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Practical Approaches to the Estimation of the Extent of Biodiversity in Speciose Groups

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CONTENTS

SUMMARY

The overall dimensions of global species richness remain very imprecisely known and the manner in which this richness is distributed only sketchily understood. This lamentable state of affairs is largely due to an inadequate appreciation of the contributions made by the most speciose groups. The most reliable, practical and cost-effective means of documenting patterns and estimating species richness in these groups is the use of a piecemeal, step by step, approach, eschewing the use of first principles, empirical relationships that are not directly amenable to calibration, diversity indices and 'short cuts' that take no account of the effects of scale. Instead, simple ratios of species richness from taxon to taxon, focal group to more inclusive group, site to site, sample to inventory, and across spatial scales provide a basis for extrapolation. Essential features of this approach are the calibration of ratios, ensuring that like is compared with like, and the fullest use of 'hands on' knowledge of the groups in question and the settings in which they are found. The choice and use of focal groups for extrapolation to larger groups and the choice and use of sampling methods to obtain reliable sample data from which to extrapolate to site inventories are considered in some detail. The way that the interplay between patchy distributions, method of sampling and sample 'dimensions' influences the reliability and precision of estimates is also discussed. The importance of appropriate rigour in assembling the species datasets that form the basis of estimates, including care in the choice and use of sampling régimes and accuracy in species recognition and sorting, is stressed. Although species richness patterns in terrestrial arthropods are used here as examples, the principle of employing simple ratios for extrapolation is also applicable to other speciose groups and other settings.

1. INTRODUCTION

Although one of the most striking and perhaps characteristic features of life on Earth is its rich variety (Wilson 1992), efforts devoted to determining the dimensions of biotic diversity and to delineating its major patterns have long been inadequate for the task in hand (May 1988). However, the value of an improved understanding of the richness of life and how it is distributed has been highlighted by current

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concerns with the threats that the world's 'biodiversity' is seen to be facing. The need for more reliable data to inform debate on how best to counter these threats and implement appropriate conservation measures is apparent. For the moment, even the approximate overall scale of global biodiversity in terms of species richness remains very imprecisely known (Hammond 1992*a*, 1994; May 1988, 1990). In large part this is due to the poverty of documentation concerning those taxonomic groups, geographic areas and biomes in which the most significant portions of the planet's biotic diversity are likely to be found (Hammond 1992*a*). Although species richness patterns exhibited by the most speciose groups of organisms are but sketchily understood, there are many indications that these patterns do not closely mirror those of the best-known but relatively species-poor groups (Abbott 1974; Yen 1987; Oliver & Beattie 1993). The reasons for a special interest in the patterns of species richness exhibited by what have been termed the 'hyper-diverse but poorly known' groups (Hammond 1992*a*) are thus obvious. They are the least understood, yet contribute most to the planet's biotic diversity, and in ways that cannot be predicted with any confidence from available data concerning, for example, large animals and vascular plants. To identify patterns of the greatest generality it is clearly essential to take into consideration at least some of the major groups in which the phenomenon of great species richness is most fully expressed. The more practical aspects of conservation evaluation would also be well served by the input of data on at least some of the more speciose groups.

Just where the major part of as yet unassessed and undescribed species richness is located, in terms of biomes, habitats or taxonomic groups, remains open to debate. However, agreement concerning possible sources of great species richness (if not concerning their relative contributions) is likely to be more general. There is no certainty, of course, that all of the 'uncharted realms' of possible biotic diversity that we recognize (Hammond 1992*a*), tropical forests and deep ocean sediments, insects, mites, nematodes, fungi, algae, microorganisms and endosymbionts in general will, in fact, prove to be especially rich in species.

This contribution is concerned with documenting and estimating species richness, at a variety of spatial scales, in what may reasonably be presumed to be the most diverse groups. To mark the distinction between this particular endeavour and the range of other activities involved in biodiversity 'appraisal', 'evaluation', 'monitoring' or 'assessment' (e.g. Anon 1993), I refer to it as *species richness assay*. Although my focus is on practical approaches to the question of assaying species richness, I inevitably touch on conceptual and other issues addressed by other contributors (e.g. Hawksworth & Harper, this volume; May, this volume), and overlap with the topics dealt with by O'Donnell *et al.* (microorganisms), and especially Colwell & Coddington (terrestrial groups) and Pearson (indicator groups), all this volume. If views that I express on these topics do not coincide with those of other contributors this may stem, at least in part, from the narrowness of my focus on species richness per se and on methods of species richness assay for speciose groups that are practical, i.e. feasible and cost-effective. Operating on a step by step basis, the principal approach advocated here aims to minimize possible margins of error, at the same time leaving the reliability of any particular estimate open to some degree of rational assessment.

Although my aim is to discuss methods of estimation applicable to speciose groups in general, problems likely to be encountered in dealing with terrestrial free-living metazoans are emphasized, and examples given are drawn largely from work on Coleoptera.

2. METHODS OF ESTIMATION

(*a*) *Sampling from scratch?*

For an extraterrestrial equipped with the means of gathering together, sorting and counting all of the species of organisms present at given points on the Earth's surface with some ease, estimation of the planet's overall species richness (and detection of its major patterns) might reasonably be seen as a straightforward and tractable sampling problem. Even so, with the discovery that the richness of life on Earth is highly clumped, that individual species are also patchy in their distribution and generally have ranges that are geographically restricted, and with ecomomy of effort in mind, the alien is likely to opt for a stratified sampling design, rather than randomly sample the globe in its entirety. For us, lacking the technical means of rapidly and reliably gathering, counting and tabulating all species of organisms present at even a few points on the Earth's surface, sampling the biota as a whole from scratch is not a practical option. However, our prior knowledge of how the variety of life is distributed means that we are better placed than the technically well endowed but naïve alien to compartmentalize the task and treat its more tractable and/or significant parts as priorities. Furthermore, if we make the most of what we already know of relevant patterns in nature, a number of short cuts are open to us, by taking advantage of the consistency that, within certain bounds, many species richness relationships exhibit (e.g. figures 5–6; table 13). Of course, the reliability of such short cuts used in species richness assay will depend on how astutely we have gauged these bounds of consistency.

(*b*) *Separate arenas*

Unless working from first principles, assays of species richness in the terrestrial and marine realms will inevitably represent separate endeavours. Within either realm, to the extent that species richness patterns involving the various speciose groups are correlated, advances made in assaying the species richness of one group may be exploited to aid the task of assay in another. However, helpful correlations are least likely where substantial differences in lifeways

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

and significant features such as body size are involved. With this as well as practical concerns and the force of tradition in mind, it may be sensible to treat the assay of species richness in groups of free-living organisms on the one hand and those, especially endosymbionts, bound in obligate and intimate associations with other organisms on the other, as distinct and separate exercises. The most speciose groups of metazoans (predominantly sexual and lacking microscopic dispersal stages) and microorganisms, including algae and fungi, also commend themselves to separate consideration.

In each operationally distinct arena, even a few significant data points with respect to the richness of one of the most speciose groups are likely to further our understanding of more general species richness patterns. As unevenness in the accumulation of relevant data is inevitable, one or more speciose groups in each major arena are likely to acquire key roles in this respect. Although self-selecting to a degree, it is clearly advantageous if such 'key groups' (see below) are among the most speciose of all and are representative in terms of significant variables such as body size, growth form, trophic group membership, vagility and mode of dispersal.

(*c*) *Practical approaches*

To be practical an approach to estimating or assaying species richness must be capable of achieving significant advances in our understanding on the basis of data that are already accessible or can be gathered with relatively modest effort. Making the most of what we already know is essential, but it is equally important that data that are not in fact up to the job should not be pressed into service just because they are there. Unfortunately, the existing record of taxonomic description for the speciose groups themselves provides us with little in the way of a reliable basis for extrapolation. The data are far too fragmentary and biased (Hammond 1994). Utilizing the relationship between numbers of described and undescribed species in samples has been suggested (Hodkinson & Casson 1991; Hodkinson 1992) as one way of making use of the existing record of description for species richness estimation. However, there are no reliable means of gauging whether samples obtained for this purpose are, in fact, representative with respect to the previous descriptive effort (Hammond 1992*a*). Just how described to undescribed species ratios in samples of restricted geographical provenance relate to similar ratios that obtain at larger scales also remains unclear (Hammond 1994). Indeed, the influence of scale on species richness relationships is sufficiently pervasive that its effects cannot be ignored safely in any type of extrapolation. Regrettably, there remains no reliable way to move from data relating to single assemblages to the global scale in one step. The equally appealing prospect of making use of turnover rates is also likely to remain no more than that, as any tolerably accurate measure of average rates demands the use of too many small scale (sample or site inventory) data points (N. Mawdsley, in preparation) to be practical for any very speciose group.

At anything other than the smallest of spatial scales, reliable species richness data in collated form are available for only a few, relatively species-poor groups such as birds and mammals. A partial exception to this generalization is provided by countries, principally those of northern and central Europe, boasting long histories of biological inventory. Data concerning at least some of the more speciose groups in these well inventoried areas offer one of the few prospects of using the best-known groups as a firm basis for extrapolation. However, in the absence of any clear support from other evidence, any assumption that species richness ratios between well known groups and very speciose groups in areas such as the British Isles hold in other contexts, notably the tropics, will generally be extremely unsafe. Relationships across spatial scales involve even greater uncertainties. In particular, there may be every reason to suppose that the species richness of such disparate groups as plants and fungi (Hawksworth 1991) or insects (Gaston 1992) scale very differently (Hammond 1994). Even a little knowledge of typical range sizes and of tropical to temperate species richness relationships in the speciose group of concern is of some service in any attempt to find a well known group that is a rough match. On the basis of such matching, somewhat greater confidence might, for example, be placed in an extrapolation from data for the British Isles involving butterflies and insects as a whole (giving a world total for insects of around 5.75 million; Hammond 1992*a*) than one involving the vascular plants and all fungi in the region (giving a world total for fungi of 1.5 million; Hawksworth 1991).

Less exploited in species richness estimation but perhaps more important is the relative wealth of more anecdotal information available for at least some of the more speciose groups. As much of this lies in the files and heads of taxonomic specialists rather than in the ecological literature, the collective views of taxonomists and others with relevant experience of speciose groups may be deserving of some attention. Indeed, the simple approach of canvassing the opinion of taxonomists has been used both formally (Gaston 1991; Andersen 1992; Winston 1992) and more informally (e.g. Hammond 1992*a*) to come up with 'working figures' for the likely species richness of various of the poorly known groups. Of course, these opinions will only be as good as the depth and breadth of the specialists' experience in relation to natural assemblages and samples drawn from them; the various biases likely to be incorporated in 'expert opinion' based estimates have been discussed by Hammond (1994). Although providing a useful point of departure for the work of species richness assay, ultimately this approach offers no serious challenge to any effective means of directly assaying species richness.

I will not go over ground already covered elsewhere (Hammond 1992, 1994) to detail the impracticality or other shortcomings of various additional approaches to estimating species richness, such as the use of host

specificity data (see also May 1990) or food web structure. With respect to the latter, Hall & Raffaelli's (1993) conclusion that food web data as they stand are largely uninformative about pattern summarizes the position well.

Ways in which sample data on their own with respect to speciose groups themselves might be used to predict their total species richness in a given arena (e.g. quadrat, plot, forest or lake) are explored by Colwell & Coddington (this volume). However, the circumstances in which statistical procedures are able to reliably predict the total species richness of a hyperdiverse group in a defined area, rather than the rate of accumulation of additional species as sampling continues, are likely to be limited. The more promising non-parametric methods have acceptable reliability only when many samples have been taken and often only when these contain 50% or more of the species in the 'population' to be assessed. This population must be small enough, therefore (see examples provided by Colwell & Coddington, this volume), to be sampled thoroughly. Just what this means will vary from group to group, but for hyperdiverse groups is unlikely to surpass the smallest of scales. For sample data to be acceptably even, methods that furnish samples amenable to quantification and at the same time ultimately obtain most if not nearly all the species of the group in question to be found in the arena under investigation will generally be required. This presents a problem with regard to many speciose groups (e.g. major groups of microorganisms, fungi and terrestrial arthropods) for which a range of disparate methods are needed for even the most approximate of inventories to be achieved.

When sample data on their own are used for extrapolation across scales or to estimate complementarity further difficulties are encountered. In particular, the problem of effectively distinguishing the accumulation of species with increased sampling effort resulting from heterogeneity *within* an assemblage or area from that which has a larger-scale spatial basis may be insuperable. Currently available sample data for the deep-sea benthos (e.g. Grassle & Maciolek 1992) face this difficulty of interpretation, leading Rex *et al.* (1993) to conclude that they cannot be used to estimate species richness of the ocean bottoms at larger scales (see May 1992).

(*d*) *Extrapolation using ratios*

The way in which ratios involving the best-known groups have been employed in species richness estimation has already been noted above. The suggestion that a more general and systematic use of ratios for extrapolation might provide an equally practical but more reliable approach is not a new one (e.g. Solbrig 1991; Hammond 1992). However, discussion of its application (Hammond 1990; Hammond & Harding 1991; di Castri *et al.* 1992; Hammond & Owen 1994; Longino 1994) has so far been limited. The use of any ratio, of course, involves the assumption that what holds in one instance also holds in another. Margins of error may be minimized by employing only the most well-grounded of assumptions, those that have been 'ground-truthed' and those that experience tells us are most reasonable and trustworthy. Clearly, like must be compared with like, and in the attempt to match situations (Eberhardt & Thomas 1991) experience and judgement are of the first importance in evaluating the prospects for bias.

Species richness ratios involve groups and contexts or settings. Those of greatest utility for extrapolations involving speciose groups fall into six general categories. Two of these are non-hierarchical (see Colwell & Coddington, this volume):

1. Group A to group B (e.g. butterflies to beetles)
2. Area A to area B (e.g. site A to site B)

The equivalent hierarchical ratios are:

3. Subgroup to group (e.g. butterflies to insects)
4. Smaller scale to larger scale (e.g. site to country)

Two further hierarchical ratios that may be regarded as special cases are:

5. Sample to inventory
6. Habitat/stratum to inventory.

Groups may be taxonomically or otherwise defined (e.g. functional groups), but the former with their relatively 'hard' edges prove easiest to work with in many instances. For extrapolation across scales, practicalities tend to dictate the choice of levels to which attention is directed: those which are unambiguously defined and for which data are easiest to collect (e.g. site, country, region, etc.). For ratios involving subgroups and samples, the way in which these elements are chosen is crucial (see below). In this context the term sample is used in a restricted sense, to mean the collection of individuals gathered by a fixed pattern and intensity of sampling with the aim of obtaining a fixed proportion of the total species present.

The essence of the approach to species richness assay outlined here – ratios and extrapolation – is simply enough stated. Its successful application, however, is likely to depend heavily on the way in which a complex series of choices and judgements are made (see below). While offering no easy answers, no rapid leaps from a handful of datasets to a comprehensive global picture, the approach has several distinct advantages. First, no use is made of uncalibrated ratios for which there are very large possible margins of error. Second, the reliability and precision of important ratios may be steadily enhanced by the acquisition of new data. Third, as well as representing steps towards establishing species richness relationships at a larger scale, many reliably established ratios will be of interest and utility in their own right. Fourth, species richness estimates, especially those for more inclusive groups and at larger scales, may be approached by a variety of routes, using different ratios and/or different datasets, thus providing additional checks on their reliability.

In summary, the principal assumptions underlying the preceding discussion, and the precepts that arise

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

from it are: (i) that the only widely applicable approach to assaying the species richness of the most diverse groups that is both practicable and reliable (however pedestrian) is the use of sample data, ratios and extrapolation; (ii) that species richness assay of speciose groups is best broken down into manageable units, with the major realms (marine, terrestrial) treated as entirely separate problems; (iii) that methods will vary in detail from taxonomic group to group, biome to biome and ecosystem to ecosystem; (iv) that the establishment of each potentially useful ratio represents a separate problem and the choice of sampling methods, focal groups, etc. should be individually tailored to its solution; and (v) that suitable reference groups can be located and sufficiently reliable sampling and sufficiently accurate inventorying are feasible (see below).

3. SPECIES DATA

Although the quality of the datasets on which species richness estimates are based is fundamental to their accuracy, this aspect of biodiversity research surprisingly often appears to be taken for granted. Some sources of data, for example concerning groups lacking adequate operational species concepts, are intrinsically unreliable, but sample or inventory data in general also varies widely in quality. Often this is a reflection of how much attention has been paid to what may be regarded as the 'nuts and bolts' of dataset compilation. Without appropriate levels of care and rigour in the choice of predictor sets, in the application as well as choice of sampling methods and régimes, in the compilation of inventories and, perhaps above all, in the basic task of species sorting, species datasets may be fundamentally flawed. An expectation on the part of non-taxonomists that samples are always well-sorted is commonly extended uncritically to all classes of identifiers or sorters. However, recognition of species limits is very much an art, and it is important to recognize that its practitioners may be of greatly varying ability.

(*a*) *Species units*

The plethora of terms applied to the units investigated in the course of biodiversity research does little to assist any judgement as to how and how well they have been sorted. The terms morphospecies, OTU (operational taxonomic unit) and RTU (recognizable taxonomic unit) tend to be used more or less interchangeably, and may represent no more than a tacit admission that taxa are unreliably sorted. It is sometimes intimated that sorting has been done to 'morphospecies' because the group in question has been little documented taxonomically and its species are largely undescribed. However, there need be no particular connection between the extent to which the species of a group have been described already and the accuracy with which samples may be sorted to species by a skilled individual. From the standpoint of species richness assays, the more closely that units conform to the biological species concept (Stanton & Lattin 1989; Wilson 1992) the better. Fortunately, experienced and skilled taxonomists working with many (although by no means all) speciose groups are able to delineate biological species on the basis of small samples as a matter of routine, and perhaps more consistently than is generally recognized.

The question of how easily and accurately 'identifiers', who are not necessarily taxonomists specializing on the group in question, are able to sort to species the samples obtained in the course of surveys or biodiversity assessments has been addressed by various authors (Anon 1993). Where operational procedures for sorting RTUs are 'standardized and calibrated' by conventional taxonomic methods the results achieved by 'biodiversity technicians' may be good (Cranston & Hillman 1992; Oliver & Beattie 1993), although this clearly varies from taxonomic group to group, and with the quality and extent of teaching and the abilities of the sorters. However, the extent to which this approach may be used for species richness assays requires more careful evaluation. The best skills available need to be applied at this, the 'sharp end' of assay work. In general, resources are probably best concentrated on obtaining and making the fullest use of available expertise, i.e. by giving skilled taxonomists extra pairs of hands rather than dispensing with their services.

The level of accuracy required in species sorting depends, of course, entirely on how the data are to be used. However, accuracy in sorting the commoner and more abundant species is often at a premium. Imagine a set of samples containing 100 species, 75 of which the sorter is able to recognize accurately, five are falsely split into two RTUs each, and the remaining 20 are grouped as seven RTUs, each containing a mixture of two or more species. Of the 92 RTUs recognized by the sorter, should the last seven be present in most samples, a situation could arise where a sample of ten RTUs contains as many as 20 species (i.e. 100% underestimate), even though the accuracy of the species total for all samples is better than 90%.

The trophic or other groups to which species belong have a role to play in some approaches to estimating species richness of diverse groups. Group membership may, for example, play a direct part in estimates (e.g. Erwin 1982) or be a factor in the choice of sampling methods or of focal groups for detailed analysis (see below). Here, it is equally important to appreciate the possible margins of error in how individuals (or species) are allotted. An illustration of the extent to which such allocations may differ is provided in table 1. It should be noted that similar proportions of species or individuals allocated to a given trophic group may mask considerable differences in how they are actually allocated using different protocols, because of a cancelling out effect. For example, very similar proportions (around 41%) of individuals are allocated to the predator category by two of the protocols (Hammond 1990; Erwin & Scott 1980), even though rather few of the species (only 42%) placed as predators using the first of these are also referred to this category using the second. On the other hand, although 74% of species referred to the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 1. *Proportional representation of major trophic groups among 1162 Coleoptera of 184 species in litter samples from lowland forest in North Sulawesi, Indonesia (see Hammond 1990, figure 11) using four different protocols*

(In general the first three protocols (Erwin & Scott 1980; Stork 1987; Hutcheson 1990) use family or other major group membership as the basis for trophic group assignments, i.e. all members of a major taxon (e.g. the family Curculionidae) are assigned to the same trophic group, whereas the protocol employed by Hammond (1990) involved the allocation of species to trophic groups on an individual basis. Not all beetle family groups represented in the Sulawesi litter samples were assigned to trophic groups by Erwin & Scott (1980), Stork (1987) or Hutcheson (1990); in these instances the allocation of species and individuals follows that employed by Hammond (1990). A = % individuals; B = % species.)

	trophic group membership					
	herbivore		scavenger/fungivore		predator	
	A	B	A	B	A	B
Erwin & Scott (1980)	7.7	12.0	51.2	46.7	41.1	41.3
Stork (1987)	5.7	9.2	74.4	52.7	19.9	38.1
Hutcheson (1990)	3.3	6.5	55.7	52.7	41.0	40.8
Hammond (1990)	5.1	6.6	53.3	41.8	41.6	51.6

predator group using the Hammond (1990) protocol are also referred to this group using that of Stork (1987), the species assigned differently do not cancel each other out in the same way, so that the number of individuals categorized as predators using the Stork protocol is lower (by *ca.* 20%).

4. FOCAL AND OTHER GROUPS

The general topic of 'indicator groups' in biodiversity studies is dealt with by Pearson (this volume), but the specific roles that selected groups play in species richness assays using ratios requires some discussion here. The term 'indicator group' has been widely employed in the literature concerning environmental and biodiversity assessment, with a variable and sometimes rather imprecise meaning. For this reason and to avoid confusion, I shall use other names for the three classes of groups, not mutually exclusive, that have a part to play in species richness assays in which extrapolations are made using ratios.

A *reference group* in this context is one used as a basis for extrapolation to a group for which less full data are available. For example, butterflies are the reference group (although by no means an ideal one) used in the simple extrapolation from species richness of beetles in the British Isles to global species richness of this group (see above). Chosen explicitly for its predictive qualities, any given reference group will typically be useful only in a specified (often narrow) range of situations. Focal groups (see below) are selected to perform a reference role, but other groups, including key groups, may also be pressed into service as appropriate. Suitable reference groups for extrapolation to the larger spatial scales (see table 14) will generally be the most difficult to locate, as the range of groups for which inventory data at the larger scales are available or can be easily assembled will always be limited.

The concept of *key groups*, whose principal role is to provide a focus for efforts made to document and estimate species richness in a given arena, has been mentioned above. They serve as touchstones and standards of comparison and may also serve as reference points where better ones are not available. However, they are not general purpose 'indicators' of the type chosen to serve a range of biodiversity assessment needs (Pearson & Cassola 1992), which by definition are too small and unrepresentative to meet the requirements of a key group. I will not presume to suggest appropriate key groups for species richness assays among microorganisms and endosymbionts or in the marine realm, but stress again the advantages likely to accrue from the choice of one of the most speciose groups and one that is as representative as possible. To be representative, a group's members should straddle the mean of significant variables and cover a good part of the range of variation found in the arena of interest as a whole. In the case of terrestrial free-living metazoans the most obvious candidates for a key group role are to be found among the major arthropod groups. The existing platform of knowledge and relative accessibility of new relevant data commends the Lepidoptera although, with most species closely associated with vascular plants, the group has a somewhat weak claim to be representative. Of the other possible choices, the Coleoptera probably best meet the criteria noted above, and have the added advantage that the group is already in relatively wide use in species richness investigations.

The term *focal group* already has some currency in the biodiversity literature, but is employed here in a somewhat restricted sense for a group that is a subdivision (often but not necessarily a taxonomic one) of a larger group of interest, selected specifically for its qualities as a predictor set (Anon 1993). The properties required of a focal group are simple: that information with respect to its richness is easily gathered, and that in at least some situations its richness is predictive of that of the more inclusive group.

I also make informal use of one additional term – *target group* – meaning one under investigation or the object of attention, and nothing more.

Before considering more closely the criteria involved

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 2. *List of major Coleoptera 'family-groups' (i.e. families and certain subfamilies), that may include 1% or more of beetle species in forest settings in tropical and/or temperate regions, with an assessment of their potential, based on ease and accuracy of sorting, as 'focal groups'*

(Family-groups in **bold** type are generally amenable to sorting with relative ease and accuracy, those in plain type sometimes so, and those in *italics* rarely if ever so. Proportional representation, based primarily on data from the Asian tropics and northern Europe, is indicated as follows: 1 = < 1%; 2 = 1–2%; 3 = 2–4%; 4 = 4–8%; 5 = > 8%. Regional variation, however, may be high for some groups with, for example, Eucnemidae often less well and Staphylininae better represented in the neotropics than the tropical assessment below suggests. The most usual feeding type(s) or 'trophic guild' membership(s) (see Hammond (1990) for further details) for each family-group is indicated in the table: F = fungivorous (including xylomycetophagy and feeding on slime moulds); H = herbivorous; Pr = predaceous; S = saprophagous; X = xylophagous. Additional family-groups that are often moderately well represented or occasionally comprise 1% or more of the beetle species in a forest setting, and are also generally amenable to sorting with relative ease and accuracy include Anthicidae, Bothrideridae, Cerylonidae, Cleridae, Colydiidae, Endomychidae, Erotylidae, Laemophloeidae, Lampyridae, Languriidae, Lucanidae, Meloidae, Melyridae, Oedemeridae, Passalidae, Platypodidae and Rhizophagidae. Although sometimes presenting difficulties in sorting, Anobiidae, Attelabidae, Biphyllidae, Brentidae, Dermestidae, Lagriidae, Mycetophagidae, Propalticidae, Scirtidae and Silvanidae might be added to this list in some instances.)

family-group	proportional representation		major feeding type
	tropical	temperate	
Aderidae	1–2	1	?S
Apionidae	1	2	H
Anthribidae	2–3	1	F, H, etc.
Buprestidae	**2**	**1**	**X, H**
Cantharidae	**1**	**1–2**	**Pr**
Carabidae	**2–3**	**3–4**	**Pr, etc.**
Cerambycidae	**3**	**1–2**	**X, H**
[Chrysomelidae]			
Alticinae	2	2–3	H
Eumolpinae	2	1	H
Galerucinae	2–3	1	H
Other subfams.	1–2	2–3	H
Cisidae	1	2	F
Coccinellidae	**2**	**2**	**Pr, etc.**
Corylophidae	2–3	1	F
[Curculionidae]			
Otiorhynchinae	**1**	**2–3**	**H**
Other subfams.	45	45	H, X
Cryptophagidae	1	3	F
Dytiscidae	**1**	**2–3**	**Pr**
Eucnemidae	2–3	1	F/X
Elateridae	2	2	H, X, etc.
Histeridae	2–3	2	Pr
[Hydrophilidae]			
Sphaeridiinae	1	2	Pr, S
Other subfams.	1	1–2	Pr, S
Lathridiidae	1	2–3	F
Leiodidae	2	3–4	F, S
Lycidae	1–2	1	?Pr
Mordellidae	2–3	1	H, F, X
Nitidulidae	2	2–3	F, S, H, Pr
Pselaphidae	3	2	Pr
Ptiliidae	2–3	2–3	S, F
Scaphidiidae	2	1	F
Scarabaeidae	**3**	**2**	**S, H, etc.**
Scolytidae	3	2	X, F
Scydmaenidae	3	1	Pr
[Staphylinidae]			
Aleocharinae	4–5	5	Pr, etc.
Omaliinae	**1**	**2**	**Pr, etc.**
Osoriinae	**2**	**0–1**	**S**
Oxytelinae	**1–2**	**2**	**S, etc.**
Paederinae	**3**	**2**	**Pr**
Staphylininae	**2**	**4**	**Pr**
Steninae	**1–2**	**3**	**Pr**
Tachyporinae	1–2	3	Pr, etc.
Tenebrionidae	**3**	**1**	**S, F, etc.**

in the selection of focal and other reference groups, it should be stressed once again that species richness assays entail a concern with *absolute* species richness at specified spatial scales. A significant correlation between the patterns of species richness exhibited by an 'indicator' group and more general patterns is sufficient for a group of this type to serve the purposes of biodiversity 'assessment', for example the comparison and ranking of sites or regions in terms of their species richness or uniqueness. However, the use of ratios for extrapolation demands a close match, at least within certain bounds, between the species richness of reference and target groups, rather than just some degree of correlation.

The criteria for the selection of focal groups include: (i) the ease and reliability with which species may be sorted; and (ii) adequate representation in conveniently taken samples; as well as (iii) matching with the target group (see table 2). In other words, groups chosen must produce enough data that are also reliable and informative for a minimum of effort. An additional criterion is the extent to which important relevant features of the biology of the focal group are known. Knowledge of feeding habits, habitat preferences, vagility and dispersal methods may all prove useful in assessing how representative the focal group is likely to be of the target group as a whole. Ultimately, however, a focal group's predictive qualities, like those of any 'indicator group' (Landres *et al.* 1988; Noss 1990), require thorough calibration.

In practice it may often prove difficult to find a single subtaxon that is able to function well as a focal group. In these circumstances it will be appropriate to select a representative 'shopping basket' of subtaxa that together serve as a composite focal group. This is the principle behind the suggestion by Sutton & Collins (1991) that a variety of groups (e.g. butterflies, dragonflies, sphingid moths, bush crickets and dung beetles among the better known, and also others such as trapdoor spiders (see Main 1987), termites, leafhoppers, carabid beetles and pyralid moths) be used as 'indicators', and the proposal by di Castri *et al.* (1992) that, for the purposes of biodiversity 'inventorying and monitoring' groups investigated should represent all major functional guilds, and cover the full range of body sizes (animals), growth forms (plants), etc.

For particular types of comparison and for particular types of sample specially tailored lists of taxa for use as a composite focal group are likely to be needed. For example, only a few of the beetle groups listed in table 2 are likely to be equally well represented in canopy fogging samples and a forest site inventory as a whole (see table 3), and even fewer if comparisons between regions or between temperate and tropical areas are involved. For comparisons of beetle species richness in the canopy between tropical sites of a similar type in the same region this need not matter, and a focal group might have as its major components (say) lamiine Cerambycidae, Coccinellidae, paederine Staphylinidae, Tenebrionidae and alticine Chrysomelidae. However, for tropical-temperate comparisons this selection will not be appropriate, and groups that are well represented in tropical but not temperate trees such as paederine Staphylinidae will need to be replaced or compensated for by the inclusion of groups such as Cantharidae or otiorhynchine Curculionidae that are proportionally better represented in temperate tree-crowns. Composite focal groups for inter-regional comparisons in the tropics will also require tailoring with inter-regional differences in mind (see table 2). Where the elements of a composite focal group are selected with care the chances of the group proving to be genuinely representative may be high, as illustrated in table 3. Here the initial choice of a shopping basket of 20 subtaxa to form a focal group was made largely on the basis of what were considered to be their typical habitat affiliations. In the event, completion of work on the full dataset (Hammond *et al.*, in preparation) revealed that a similar proportion (*ca.* 20%) of canopy specialists, of all Coleoptera species in canopy samples and of species in the site inventory as a whole belonged to the focal group.

Table 3. *List of focal Coleoptera 'family-groups' (i.e. families and certain subfamilies) selected for detailed analysis in connection with a comparison of Coleoptera assemblages in the canopy and lower strata of a lowland tropical forest in Sulawesi, Indonesia (Hammond* et al.*, in preparation)*

(The groups are selected from a pool of family-groups for which sorting to species is considered to be generally reliable (see table 2), with the aim of achieving a representative subset of the species of Coleoptera both in the canopy and in the forest inventory as a whole.)

family-group	total %	canopy %	canopy only %
Anthicidae	0.5	0.4	0.2
Buprestidae	1.4	1.9	2.9
Cantharidae	0.3	0.6	0.2
Cerambycinae	0.6	0.4	1.0
Cicindelinae	0.4	0.1	0.2
Cleridae	0.8	1.1	0.6
Coccinellidae	1.4	3.0	2.1
Endomychidae	0.9	0.6	1.3
Erotylidae	0.6	0.3	0.4
Hydrophilidae	0.8	0.3	—
Lagriidae	0.5	0.6	0.4
Lamiinae	2.8	4.2	5.6
Osoriinae	1.1	0.8	0.8
Otiorhynchinae	0.5	1.2	1.0
Oxytelinae	0.8	1.0	0.2
Paederinae	2.0	1.6	2.3
Platypodidae	0.6	0.8	1.0
Scarabaeinae	0.8	0.1	—
Staphylininae	1.3	0.4	0.4
Tenebrionidae	2.0	1.1	1.0
total	20.9	20.3	21.6

5. SAMPLING

Quantitative sample data concerning numbers of

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

species and pertaining to a single site or area may be gathered for a variety of purposes: for modelling or the investigation of pattern as well as for inventory or comparison (Eberhardt & Thomas 1991). The use of ratios for extrapolation in species richness assays involves the acquisition of both sample and inventory data with respect to individual sites. The distinction between 'sampling' and 'inventorying' in this context is fundamental. The two exercises have independent and very different objectives. In gathering sample data the aim is not to obtain the maximum number of species of the target group nor, for example, to reveal whether particular species are present or to examine sample characteristics such as equitability. The purpose of sampling is simply to obtain a fixed proportion of target group species present at a site, to do this reliably, with some precision and with a minimum of effort. Many of the criteria involved in the choice of sampling methods (see below) reflect this aim. Some requirements, of course, are much the same as in other types of investigation; methods used must furnish enough data (i.e. samples must be of a type and size to include a sufficient number of target group species), and must be informative (i.e. reflect real differences between sites or areas). Practical considerations with respect to cost and effort are also of significance, and it is often advantageous for methods to be robust (i.e. usable by the inexpert in a consistent manner, and not readily compromised by disruptions such as bad weather or vandalism).

(*a*) *Units of study*

The basic spatial unit of study for species richness assays is, in some sense or other, a 'site'. As the eventual aim is to relate species richness figures for these basic units to regional totals it is essential that there is some consistency in how they are delimited in any particular arena of investigation. Although optimal dimensions vary from taxon to taxon, there are clear advantages to be gained from using the same sites and types of site for as many target speciose groups as possible. In general, the most convenient and informative level at which to describe local species richness for assay purposes is between what are generally described as habitats and landscapes. More significant than the precise area that they cover is that they should be natural units. 'Extended sites,' those (however small) that include different major vegetation types and/or elevational assemblages, may in fact encompass much of the variability that exists at regional level. Many biodiversity 'hotspots' have this character (see, for example, Lamas *et al.* 1991), and although of special interest in conservation terms, they are unlikely to provide a good basis for site-to-site comparisons, for example between regions. The relatively large areas currently proposed for ATBI (all taxon biological inventory) investigations also cover terrain that is too varied for them to be used as the basic unit for species richness assays. In some arenas, such as the deep-sea benthos, setting suitable spatial bounds for assaying local species richness remains a challenge, but this will need to be met if the sample to inventory ratio approach is to be used successfully.

(*b*) *Choice of methods*

No sampling method evenly covers all habitats or habitat patches that occur at a site, and most sample a restricted component of the target group species present. This selectivity may be determined largely by the behaviour of the organisms themselves (e.g. when trapping methods, especially those employing attractants, are used), or by the way in which organisms are extracted or isolated from samples, as well as by the range of habitats and/or strata from which samples are drawn. Each method is likely to display some advantage, but the most suitable for sampling in connection with single site assays will, in general, need to: (i) sample a component that represents a reasonably large and constant proportion of the whole; (ii) cope with within-site heterogeneity in a manner that minimizes the risk of bias introduced by pattern of sampling; (iii) be free of strong biases resulting from inter-site differences that are not correlated with species richness; and (iv) be little influenced by incidental variables (e.g. weather).

In practice, wherever possible, the attempt should be made to rule out methods that involve a strong user variable (e.g. general searching, sweeping vegetation) or sampling point or site specific variables that affect sampling efficiency (e.g. trap apparency). Of course, various practical considerations, especially ones relating to cost, effort and user friendliness, will also be a factor in the choice of methods.

(*c*) *Sampling régimes and protocols*

As the aims of assays are to estimate species richness directly, rather than employ some form of index (Whittaker 1972), a precisely equivalent sampling effort is required at each site. The constants here are the intensity and spread of sampling, rather than sample size in the most usual sense (i.e. the number of individual organisms). Of course, large differences in the mean size of samples obtained at different sites may indicate that the aim of excluding the influence of incidental variables (e.g. weather) has not been achieved. Sample size differences, however, may also arise in a number of ways that have no direct bearing on the relationship between sample species richness and site species richness. To take an extreme example, mass flights of one or a few insect species that are present at one site but absent at a neighbouring one might have a profound influence on the size of Malaise trap samples obtained concurrently at the two sites.

One of the more important practical considerations involved in the choice of sampling methods is the number and the dimensions of samples needed to obtain reliable results. Where between-sample variation in species richness is great, a larger sampling effort will generally be required. Equally, where sample complementarity (see Colwell & Coddington, this volume) is high, the spread of sampling through

space and/or time must take this into account. In short, the sampling effort has to be sufficient to eliminate or minimize bias. Although to some extent the most appropriate intensity and pattern of sampling for a given method may be deduced *a priori*, testing against real sample and inventory data may prove essential.

In a typical habitat mosaic spot samples of the 'standing crop' type (e.g. soil cores) are particularly likely to exhibit high complementarity. This may or may not present a problem for sampling in connection with site assays, depending on whether the pattern of complementarity differs between sites in a way that does not correlate with species richness. Samples obtained by some activity-based trapping methods (e.g. Malaise traps) may also exhibit relatively high complementarity (see below) but most such methods effectively sample from a larger scale than that evident from the simple distribution of sampling sites. Although this characteristic renders activity-based traps unsuitable sources of samples for some purposes, it may make them especially appropriate for others. Species richness assays of individual sites are a case in point, as the population (in the statistical sense) sampled by some trapping methods more or less equates with the 'target' population (see Eberhardt & Thomas 1991), i.e. that of the whole site. Large area flight interception traps provide a particularly good example of how an appropriate method may produce samples of relatively unvarying species composition and richness even in an extremely patchy environment. First developed as a means of collecting small insects difficult to obtain by other means (Peck & Davis 1980; Masner & Goulet 1981), large area flight interception traps are an effective means of obtaining quantitative samples rich in some groups of flying insects, notably Coleoptera and Diptera, and not especially influenced by incidental variables. The particular model developed for comparing the species richness of beetle assemblages in tropical and temperate forests (Hammond 1990; Hammond & Owen 1994) has now been used successfully at a wide range of sites in the Old and New World tropics. Effective use has also been made of the sampling method for comparisons of assemblage composition (Chandler 1987, 1991; Jessop & Hammond 1993). The crucial characteristic of flight interception trap samples with respect to local species richness investigations is that they are largely composed of low flying insects that forage relatively widely, mostly using olfaction, for sparsely distributed resources that are not generally particularly clumped in their occurrence (see Hammond 1990, 1992*b*; Hammond & Owen 1994; Owen 1992, 1993). Although samples from different sites may differ greatly in composition (Jessop & Hammond 1993), those taken concurrently at the same site in randomly sited traps that are several hundred metres apart are generally very alike in species composition and species richness (Hammond & Owen 1994). Malaise traps (see Matthews & Matthews 1971, 1983; Townes 1972) generally obtain a very different range of flying insect species, many of which are plant-associated, and thus may usefully complement flight interception traps as a means of sampling for species richness assays. However, as many of the insects present in Malaise trap samples forage (e.g. for flowers) using vision along particular lines of flight, traps that are even a few metres apart may obtain very different catches. Nevertheless, if sufficient subsamples are taken, Malaise traps may be used successfully for inter-site comparisons (Neumann 1979; Hutcheson 1990; Hammond 1990).

Table 4. *Comparison of beetle species richness in Malaise trap samples from lowland forest, Sulawesi, Indonesia (see Hammond 1990), at six different scales of measurement*

(Trap A, operated at forest floor level, obtained 350 species in 43 weeks of trapping; trap B, operated at canopy level, obtained 172 species in 29 weeks.)

sampling effort (trap weeks)	no. of samples per trap	mean no. species		increment (%)	
		trap A	trap B	trap A	trap B
1	16	36	14	—	—
2	8	62	24	73	76
4	4	104	42	68	75
8	2	170	71	63	69
16	1	269	116	59	63
29	1	308	172	14	48

(*d*) *Sample 'dimensions' and species richness ratios*

As well as the 'dimensions' and number of subsamples necessary for reliable mean sample species richness figures to be obtained, the sample dimensions which most accurately reflect inter-site species richness relationships also vary with sampling method. Again, samples produced by standing crop methods that directly reflect the mosaic nature of a site and those, on the other hand, that are effectively drawn from a relatively large area (e.g. many activity-based trapping methods) generally exhibit the greatest differences.

The pattern of accumulation of species with increasing sample dimensions for an activity-based method (Malaise trapping) at a species rich and less species rich site are depicted in table 4, illustrating how the rate of accumulation diminishes much more sharply at the richer site. The inter-site species

Table 5. *Species richness of Coleoptera in canopy-level Malaise traps (B, C & D) in relation to a forest floor Malaise trap (A), in Sulawesi, Indonesia (see Hammond 1990), at six different scales of measurement (as in table 4)*

sampling effort (trap weeks)	mean species richness ratio		
	A : B	A : C	A : D
1	2.63	3.06	3.86
2	2.58	2.92	3.59
4	2.48	2.68	3.50
8	2.39	2.67	3.14
16	2.32	2.40	2.92
32	1.74	—	2.48

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 6. *Species richness of Coleoptera in pitfall-trap samples from three sites (A, B & C) at Burnham Beeches, U.K., at five different scales of measurement (P. M. Hammond, unpublished data)*

sampling effort (trap weeks)	no. of samples per site	mean species richness ratio A : B	A : C	B : C
10	20	1.30	1.22	1.07
20	10	1.20	1.11	1.08
50	4	1.12	1.01	1.11
100	2	1.08	1.10	1.05
200	1	1.03	1.08	0.96

Table 8. *Species richness of Coleoptera in insecticide fogging samples from beech canopy in a wood-ant infested area (B) in relation to species richness in an area free of Wood Ants (A) at Burnham Beeches, U.K., at four different scales of measurement (P. M. Hammond, unpublished data)*

sample dimensions/m^2	no. of samples per site	mean species richness ratio A : B
1	15	1.32
6.5	6	1.62
20	3	1.62
60	1	1.65

richness ratios (table 5) that obtain for different sampling efforts reveal the influence of scale of measurement particularly clearly. In the instances depicted (table 5), there is no initial increase in ratios and these fall steadily up to a sampling effort of around 16 trap weeks where a much steeper fall is observed. In the case of the pitfall-trap samples illustrated in table 6, the modest between-site differences in species richness observed at a sampling effort of 10 trap weeks are no longer evident when samples of much larger dimensions are compared. Between-site species richness ratios of flight interception trap samples tend to be more stable, but at very large sampling efforts also fall (table 7).

For terrestrial arthropods canopy fogging approximates to a 'standing crop' method of sampling, and the influence of sample dimensions on site to site ratios of species richness is illustrated in table 8. At the smallest scale measured (1 m^2), the difference in beetle species richness between the two sites was distinctly less marked than at any of the larger scales. Other U.K. fogging samples taken from single species of trees confirm this pattern with, for example, beetle species richness in June–July samples from oak trees consistently around 2.2 times greater than in September–October samples at all scales except the smallest. Litter samples provide another example of a standing crop sampling method in which a similar relationship between sampling effort and species richness is found (table 9). The observed pattern here resembles the effect of sample plot size on species richness relationships that has been well documented for plants. However, where differences in habitat heterogeneity at intermediate and larger scales contribute to the differences in species numbers between richer and poorer sites, some growth in inter-site species richness ratios may be expected to persist up to relatively large sampling efforts. Finally, however, even in the case of litter samples (or other standing crop methods), if sufficient and large enough samples are taken for virtually all resident species to be found, differences between richer and poorer sites may become less marked. An example of this is provided by the datasets of Longino & Nadkarni (1990) for ants in neotropical forest floor litter samples (richer) and suspended litter samples (less rich).

The general conclusion from these observations is that, apart from very small samples, species richness relationships between sites are typically best indicated by samples of relatively modest dimensions. This is particularly true of the activity-based trapping methods considered (tables 4–7). The explanation for this is likely to lie in the way that the representation of common and less common species and also those that are in some sense intruders varies, as sample dimensions change. If, unlike the species that 'belong', intruder or vagrant species generally accumulate at approximately the same rate with increasing sample dimensions or sampling effort at sites differing in species richness, their influence on inter-site species richness ratios may be marked, as illustrated for a hypothetical instance in table 10. Close examination of the species composition of Malaise trap and flight interception trap samples from well known sites (P. M. Hammond, unpublished data) suggests that this pattern of accumulation of vagrants may indeed take place.

Table 7. *Species richness of Coleoptera in flight interception trap catches at two woodland sites in the U.K.: Burnham Beeches, Bucks. (A) (see Hammond 1992b) and Gosforth Park, Northumbria (B) (see Jessop & Hammond 1992), at three different scales of measurement*

sampling effort (trap weeks)	no. of samples per site	mean species richness ratio A : B
2	4	3.48
4	2	3.42
8	1	3.09

Table 9. *Species richness of Coleoptera in litter samples from lowland forest in Sulawesi, Indonesia (A) (see Hammond 1990) and from Burnham Beeches, U.K. (B), at two different scales of measurement*

sample dimensions/m^2	no. of samples per site	mean species richness ratio A : B
2.5	4	1.50
10.0	1	1.76

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 10. *Hypothetical assemblages of 130 (A) and 65 (B) species, illustrating how the inclusion of vagrants might influence inter-site species richness ratios measured at different scales*

	sample size									
	very small		small		medium		large		inventory	
species status	A	B	A	B	A	B	A	B	A	B
very common	5	7	5	7	5	7	5	7	5	7
common	1	2	5	11	8	16	10	18	10	18
rare	0	0	5	11	10	20	25	50	50	105
vagrant	0	0	1	1	5	5	25	25	—	—
total	6	9	16	30	28	48	65	100	65	130
ratio A : B	1.5		1.88		1.71		1.54		2.0	

6. CALIBRATION AND INVENTORIES

Inventories of one type or another furnish most of the reference points on which species richness assays employing ratios are based. Single site inventories for speciose groups represent the 'knowns' against which the results of sampling are calibrated (see table 13), while inventory data for selected reference groups at larger scales (country, region) provide the basis for working species richness ratios across scales (see table 14). Inventory data, as they accumulate, may also provide the means of confirming the appropriateness of choices made with respect to focal groups and to sampling methods and régimes, and of gauging the bounds within which a given relationship might be expected to hold. The discussion that follows is based on the assumption that inventorying will normally involve the attempt to census the species of a taxonomically defined group, this target group being either a speciose group as a whole or some of its component (focal) taxa. The alternative approach of employing groups at least partially defined in other terms, for example plant-associated mites, or nematodes retained in sieves of given mesh size, may make the initial task of inventorying easier, but is likely to create greater difficulties when the resulting inventory data are related to reference points, generally concerning taxonomic groups, at larger scales.

(*a*) *Site inventories*

Although inventories that break important new ground (e.g. mites at a moist tropical forest site, nematodes in a well-defined area of deep ocean floor) are the most obvious and urgent need, single site inventories made in already relatively well-investigated settings also have a vital role to play. In the best-known areas of the world, such as the British Isles, site inventories are easier to make and, except for the most poorly known groups of microorganisms, their completeness much easier to judge, especially if moderately reliable inventories at country or region level already exist. Extensive calibration of sample data and the honing of sampling methods are also likely to be more feasible in these circumstances. Where inventories need to be compiled from scratch, it makes sense for the exercise to proceed in tandem with the quantitative sampling that is to be calibrated (Coddington *et al.* 1991; Hammond 1990; Hammond & Owen 1994; Longino 1994).

Appropriate spatial bounds for species richness assays of single sites have already been discussed in connection with sampling. With inventories the question of temporal limits also arises. Typically, exhaustive surveys extend over several years, but the longer an inventory period the greater the likelihood that species not usually present will be included. This problem may be particularly acute for small 'island' sites, for organisms that are are vagile and have large trivial ranges, and where standard inventory methods involve powerful attractants (e.g. Lepidoptera flying to light traps). Inventories of Lepidoptera (e.g. Barlow & Woiwod 1989, 1990), and the results obtained by Owen & Owen (1990) for Diptera, Hymenoptera and other flying insects such as Hymenoptera and Diptera by using a single Malaise trap in a suburban garden in the U.K. over two decades illustrate this point well. In such instances the number of vagrants, visitors and temporary residents (not present in every year) claiming a place in the site list may be great if the inventory period is not strictly limited. In practice, however, the ideal of a short but intensive inventory may be difficult to achieve, especially where diagnostic life stages are seasonally limited in their appearance or, like the fruiting bodies

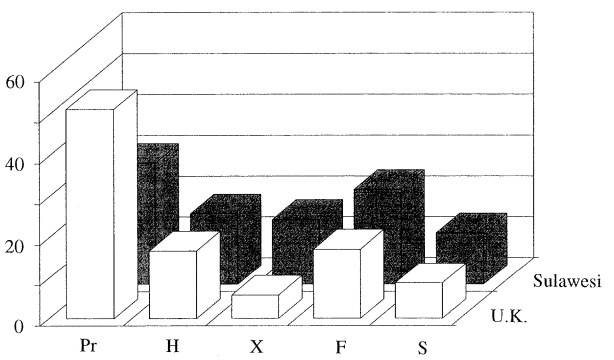

Figure 1. Proportional representation of feeding-groups among the beetle species found in a 200 hectare area of deciduous woodland at Burnham Beeches, U.K. (front) and in a 500 hectare area of relatively uniform moist tropical forest in Sulawesi (back). Data from Hammond (1990, 1991, unpublished). Pr = predators; H = herbivores; X = xylophages; F = fungivores; S = saprophages.

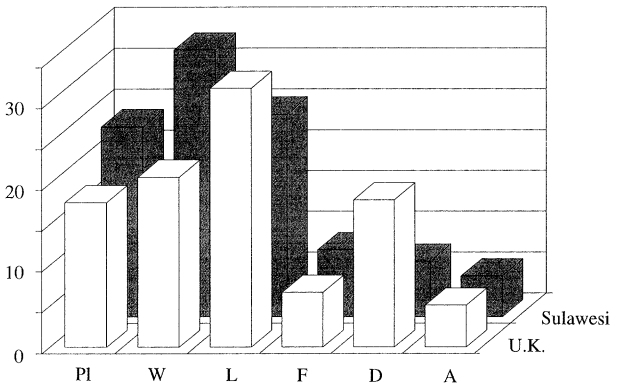

Figure 2. Proportional representation of 'habitat-groups' among the beetle species found in a 200 hectare area of deciduous woodland at Burnham Beeches, U.K. (front) and in a 500 hectare area of relatively uniform moist tropical forest in Sulawesi (back). Data from Hammond (1990, 1991, unpublished). Pl = non-woody parts of vascular plants; W = wood; L = litter, including soil and soil surface; F = large fungus fruiting bodies; D = decaying matter such as dung, carrion, etc.; A = aquatic.

of some fungi, appear only in certain years (Hawksworth 1991).

Gauging the reliability of site inventory data, especially those for the least known groups and settings, presents a further challenge. Where the data are appropriate, statistical techniques (Baltanas 1992; Palmer 1990), notably the simple non-parametric methods of extrapolation described by Coddington *et al.* (1991), may assist in determining how closely an inventory has approached completeness. However, in the common situation where many different inventory techniques have been employed and few data are for comparable quantitative samples, educated guesses have the most important part to play. These will be most firmly grounded where field lore and natural history know-how are fully exploited and a good knowledge of the occurrence of the target group in surrounding areas and at similar sites already exists. Where sites are of a similar general type, great regularities may exist in the proportions of species associated with particular habitats or belonging to particular trophic groups, and an analysis of survey results in these terms is another way of detecting biases or shortcomings in inventorying (see figures 3–6).

(*b*) *Inventory methods*

Inventory methods tend to be highly group and situation specific. At the same time, successful inventorying of even one hyper-diverse group may

Table 11. *Numbers of species of Coleoptera collected by various methods and/or from various sources during an intensive five-and-a-half year survey of Richmond Park, U.K. (Hammond & Owen 1994)*

(Figures in parentheses are percentages of the total of 959 species. Figures in the 'exclusive' columns are for species collected exclusively by the method in question. Sampling 'effort' is indicated as high (H), medium (M) or low (L). The 'extra' column provides a subjective measure of adequacy of sampling effort; the plus signs indicate that a considerably greater effort than that actually employed would have increased the number of species obtained by that method by 60 + % (+ + +), 30 + % (++), or less than 30% (+). The sampling methods and/or sample sources are as follows (see Hammond & Owen (1994) for details): 1, wood/fungi (includes slime mould fruiting bodies, litter inside hollow trees, etc.); 2, FITs (two large-area flight interception traps operated for a total of 500 trap-days); 3, fogging (insecticide fogging of 72 trees, mostly oaks); 4, plants (from living parts of vascular plants, by searching, sweeping, beating, etc.); 5, litter (soil, humus, leaf litter, etc. samples); 6, wetland (from waterside or marshy situations by washing, searching, etc.); 7, dung; 8, nests (including those in tree-holes); 9, snanthropic (from man-made accumulations of cut grass, manure, stable debris, etc.); 10, baits (from carrion or from traps baited with carrion, fruit, etc.); 11, flood debris; 12, aquatic (from ponds or streams, mostly by netting); 13, stones (by searching under stones, logs, etc.); 14, grubbing (by 'grubbing' under mat or rosette plants, at the base of trees or large plants, etc.).)

	total spp.		exclusive spp.		sampling	
sample type	no.	%	no.	%	'effort'	extra
1 wood/fungi	211	(22)	59	(6)	H	+
2 FITs	317	(33)	44	(5)	H	++
3 fogging	198	(21)	35	(4)	H	+
4 plants	226	(24)	78	(8)	H	+
5 litter	229	(24)	23	(2)	H	+
6 wetland	122	(13)	57	(6)	H	+
7 dung	83	(9)	24	(3)	M	++
8 nests	35	(4)	6	(< 1)	L	+
9 synanthropic	115	(12)	41	(4)	M	++
10 baits	85	(9)	12	(1)	M	+
11 flood debris	170	(18)	34	(4)	M	++
12 aquatic	14	(1)	8	(< 1)	L	+ + +
13 stones	59	(6)	6	(< 1)	M	++
14 grubbing	46	(5)	5	(< 1)	L	++
all samples	959	(100)	442	(46)	H	+

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 12. *Representation of species of 15 relatively well inventoried Coleoptera family-groups in samples taken from a 500 hectare area of relatively uniform lowland forest in Sulawesi (see Hammond 1990)*

(The sampling methods (columns 1 to 8) are: (1) light traps; (2) Malaise traps; (3) flight interception traps; (4) canopy fogging; (5) samples of litter/wood/fungi/etc.; (6) samples of dung/carrion/etc., and from baited traps; (7) samples taken directly from plants by sweeping, etc.; and (8) samples taken from water bodies or the banks of water. Figures in parentheses are numbers of species collected exclusively by the method in question.)

'family-group'	1	2	3	4	5	6	7	8	total
Dytiscidae	26 (13)	3 (0)	3 (1)	0 (0)	1 (0)	0 (0)	0 (0)	8 (0)	28
Osoriinae	4 (0)	10 (5)	23 (7)	9 (2)	34 (11)	3 (0)	0 (0)	0 (0)	53
Oxytelinae	18 (6)	9 (0)	15 (2)	14 (1)	14 (2)	13 (0)	0 (0)	2 (0)	36
Paederinae	42 (12)	29 (2)	32 (3)	23 (9)	29 (7)	9 (0)	19 (3)	13 (2)	93
Staphylininae	12 (3)	19 (1)	38 (13)	5 (0)	20 (3)	15 (0)	1 (0)	6 (0)	61
Scarabaeinae	15 (4)	5 (0)	30 (6)	0 (0)	1 (0)	22 (0)	9 (0)	0 (0)	36
Buprestidae	13 (4)	43 (19)	4 (0)	26 (13)	1 (0)	1 (0)	7 (2)	0 (0)	69
Cleridae	11 (3)	31 (11)	1 (0)	15 (1)	1 (0)	1 (0)	0 (0)	0 (0)	38
Erotylidae	8 (5)	16 (3)	10 (3)	4 (1)	6 (0)	2 (2)	3 (1)	0 (0)	31
Endomychidae	10 (3)	17 (3)	19 (6)	9 (7)	19 (4)	0 (0)	0 (0)	0 (0)	41
Coccinellidae	21 (2)	42 (7)	7 (0)	42 (11)	3 (1)	0 (0)	10 (0)	0 (0)	66
Colydiidae	20 (11)	7 (1)	10 (6)	5 (4)	6 (2)	0 (0)	1 (0)	0 (0)	36
Cerambycinae	7 (2)	25 (15)	0 (0)	11 (5)	2 (0)	0 (0)	4 (1)	0 (0)	38
Lamiinae	35 (4)	105 (54)	5 (0)	59 (28)	14 (1)	0 (0)	10 (3)	0 (0)	150
Otiorhynchinae	11 (2)	10 (0)	1 (0)	17 (5)	3 (1)	2 (0)	6 (2)	0 (0)	26
total	252 (74)	371 (121)	198 (47)	239 (87)	153 (32)	68 (2)	70 (12)	29 (2)	802

involve a wide range of methods. Comment here is thus restricted to a few generalities, illustrated by reference to temperate and tropical site inventories for Coleoptera (Hammond 1990, 1991; Hammond & Owen 1994). First, as the distinction is generally not made in discussions of survey and inventory methods (Anon 1993; Disney *et al.* 1982; Majer 1987), it should be stressed that in the context of species richness assays, inventorying and quantitative sampling are separate and distinct activities. The criteria employed in the choice of methods for obtaining quantitative sample data (see above) may be of little direct relevance to inventorying. Here, the first consideration is the return for cost/effort, not only in terms of the number of species obtained but also the numbers difficult or impossible to obtain by other means (tables 11 and 12). Inventories do not have to be compiled building block by building block, each habitat type being dealt with separately, although knowledge of the components of the inventory in these terms is likely to prove useful in various ways, for example in checking for completeness.

Making use of the results of an inventory of Coleoptera at one temperate site, Richmond Park, Surrey, U.K. (Hammond & Owen 1994), a few further points concerning inventory methods may be made. First, as 'sampling effort' – the combination of intensity and pattern of sampling – is often difficult to quantify and compare, the relative efficacy of inventory methods can be assessed only in the most general terms (table 11). The nature of the contribution made by a given method will, of course, always depend on which other methods have also been used. However, even where many different types of sample are taken and sampling effort is generally high, methods may still complement each other in large measure, if efforts have been judiciously apportioned. In the case of the Richmond inventory no more than one-third of the species were present in any one of 14 broad categories of sample, and around half of the species were restricted to one sample type (table 11). However, not all methods are equally complementary, and various combinations of methods may be used to achieve a similar result. In an inventory of Coleoptera at a second U.K. site of a similar type, Burnham Beeches (Hammond 1991), methods used differed substantially from the Richmond survey (figures 3 and 4), but the results, in terms of

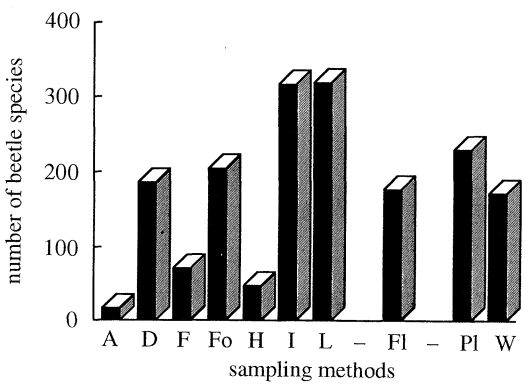

Figure 3. Numbers of beetle species taken by various sampling methods during an intensive survey of Richmond Park, U.K. (Hammond & Owen 1994). A = from fresh water; D = from decaying matter such as dung, carrion, etc.; F = from fungus fruiting bodies; Fl = flood debris; Fo = canopy fogging; H = litter and wood-mould inside hollow trees; I = flight interception traps; L = woodland floor soil and litter samples; Lt = light traps; M = Malaise traps; P = pitfall traps; Pl = from foliage, flowers, etc. of vascular plants; W = collected directly from wood.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

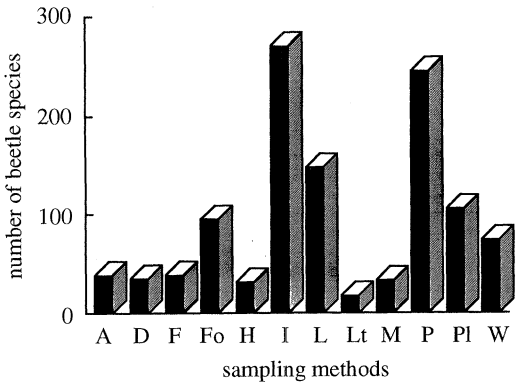

Figure 4. Numbers of beetle species taken by various sampling methods during an intensive survey of Burnham Beeches, U.K. (Hammond 1991, unpublished). See figure 3 for explanation of symbols.

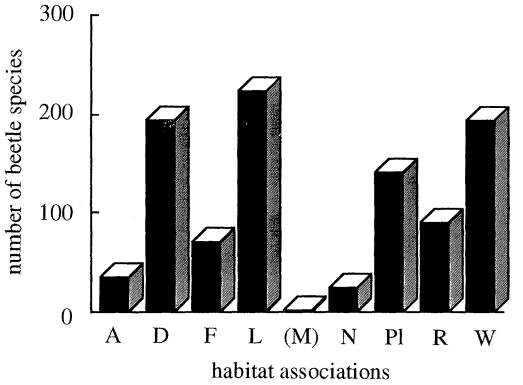

Figure 5. Habitat associations of beetle species taken during an intensive survey of Richmond Park, U.K. (Hammond & Owen 1994). A = aquatic; D = decaying matter such as dung, carrion, etc.; F = large fungus fruiting bodies; L = litter, including soil and soil surface; M = myrmecophilous (ant-associated); Pl = non-woody parts of vascular plants; R = riparian and wetland (excluding truly aquatic species); W = wood.

completeness, are likely to be comparable, as strongly suggested by the strikingly similar patterns of species' habitat associations (figures 5 and 6). Inventories of richer sites in less well known territory present greater challenges and are less likely to be truly exhaustive. The contributions made by particular inventory methods may also be expected to differ (see tables 11 and 12). Although in part due to the influence of variables such as climate on the efficacy of trapping methods, such differences also reflect the proportional representation of trophic and 'habitat' groups (figures 1 and 2).

7. APPLICATIONS AND PROSPECTS

The approach to estimating species richness described above has its most immediate application in using sample to inventory ratios (see table 13) to assay the numbers of species of a target taxon at a range of individual sites. Beginning with similar sites within the same biome and region, these investigations will duly furnish information on: (i) relationships between sites of different type (e.g. moist and dry forests) within the same biome; (ii) 'typical' relationships between regions (e.g. Afrotropical and Neotropical) for sites of a similar type; and (iii) 'typical' relationships between sites in different latitudinal zones.

As site inventory data accumulate they may be used to assess constancy of representation of taxonomic groups, size classes, trophic, 'habitat' (see figures 1 and 2) or other groups at sites that are in some sense alike. Figures 5 and 6 illustrate how similar such representation may be at individual site level. Progressing to sites that are less alike, any substantial differences in these patterns that emerge may be scrutinized to gauge how they might influence the performance of sampling methods, and reveal the extent to which independent calibration of samples at less alike sites is to be desired.

Single site assays for a target taxon or key group also represent the first stepping stones towards estimating species richness of these groups at larger spatial scales. In a global context, the most informative extrapolations will be those involving the regions of greatest species richness which, for most speciose terrestrial groups at least, are likely to be the moist tropics. In the absence of direct calibration, extra-

Table 13. *Representation of Coleoptera species in flight interception trap samples in moist temperate forests (U.K.) as proportion of total Coleoptera species present*

(The representation is similar in at least some moist tropical forests. The ranges given are for mean species richness during an 8 week period from early June to early August at five sites for which inventories have been made or total species present estimated. Note that peak figures for the shorter trapping periods may be much higher.)

		% beetle species present in:		
no. traps	no. weeks	1 ha	50 ha	500 ha
1	2	12–15	10–12	7–8.5
1	4	18–22	15–17	11–12.5
1	8	26–32	20–25	15–17
2	2	18–21	15–17	11–12.5

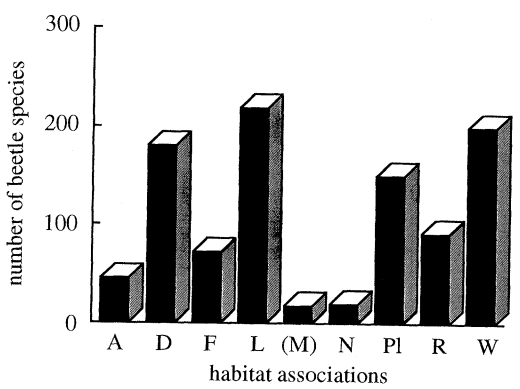

Figure 6. Habitat associations of beetle species taken during an intensive survey of Burnham Beeches, U.K. (Hammond 1991, unpublished). See figure 5 for explanation of symbols.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 14. *Extrapolation of Coleoptera species numbers from a single site inventory in Sulawesi, Indonesia (Hammond 1990, unpublished data), to province, country, subregion, region and world totals, employing estimated tiger beetle (Cicindelinae) species numbers (from data in Cassola 1991; Pearson & Cassola 1992) at these scales as reference*

(Extrapolated numbers of beetle species are indicated in bold type.)

	tiger beetles			
scale	known species	estimated species	beetles no. spp.	increment (x)
Toraut lowland forest (500 ha)	17	18	6500	—
N. Sulawesi (Utara)	35	37	**13 361**	2.06
Sulawesi	81	86	**31 056**	2.32
Indonesia	217	250	**90 278**	2.91
Oriental–Australian region	*ca.* 900	1100	**397 222**	4.40
World	2028	2400	**866 667**	2.18

polation from local species richness of a target group to that obtaining at larger scales requires the use of reference groups. An example of how single site data (from the Sulawesi Coleoptera inventory already mentioned) might be put to use in this way is provided in table 14. The global figure of 870 000 beetle species reached using tiger beetles as a reference group contrasts with that of 2.3 million arrived at by Hammond (1992*a*) from the same starting point (6500 species at the Sulawesi site), but using a broader range of reference data. At intermediate scales (N. Sulawesi to the Oriental–Australian region) the two extrapolations involve very similar increments. However, at both the smallest (site to N. Sulawesi) and largest (region to globe) scales for which data are provided in table 14, the increments for tiger beetles were much lower than those assumed using information on species turnover patched together, in a rough and ready way, from a number of groups. While no particular claim of reliability can be made for this latter approach, the disparities illustrate the possible shortcomings of employing just one small reference group for extrapolation across scales. Tiger beetles, like many groups of similar size and/or taxonomic rank, do not exploit as wide a range of resources as larger and biologically less uniform groups. For example, whereas some tiger beetles are closed forest specialists and others favour open ground or river banks, relatively few (at least in N. Sulawesi) are specialist members of higher elevation, coastal, marshland and other assemblages which make a notable contribution to species totals for large groups such as the Coleoptera in an area like N. Sulawesi. At the largest spatial scales, where historical factors play a paramount role, small specialized groups are always likely to exhibit highly individual patterns. With almost half of their species occurring in the Oriental–Australian region, a distinctly greater proportion than for higher plants, vertebrates and no doubt most other large groups, tiger beetles appear to be no exception.

Finally, there are immediate and practical 'biodiversity assessment' uses to which methods developed for rigorous species richness assays may be put. Pared down to their essentials, protocols that have proved reliable for assay purposes may be used as the elements of 'sampling packages' dedicated to the rapid comparison of species richness at numbers of individual sites. A simple sampling package for a representative speciose group could thus take its place alongside and complement the RAPS (rapid assessment programmes) for groups such as birds and flowering plants that are already in operation.

The immediate prospects of substantially advancing our understanding of the scale and pattern of species richness in the most diverse groups of organisms using the practical step-by-step approach discussed above depend, of course, on the priority such endeavours are accorded. A perception that the problems involved are insuperable may be responsible for the current lack of anything approaching an exhaustive inventory for such groups as bacteria, protozoa, nematodes or mites at any terrestrial site. However, many evidently more tractable inventorying tasks, for example with respect to some of the major insect groups at tropical sites, also remain unattempted, despite the relatively long histories of biological investigation at field stations such as that at Barro Colorado, Panama. Current concerns with 'biodiversity conservation' have highlighted the potential interest and utility of inventory data on the most speciose groups (e.g. May 1988), and generated a good deal of discussion as to how these may be obtained (e.g. Solbrig 1991; di Castri *et al.* 1992). On the ground, however, there remains little to indicate that the necessary resources, including the best field-work know-how and taxonomic expertise available, are being or are about to be applied to the task of acquiring these data. The extent of the personal and institutional investment required, coupled with the painstaking but unspectacular nature of the work, may explain this apparent hesitation.

Among the more obvious priorities, once the assay of speciose groups seriously gets under way, are inventories for single terrestrial sites in both temperate and tropical areas of those groups, e.g. nematodes, mites, Diptera, fungi, for which these are clearly feasible but reliable data on local species richness is almost totally lacking. The development of appropriate inventory know-how is a prior requirement for some groups, especially microorganisms (Veal 1993), and it may prove advantageous to compile group and biome dedicated inventorying/sampling manuals in some instances. The oceans present a separate series of challenges, not least in the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

setting of suitable bounds for inventories. With few possibilities for direct calibration, extrapolation from single site data concerning speciose groups to larger scales is likely to remain the most problematic aspect of using the ratio approach to species richness estimation. The search for and acquisition of the most appropriate reference data for the larger spatial scales (country, region, etc.) thus takes on a particular importance.

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