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Representing Biodiversity

The specific problem the biodiversity project sought to address is how to identify and map a set of areas within a defined region which together represent all, or as much as possible, of the biological diversity of that region. We call such areas biodiversity priority areas because they should have priority for protection and/or appropriate management. Such areas alone will not be sufficient for the long-term maintenance of biological diversity and should not, therefore, be seen as a solution to the greater problem of general biodiversity protection. Overall protection will require much more than the identification and management of priority areas. Priority areas will never encompass all of biodiversity nor will they sustain the biodiversity they do encompass over time if they are managed in isolation from the surrounding matrix of other natural, semi-natural and production lands. However, priority areas should form the core of conservation plans for biodiversity protection.

The book and its contents were conceived in the light of three realities affecting biodiversity conservation: biological resources will continue to be used for human necessities and comforts, so land use change will continue apace (at least in the short to medium term) regardless of calls for it not to; there is some as yet undefined upper limit on the total area that will be managed or maintained primarily for the protection of nature; thorough inventories of all organisms (taxa) at all places is not an achievable goal in the short to medium term, if at all.

To attain the goal of identifying and mapping priority areas there must be an acceptable way of measuring biological diversity, a way of determining an acceptable level of representation and, having determined that level, a cost-effective way of allocating limited resources to secure it. Various partial yet practical and realistic measurements for biodiversity were devised, together with methods for deciding where in the landscape priority areas should be located so that a given level of representation can be achieved. There is no proposed single best measure or single sufficient level of representation, and no perfect means of deciding where priority areas should be located. As knowledge accumulates and scientific methods are refined, different measures and levels will seem to be appropriate. However, current biological theory and up-to-date scientific practice have been brought to bear now because the need is pressing. Decisions are being made now to designate areas for protection or exploitation, and it is

desirable that these decisions be informed by all available knowledge. Because the need is urgent in the face of continuing land use change and because biodiversity protection competes with legitimate alternative uses of biological resources, the methods for identifying priority areas have to be explicit, efficient, cost-effective and flexible. In addition, because data are incomplete and knowledge is limited, they have to make the most effective use of available data and it will always be necessary to re-examine priorities as knowledge accumulates.

Biological diversity protection has tended to be *ad hoc* in the past, favouring the biodiversity of areas with least potential for extractive uses. Increasingly, protection is being advocated in response to threatened land use change or biological resource utilisation, but without clear measures of the contribution different areas could make to an overall representation goal. Our objective here is to describe suitable methods for deriving explicit statements about the relative contribution different areas, both alone and in combination, can make to the protection of biological diversity. Armed with such statements the return on any given conservation investment can be measured and enlightened trade-offs can be made. Negotiation can be entered into in the early stages of land use planning and policy-making, and initiatives can be taken to protect, or manage sympathetically, areas which make an appropriate, significant or unique contribution to the overall goal.

Recognising that competing land uses are a severe constraint on biodiversity protection, to facilitate negotiation the methods provide maximum flexibility in the location of priority areas. In accepting this need it must also be acknowledged that some areas in any region, country or locality are indispensable if full protection is to be achieved. No other areas can be substituted for them because, for example, they contain unique components of biodiversity. Such places are also identified by the methods.

Biodiversity Priority Areas

The basic components of biological diversity are interpreted here as the characters that confer variety on or amongst taxa; that is, the differences among organisms which govern their functional interactions. The number of characters is phenomenally large and in practice unknown. Yet sustaining this variety, unknown and unmeasured, the variety of life on earth, is the goal of biodiversity protection. To achieve this it will be necessary to maintain the complex hierarchical biological organisation that sustains characters within taxa, taxa within communities or assemblages, and such

communities within ecosystems. It is not reasonable to expect networks of biodiversity priority areas alone to maintain such complexity. What, then, should their role be? Ideally, they should encompass a sample of biodiversity. In practice, they will only contribute, within the limitations of current knowledge, to encompassing that sample.

Theoretically, phylogenetic pattern can be used to predict the distribution of characters among taxa. Figure 1 depicts the phylogenetic pattern among 10 African milkweed butterflies (Nymphalidae) as an example. This pattern can be interpreted as an estimate of the overall character difference between terminal taxa (usually called species) and can therefore be used to compare the overall biological diversity contained within sub-sets of those taxa. In practice — in the field — it is the persistence, hybridisation or extinction of populations that will determine the fate of characters. It is at the population level that biodiversity protection will succeed or fail. If populations of all species persist, or are allowed to pursue an unimpeded course of events to extinction, wider dispersal, hybridisation or some other form of evolution, then biodiversity will have been successfully protected. Thus, an ideal goal for biodiversity priority areas might be that, together, they should sample and maintain populations of all (known or extant) terminal taxa. Such a sample would have the same mean and variance as the wider populations; the same genetic, morphological and demographic means and variances (Margules et al., 1994). A sample does not imply sufficiency and a sample alone will not sustain biodiversity but a sample of populations of all terminal taxa is a rational goal for biodiversity priority areas.

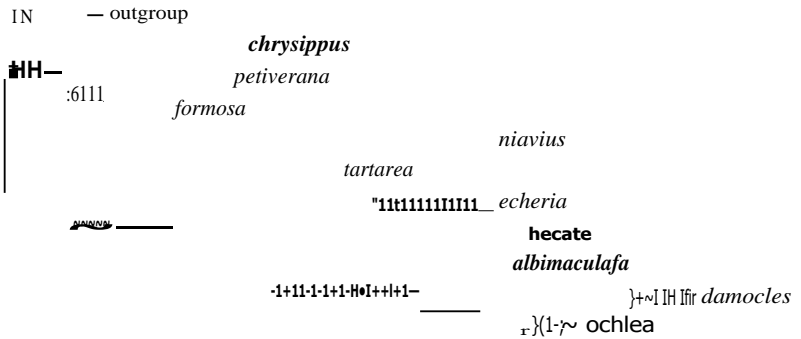


Figure 1. — Hierarchical classification (cladogram) for the 10 (out of 15) species of African milkweed butterflies for which data on both adult morphology *and* male pheromone volatiles are available. Each cross-hatch signifies one character (autapomorphy, synapomorphy, reversal, homoplasy) unique to individual species (terminal branches) or shared by two or more species at the internodes (subterminal branches). Data from Ackery & Vane-Wright (1984) and Schulz et al. (1993), for *Danaus chrysipus*, *Tirumala petiverana*, *T. formosa*, *Amauris niavius*, *A. tartarea*, *A. echeria*, *A. hecate*, *A. albimaculata*, *A. damocles* and *A. ochlea*. Character state changes per branch vary within *Amauris* from a maximum of 39 (*A. echeria*) to a minimum of 5 (internode for *damocles* + *ochlea*).

Implementation of this goal is hampered by a lack of knowledge, both theoretical and empirical. With adequate knowledge, it should be possible to identify a set of areas throughout the world which together contain all the millions of terminal taxa, as exemplified by Figure 1, and hence all of the underlying characters. It should then be possible, with adequate knowledge, to locate areas within those regions which sampled populations of those taxa and were capable of maintaining such sub-populations over time. However, knowledge is limited. Figure 1 is the best estimate, based on current knowledge, of the phylogenetic pattern amongst the given subset of 10 African milkweed butterflies, but it is not necessarily the true one. Not only the interrelations of the terminal taxa, but even the number of terminal taxa recognised within such a subset, are all subject to re-assessment and revision. In addition, current records of geographical locations are likely to be biased, at least on spatial scales useful for conservation planning. Most field records are collected in a haphazard manner from locations where the species of interest are likely to be found, or are conveniently accessible. Locations with butterfly records are probably only a sub-set of the locations where butterflies actually occur and there are probably few records of where they were looked for but not found. Recorded absences are necessary to establish geographical ranges and recorded absences are rare in biological collections (Margules & Austin, 1994). At the coarse global scale this may not be much of a problem. We can be almost certain that there are no wild lions (or pseudopontiine butterflies) in Australia, no koalas (or trapezitine butterflies) in China, and no pandas (or calinagine butterflies) in Africa, but at finer scales, e. g. the distribution of koalas within south-eastern Australia or the distribution of purple hairstreak butterflies in the U. K., recorded absences are needed to establish the limits of species' ranges. The milkweed butterfly phylogenetic pattern is only one of millions and the same comments apply to all of them. Similarly, the descriptive knowledge needed to identify a sample of a population and the ecological knowledge needed to manage populations so that they remain viable and their evolutionary options are kept open is lacking for all but a very few species.

In summary, the goal of conserving characters by protecting samples of populations of terminal taxa (species) has to be revised because of: imperfect knowledge of terminal taxa and their phylogenetic relationships; biased data on the geographical ranges of occurrences of taxa; and inadequate management prescriptions for ensuring the persistence of populations.

From this it is apparent that some form of compromise is necessary. Hence the term 'represent'. An appropriate revised goal for biodiversity priority areas is to represent the known biodiversity of a region, country or

biome. At this time, only a sub-set of taxa are sufficiently well known and well mapped to be represented with confidence in priority areas. Indeed, based on the inadequacy of distributional data at the taxon level in many parts of the world, strong cases can be made for working with assemblages of taxa or environmental classes, in which case the aim becomes to represent each assemblage or each environmental class in the priority area network. These sub-sets of taxa, assemblages, types of environments, etc. are the currently known and therefore measurable components of biodiversity.

Most research in conservation biology is aimed at managing populations in the wild. A widely used product of this research is population viability analysis, which tries to predict likely time to extinction under different management regimes. This is the 'how' of conservation biology. Our purpose is to ask the question, 'where should we locate priority areas in the first place and, therefore, where should this management take place?' The tools available for doing this fall into two distinct but interdependent classes. One encompasses the methods for acquiring suitable data sets, and the other comprises the methods for using those data sets to identify priority areas. Considerable effort has gone into improving the first class of methods in recent years, particularly in the field of computer technology. Much of the software and associated activities now familiar to conservation biologists and planners consist essentially of tools for compiling better data sets. Some well known examples include MASS (MacKinnon, 1994), BIOCLIM (Nix, 1986; Busby, 1991) and Conservation International's RAP (Rapid Assessment of Biodiversity Priority Areas). Improvements have been made in the display and manipulation of data using sophisticated Geographic Information Systems (GIS) and more are on the way, e.g. ERMS (Pressey et al., 1995). Investment in improving the second class of methods has been small in comparison, but is now picking up (e. g. Kirkpatrick, 1983; Ackery & Vane-Wright, 1984; Margules et al., 1988; Margules, 1989; Rebelo & Siegfried, 1990; Vane-Wright et al., 1991; Rebelo & Siegfried, 1992; Scott et al., 1993; Williams et al., 1993; Pressey et al., 1993; Faith & Walker, 1994). Both sets of tools are necessary but quite different. They are considered briefly in turn below and in detail in the forthcoming book.

(a)

Attributes	Sites													
	AB	C	D	EF	GHI	J	K	L	M	N	O	P		
1	1	1	1	1	1	1	1	1	1	1	1	1		
2			1	1	1	1	1	1	1	1	1	1		
3					1	1	1	1	1					
4					1	1	1	1						
5						1	1							
6							1							
7								1						
8									1	1	1	1		
9										1				
10											1			
11												1		
12													1	
13														1
14														1
15														1

(b)

Attributes	Sites															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
2	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
3	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
4	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0
5	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
9	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
10	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0
11	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

(c)

Attributes	Sites															
	AB	C	D	EF	GH	I	J	KL	MN	O	P					
1	1	10	25	12	18	21	31	11	17	12	10	6	5	4	0	0
2	0	0	100	19	15	17	13	31	23	34	15	9	71	0	0	0
3	0	0	0	0	0	1	197	31	182	114	45	0	0	0	0	0
4	0	0	0	0	0	12	14	16	15	14	0	0	0	0	0	0
5	0	0	0	0	0	0	176	230	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	1785	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	14	780	71	179	0	0	0	0	0	0
9	0	0	0	0	0	0	19	100	0	0	0	0	0	0	1	0
10	0	0	0	0	0	0	4	11	0	0	0	0	0	0	1	0
11	0	0	0	0	0	0	0	0	0	140	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	845	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	98	71	169	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	981	19
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	67	183

Figure 2. – Three areas x attributes matrices showing (a) presence only data; (b) presence/absence data; and (c) abundance data.

Data Sets

Data sets consist of objects and attributes. Objects for the present purpose are areas; geographically (or biogeographically) defined units of land or water. They may be large or small and regular or irregular. Grid cells, catchments, tenure classes and habitat patches are some of the different kinds of areas used in later examples. Attributes are the properties of areas. They may be taxa or the characters they represent, or they may be more heterogeneous entities such as assemblages or environmental classes. Data sets should convey a consistent level of detail across the localities, biomes or countries they cover because the identification of biodiversity priority areas requires a comparison across all such regions. This means that they will have to be derived from some set or sets of raw data, involving some form of raw data analysis. The analysis can include one or more of the following: classification of environmental variables; classification of biological records to derive, for example, species assemblages; and the estimation of wider spatial distribution patterns of species or assemblages with statistical or empirical models relating records of occurrence to environmental variables.

Information about areas and attributes is most conveniently recorded and stored in an 'areas by attributes' matrix. Attributes themselves can have different states. Figure 2 depicts three areas by attribute matrices. One (Fig. 2a) contains attributes of the 'presence only' kind. Attributes such as species have been recorded as present in some areas, but there is no indication of abundance or extent, and the lack of a recorded presence within other areas does not imply absence. Rather, it means that it is not known whether the attribute occurs there or not. The second matrix (Fig. 2b) contains 'presence/absence' attributes. In this case the absences are real within the limits of sampling intensity, meaning that the attributes were looked for, recorded as present where they were found and recorded as absent where they were not. The third matrix (Fig. 2c) contains estimates of abundance or extent, as well as absences. The methods for identifying priority areas (section "Identifying Biodiversity Priority Areas" below) can be applied to data sets with all three kinds of attributes with, successively, more confidence in the results. Unfortunately, almost all records of taxa are of the presence only kind. Most field records have been collected opportunistically, and the species collected are often the ones of interest to the collector. Figure 3 is a map of koala records from part of northern coastal New South Wales, Australia, showing how those records closely map the road network (from Margules & Austin, 1994). From this set of records, it is not possible to define the range of this species in this

area because there are few, if any, records of where it was looked for but not found. More systematic data collection methods have to be devised and implemented (see also Gillison & Brewer, 1985; Austin & Heyligers, 1989; 1991; Margules & Austin, 1994). In the meantime, the best use has to be made of existing data, even if field records are geographically biased and incomplete. There are techniques available to estimate spatial distribution patterns from presence only data and there are techniques for estimating underlying character difference among taxa. Both add value to existing data sets.

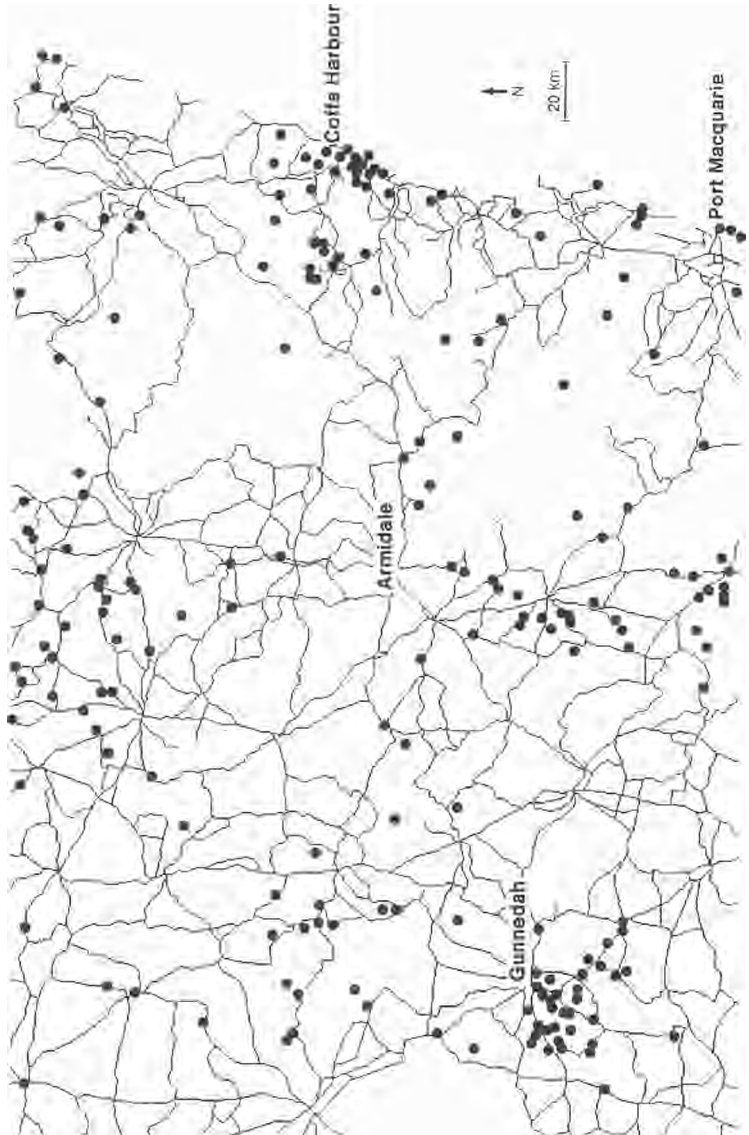


Figure 3. — A map of Koala records from part of northern coastal New South Wales, Australia, showing how the records closely follow roads. — Reproduced from Margules & Austin (1994a), with permission of the Royal Society of London.

Biodiversity Surrogates

The task of discovering, naming and then determining the systematic affinities of all species is daunting. Scientific names have been given to approximately 1.4 million species of plants, animals and micro-organisms (Wilson & Peters, 1988; Ehrlich & Wilson, 1991), but this is only a fraction of all species. Estimates of arthropod diversity in tropical forests alone range from about 7-80 million (Erwin, 1982; 1983; Stork, 1988), and knowledge of other invertebrate phyla is even poorer. Estimates have been made that if the collection and description of new species was to continue at the current rate, using traditional methods, it would take several thousand years to catalogue the world's biodiversity (e. g. Soulé, 1990) and in fact the rate is slowing because funding for taxonomy has declined (e. g. Stork & Gaston, 1990; Whitehead, 1990).

Urgency has led to the development of methods for rapid biodiversity assessment. The idea is that semi-professionals, variously referred to as apprentice curators (e. g. Sandlund, 1991) or biodiversity technicians (Oliver & Beattie, 1993), receive only basic training in field biology and systematics. They make field collections which are then sorted into broad taxonomic groups and morpho-species or recognisable taxonomic units (Oliver & Beattie, 1993). In this way rapid estimates of the total biological diversity at particular sites or over particular areas can be made.

The best developed programme is in Costa Rica, where the goal is to obtain an inventory of Costa Rica's biodiversity by the year 2000 (Janzen, 1991). The energy and commitment of those involved in the Costa Rican enterprise (see Gamez, 1991; Sandlund, 1991; Hovore, 1991; Janzen, 1991; and Wille, 1993, for comprehensive accounts) may well see it through and it may, in time, prove to be a model for other countries. Oliver & Beattie (1993) offer support with their finding that with only basic training biodiversity technicians estimated to within 13 % the actual number of spider species, to within 6 % the actual number of ants, to within 38 % the actual number of polychaetes, and to within 1 % the actual number of mosses, in samples from Australia. However, such approaches raise a variety of problems and their adequacy is questionable (Cranston & Hillman, 1992).

Even if Costa Rica reaches its goal by the year 2000 and even if biodiversity technicians can be enlisted and trained at a fast rate, the likelihood that approximate inventories will be available for most parts of the world in the short term, say, 20 to 50 years, seems remote. Even when inventories do become available they will be catalogues or lists of species or, far less helpful, merely estimates of numbers of taxa from particular locations. There is a lack of identity across samples from different areas so they cannot be compared validly. Wider spatial distribution patterns will still have to be estimated (i.e. those raw data would still have to be analysed using

spatial modelling techniques) before they could form an adequate data set for identifying biodiversity priority areas. In the short to medium term, only groups of taxa representing a very small proportion of total biodiversity will be available for priority area identification.

Since complete inventories are not a practical option, yet land use change is proceeding apace, some measurable biodiversity surrogate is required. Realistically, there are three kinds available: sub-sets of taxa or higher taxa, assemblages, and environmental variables or classes. It is not possible at this stage to nominate one as better than the others because there are valid arguments, summarised below, for and against each of them. In reality it seems likely that some combination will be used because the data available will normally come from a variety of sources.

Taxa

Although there is disagreement among biologists about the definition of species, most people recognise the term and think they understand it. Species are usually the units with which diversity has been measured (Vane-Wright, 1992). Higher taxa may also be used if a relationship between the distribution patterns of higher taxa and the distribution patterns of species can be demonstrated (Williams et al., 1994). It would be cheaper and easier to identify samples at higher taxon levels (Williams & Gaston, 1994). In the short to medium term, there may be little choice as to the sub-set of taxa, because it depends on available data and available experts. However, if there is the opportunity to choose, then consideration should be given to both focal taxa (those we have good information about and which are taxonomically tractable such as birds and vascular plants), and target taxa (*sensu* Kremen, 1992 — those that can be demonstrated to be better than average indicators of a wider range of biodiversity).

Most taxa remain undescribed and even of the taxa that are known, only a small sub-set is sufficiently well studied, both in terms of taxonomic status and geographic distribution, to be used to identify biodiversity priority areas. Unfortunately, there is no evidence that sub-sets of taxa represent biological diversity as a whole. Vane-Wright (1978) pointed out that, despite the coevolution theory for butterflies and plants, overall plant diversity was a poor predictor of butterfly diversity on a global scale. Majer (1983) showed that variation in plant diversity accounted for only 24 % of the variation in ant diversity in part of Western Australia. Yen (1987) found no correlation between the number of vertebrate species and the number of beetle species and further, that neither beetle nor vertebrate communities corresponded to plant communities in south-eastern Australia. Prendergast et al. (1994) showed only partial correspondence between areas rich in butterflies, dragonflies, liverworts, aquatic plants and breed-

ing birds in the U.K. It seems unlikely that priority areas identified using one or a few taxonomic groups as surrogates will adequately represent biodiversity as a whole, even though such analyses are valuable for action plans centred on particular groups, such as birds, for example.

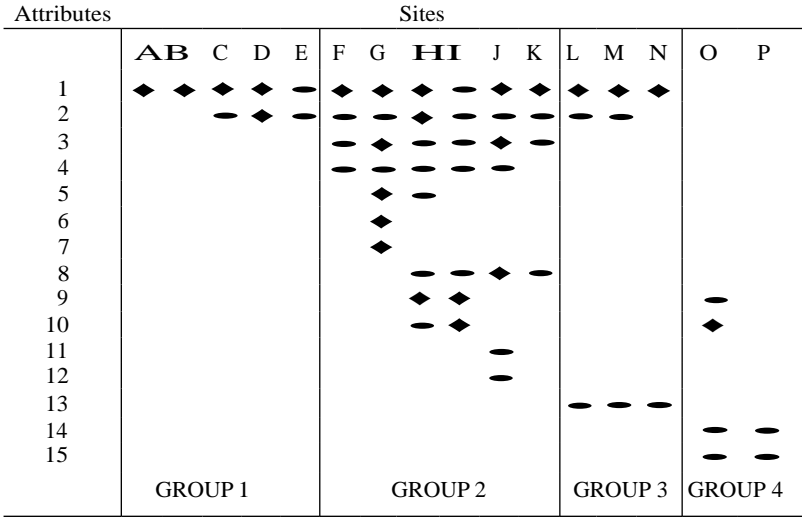


Figure 4. — Four groups of areas that might be identified using numerical clustering, based on shared attributes.

Assemblages

The term assemblages is used here generically to cover a range of ill-defined classifications such as community, association, habitat type, etc. They are generalised entities more heterogeneous than taxa. Taxa are distributed patchily within them and may only be present at some places and at some times. Assemblages can be subjectively derived using a small number of dominant or prominent species or they can be produced with numerical pattern analysis techniques.

Figure 4 is one classification that might result from a numerical pattern analysis of the data set illustrated in Fig. 2. Four classes have been recognised based on the attributes they have in common. Areas O and P have two attributes in common not shared by any other areas. Areas L, M and N have one attribute in common not shared by any other areas. Areas F, G, H, I, J and K all have at least three attributes in common and, although two of those are shared by some other areas, they also share a number of other attributes in various combinations. Areas A, B, C, D and E share one attribute also shared by most other sites, but what they have in common is the absence of most other attributes. This class illustrates one of the dangers of using classes as surrogates for biodiversity. It contributes nothing to the representation of the data set in Fig. 4 and by representing this particular class in a priority area, the opportunity to represent more of another class with more attributes might be foregone. In real data sets, areas and attributes can number in the order of thousands and classification (or ordination) can help simplify such complex multi-variate data and help reveal underlying trends. Basic texts on these kinds of analyses with a biological emphasis include Clifford & Stephenson (1975), Williams (1976) and Gauch (1982).

Assemblages represent various alternative combinations of species and the interactions between them and, therefore, more ecological complexity than individual taxa. Larger organisms such as vascular plants and vertebrates, most often used to delineate assemblages, are nested ecologically within interactions between smaller organisms such as nematodes, arthropods, fungi, protozoa and bacteria, and they have diminutive radiations in comparison (McKenzie et al., 1989). On the other hand, protecting a single area as a representation of an assemblage is likely to miss some species (Presley, 1994a) and some ecological complexity because it may be impossible to judge whether a given part of an assemblage is an adequate representation of the whole.

Environments

Environment is also a generic term covering land classifications based primarily on physical and climatic variables, numerical or intuitive, which

may or may not incorporate some biotic variables such as vegetation. Land systems (Christian & Stewart, 1968) are examples of intuitive classifications, while environmental domains (Richards et al., 1990; Belbin, 1993) are examples of numerical classifications. Environmental variables may also be used, unclassified, to estimate unmapped species distribution patterns (Walker & Faith, 1993). Different kinds of environments are assumed to support different sets of species (with some overlap) and have been used at broad scales as biodiversity surrogates (e.g. Mackey et al., 1989; Richards et al., 1990; Belbin, 1993).

There is strong theoretical support for the use of environments as biodiversity surrogates, which can be summarised as follows: each species has a unique distribution within environmental space determined by its genetic make-up and its physiological requirements. This distribution is, in turn, constrained by ecological interactions with other species. This is the concept of the niche (Hutchinson, 1958). Plant ecologists use the term "individualistic continuum" for essentially the same concept (Austin 1985). Species respond individually in, say, abundance or frequency, to resource gradients, and that response is constrained by interactions with other species. The implications are threefold: each species occupies a unique niche not readily predicted from that of other species (i.e. there is little overlap in environmental space); therefore, species distribution patterns are most accurately measured in multi-dimensional environmental space and only then translated to geographic space; the resultant spatial pattern shows high or dense populations in scattered locations representing most favourable habitat (or mix of environmental variables), and lower, more sparse populations in areas of more marginal habitat.

Thus, geographic distribution patterns can be linked to variation in the environment. Whittaker (e.g. 1956; 1960), Perring (e.g. 1958; 1959), Austin et al. (1984) and Austin et al. (1990), among others, provide empirical support. Nix (1982; 1986) has argued that for many purposes, including estimating the spatial distribution patterns of taxa, complete niche specification is unnecessary and that in most cases, five regimes, namely solar radiation, temperature, moisture, mineral nutrients and other components of the biota, are sufficient.

A network of priority areas representing the range of environmental combinations in a region is likely to encompass unknown species and known species with unmapped distribution patterns. Furthermore, the data needed to delineate environments (e. g. climatic data, geology maps, etc.) are more widely available than unbiased biological data and are often available at a consistent level of detail across wide geographic areas. On the other hand, as is the case with assemblages, protecting a single area as a representation of an environment is likely to miss some species because it

is not clear what an adequate representation might be. Similarly, the relationships between environmental classes and the distribution and abundance patterns of taxa are difficult to quantify, and some species may require a combination of environmental variables not recognised by a classification (Pressey, 1994a).

Combinations of surrogates

Taking into account the limitations on current knowledge, the limited resources for acquiring new data and the goal of adequately representing each surrogate, it seems likely that in practice some combination of these surrogates will be most widely applicable. In many localities, some data on the distributions of taxa are available but at an inconsistent level of detail and geographically biased. More usually, at least some environmental data are available at a consistent level of detail and it may be that assemblages have been mapped as, for example, vegetation or habitat types. A rational way to proceed in such cases would be to represent each environment or assemblage, overlay available distribution maps of taxa to see which, if any, were still not represented, and add areas to complete the representation (e.g. Nicholls & Margules, 1993). Alternatively, the geographic locations of selected taxa, such as rare or vulnerable species, could be used as seed points around which to build up a representation of each environment.

Collecting New Data

It may be necessary or desirable to collect new biological data. If the resources are available for doing so, then the most effective use should be made of those resources and any new collecting activities should provide data that can be analysed to maximise the information gained. In particular, new data should be collected in a way that facilitates accurate estimation of the spatial distribution patterns of species. This can be achieved with the following protocol: a conceptual framework, based on current ecological theory; field survey design principles based explicitly on the conceptual framework for locating field sample sites; a rationale for deciding which measurements should be made at field sample sites in addition to records of the target species; and appropriate analytical methods for estimating wider spatial distribution patterns from the point records that field sample sites represent (Margules & Austin, 1994). One chapter in the book is devoted to collecting new data and will consider each of these needs, covering theoretical, statistical and practical issues in describing some recent advances in the design of biological surveys and the analysis of survey data (see also Austin & Heyligers, 1989; 1991; Nicholls, 1989).

Summary of Data Requirements

Biodiversity surrogates may be taxa (e.g. species), species assemblages or environmental classes or variables, or they may be combinations of these. Compiling a data set is a process that includes both acquiring relevant raw data and, in most cases, analysing those data (classification, ordination and/or mapping) so that they are in a form suitable for identifying biodiversity priority areas. Raw biological data are records of the geographic locations of taxa, which may be available from previous collecting expeditions or surveys, or collected during new surveys. Raw environmental data may be extracted, for example, from meteorological records, or perhaps from existing thematic maps of geology, soils etc. Although thematic maps depict classes, they can be treated as raw data for the purpose at hand.

For the analysis of biological data there are two general options. One is to estimate the geographic distribution patterns of taxa, either intuitively, or by relating actual records of locations to environmental variables using predictive empirical models such as BIOCLIM (Nix, 1986; Busby, 1991) or statistical models such as GLMs (e.g. Nicholls; 1989). Empirical models are for data of the presence only kind. That is, there are records of where a taxon occurs but it is not known whether a non-occurrence is a true absence or simply a result of the taxon not having been looked for there. Almost all museum and herbarium data sets, the most common and widely available biological data source, are of this kind. Statistical models are appropriate for data of the presence/absence kind. That is, the absence of a species is the result of it having been looked for but not found.

The other option for analysis of biological data is to classify the data into assemblages and map the boundaries of assemblages. Classification can be done intuitively or with numerical methods, and mapping can be intuitive or it can utilise computer based empirical or statistical methods. Similarly, if the intention is to use environmental classes, classification can be intuitive or numerical and mapping can be manual or computer based.

Whether it is biological, environmental or a combination of both, the end result is a data set, either in raw form or derived from raw data records, that contains maps, on paper or in electronic form, of the chosen biodiversity surrogates. This data set can then be used, with the methods summarised below and detailed in the forthcoming book, to identify biodiversity priority areas.

Identifying Biodiversity Priority Areas

Biodiversity priority areas should, collectively, represent the biodiversity of the locality or region they are situated in; that is, they should encompass all of the attributes in the data set. Effective protection need not necessarily require formal reservation, because in some cases it may be possible to treat areas as protected if current land use is compatible and likely to continue. Methods for identifying priority areas are only one aspect of overall biological conservation planning and management.

In the past, parks and reserves, areas currently protecting components of biodiversity, have been set aside primarily for reasons other than the representation of biological diversity. The earliest National Parks, e.g. Yellowstone in the USA and Royal, near Sydney, Australia, were chosen for their outstanding natural features and beauty. Many areas throughout the world continue to be set aside for similar reasons or, for example, because they protect particular rare species or wilderness areas. The most common reason, however, appears to be that the land concerned was of little use for commercial exploitation or human habitation (Runte, 1979; Pressey, 1994b). Thus, in general, reserve selection has tended to be opportunistic, *ad hoc*, or in response to some perceived external threat. This has had three unfortunate results. Firstly, the biodiversity (taxa, assemblages, environments) most in need of strict reservation is not protected. Consequently, limited conservation resources have been used inefficiently, in that current protected areas protect relatively few attributes. Thirdly, therefore, there is now a very uneven representation of biodiversity in existing reserves (Pressey et al., 1993).

Scoring and ranking procedures were developed in an attempt to make priority setting more systematic. In these procedures, multiple criteria, e. g. diversity, rarity, naturalness and size, among others, are given scores, the scores are combined and candidate areas are ranked with highest priority going to the area with the highest score. Many studies have reviewed these procedures or the criteria used (e. g. Margules & Usher, 1981; Margules 1986; Usher, 1986) but it was not until 1989 that Pressey & Nicholls (1989) examined their efficiency in achieving the goal of full representation of natural features. In summary, they found that selecting areas from the top ranked down, based on a variety of different multi-criteria scores, require at least a fifth, but in most cases more than half, of all areas if full representation was to be achieved. Application of scoring and ranking procedures does not improve efficiency greatly over *ad hoc* representation.

Four principles

The selection methods to be described in the book are designed to help remedy current uneven representation and to promote efficiency. They are based on four principles: vulnerability, complementarity, flexibility and irreplaceability, summarised below. The methods are efficient and explicit. Efficiency is needed because the amount of land or water realistically available primarily for biodiversity protection is limited. The real prospect exists that the upper limit will be reached well before biodiversity is adequately represented. It is important that the methods be explicit for two reasons. First, for the results to be independently verifiable they must be repeatable. Second, the priority area network so identified can be justified more easily and defended more readily (Margules et al., 1994).

Vulnerability

Some ecosystems and the biota they contain are more vulnerable to threatening processes than others. Fertile soils and good rainfall are conducive to agricultural production, for example. Similarly, some species cope with impacts such as habitat fragmentation, grazing, etc. well, being favoured by the changed conditions, while others suffer a reduction in abundance and a contraction of range. In many cases it is possible to predict which kinds of habitats or ecosystems are most likely to be exploited and in some cases it is possible to predict which species will cope well with exploitation of their habitat and which species won't.

This kind of information on vulnerability or threat can be used to help set the goals of a priority area selection procedure. Because resources for conservation planning are limited, not all biomes, parts of countries, countries or regions can be dealt with equally or at the same time. Priority for identifying priority area networks should be assigned to places that are vulnerable to threatening process such as land clearing for agriculture, and the goal might be to represent all species that are vulnerable to threatening processes, rather than all species willy-nilly, in which case the data set being used would contain only those species. One chapter of the forthcoming book is devoted to vulnerability and goal setting.

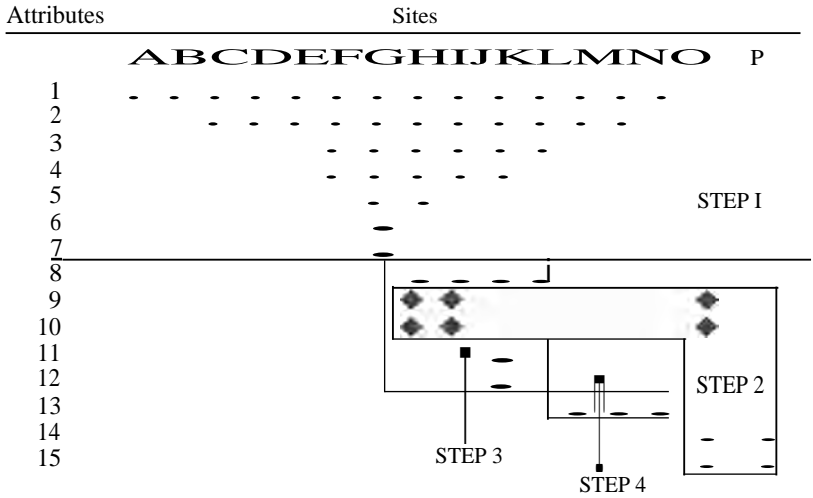


Figure 5. — The species represented at each step in an application of complementarity.

Area G, selected at the first step (see text) represents species 1-7.

Area O, selected at the second step, adds species 9, 10, 14 and 15.

Area J, selected next, adds species 8, 11 and 12.

At the fourth step, any one of areas L, M or N would add species 13.

Complementarity

The selection of biodiversity priority areas has to proceed from the goal of representing all attributes in the data base and not be side-tracked by other equally legitimate but different goals, such as the preservation of natural scenery or wilderness areas. It follows from this goal that any new areas added to an existing protected area network should contribute new attributes (unless all of them are already represented). This common sense observation reflects the principle of complementarity. Priority areas should complement one another in terms of the attributes they contain; the characters, taxa, assemblages, environments, etc. It follows that an area contributing most to completing a full complement will not necessarily be the richest area (which is, in fact, often the case). This is why ranking procedures, such as selecting a sub-set of richest areas, are often so inefficient. They fail to take account of spatial heterogeneity and the turnover in species (or other attributes) from area to area.

Complementarity is a property of the areas x attributes matrix. It is a measure of the extent to which an area, or set of areas, contributes unrepresented attributes to an existing set of areas (Faith, 1994). Figure 5 is another representation of the data matrix shown in Figs 2 and 4. There is a total of 15 species in the matrix in Figure 5. Area G has two unique species and five others shared by one or more other areas. Imagine area G has been identified as a biodiversity priority area, which seems likely as it has two unique species. Seven of the 15 species are represented in area G. The remainder is the residual complement, comprising species 8 to 15. Area O contains four species from that unrepresented complement, more than any other area. If area O was added to area G as a second biodiversity priority area, 11 species would be represented, leaving a residual complement of just four. Area J contains three of those four. If area J was added to the network it would leave a residual complement of just one species, which could be represented by any one of areas L, M or N.

This illustrates an iterative heuristic procedure which measures the unrepresented complement in each area at each step and adds the area with the largest unrepresented complement until the total complement is represented (e.g. Kirkpatrick, 1983). A similar heuristic algorithm, which is explained in detail in the book, takes areas with the rarest species first and then adds areas with the rarest remaining unrepresented species until all are represented. Thus, area G would still be chosen first but J would be chosen second. They both have seven species and both have two unique species, but G contains one species (species 5) represented in only two areas, whereas the next rarest species in area J is represented in four areas altogether (species 8). The next choice would be between areas O and P which both have the rarest remaining species (species 14 and 15) and O

would be chosen because it contributes those two next rarest species plus two others not yet represented (species 9 and 10). Once again, the last unrepresented species (species 13) could be represented by any one of areas L, M or N. In this example the list of sites chosen is the same, but the order is different. Using other data sets, the lists might differ between the two algorithms.

Complementarity is very important because it leads to an efficient representation of biodiversity surrogates and, therefore, to an efficient use of limited conservation resources such as land (or water) and funds. Algorithms which incorporate complementarity procedures are much more efficient than *ad hoc* approaches and scoring and ranking approaches (Pressey & Nicholls, 1989; Pressey, 1994b).

Replaceability, Irreplaceability and Flexibility

Figure 5 also illustrates the principles of flexibility and irreplaceability. Areas G and J are irreplaceable because they contain unique species (species 6 and 7 and species 11 and 12 respectively). Areas L, M and N all contribute the same species to the full complement so they can be substituted for one another. They are replaceable. Area O is also replaceable, though less so than L, M or N. Area O contributes four species to the full complement. Those same four could not be contributed by any other single area, but area P plus either H or I could be substituted for O. These have been described as different levels of irreplaceability (e.g. Pressey et al., 1993). Areas G and J are globally irreplaceable. Area O is goal irreplaceable because the goal is to find the fewest areas that represent all species. It would cost an extra area to replace O. Areas L, N and M are all replaceable (in this case, each one with one of the other two).

The existence of replaceable areas, which may be rare in some cases but seem to be common in many data sets, facilitates negotiation with alternative competing land uses. All replaceable areas are negotiable, though some have associated costs, such as the extra area needed if O was not available. Irreplaceable areas are not negotiable because without them it would be impossible to achieve the goal of representing all attributes. The fate of irreplaceable areas is a matter of policy, not planning. They should form the core around which the rest of a priority area network is built up. Flexibility is a property of the network of areas. It arises because many areas can be substituted with one or more others. Flexibility refers to the different spatial arrangements of areas available to achieve the overall goal.

Priorities within Networks

Fully complementary priority area networks can be identified using heuristic iterative procedures. While the results may be close to optimal in the sense that a minimum or near minimum set of areas is identified that together represent all attributes, implementation in the real world may be difficult. Some areas may be unsuitable because, for example, they are degraded, or simply unavailable for compelling social, economic or political reasons. Flexibility in spatial configuration can help towards practical solutions, but even when pragmatic compromises have been made, not all preferred areas will have equal status. It is likely that priorities within the identified network will have to be set. The impacts of any threatening processes will affect both the timing of protection and the type of protection measure.

Areas that are threatened or more vulnerable to threatening processes in general would have a high priority, but it may be necessary to examine them closely before coming to any final decision. For example, consider a habitat remnant in cropland and a more remote area in rugged terrain. They occupy different environments and contribute different sets of taxa to the full complement but the habitat remnant is more vulnerable simply because of its location. If it was determined that the habitat remnant was seriously threatened, or that populations of taxa there had low probabilities of persistence unaided, then it might be accorded priority and scarce management resources might be allocated in an attempt to protect it. On the other hand, if the area occupied by the remnant was not irreplaceable, alternatives could be sought. Even if the remnant was irreplaceable, it is conceivable that a greater contribution to the overall conservation goal might be obtained by abandoning it and diverting scarce management resources elsewhere, particularly if it was assessed to have low viability even if aided on a large scale. However, it is better to have known in the first place which set of species the remnant contributed and whether it was flexible or irreplaceable, so that the trade-off between allocating management resources and sacrificing the goal of representing all attributes could be made on the basis of all possible information.

Summary

The problem addressed by the biodiversity 'Schwerpunkt' and developed in the forthcoming book is how to identify a sub-set of areas within a specified region which together represent as much as possible of the biological diversity of that region. Such areas are called biodiversity priority areas. This is an immensely practical problem soluble only through both theoret-

ical and empirical investigation. Because total biodiversity as we have interpreted it is not directly measurable, it will only ever be possible to represent surrogates; sub-sets of taxa, assemblages, and/or environments. Two classes of methods are required. The first represents methods for deriving suitable data sets; the second, methods for using those data to identify priority areas. Raw data such as field records of the locations of taxa can be treated in various ways to improve their quality, such as modelling wider spatial distribution patterns and estimating character diversity from phylogenetic patterns. New data should be collected in a more systematic and cost-effective way than they have been in the past, enabling more accurate statistical models of spatial distribution patterns. The methods described for identifying priority areas are efficient and explicit heuristic algorithms. They employ the principles of vulnerability, complementarity, flexibility and irreplaceability. Their goal is to represent all of the attributes in the available data set in a minimum or near minimum set of areas, which should be the starting point for biodiversity conservation planning. Preferred biodiversity priority areas can then be determined via an exploration of flexibility and possible alternative configurations, and an assessment of the costs associated with controlled departures from the most efficient representation, to facilitate negotiation with competing land uses.

Biodiversity priority areas are necessary but not sufficient for the long-term maintenance of biological diversity. The methods and procedures to be described in the book are some of the tools needed by conservation biologists to help them identify priority areas. Other tools, such as planning procedures incorporating competing land uses, and management prescriptions to minimise the risk of extinction of local populations, can then be focused more sharply on the places and populations in greatest need.

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