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Beyond Opportunism: Key Principles For Systematic Reserve Selection*

The intention and practice of conservation reserve selection are different. A major reason for establishing systems of conservation reserves is to sustain biological diversity. This involves protecting examples of as many natural features, e.g. species, communities or environments, as possible. In reality, however, new reserves have rarely been dedicated for their representation of features. Furthermore, the opportunism that has characterized the development of reserve systems can actually jeopardize the representation of all features in reserves through the inefficient allocation of limited resources. More systematic approaches are essential if reserves are to play their role in protecting biodiversity. Some basic principles for conservation planning are emerging from recent systematic procedures for reserve selection. These principles will help to link intention and practice.

The conservation of biodiversity is a major challenge for the forthcoming decades and a wide array of approaches will be necessary to address it. These include research, education, *ex situ* collections, economic incentives and the establishment of protected areas. Of this variety of approaches, *in situ* protection will play the most crucial role^{2,3}.

The term 'reserves' is used here to describe areas under a range of *in situ* protection measures, from wilderness to managed extraction of resources for commerce or subsistence. Determining the boundaries of reserves has two aspects: design and location. Design criteria such as size, shape and connectedness have been widely discussed. The location of reserves, or reserve selection, is currently receiving increased attention and is the concern of this article.

Reserves are most likely to fulfil their critical role in conserving biodiversity if reserve systems become as representative as possible; that is, if they contain examples of as many elements of biodiversity as possible.

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This will partly depend on how well biodiversity can be measured for the purposes of conservation planning (see box at the end). It also depends heavily on how available data are used to make decisions on reservation. Representative reserve systems must be achieved with economic resources which are only a tiny fraction of those devoted to activities destructive of nature³. Moreover, the options for reservation are diminishing steadily as intact habitats are reduced and competition with alternative land uses increases.

New reserves must therefore be selected carefully so that limited resources are deployed most effectively. More importantly, reserve selection must do more than react to threats: land must be allocated to conservation at least as assertively as to competing uses, and conflicts must be resolved explicitly. These needs will not be met by the widely-used opportunistic approaches that have led to very uneven representation of natural features in reserve systems¹⁵ and do not stand up against well-argued cases for other land uses.

Recognition of these limitations has led to the development of systematic, explicit procedures for assigning conservation value and selecting reserves. The more recent of these have concentrated not on individual sites but on the problems of combining sites into representative networks. From this new perspective have emerged some fundamental principles for selecting reserves, principles that reflect the ways in which individual sites relate to one another as members of networks.

Three principles for selecting priority regions and regional reserves

The three principles discussed below concern reserves as a means of conserving biodiversity, although reserves also have other purposes in protecting scenic, recreational or inspirational values. Application of the principles requires an explicit statement of the representation target of a reserve network, which can be all or a subset of the features in a geographical area and any proportion of population size or geographical extent.

Complementarity

With limited options and resources for reservation, an intelligent strategy is to assess the content of any existing reserves and then to proceed in a stepwise fashion, selecting at each step the site that is most complementary in the features it contains. Iterative procedures emphasizing complementarity in selecting reserves have been devised independently at least four

times: twice in Australia^{16,17}, in Britain¹⁸ and in South Africa¹⁹, although the term was not coined until 1991¹³. The algorithms and selection of specific sites differ among the procedures described, but all demonstrate that the features of a region can be represented in a minimal or near-minimal set of sites if they are highly complementary.

Complementarity is closely related to the notion of efficiency, expressed by $1 - (x/t)$, where x is the number or area of sites needed to achieve a representation target and t is the total number or area of sites²⁰. High efficiency is therefore achieved with procedures that emphasize complementarity. Scoring procedures that neglect the complementarity of sites²¹ can be highly inefficient in delineating reserve networks²⁰, as can opportunistic reserve selection²²⁻²⁴.

Efficiency, and therefore complementarity, are very important because in most regions there is a limit, however ill-defined, to the land or water area which will be devoted to conservation. Efficient solutions to the problem of representing all features in an area are not only more defensible but also minimize the risk of reaching a ceiling of acceptable reserve area before all features are protected (Fig. 1).

Efficiency is highly dependent on the size of the geographical units used in the selection exercise and the indices of biodiversity used as targets for reserves. Large selection units requiring little or no amalgamation to produce viable reserves inevitably overrepresent some features and result in lower efficiencies to achieve the same target than very small units²⁷. Efficiency will also vary with identical selection units according to whether the target features are, for example, a few widespread and co-occurring vegetation types or many plant species including narrow endemics which rarely co-occur. In addition, if the selection units vary in size, numerical and areal efficiencies are likely to differ²⁰.

With these factors considered, efficiency can be used to demonstrate the relative effectiveness of alternative approaches to reserve selection. Thus, the numerical value of an iterative selection of all landscape types in semi-arid Australia was 0.969 compared to 0.786-0.078 for scoring procedures²⁰. In the Cape Floristic Region of South Africa, two iterative algorithms represented all Proteaceae species with efficiencies of 0.904 and 0.898 compared to 0.822 for a random selection, the high values being due to the clumped distribution of the species²⁴.

Flexibility

In most regions, there are many ways of combining sites to form representative networks of reserves. An example for a small data set (Table 1) shows that there is a minimum combination size (size = number of component sites) below which no combinations are representative. This is the

'minimum set' of sites which can be identified with procedures using the principle of complementarity.

An analysis of site combinations shows, -however, that there can be more than one minimum set — seven in the case of Table 1— and hundreds or thousands of potential reserve networks larger than the minimum. In large data sets, there will be many more representative combinations, although in practice the number of these alternative reserve networks will be strongly constrained by considering only those combinations which contain essential sites for conservation, defined in various ways, and exclude sites which are unsuitable as reserves.

The principle of flexibility refers to this diversity of potential networks and has implications for selection procedures. Procedures giving only one answer to the problem of representing all features in an area can be indispensable in indicating the requirements of representation targets and in comparative analyses. Nevertheless, for the design of a real network, the exploration of the flexibility inherent in reserve networks is important. The more alternative networks that can be appraised, the more likely the planner is to find one which is not only representative but also maximizes values of design and land suitability and/or minimizes costs. Achievement of these other objectives will probably lower the efficiency of representation. The assessment of alternative networks should therefore allow the planner to determine the extent to which this occurs.

The range of alternative networks can be partly explored by constraining iterative analyses (excluding or forcing the inclusion of sites) and comparing the results to those from other starting conditions. This is a useful adaptation to changes in the availability of sites as, for example, some are destroyed or offered for reservation. It can also quickly demonstrate the implications of acquiring particular areas of interest or building on the existing reserve system rather than exchanging present reserves for new areas. If an iterative analysis is constrained repeatedly and systematically and/or the alternative sites considered at certain steps of the algorithm are recorded, a larger subset of the representative combinations of sites can be generated²⁴. The CODA procedure (Conservation Options and Decisions Analysis)²⁷ is a more explicit way of exploring the flexibility of networks. It displays alternatives to selected sites and allows initial selections to be changed while calculating the degree to which targets for each feature have been achieved.

Flexibility arises from the non-unique occurrences of many indices of biodiversity. A critical implication of flexibility is that most reserve plans are fluid to some extent. Some component sites are fixed but others can be replaced. This variety of possible configurations gives scope for sensible resolutions of land use conflicts.

Irreplaceability

All sites occur with equal frequency when all possible combinations of a given size (number of component sites) are considered. This frequency is nC/t , where t is the total number of sites in the region, n is the size of combination and C is the total number of possible combinations of a given size (see Table 1). An important question for conservation planning is whether each site occurs with equal frequency in the set of representative combinations or alternative reserve networks (right hand column in Table 1). Sites actually occur with widely different frequencies in representative combinations. For example, at a combination size of seven in Table 1, there are 1150 representative combinations. In this set of potential reserve networks, sites are distributed in ten levels of frequency, from 11-100 %, with most sites occurring in relatively few combinations.

Frequencies of occurrence in representative combinations can be called levels of irreplaceability²⁸ with irreplaceability defined in two ways: (i) the potential contribution of a site to a reservation goal; and (ii) the extent to which the options for reservation are lost if the site is lost. Irreplaceability therefore provides a fundamental way of measuring the conservation value of any site.

For regional data sets with many sites, direct measurement of irreplaceability is impossible because of the vast numbers of possible combinations that would have to be generated and analysed. However, an accurate predictor of irreplaceability has been developed for small data sets which is probably also accurate for whole regions. The present predictor can be used to approximate levels of irreplaceability and display a 'landscape' of conservation value (Fig. 2).

Irreplaceability has also been approximated by displaying alternative results of iterative algorithms²⁴. This approach will certainly identify the unique sites with irreplaceabilities of 100 %, although several issues remain unresolved: its effectiveness in distinguishing lower levels of irreplaceability; the influence of the particular rules and measures employed; and the correspondence of the results with a combinatorial analysis (e.g. for Table 1), which is the most fundamental and accurate way of identifying the frequency of occurrence of sites in the optional networks.

Levels of irreplaceability such as those in Figure 2 can guide the design of whole reserve networks, with choices proceeding from the most to the least irreplaceable. They also provide a way of anticipating conservation value when decisions are necessary on individual sites or when real-world constraints force departures from an original network design. In conservation planning, the notion of a gradient of irreplaceability is also compatible with the more traditional concepts of sites which have outstand-

ing value for a variety of reasons — these sites can be regarded as equivalent to those with maximum quantitative irreplaceability.

Principles in practice

These three principles can be applied at different scales. On a broad scale, they can identify priority regions for conservation efforts in a global or national context. On a finer scale, within regions, they can determine the locations of sites comprising representative networks.

The big picture -- identifying priority regions

The WORLDMAP computer program¹³ identifies key regions for conserving the biodiversity of one or more taxonomic groups at global or national scales. Biodiversity is measured as a combination of the number of species or higher taxa in a region and the taxonomic differences between them⁷, although endemism measures are also supported. A critical aspect of the system is the implementation of the principle of complementarity. This is used to find a priority sequence of regions to represent all taxa by identifying the maximum increment of unrepresented biodiversity possible at each step (Fig. 3).

An important consideration is the degree to which areas prioritized for one taxonomic group are congruent with those for another. In general, they only partially coincide, so different distributional patterns of groups influence the priority order of regions and the number of complementary regions necessary to represent all taxa. Three direct solutions to the problem of assessing total diversity are being investigated: summation techniques for combining data from several, but ideally many, different groups; reliance on indicator groups, chosen either because they are well known²⁹ or because of demonstrated correlations³⁰; and the use of more inclusive taxa. Another major influence on the results of WORLDMAP is that, as regions are defined at broader scales, a greater proportion will be totally irreplaceable because more will have endemics.

Recent applications of WORLDMAP include analyses of Old World fruit bats and African antelopes for the IUCN Species Survival Commission and South American trees in collaboration with the Royal Botanic Gardens, Kew, UK. Future applications will also investigate the irreplaceability of regions for representing biotas.

A previous method for identifying global conservation priorities is the 'hotspots' approach using data on plant species. The IUCN study³¹ proposes two main criteria for choosing important regions — species richness and number of endemics — with several subsidiary criteria. Myers³² uses

two criteria — degree of endemism and severity of threat. There is no doubt that both studies have identified globally important areas for conservation, but the arbitrary selection of sites raises questions about which other critical areas would emerge from a more exhaustive compilation of data and more systematic analyses.

Another global approach has identified centres of endemism for birds²⁹. This improves on the 'hotspots' approach by systematically using data on about one quarter of bird species — those with total geographical ranges smaller than an arbitrary threshold. Other systematic assessments are underway at global or continental scales. Some are likely to be more effective than others, just as regional selection procedures differ in efficiencies (see above). Given the significance and urgency of global assessments of conservation priority, there is a pressing need to compare the alternative evaluation methods so that their implications for conserving biodiversity can be clearly understood.

The regional picture — selecting reserve networks

Once a priority region has been identified, the problem remains to delineate a network of reserves capable of representing all the features requiring protection. The principle of complementarity has been applied with several iterative analyses of regions in south-eastern Australia, for example in South Australia³³ and on the south coast of New South Wales³⁴. Another recent application has been in South Africa²⁴. Such analyses provide rapid indicative pictures of the minimum requirements for representative reserve networks and are valuable for comparing scenarios with different representation targets or with certain sites included or excluded.

The CODA procedure has applied both complementarity and flexibility to the South-East Forests of New South Wales to find a network of sites which represent a minimum percentage area of all environments, as well as occurrences of rare species and other important features²⁷. Irreplaceability has only recently been tested on data from the Western Division of New South Wales²⁸, but its potential value in planning applications is established. Extensive trials are underway to validate the present predictions of irreplaceability levels for large data sets and to develop models for a wider variety of reservation goals.

Because regional methodologies differ not only in the configuration and content of the resultant reserve networks but also in the likelihood of achieving reservation goals²⁰, comparative trials are also desirable at this scale.

The way ahead

Application of the principles of complementarity, flexibility and irreplaceability will maximize the chances of achieving representative networks of reserves — something that many scientists and conservationists regard as an important, if difficult, goal. This benefit will come from increased effectiveness of planning that employs these principles and an improved ability to lobby and negotiate using systematic, defensible and flexible reserve plans.

In actual planning exercises, these principles will have to be applied with due consideration of other factors, such as design criteria which might determine the viability of reserved populations. At the selection stage, as much information as possible is needed on the areas and combinations of habitats required by certain species and on the existing and future impacts of natural disturbances and extractive land uses on the proposed reserves. The definition of 'representative' needs to be extended to cover not only examples of land types or populations of species, but also the spatial and temporal dynamics addressed by landscape ecology and metapopulation studies.

Priorities will also have to be adjusted on a global scale according to the apparent threats to regions¹⁴ and, on regional scales, in response to threats and differences in the most appropriate form of protection. The success of reserve location, design and management will have to be measured by monitoring the features and qualities for which the reserves are initially dedicated.

Improved procedures are being developed to apply the three key principles outlined here, and trials are underway on a wide variety of data sets. While ideas on each of the principles are being refined, work is also proceeding to integrate their application at a range of scales in Australia, Britain, South Africa, Uganda, South East Asia and South America.

Definitions of biodiversity and their use in reserve selection

There are several ways of defining biodiversity, which is itself a rubric to cover all of nature's variety. For any measure of diversity to be useful for conservation evaluation, it should be able to represent both alpha, or local, diversity and beta diversity — variety among areas (gamma diversity at larger spatial scales) .

One of the simplest measures of diversity is species richness, a count of the number of species⁴. Ecologists interested in community structure have also included the relative abundances of species in composite measures. More appropriate measures of ecological diversity would represent the functional diversity of what the species do^{3,54} although sufficiently detailed information is likely to be very difficult to obtain for large numbers of species.

Another approach to diversity is to measure the variety or pattern of taxonomic differences among the organisms themselves. Biological classifications, of differing quality, are available for all groups of organisms to summarize these differences and new taxonomic diversity measures are able to cater for a broad range of data qualities? 1a

Regardless of definition, conservation planning requires indices of biodiversity to be distinguished, labelled and related to specific areas. These tasks therefore become central problems in the conservation of features such as species¹¹ and communities¹².

Different indices vary in utility at different scales. For example, taxonomic richness on a global scale can focus attention on priority regions for individual groups of organisms¹³ but, on the local scale, the density of this information is generally insufficient for decisions on actual reserve boundaries. Some indices, such as DNA variation within species, will remain largely inaccessible. Similarly, the sheer number of living organisms will preclude complete enumeration and geographic referencing before crucial conservation decisions have been implemented¹⁴.

The practice of conservation therefore uses various approximations of biodiversity depending on the available data. Aspects of biodiversity which are not considered directly will be protected only incidentally, if at all.

Table 1. Possible and representative combinations of sites for a range of combination sizes' in an environmental province in western New South Wales, Australia^b

Combination size (no. sites)	Possible combinations	Representative combinations ^a
1	24	
2	276	
3	2 024	
4	10 626	
5	42 504	7
6	134 596	134
7	346 104	1 150
8	735 471	5 980
9	1 307 504	21 457
10	1 961 256	57 043

^a Combination size is the number of component sites.

^b The province (4CB; Ref. 25) has a total area of 3820 square km, comprises 24 pastoral holdings and contains 17 land systems'.

Representative combinations are those which represent every land system at least once.

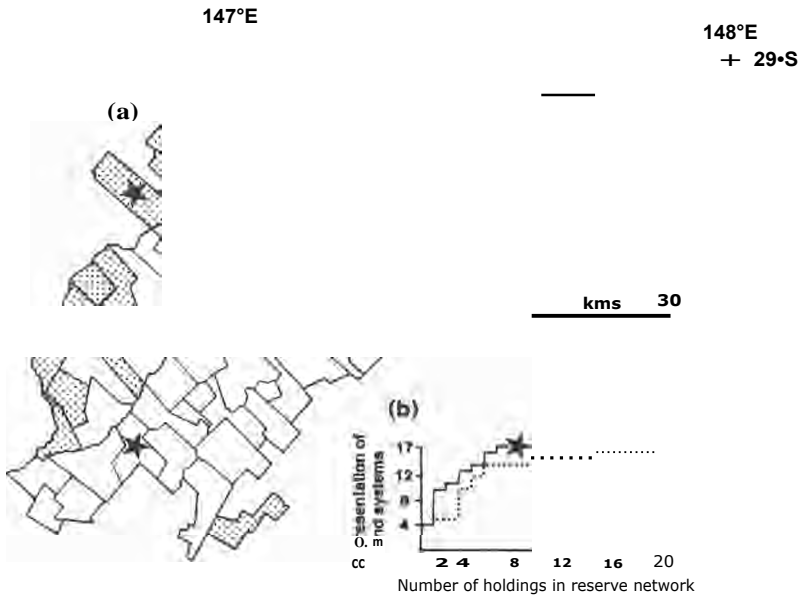


Figure 1

(a) An environmental province in the Western Division of New South Wales (Province IAC)²⁵ consisting of 95 pastoral holdings with a total area of 6625 square km (the northern edge is the Queensland border); the map shows two indicative sets of holdings needed to represent all land systems²⁶ in the region at least once: (i) stars indicate a minimum set identified by a simple algorithm which selects sites with unique land systems and then proceeds stepwise to select the site with the rarest unrepresented land system; if there is a choice, it selects the site which adds the most unrepresented land systems; (ii) shading indicates the set required if all holdings are scored according to the average rarity of the land systems they contain (in terms of frequency within the region) and reserved in order of score; note that reservation in order of scores for richness (number of land systems) requires 87 sites (92 % of total) to represent all land systems.

(b) Cumulative representation of land systems if holdings are added to a reserve network according to minimum set selection (stars) and scoring (shading).

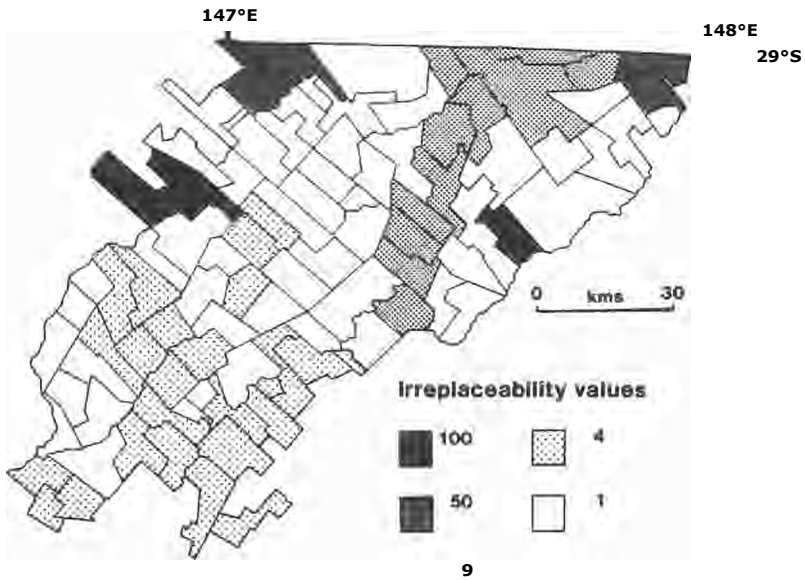


Figure 2

A 'landscape' of conservation value for the environmental region in Fig. 1 derived from predicted irreplaceability levels²⁸.

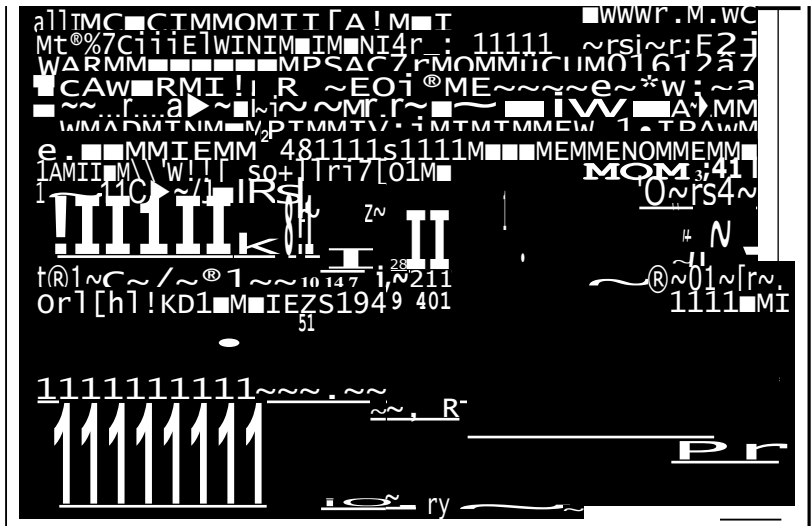


Figure 3
 WORLDMAP¹³ output showing the sequence of 58 priority regions needed to represent efficiently all the owl (*Strigiformes*) species of the world.

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