecosystems. But as we have already seen, it is the task of systematics to describe and relate the difference between organisms. Thus we should not be surprised on this basis that systematics is at the heart of the functional description of ecosystems. The currently perceived mismatch of ecology and systematics comes instead, I suggest, from that old debate of structure versus function and therefore represents a false dichotomy.

Structure is measured in the three dimensions of space, whereas function is measured in four dimensions (i.e. space plus time). Thus, for example, if we view the live mammalian heart at any one time a structure of valves and chambers will be seen which, if we then view at successive times, will change shape and position such that we observe the function of pumping. More generally, energizing a biological structure within a suitable environment generates, when viewed over successive times, function.

A comparable summary of the distinctive features of the systematic (genealogical) and ecological (economic) hierarchies in terms of the dimensions of space and time is given by Eldredge (1992):

Thus economic biotic systems are inherently spatial—and though they persist for periods of time, their hallmark is definitely moment-by-moment interactions.

Genealogical systems, in contrast, are the by-product of history that act as reservoirs of genetic information.

I interpret these observations simply to mean that the structure of the organism is predominately influenced by genetics, but when this structure (the organism) is viewed moment-by-moment in time, then economic or ecological interactions are observed.

The really interesting question is whether organisms in higher taxonomic classes (structures) when viewed in moment-to-moment interactions create ecosystem function. Snaydon (1973) was perhaps the first to explore this idea, however briefly:

There is still a surprising similarity between taxonomic groupings and ecological behaviour; plants, animals, fungi and bacteria are broadly equivalent to producer, consumer and decomposer levels in ecosystems. Within each of these groups there are also broadly equivalent taxonomic and ecological groupings; for example the taxonomic grouping into algae, bryophytes and angiosperms broadly corresponds to ecological differences and the major taxonomic groupings with the algae broadly corresponds to ecological differences.

A much larger body of knowledge linking the ecological and the taxonomic arises from the study of body size linked phenomena, or biological allometry. Early work related key ecological parameters such as reproductive rate and metabolic rate to body size. In the case of metabolic rate three taxonomically distinct categories were proposed (Fenchel 1974): unicells, multicellular poikilotherms, and multicellular homiotherms, since these three categories radically improved the fit of the data. Over 1000 allometric relationships with ecological relevance were listed by Peters (1983). The abundance of these relationships was caused primarily by refining particular relationships through partitioning the data into particular taxonomic groups. As I wrote at the time (Cousins 1983), the discovery of allometric ecology is the discovery of taxonomic ecology since allometric relationships hold more precisely within taxonomic groups.

Using body-size based parameters for taxonomic categories it is possible to model whole ecosystems on land (Parkin and Cousins 1981) and in the ocean (Platt 1985; Cousins 1985). Size relates the fundamental ecological interactions of who can eat whom, how much food each requires to meet its own metabolic demands, and how much food each represents when eaten; reproductive rates are also likely to be size related within the taxon. The importance of body size in ecology is now well established in the central core of ecological science, trophic ecology (Lawton 1989).

Finally, the difference between a single view of a biotic hierarchy and the dual hierarchy of Eldredge and associated workers amounts to a difference in how organizational levels above the individual organism are treated, since it is assumed (see Eldredge 1992) that the two hierarchies are linked at the

level of the organism itself. Hierarchies appear inherently convergent and truncated, which is to say that in a nested hierarchy of parts containing parts, there have to be fewer larger parts at each successive level. Thus categories of parts drop out or truncate at each level. For example, the organs in our own bodies (liver, heart, sexual organs) have a distinct hierarchy of component cell types and cell internal structures. In sum and in interaction they create a whole organism. But the liver has truncated at the organ level; we do not project, except in the arts, a 'liverish' group of adults who form a distinct economic or ecological group. The sexual organs do have a relevance because they commonly form two distinct groups of adults, male and female, but these 'truncate' at the social or reproductive group. Even ecological systems in Eldredge's dual hierarchy truncate biologically at the Earth as a whole, although the solar system plainly has importance in energy transfer to the Earth itself.

In the single hierarchy (Cousins 1990) the ecological object truncates at a much smaller scale than the whole Earth, namely at the area occupied by the social group of the top predator. The ecological object includes all organisms of all taxa found within this area and is named the ecosystem trophic module (ecotrophic module or ETM). The size of the ETM will vary between sites and be dependent on the degree of human interference. There are no larger *ecological* objects than these; there may be larger lakes, oceans, or deserts but these are variously parts of the global climate and water distribution system of weather structures such as cyclones, currents, and watersheds upon the Earth's mantle. ETMs will sit upon or in these structures, but it will not make them any larger as an ecological object. I argue therefore that any biological assemblies larger than the local ETM are aggregates (Rowe 1961) such as forests, breeding colonies of sea-birds, or migrating organisms, but not integrated objects formed by functionally connected and distinct parts (Salthe 1985).

Ecological diversity measurement

So far we have concentrated on showing how systematics and ecology are linked. One of the benefits of the newly developed methods of systematics suggest that it is possible to move away from treating all species as equal, and instead, treat species as being of different relative importance. An equivalent development has been occurring in ecological diversity measurement. These changes are of interest in their own right for the purpose of conservation evaluation. Later they are also examined to see how they might be linked to the systematics approach.

It is noted that mechanism of functional interaction will differ at the global, ecosystem, and local levels of organization. This points to the need for distinctly different conservation evaluation techniques at each scale if the

goal of conserving global biodiversity is to be attained. These scale-dependent functional measures may place different priorities for conservation than the scale independent methods arising from measures of taxonomic distinctiveness developed from systematics. Neither is sufficient alone.

Local evaluation

Apart from particularly glamorous species, conservation priorities at the local level are set by some kind of species diversity measure, or by non-specific attributes such as landscape features. We will only consider species diversity measures. The traditional approaches are to make species counts or to use species diversity indices which, as well as being responsive to the number of species in the sample, take into account the relative commonness and rarity of species, that is they include a measure of the abundance of individuals in each species. This was a popular area of research in the 1960s and 1970s which received very full attention from the ecological research community at that time. However, the results have not really met expectations. Some simple modifications to standard practice are possible which may significantly improve the efficacy of species diversity measurement as a conservation evaluation tool at the local level, using selective elements of the now traditional indices. We now consider these.

Species diversity measurement is based around the species number curve. Each time an individual organism is added to a count (N) of organisms in an observed sample, it can be of the same species as organisms already present or it can be a new species in which case (S), the number of species in the observed sample, increases by one also. As N increases S can also increase although it is progressively less likely that, as the number of individuals in the sample increases, the next individual encountered will be of a species not previously met. Functionally, N is proportional to area, such that if the area is doubled within a similar kind of habitat the number of individuals encountered is likely to double also although, for the reasons given above, the number of species increases by a lesser amount.

In summary:

$$N = k \cdot \text{Area} \quad (25.1)$$

$$S = f(N) \quad (25.2)$$

$$S = f(\text{Area}) \quad (25.3)$$

This simple set of relationships has had two basic effects on the measurement of species diversity. While the number of individuals is proportional to the area sampled and measurement achieved by number per unit area, i.e. a number density with units of N/m^2 , the approach to measuring species diversity has been twofold. Species diversity is described

either as a measure of the number of species per unit area giving a species density measure with units of S/m^2 as typified by species atlases (Sharrock 1976; Dony 1976), or by making measures which are assumed to be sample size independent and are described by the function f as typified by Williams' α (Williams 1964). The frequently used Shannon index is assumed (Pielou 1975) to fall into the class of sample size independent indices although, as will be shown below, this is not the case for samples of the size normally encountered in the ecological literature.

In a study (Cousins 1977) of breeding birds on farms in the United Kingdom using Common Bird Census data from the British Trust for Ornithology, the Shannon index H' , and the related J , were analysed for sample size effects. From the simple relationship which defines H' and J ,

$$H' = J \log_2 S \quad (25.4)$$

we know that S increases with sample size and that therefore, from (4), H' and J cannot both be constants, and either H' or J or both are sample-size dependent.

Figure 25.1 shows that for the 85 farm plots (average area 40 hectares), as S increases so does H' . When individual farms are analysed for sample-size effect through the random aggregation of sub-samples, the sample-size dependence is clearly shown in Fig. 25.2 for both S and H' , while J is inversely related to the number of species in the sample and therefore again sample size related, Fig. 25.3. As a conservation evaluation technique the

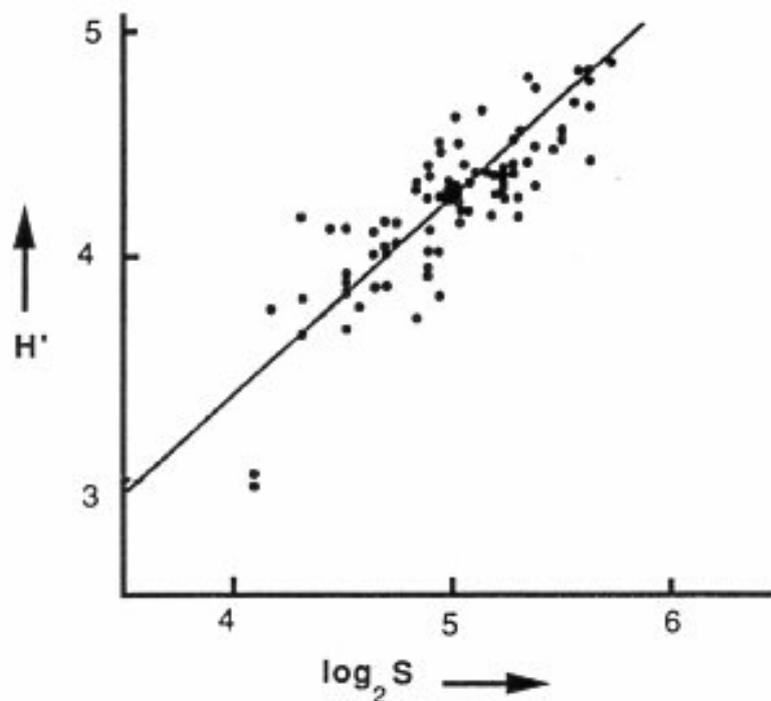


Fig. 25.1 The relationship between H' and S , the number of species in each BTO farm census plot in 1973. (From Cousins 1977)

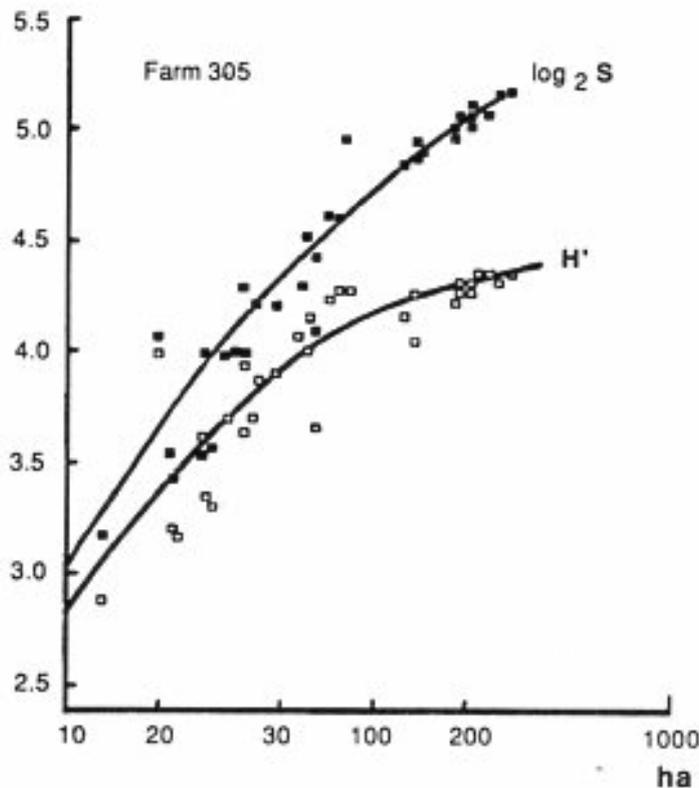


Fig. 25.2 The effect of area sampled on H' and $\log_2 S$ for a single farm determined by random aggregation of sub-samples. (From Cousins 1977)

Shannon derived indices are therefore very difficult to interpret. At least the area of the sample should be specified. The comparison between samples remains difficult if the sampling is not standardized, or compensated for, as shown in Table 25.1 where three farms are compared.

The highest diversity measured by H' is 4.28 for farm 209. This is a particularly large farm with the highest total number of individuals (N) and species (S) identified. However, Farm 209 has the lowest evenness value (J). We need to know if this is an artefact of sample size, as would be expected from the relationship of J with S shown in Fig. 25.3, or whether it is really different to the value of J for the other two farms. Clearly the most even distribution, $J = 0.86$, is produced by farm 315, but this similarly could be a result of the low number of species (23) found in that plot. In fact, when we compare the species densities at 10–40 ha, farms 133 and 209 are in effect identical in their species densities. Although J values were not calculated for sub-samples corresponding to these species densities, the J value for farm 209 would be expected to rise if that farm were sampled at the same scale as farm 315. Finally, it is farm 072 which turns out to have a much greater species density than the other two. The lack of sample size independence of H' , $\log_2 S$ and J requires that each of these parameters be plotted against sample area to establish comparability between sites as occurs in Fig. 25.2, although the ratio of H' to $\log_2 S$ would also require plotting to give J .

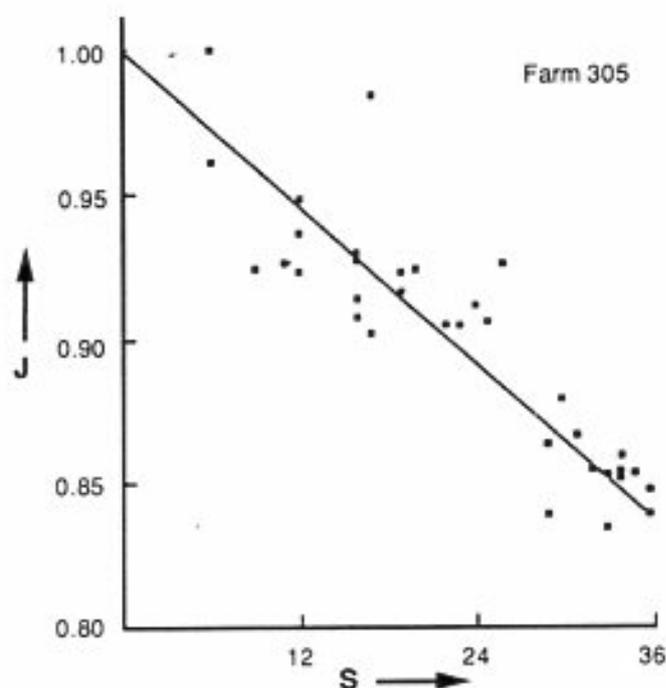


Fig. 25.3 The relationship between J and the number of species present on a single farm determined by random aggregation of sub-samples. (From Cousins 1977)

Table 25.1 Comparison of representations of biodiversity on three farms; S , number of species, N number of individuals. Species densities were obtained from averages of repeated random selection of equal area segments of mapped territory distributions. (After Cousins 1977)

Farm code	315	209	072
N	133	736	250
S	23	41	34
H	3.90	4.28	4.22
J	0.86	0.80	0.83
$S/10$ ha	9	9	15
$S/20$ ha	14	15	22
$S/40$ ha	21	22	30

Given these sample size problems for H' and J , it is preferable to use clearly understood measures such as species density and the density of individuals to describe the variety and quantity of biota present in an area. A measure of the relative abundance is provided by Williams (1964) alpha,

$$S = \alpha \log_e (1 + N/\alpha) \quad (25.5)$$

which can be used as a sample size independent measure and, more importantly, can be used to calculate species densities at a common scale by substituting (N'), the number of individuals for the base area, in equation (25.5), where S and N are known for the whole sample. In some habitats strong edge effects of the sample plot need to be removed from the data before calculating the density, N'/m^2 (Cousins 1977). Rarefaction offers an alternative technique for common scaling of diversity (Magurran 1988).

Each of the above methods are cardinal measures of species diversity in which each species is treated as equal and additive, in forming a count or index. A second group of methods is possible, where ordinal measures of species diversity (Cousins 1991) are used and species are ranked in an order and not added together. This difference is important for functional biotic measurement. Earlier it was stated that if species diversity is measured as a species density then this represents in some way the variety of energy paths present in an given area. Members of species of different sizes or of different trophic habit also have different quantitative effects on those energy flows and these can be represented in an ordinal index.

Within the cardinal indices, a sparrow counts the same as an eagle in the count of number of species present. In an ordinal representation, such as the number of species in weight classes, different levels of importance can be attached to species which individually have very different impacts on energy flow.

It is important to make one further relationship explicit between biodiversity and ecosystem function. Biodiversity describes the number of types of organism present in an area; it is the number of individuals of each of these organisms, i.e. the quantity of the biota, which determine the functional consequences of the biodiversity. In the section on taxonomic ecology the importance of body size classes with a taxon has already been identified. This provides an ordinal representation of biodiversity if we plot the number of species against weight, giving the species weight-distribution ($S(w)$). The plot of numbers of individuals of those weights, gives the individuals weight-distribution ($N(w)$), which provides the functional description since it is the number of individuals of different weights that are feeding, respiring, and so on. Because it is easier to count the number of types rather than the total number of individuals in an area, it would be useful to know the relationship between $N(w)$ and $S(w)$ for a given sample. For the 85



Fig. 25.4 Mean species weight of the British breeding bird land fauna. Small dots, 115.8–153.0 g; open circles, 153.0–191.3 g; circles with bar 191.3–229.1 g; filled symbols, 229.1–266.9 g. (From Cousins 1989)

farms above, the distributions have correlated medians ($r = 0.70$ $p < 0.001$) and a Chi-squared test showed no difference of medians between the distributions (Cousins 1989). Thus it may be possible to infer functional consequences from biodiversity distributions if the relationship between $N(w)$ and $S(w)$ is known. As an example, the species distribution of body size in UK breeding land birds, Fig. 25.4, would suggest that the distribution of body size of the numbers of individuals of UK breeding land birds also follows that distribution, if the medians of the two distributions are common. This remains to be tested further.

Finally, evidence from a survey of the feeding habits of British insects (Price 1977) shows that species of parasite (72.1 per cent of the fauna) are much more numerous than species of predator (6.3 per cent of the fauna including non-parasitic herbivores). In this case parasites are about 10 times as numerous as predators; the remaining species are saprophytes. Whereas parasites tend to be taxonomically specific in their hosts, foraging theory (Pulliam 1974; Charnov 1976) points to predators including any species in their diet provided that the predator can encounter and capture the prey, and that the rate of energy gain from eating the prey exceeds a threshold value. This comparison of parasitic specificity and predatory opportunism may account for the substantially different number of species in these two categories. Whatever the cause, there is a need to distinguish these two diversities since data on parasites could swamp predator data where they are combined. Warren and Gaston (1992) examine a related issue, the correlation between species richness in different trophic guilds in ecosystems.

This brief review of 'ecological' biodiversity indices has suggested simple alternatives to the more familiar Shannon index. The emphasis on species density, species size, and species as predators, saprophytes, or parasites provides functional descriptors. These labels may also be applied to the relations in a taxonomic hierarchy and used to redefine conservation priorities. A closely related but very differently sized organism may change its ranking in a species priority list for example.

Ecosystem and regional scale evaluation

It has already been noted that one of the differences between ecological and systematic methods for conservation evaluation is that ecological methods are scale specific, while systematic relationships are scale independent. Thus the application of the ecological methods involves different phenomena at the ecosystem level compared to the local scale. By contrast, scale change in systematics requires the introduction of a set of (arbitrary) system boundaries from outside biology, e.g. regional or national boundaries within which to set the priorities for conservation using the new systematic methods.

In terms of the politics of conservation, national or regional boundaries are far from arbitrary and are clearly very important. Funds which are raised locally or nationally are mainly spent locally or nationally. Whereas from the viewpoint of the systematic methods biodiversity priorities are international and predominately located in the tropical and sub-tropical regions, the funds for conservation are sourced and spent disproportionately in Europe and North America. There are, however, larger issues of biological principle present in this problem. There is no doubt that if the systematic methods were applied globally without reference to national interest, and expenditure was made on the basis of where there was the marginally best application, then maximal effect in terms of getting the most diversity of biological form into a minimum number of non-overlapping reserves would be achieved. However, this distribution of reserves may not include a single one in Britain and other large parts of Europe. The question that arises is: when national interest is removed from the analysis, does the 'pure' application of the technique still identify an optimal biological distribution of reserves? Are there functional attributes of the biota which require a different biodiversity strategy?

To gain an insight into this problem let us tackle the question of conservation evaluation at the ecosystem level. The Lindeman (1942) definition of ecosystem, 'the system of physical-chemical-biological processes active within a space time unit of any magnitude' is problematic for conservation evaluation since, whatever change occurs, the 'ecosystem' always remains. The ecosystem object, i.e. the ETM (Cousins 1990), unlike Lindeman's ecosystem concept, is countable and has a characteristic spatial scale. It therefore becomes possible to evaluate particular effects on ecosystems including the loss of an ETM, or its downgrading to a smaller scale, by the extinction of the primitively largest species of predator and its replacement by smaller predators.

In Britain the top predators were, until recent times, brown bears (*Ursus arctos*) and wolves (*Canis lupus*), although their abundance prior to extensive human modification of the landscape is not known. Harting (1894) reports that it was probable that bears were extinct in Britain by the tenth century, whereas the wolf survived until about 1500 in England and Wales, 1740 in Scotland, and 1770 in Ireland. In contemporary Britain the fox is the largest predator; a map of the estimated fox population is shown in Fig. 25.5.

The loss of the primitive top predators from the UK is a total one. In some parts of the world the regional count of ecosystem objects defined by the primitive top predator social groups is still possible, and is an important conservation evaluation technique to assess the status of the natural world. Since these are the largest ecological objects it is interesting to know the biodiversity present at the scale defined by the ETM. Indeed it may eventually be possible to suggest standards for biodiversity that are desirable



Fig. 25.5 Estimated adult fox densities divided into six intervals; light, zero to less than 4 ranging to 20–24 foxes per km² for the darkest symbols. (From Macdonald *et al.* 1981)

to provide a 'healthy' ETM akin to the concept of a healthy ecosystem (Cowie 1992) called for elsewhere. Such a 'standard' would need to reflect the latitude and other climatic effects on biodiversity. Each of the ways of classifying biodiversity outlined above could contribute to this; a well-spaced size distribution of species in a full set of expected higher taxa for the location; a balance of predator, saprophyte, and parasite biodiversity; a high biodiversity of biological form as defined by the systematic indices.

Before returning to the relationship between systematics and local biodiversity measurement one further aspect of the ETM needs to be considered. Top predators tend to have extensive species distributions. Thus in the case of the fox in the UK, apart from its absence from some mountainous regions, the fox is ubiquitous. This does not mean, however, that there is only one type of ETM in the UK. The ETM, although defined by the area occupied by the social group of the top predator, includes among its parts all individuals of whatever species present in that area at any given time. Traditionally, plant functional types have defined biomes and at a smaller scale plant taxonomic categories have defined UK ecosystem types (grassland, oak woodland, heather moorland, and so on). In maintaining this tradition, there is a useful parallel to be drawn between the measurement of species biodiversity using the primary variables number of individuals (N), and number of species (S), with the number of ecosystem objects (N_e), and the number of plant-defined types of ecosystem object (S_e), found in a given area. Both quantities are potentially useful tools for conservation evaluation. A similar system of plant defined ecological zones is currently under development by English Nature.

The case has been made earlier that systematics and ecology are the other sides of the same coin, that the biological structures, aptly described by systematics, when viewed moment-to-moment in time create the interactions we call ecology. It follows therefore that spatial boundaries which exist in ecosystems also exist for systematic descriptions. Thus when Vane-Wright *et al.* (1991) use their systematic methods to determine priority locations for conserving critical faunas, they are in fact selecting a particular, or several ETMs, since they also require that 'once identified, the whole biota of a priority reserve area needs adequate protection as a functional ecological system, or set of such systems'.

The use of political borders to distribute local priorities for conservation using systematic methods will again select particular whole or parts of ETMs within each country. Adding the countries together this approximates to a global collection of ecosystem types and may more usefully be approached, and selected, as such. Because of the relationship to function implicit in the systematic approach this suggests the hypothesis: that the selection of conservation priorities by the representation of ecosystem types offers a minimum area solution within a political boundary, but with the additional

benefit of selecting a full range of ecosystems as part of the biodiversity conserved.

The only major functional analysis programme to have occurred at the ecosystem level was the International Biological Programme IBP (carried out 1964–1974). An objective of IBP was to determine a functional description of each of the world's major ecosystem types. IBP was to provide a comparative description of ecosystems using a common methodology, and it was comprehensive in its coverage of the world's biomes. Unfortunately, there were shortcomings in the trophic level methodology (Lindeman 1942; Cousins 1987) and the proposed comparison of systems was not possible at the completion of the study; instead, a trophic-taxonomic analysis was made. This work by Heal and MacClean (1975), must rank as a milestone in taxonomic ecology. However, this solution arose out of the problems with the programme's central methodology. The taxonomic ecology approach if adopted from the start of such a programme would have a very different structure of analysis. It is hard to see how comparative ecology and conservation ecology can proceed without a baseline research description of the world's ecosystems. This is perhaps the most serious gap in our ability to undertake conservation evaluation. The objective which IBP set itself of obtaining a functional description of the world's ecosystems has yet to be fulfilled; the present international geosphere-biosphere programme (IGBP) or global change programmes do not fill this gap left by IBP, and a new initiative is needed.

Human impact assessment

The measurement of biodiversity has itself been commonly used as an index of human impact on the environment. However, for the purposes of conservation evaluation, human impact needs to be seen as an independent variable which is measured and capable of being equated against the results of different conservation strategies. There is no consensus on how definitive measurement of human impact could be achieved, although a number of lines of inquiry are opening up which need to be fully explored. The ecosystem object, the ETM, provides one framework to examine these issues.

The density of top predators forming the social group of the top predator species is the largest organized structure generated by the passage of energy through the food chain. This structure can be disrupted by three primary forms of human impact. The first is direct hunting of the top predators; the second is harvesting other organisms lower in the food chain thereby reducing food availability to the top predators; thirdly, by pollutants reducing the productivity of plants and animals. Data on hunting are available as typified by fur trapping records. Vitousek *et al.* (1986) have made calculations, in a variety of ways, to quantify the proportion of the total

incoming solar radiation incident on the land surface that is used by human populations rather than flowing through to top predators, and they calculate that humans may have appropriated 40 per cent of the products of terrestrial photosynthesis. The distribution of pollutants of many kinds is gaining widespread analysis and documentation (UNEP 1991). Agricultural databases form an important measure of human impact on the natural environment. A further group of *ad hoc* measures of human disturbance to natural systems have been developed for specific purposes. A built environment index for the city of London (Sandford 1975) was used as the basis for Fig. 25.6 and produced a negative Spearman correlation (-0.90 , $p = 0.001$) with the species density of land birds (Cousins 1982). If cities are the most dense human distribution, the opposite extreme has been quantified by McCloskey and Spalding (1989) who estimated the areas of the Earth's surface which are wilderness, defined as having no roads or human settlements, in areas of 400 000 hectares or more. Table 25.2 shows how these areas of wilderness relate to biome distributions and may indicate priorities for conservation. Between these extremes of city settlement and wilderness, suitable measures need to be established to measure human impact as it affects biodiversity.

Hunting, appropriation of the products of photosynthesis, and pollution in total reduce the possible density of primitive top predators or ultimately the size of top predator species that can be sustained on an area. Counts of top predators also provide an integrative measure of status of natural ecosystems (Cousins 1990) suitable as a conservation evaluation tool. Again it is not the



Fig. 25.6 An index of the built environment of London derived from Sandford (1975). Four intervals from light, least dense settlements to dark, most dense. Corresponding land bird species densities, light to dark, 43–51 species; 52–60 species; 61–68 species; 69–77 species. (From Cousins 1982)

Table 25.2 Wilderness distribution by biomes. (From McCloskey and Spalding 1989)

Biome	Wilderness distribution by biomes		
	km ²	% total	Count
Tundra Communities	20 047 533	41.7	100
Warm Deserts/Semi Deserts	9 329 531	19.4	389
Temperate Needleleaf Forests	8 799 312	18.3	120
Tropical Humid Forests	3 006 855	6.3	77
Mixed Mountain Systems	1 973 391	4.1	76
Cold Winter Deserts	1 478 494	3.1	51
Tropical Dry Forests	1 424 099	3.0	120
Tropical Grasslands/Savannahs	735 331	1.5	33
Temperate Rainforests	450 215	0.9	15
Temperate Broadleaf Forests	290 646	0.6	20
Temperate Grasslands	272 016	0.6	24
Evergreen Sclerophyllus Forests	170 885	0.4	7
Mixed Island Systems	91 647	0	7
	48 069 951	100.0	1039

number of types of top predator that is important, but the quantity of top predators that provides the evaluation measure.

Each of these techniques capture an aspect of human impact on the existing environment against which the success or failure of conservation management can be evaluated. Since it is the human realm which is driving the reduction in biodiversity, the reasonable economic aspirations of populations, estimated to reach 12 billion by 2150 (Bulatao *et al.* 1990), will generate demands on the natural environment which will need to be anticipated in order to devise appropriate conservation policies. Modestly declining biodiversity may represent a major success against this background.

Global biological function

There is a picture on the front of the paperback edition of *Five Kingdoms* (Margulis and Schwartz 1988) showing the Earth with its climate against a background of stars held in position by the thumb and forefinger of a human hand. On each digit is a symbol representing one of five kingdoms. As well as being a human hand, profiles of the heads of the human male and female are visible as outlines of the forefinger.

This powerful graphic concisely represents the role of life in maintaining the climate of the earth within an otherwise inhospitable void. The influence of life in creating the present proportions of the Earth's atmosphere has been profound (Berkner and Marshall 1965) notably in the creation of an oxygen rich atmosphere with sufficient ozone to substantially reduce the level of ultra-violet reaching the Earth's surface. Without this attenuation of UV, higher plant life would be prevented from existing on land. The present interaction of life and the atmosphere is still closely bound up with the 'five kingdoms'. It is this functional role of life at the planetary level that forms the final case for conservation evaluation.

Here, it is the quantity of life and its appropriate spatial distribution which is important rather than how many species of life there are. Technically, whether the five kingdoms were represented by only five species, or by single local populations of all species, neither case would fulfil the function represented by the hand holding the Earth in space. It is the quantity of active biomass that is determining the physical properties of the Earth's surface and atmosphere. Shukla and Mintz (1982) provided early evidence for the effect on global climate of the removal of existing vegetation from large areas of the Earth's surface. Their model showed that the global distribution of rainfall, temperature, and air motion strongly depend on the land surface evapotranspiration, thus confirming the importance of vegetation to climate. A similar call for the conservation of vegetation to preserve global climate has been made by Lovelock (1988).

As global models of climate improve and the role of vegetation in determining climate is better understood, then the consequences, including economic consequences, of anthropomorphic vegetation change upon remote as well as local environments will become calculable. Conservation evaluation on this basis could provide an alternative path to prioritizing land areas for conservation for reasons of the environmental services, such as climate stabilization, that they provide. It is the quantity of life and not its diversity which provide these services. Paradoxically, this approach should justify the continued existence much larger areas of natural and semi-natural land including its inherent biodiversity. The process of selection of priority biodiversity reserves within 'climate reserves' could further be made using the ecosystem-systematics methodology outlined above.

Conclusion

The new systematic methods for prioritising species conservation may be applied at any spatial scale. In this paper the importance of the ecosystem scale, defined by the size of the ecotrophic module, has been stressed as being of particular importance. It is suggested that the systematic methods, in combination with body size and trophic categories of predator, parasite, or

saprophyte, ensure a sound functional basis for choice between ecosystem parts or wholes. The case is made for improving local conservation evaluation by using species density measures and Williams' α rather than the Shannon H' and J indices.

There is a profound role for systematics at the heart of functional ecology. This is not through the conventional task of naming species, but relies on the importance of higher taxonomic structure which, when viewed moment-to-moment in time, creates ecosystem function. The congruence should point to a non-problem in the priorities of critical faunas over critical ecosystems, at least for local or regional conservation purposes made, say, within nations.

Globally, the systematic methods provide a fascinating picture of the location of biological form. However, the economy with which the method assembles the ark may not in the end be to the advantage of its inhabitants. In effect, the careful selection of reserves creates very high biodiversity for a small total area and thus 'cheats' the species-area curve. At the global level it is the quantity and distribution of biota, particularly plant life and microbes, that determine the biological influences upon the world's climate. Without relative climatic stability, carefully optimized biodiversity reserves risk losing species and returning eventually to the expected point on the species-area curve for the total area conserved.

The problem of conserving global biodiversity presents an almost overwhelmingly difficult task. An approach to biotic measurement has been proposed which includes the new systematic techniques, but for functional or dynamic reasons, focuses on the ecosystem level. Despite the urgency of this issue, uncertainties mean that major research efforts are needed for practically every aspect if real progress is to be made. The systematic approaches need testing and validating, ecosystems need benchmark and comparative analysis preferably in the taxonomic ecology or ecosystem-systematics framework, human impact measurement needs refining, while climatic and landscape level ecology and economics are yet other planks needed for the ark.

References

- Berkner, L. V. and Marshall, L. C. (1965). On the origin and rise of oxygen concentration in the Earth's atmosphere. *Journal of Atmospheric Science*, **22**, 225-61.
- Bulatao, R. A., Bos, E., Stephens, P. W., and Vu, M. T. (1990). *World population projections 1989-1990 edition Short and long-term estimates*. World Bank, New York.
- Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Journal of Theoretical Population Biology*, **9**, 129-36.
- Cousins, S. H. (1977). Sample size and edge effect on community measures of farm bird populations. *Polish Ecological Studies*, **3**, 27-35.
- Cousins, S. H. (1982). Species size distributions of birds and snails in an urban area.

- In *Urban Ecology* (ed. R. Bornkamm, J. A. Lee and M. R. D. Seaward), pp. 99–109. Blackwell Scientific, Oxford.
- Cousins, S. H. (1983). An alignment of energy and diversity models of ecosystems. PhD Thesis, The Open University, Milton Keynes.
- Cousins, S. H. (1985). The trophic continuum in marine ecosystems: structure and equations for a dynamic model. *Canadian Bulletin of Fisheries and Aquatic Sciences*, **213**, 76–93.
- Cousins, S. H. (1987). The decline of the trophic level concept. *Trends in Ecology and Evolution*, **2**, 312–16.
- Cousins, S. H. (1988). Fundamental components in ecology and evolution. In *Ecodynamics* (ed. C. J. Soeder and W. F. Wolff), pp. 60–8. Springer-Verlag, Berlin.
- Cousins, S. H. (1989). Species diversity and the energy theory. *Nature*, **340**, 350–1.
- Cousins, S. H. (1990). Countable ecosystems deriving from a new food web entity. *Oikos*, **57**, 270–5.
- Cousins, S. H. (1991). Species diversity measurement: choosing the right index. *Trends in Ecology and Evolution*, **6**, 190–2.
- Cowie, J. (1992). Conserving biodiversity. *Biologist*, **39**, 148.
- Damuth, J. (1985). Selection among 'species': a formulation in terms of natural functional units. *Evolution*, **39**, 1132–46.
- Dony, J. G. (1976). *Bedfordshire plant atlas*. Luton Museum and Art Gallery, Luton.
- Eldredge, N. (1992). Where the twain meet: causal intersections between the genealogical and ecological realms. In *Systematics, ecology and the biodiversity crisis* (ed. N. Eldredge), pp. 1–14. Columbia University Press, New York.
- Eldredge, N. and Salthe, S. N. (1984). Hierarchy in evolution. *Oxford surveys of Evolutionary Biology*, **1**, 184–208.
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.
- Fenchel, T. (1974). Intrinsic rate of natural increase: the relationship with body size. *Oecologia*, **14**, 317–26.
- Grene, M. (1987). Hierarchies in biology. *American Scientist*, **75**, 504–10.
- Harting, J. E. (1894). *British animals extinct within recent times*. Trubner, London.
- Heal, W. O. and MacLean Jr., S. F. (1975). Comparative productivity in ecosystems—secondary productivity. In *Unifying concepts in ecology* (ed. W. H. van Dobben and R. H. Lowe-McConnell), pp. 89–108. Junk, The Hague.
- Lawton, J. H. (1989). Food webs. In *Ecological concepts* (ed. J. M. Cherrett), pp. 43–78. Blackwell Scientific Publishers, Oxford.
- Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, **23**, 399–418.
- Lovelock, J. E. (1988). The earth as a living organism. In *Biodiversity* (ed. E. O. Wilson and F. M. Peter), pp. 486–9. National Academy Press, Washington, DC.
- McCloskey, J. M. and Spalding, H. (1989). A reconnaissance-level inventory of the amount of wilderness remaining in the world. *Ambio*, **18**, 221–7.
- Macdonald, D. W., Bunce, R. G. H., and Bacon, P. J. (1981). Fox populations, habitat characterization and rabies control. *Journal of Biogeography*, **8**, 145–51.
- McNaughton, S. J. (1989). Ecosystems and conservation in the twenty-first century. In *Conservation for the Twenty-First Century* (ed. D. Western and M. Pearl), pp. 109–20. Oxford University Press, New York.

- Magurran, A. E. (1988.) *Ecological diversity and its measurement*. Croom Helm, London.
- Margulis, L. and Schwartz, K. V. (1988). *Five Kingdoms: an illustrated guide to the phyla of life on earth*. Freeman, New York.
- Parkin, H. and Cousins, S. H. (1981). Towards a global model of large ecosystems. *ERG Report*, **41**, The Open University, Milton Keynes, UK.
- Peters, R. H. (1983). *The ecological importance of body size*. Cambridge University Press.
- Pielou, E. C. (1975). *Ecological diversity*. Wiley, London.
- Platt, T. (1985). Structure of marine ecosystems: its allometric basis. *Canadian Bulletin of Fisheries and Aquatic Sciences*, **213**, 55–64.
- Pressey, R. L. and Nicholls, A. O. (1989). Efficiency in conservation evaluation: scoring vs. iterative approaches. *Biological Conservation*, **50**, 199–218.
- Price, P. W. (1977). General concepts on the evolutionary biology of parasites. *Evolution*, **31**, 405–20.
- Pulliam H. R. (1974). On the theory of optimal diets. *American Naturalist*, **108**, 59–75.
- Rowe, J. S. (1961). The level-of-integration concept in ecology. *Ecology*, **42**, 420–7.
- Salthe, S. N. (1985). *Evolving hierarchical systems*. Columbia University Press, New York.
- Sandford, H. A. (1975). Habitat overlay. *London Naturalist*, **54**, 72–3.
- Sharrock, J. T. R. (1976). *The atlas of breeding birds in Britain and Ireland*. British Trust for Ornithology, Tring, UK.
- Shukla, J. and Mintz, Y. (1982). Influence of land-surface evapotranspiration on the earth's climate. *Science*, **215**, 1498–501.
- Snaydon, R. W. (1973). Ecological factors, genetic variation and speciation in plants. In *Taxonomy and Ecology* (ed. V. H. Heywood), pp. 1–29. Academic Press, London.
- Warren, P. H. and Gaston, K. J. (1992). Predator-prey ratios: a special case of a general pattern? *Philosophical Transactions of the Royal Society of London*, **B 338**, 113–30.
- Vane-Wright, R. I., Humphries, C. J., and Williams, P. H. (1991). What to protect—systematics and the agony of choice. *Biological Conservation*, **55**, 235–54.
- Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H., and Matson P. A. (1986). Human appropriation of the products of photosynthesis. *BioScience*, **36**, 368–73.
- Williams, C. B. (1964). *Patterns in the balance of nature*. Academic Press, London.
- Vrba, E. S. (1984). Evolutionary pattern and process in the sister group Alcelaphini-Aepycerotini (Mammalia:Bovidae). In *Living fossils* (ed. N. Eldredge and S. M. Stanley), pp. 62–79. Springer-Verlag, New York.
- UNEP (1991) *Environmental data report*. Basil Blackwell, Oxford.