The principle of complementarity in the design of reserve networks to conserve biodiversity: a preliminary history

JAMES JUSTUS and SAHOTRA SARKAR*

Biodiversity and Biocultural Conservation Laboratory, Program in the History and Philosophy of Science, University of Texas at Austin, Waggener 316, Austin, TX 78712-1180, USA

**Corresponding author (Fax, 512-471-4806; Email, sarkar@mail.utexas.edu)*

Explicit, quantitative procedures for identifying biodiversity priority areas are replacing the often ad hoc procedures used in the past to design networks of reserves to conserve biodiversity. This change facilitates more informed choices by policy makers, and thereby makes possible greater satisfaction of conservation goals with increased efficiency. A key feature of these procedures is the use of the principle of complementarity, which ensures that areas chosen for inclusion in a reserve network complement those already selected. This paper sketches the historical development of the principle of complementarity and its applications in practical policy decisions. In the first section a brief account is given of the circumstances out of which concerns for more explicit systematic methods for the assessment of the conservation value of different areas arose. The second section details the emergence of the principle of complementarity in four independent contexts. The third section consists of case studies of the use of the principle of complementarity to make practical policy decisions in Australasia, Africa, and America. In the last section, an assessment is made of the extent to which the principle of complementarity transformed the practice of conservation biology by introducing new standards of rigor and explicitness.

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1. Introduction

On 4 September 1970 the British Association held a symposium at Durham on "Conservation and Productivity" as part of the European Conservation Year (Poore 1971). Poore, President of the Nature Conservancy (UK), introduced the session by noting the many different ways in which the word "conservation" can be used:

> "Conservation is a word which has come to be used in many senses. I take it to mean the husbandry of resources – use in such a way that the potential of the resource remains unimpaired. But the conservation of one resource may compete with the conservation of another. . . . Conservation of all resources . . . must, therefore, include an element . . . of choice" (Poore 1971, p. 291).

Though the main focus of the symposium was on the potential conflicts between various land use options, the most influential contribution was a paper by Ratcliffe (1971) that laid out criteria for the comparative evaluation and selection of sites to be targeted for conservation. Ratcliffe envisioned a three-stage selection process: (i) field surveys, (ii) the application of explicitly agreed criteria for the site prioritization, and (iii) a final choice of a set of high-quality sites. For the second stage he listed nine criteria. What makes Ratcliffe's discussion historically important, and is one reason why this paper begins with it, is that it marks the first time that the prioritization of sites was required to be based on explicit

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public criteria rather than intuitive judgments. It began the transformation of the problem of biological reserve design to a technical problem from an intuitive one.

In 1977, Ratcliffe edited the two-volume Nature Conservancy (UK) report, *The Selection of Biological Sites of National Importance to Nature Conservation in Britain*, which identified 984 sites in Britain as worthy of conservation attention, primarily based on biological interest. He graded the sites into four categories on the basis of their presumed conservation importance: (i) sites of international or national importance; (ii) sites of similar, but slightly inferior, importance; (iii) sites of high regional importance; and (iv) sites of lower regional importance. This was done in accordance with his 1971 scheme, which thereby became the first set of explicit site evaluation criteria to be used on a large spatial scale in a practical policy-making context. Since the publication of *Conservation of Nature in England and Wales* (Ministry of Town and Country Planning 1947a) and *National Parks and the Conservation of Nature in Scotland* (Ministry of Town and Country Planning 1947b), nature conservation in Britain had been guided by an official policy that put a premium on safeguarding a number of "key areas". These were to represent adequately "the main types of community and kinds of wild plants and animals represented (in Britain), both common and rare, typical and unusual, as well as places which contain physical features of special or outstanding interest" [as quoted in Ratcliffe (1977) V 1, p. 3.]. While the concept of "key area" seems clear enough, "the actual process of choosing sites and compiling an adequate national sample of all major ecosystems", as Ratcliffe noted, "raise(d) some extremely complex and difficult problems, both conceptual and practical" (Ratcliffe 1977 V 1, p. 1). Before the 1977 report, sites were selected on a semi-intuitive basis, that is, whenever it seemed reasonable that a chosen site met the general objectives enshrined in policy.

In 1977 Ratcliffe analysed the second stage of the site selection process, the initial selection of sites on the basis of data, in much more detail than in 1971. He used ten criteria (only the last of which was new): (i) size – larger sites were to be preferred over smaller ones and "the concept of the 'viable unit' embodies the view that there is a minimum acceptable size for areas" (p. 7); (ii) diversity – this was interpreted as the richness of communities and species, "which are usually closely related and in turn depend largely on diversity of habitat" (p. 7); (iii) naturalness – this was implicitly defined by the claim that it "has been customary to use the term natural for vegetation or habitat which appears to be unmodified by human influence" (p. 7). Areas were classified as natural, semi-natural, or artificial; (iv) rarity – "the presence of even one rare species on a site gives it higher value than another comparable site with no rarities" (p. 8); (v) fragility – this was supposed to reflect the "sensitivity of habitats, communities and species to environmental change" (p. 8); fragility made the viability of even otherwise valuable sites doubtful; (vi) typicalness – this ensured that all species or other surrogates of a region were represented; (vii) recorded history – this was supposed to capture the belief that a well-kept scientific records made a site valuable; (viii) position in an ecological/geographical unit – this was reduced to an emphasis on the "contiguity of one site with a highly rated example of another formation" (p. 9); (ix) potential value – this was supposed to capture the possibility that good management may add to the value of a site; (x) intrinsic value: "(t)here is finally the awkward philosophical point that different kinds of organism do not rate equally in value because of bias in human interest, as regards number of people concerned" (p. 10); however, Ratcliffe explicitly emphasized the importance of saving less charismatic biological units. All ten criteria were not to be taken as being on a par with each other. Implicit in Ratcliffe's discussion is a partial hierarchy: intrinsic appeal has less weight than rarity, fragility is presumably not relevant unless a site is important for other reasons, and so on. What is striking about Ratcliffe's discussion is that these criteria were generally pragmatic: biological considerations were neither clearly distinguished from nor always explicitly preferred to sociopolitical ones.

Ratcliffe's scheme was articulated in the context of a growing concern for expanding nature reserve networks in the late 1960s, accompanied by a realization that it would not be economically feasible to conserve every site of biological interest. This situation underscored the importance of having explicit criteria for evaluating potential sites for selection. As noted earlier, it is precisely because it systematically does so that Ratcliffe's 1971 discussion and his 1977 two volume review of nature conservation in Britain are historically important. This growing concern for conservation reflected the increased rate of utilization of natural resources, particularly in the south, after the end of colonialism led to attempts at rapid industrialization and development. (A detailed social history of these developments remains to be written.) Ratcliffe was not alone in suggesting criteria for estimating biological conservation value. Between 1971 and 1978, seven other studies proposed the use of richness and/or diversity (including both species richness and habitat diversity) (Tubbs and Blackwood 1971; Tans 1974; Gehlbach 1975; Goldsmith 1975; Wright 1977; van der Ploeg and Vlijm 1978; Everett 1978); six suggested rarity (Tubbs and Blackwood 1971; Gehlbach 1975; Goldsmith 1975; Wright 1977; van der Ploeg and Vlijm 1978; Austin and Miller 1978); five proposed area (Tans 1974; Gehlbach 1975; Goldsmith 1975; van der

Ploeg and Vlijm 1978; Austin and Miller 1978); five worried about the threat of human impact (Tans 1974; Gehlbach 1975; Wright 1977; van der Ploeg and Vlijm 1978; Austin and Miller 1978); four explicitly suggested naturalness (Tans 1974; Gehlbach 1975; Wright 1977; Everett 1978); and four suggested representativeness or typicalness (Gehlbach 1975; Wright 1977; van der Ploeg and Vlijm 1978; Austin and Miller 1978; Everett 1978). Other criteria invoked in these proposals included scientific value, educational value, amenity value, recorded history, uniqueness, wildlife reservoir potential, ecological fragility, position in ecogeographical units, potential value, availability, replaceability, and management considerations (Margules and Usher 1981). Ratcliffe's scheme was the most comprehensive, besides being important as a tool of practical policy (as noted before).

These early efforts were reviewed by Margules and Usher (1981) who made a critical distinction between scientific and political criteria. This paved the way for reserve selection and design to become an applied natural science (say, on a par with forestry). Concentrating on the science, they arranged the scientific criteria into three categories: (i) criteria which could be assessed in one site visit (diversity and area); (ii) criteria which required extensive surveys for assessment (rarity, naturalness, and representativeness); and (iii) criteria which required case histories of sites for assessment (recorded history, potential value, and ecological fragility). Each of these categories progressively specified criteria which required more effort for assessment. Margules and Usher (1981) emphasized that case history data, often discarded after treatment for the purpose at hand, should always be preserved for future use. Political criteria are not completely irrelevant: they may "play an essential role in a final decision on conserving a site, a decision taken by government, councils or committees which are not composed of ecologists" (p. 104).

In the context of Margules and Usher's (1981) clear separation of political and scientific criteria for reserve selection, during the 1980s attempts to use only scientific criteria for prioritizing areas for potential inclusion in reserve networks became common practice. Planning gradually moved from an almost completely intuitive approach to an algorithmic one in which the criteria invoked were applied mechanically to remove any residue of intuitive judgment. This process was greatly aided by the increased availability and sophistication of microcomputers and, above all, by the development of Geographical Information System (GIS) during, roughly, the same period. Sarkar (2002) has argued that the development of GIS was the technological innovation that made a science of conservation biology possible. It marked a radical methodological innovation in the techniques of biological conservation.

With hindsight, it is possible to detect a conceptual tension throughout this period between: (i) representing in reserves the maximum number of species; and (ii) maintaining representative samples of a region, nation or biome's habitats or ecological communities and the species that characterize them. The second goal can be traced back directly to the UK Ministry of Town and Country Planning document (1974a) cited above. Although the two goals appear to have the same outcome – protecting the most possible species – one led to the use of species richness as a criterion of value, while the other led to complementarity. A crucial conceptual breakthrough was the realization that the use of species richness, led to the inefficient representation of the greatest number of species in reserve networks. For instance, two areas may both be very rich in species but contain the same set of species. If one of those areas is selected, then, if maximizing the total number of species protected is the goal, the next area to be selected should be the one that adds the most species that have not already been represented. Thus, the second area with highest richness should not be selected if it contained the same species as the first one selected. This is the principle of complementarity, which has led to a fundamental change in the design of reserve networks. This principle, obvious once stated, was independently discovered at least four times: twice in Australia, and once each in South Africa and the United Kingdom. Once explicitly stated, this principle is not only intuitively easy to grasp and use, but its advantages over the use of richness for the protection of the greatest number of species is also obvious. It is not surprising, then, that it rapidly became a staple of reserve network design. The idea that complementarity rather than richness should be used for iterative place selection probably was independently recognized almost simultaneously because, by this time, explicit targets of conservation (the number or percentage of surrogates) were routinely being set for conservation plans.

This paper is a preliminary history of the use of the principle of complementarity in reserve network design to date. Section 2 describes the history of the theoretical innovations involved in its use. These consisted of algorithms devised to incorporate the principle of complementarity in various ways. Section 3 is a preliminary – and almost certainly incomplete – history of the use of complementarity-based algorithms in practical policy making situations. Finally, section 4 discusses some criticisms of algorithmic approaches to biological reserve network design and responses to them.

2. Theory

The first use of complementarity was by Kirkpatrick (1983) in Tasmania (Australia). Kirkpatrick pointed out that a non-iterative procedure for place selection was inefficient insofar as it might not achieve adequate representation of biological features in the least possible set of sites. As he put it: "A major drawback of a listing of priority areas on the basis of a single application formula is that there is no guarantee that the priority area second or third on the list might not duplicate the species, communities or habitats that could successfully be preserved in the first priority area". (p. 128). In other words, the use of richness (the non-iterative formula Kirkpatrick had in mind) had to be replaced by an iterative procedure. Kirkpatrick provided such an iterative procedure, but its use of complementarity was only implicit. In Kirkpatrick's words:

> "Methods of data collection, weighting of attributes and formula selection are subjectively chosen to best fit the intensity, scope and purpose of the study. The first priority area revealed by the working of the formula is then chosen. It is then assumed that this first priority area will be preserved. Thus, species, communities or habitats that had high weightings because of their poor preservation status, and that are in the first priority reserve, will not merit the same weightings in the selection of a second priority reserve. Thus, in the first round the presence of a particular species may add 100 to the value of a site, because the species was totally unpreserved. In the second round the same species could only be worth 50 because it is now within one notional reserve. If this species also occurs in the second priority area, its worth in the third round could be assessed as zero. Thus, the site scores are adjusted at each stage of the analysis by adjusting the weighting of attributes on the assumption that the higher priority areas will be preserved, and this iterative process continues until all species, communities, or habitats are notionally preserved to a predetermined adequate level" (p. 128).

This procedure does not fully reject the use of richness. The number of different species at a site enters into the computation, though the weight given to each species declines as its representation in the selected sites increases. It is this decline in weight that implicitly invokes complementarity.

Kirkpatrick applied this iterative method to the central east coast of Tasmania, for which data were available on the distribution and abundance of some species. The sites consisted of 1 sq. km cells. The cells were weighted according to how they represented 24 poorly preserved species of vascular plants, of which 23 were endemic. To determine the weight of a cell, each species was first allocated to one of four groups: (i) those not in reserves and mostly confined to the land studied; (ii) those poorly represented in reserves and mostly confined to the land studied; (iii) those not in reserves and more common outside than inside the land studied; (iv) those poorly represented in reserves and more common outside than inside the land studied. Second, each cell was weighted according to how it represented these four groups of species. A cell containing a species of group (i) is given a score of 100; 50 for (ii); 25 for (iii); and 10 for (iv), respectively. Kirkpatrick iterated this procedure until the weight of the top scoring cell was less than 30. This benchmark ensured adequate representation for all species not adequately represented outside the area being analysed.

Based on this analysis Kirkpatrick targeted seven areas of decreasing importance for conservation. He gave two reasons for the superiority of his iterative method over past methods. First, "In the case of the study area, an adoption of the methods previously used for allocation of preservation priorities would have led to the over-representation of some of the unpreserved and poorly preserved endemic species, and to the non-representation of others" (p. 131). Second, "The iterative method provides for the maximum nature conservation values per unit area preserved", subsequently, "for this reason alone it may be of considerable value in the land use decision-making process" (p. 131).

One year later, in their book, *Milkweed Butterflies*, Ackery and Vane-Wright (1984) again invoked complementarity. While the book is primarily concerned with the cladistics and biology of danaine butterflies, one section concerned the problem of conserving these species and recommended a set of selected areas. Ackery and Vane-Wright were primarily concerned with the representation of endemic danaine species. While they presented no explicit algorithm, the procedure they followed also implicitly used complementarity:

> "All but 32 of (the species considered) occur in the Indo–Pacific region. . . . [T]he four with the highest danaine species endemism are Sulawesi (9 endemics), Biak (4), Mindanao (3) and New Guinea (3). Between them, the combined faunas of these four territories include 69 danaine species. Thus, if these four faunas could be conserved, this would ensure the survival of over half of the danaine species found in the Indo–Pacific region (and over 40% of the world danaine fauna). Adding the 14 other endemic areas of the region (Sri Lanka, 2; southern India, 2; Borneo, 1; Luzon, 1; Negros, 1; Sumatra, 2; Java, 2; Sumbawa, 1; Sumba, 1; Flores, 1; Timor, 1; Seram, 2; New Ireland, 1; Guadalacanal, 1) brings the regional total to 115 – or 92%. The addition of the faunas of Nepal, Burma, New Britain, New Caledonia and San Cristobal is the minimum needed to secure the remaining ten Indo–Pacific species. Applying the same method to Africa,

> at a minimum we need to conserve the faunas of four regions: the Comoro Islands (1), the Seychelles (1), Mauritius (1) and Zaire. For the Americas we need Hispaniola (1) Cuba (1), Costa Rica and Bolivia" (p. 156).

Besides complementarity, Ackery and Vane-Wright endorsed the use of several other principles for conservation planning including rarity, richness, viability, and feasibility.

The first complete statement of a complementarity-based algorithm was due to Margules *et al* (1988). Their analysis was designed to select a subset of wetlands for protection from the complete set of wetlands on the Macleay Valley Floodplain in Australia. They presented two algorithms both of which used complementarity explicitly; however, rarity was privileged in the first algorithm. The first algorithm was a four-step procedure to ensure the representation of all 98 native plant species:

> "1. Select all wetlands with any species which occur only once. 2. Starting with the rarest (i.e. the least frequent species in the data matrix) unrepresented species, select from all wetlands on which it occurs, the wetland contributing the maximum number of additional (i.e. unrepresented) species. 3. Where two or more wetlands contribute an equal number of additional species, select the wetland with the least frequent group of species. The least frequent group was defined as that group having the smallest sum of frequencies of occurrence in the remaining unselected wetlands. 4. Where two or more wetlands contribute an equal number of infrequent species, select the first wetland encountered" (p. 65).

Step 2 uses complementarity though rarity gets precedence (as it does in every other step). The second algorithm, a three-step procedure, was designed to represent each of nine wetland types and each of the plant species at least once:

> "1. Select the wetland from each habitat type which has the greatest number of plant species. If all species are included, then stop. 2. Select a second wetland from each type which adds the most new species. A habitat type will be passed over if there are not wetlands from that type that add new species. If all species are included then stop. 3. Continue to select a third or fourth, etc., from each habitat type which adds the most new species, until all species are represented" (p. 69).

Step 2 constituted the first ever explicit use of complementarity by itself, that is, without also using rarity (as in the first algorithm).

At the practical level, the result was somewhat unsettling: it conclusively demonstrated that the idea that "biological diversity is 'reasonably secure' or 'as well taken care of as possible' with the dedication of one or a few well chosen reserves in an ecological domain", was thoroughly misguided (Margules *et al* 1988, p. 71). The first algorithm selected 20 wetlands or 44·9% of the total wetland area and the second selected 29 wetlands or 75·3% of the total wetland area, even with a target of only one representation for each species. This could hardly be regarded as feasible for conservation purposes.

Margules *et al* (1988, p. 73) went on to note that, with Kirkpatrick's (1983) "approach, wetlands with unique species tend to be added late in the selection procedure, and . . . add a disproportionate number of wetlands . . . (because) species with unique occurrences may not be included until towards the end of the procedure, so stopping anywhere before the end will ignore some species, including the very rare ones". This happens because Kirkpatrick's algorithm implicitly used richness (as noted above), rather than rarity, in addition to complementarity. Their rarity based approach (the first algorithm) is supposed to ensure that rare species are included in the first stages of the algorithm. They also noted another difference between Kirkpatrick's method and their first algorithm: the latter finds the smallest number of wetlands that represent all the species within a study area regardless of the representation status elsewhere, whereas the former considered whether a species was represented poorly or not at all outside of the study area.

The Margules-Nicholls-Pressey (MNP) algorithm was subsequently modified in a variety of ways, mainly to improve efficiency (Pressey and Nicholls 1989), but also to incorporate other criteria such as adjacency (Nicholls and Margules 1993), which puts a premium on a site being next to one already selected, all other things being equal. This leads to the creation of larger reserves. The MNP algorithm has been the basis for many of the publicly-available software packages for place prioritization, including C-Plan and ResNet; a variant approach which uses a different interpretation of complementarity is used in Target (see below).

Complementarity was independently rediscovered in South Africa by Rebelo and Siegfried (1990) during an analysis designed to select sites for the protection of Fynbos vegetation in the Cape Floristic region, which covers 90,000 sq. km. Their algorithm, though it used complementarity, was not as explicit or clearly stated as the MNP algorithm. First, core squares were selected on the basis of endemism and richness. Then:

> "A list of species present . . . in each of the assigned core squares was then compiled, and the distribution of species not present in core squares plotted. The grid

square with the most species not present in the core squares was designated as a 'secondary core square'. Its species were removed from the map, and the procedure was repeated. Where ties occurred, grid squares with the highest species richness were selected; where species richness was equal, the square containing the most Fynbos vegetation was chosen" (p. 21).

Rebelo and Siegfried (1990) applied this procedure to 12 km × 12 km cells, using 326 taxa (species and subspecies) of Fynbos vascular plants as biodiversity surrogates, and very convincingly showed that the designation of existing reserves had been inefficient and the plans then under consideration only slightly better: "Less than 27% of the area reserved for nature conservation and less than 50% of that proposed for conservation in the district lie in the area of high Proteaceae endemism" (p. 28). Nevertheless, the analysis had little practical impact.

None of these approaches used the term "complementarity". Finally, in 1991, Vane-Wright *et al* (1991) introduced that term to describe the principle that was implicit in all these procedures. Vane-Wright *et al* do not explicitly mention Ackery and Vane-Wright (1984) or Rebelo and Siegfried (1990) but, referring to the other two approaches [Kirkpatrick (1983) and Margules *et al* (1988)], observe:

"both procedures are based on a basic guiding principle – which we call complementarity.

In carrying out a simple faunal [sic] analysis, once the first choice has been made, all further consideration of species included within that region are eliminated. The second area is then drawn from the taxonomic complement of the first – the remaining fauna with the higher number of endemics, and all additional non-endemics that the area happens to contain. Once the first two faunas have been added, the reduced complement is then searched for the third area. This algorithmic procedure is repeated until all species are accounted for (the total complement)" (p. 245).

It was a happy choice of term, in full concordance with the use of "complement" in set theory within mathematics, where it is also taken to designate the remainder of an original set. The term was influential enough that even when an algorithm incorporated many other principles, for instance, rarity or even richness (sometimes still used to select the first site), it came to be called a "complementarity-based" algorithm.

That complementarity-based algorithms would outperform richness-based algorithms in minimizing the number of sites selected to achieve a required level of representation for species (or other biological surrogates) was clear to its proponents from the beginning [recall the statement of Kirkpatrick (1983)]. Explicit analysis of field data to show that this intuition was correct was first performed by Williams *et al* (1996) using distribution data for British birds. It has been repeated with the same result using modelled vertebrate data for Oregon by Csuti *et al* (1997). These results, though only of academic rather than direct policy interest, have nevertheless played a role in the gradual adoption of complementarity-based algorithms for actual reserve network design. These applications will be discussed in the next section.

However, complementarity-based algorithms are heuristic in the sense that they do not guarantee that the set of sites selected is the most efficient possible (the "global optimum") (Underhill 1994). It may even be the case that, as a set of sites is sequentially selected, some new site makes a prior selected one redundant, that is, the latter can be dropped without dropping the level of representation of any species beneath the set target. Some recent complementarity-based algorithms check for such redundancy (Aggarwal *et al* 2000). However, even removing such redundancy does not guarantee that the global optimum is achieved. If the required level of representation is 1, that is, the target of representation for each surrogate is 1, it can be shown that the problem of obtaining the global optimum is formally identical to the "maximal covering" problem of the theory of algorithms (Church *et al* 1996) which has an exact solution using integer linear programming (Cocks and Baird 1989). Csuti *et al* (1997) showed that this exact method does slightly better than some complementarity-based algorithms but they are known to be much more computationally intensive. It is an open question whether exact methods exist when targets are not equal to 1, for instance, when they are set to a specified percentage of surrogate records. Finally, there exist other heuristic procedures for reserve selection, for instance, some based on the optimization procedure of simulated annealing (Andelman *et al* 1999). The relation of these to complementarity-based algorithms remains unclear.

3. Policy applications

Analyses of data sets using complementarity-based algorithms for academic purposes have been performed for areas in at least ten countries: Australia (Kirkpatrick 1983; Margules and Nicholls 1988; Nicholls and Margules 1993; Pressey *et al* 1997; Pressey 1998, 1999), Canada (Sarakinos *et al* 2001), Guyana (Richardson and Funk 1999), Namibia (Sarkar *et al* 2002), the Falkland Islands/Islas Malvinas (Sarkar *et al* 2002), Papua New Guinea (Nix *et al* 2000), South Africa (Rebelo 1989; Lombard *et al* 1996; Cowling 1999; Cowling *et al* 1999; Lombard *et al* 1999; Cowling and Pressey 2000), Uganda (Howard *et al* 1998), the United

Kingdom (Williams *et al* 1996), and the United States (Csuti *et al* 1997; Clark and Slusher 2000; Sarkar *et al* 2000). Applications on a continental scale include an analysis of bird and mammal distributions of sub-Saharan Africa (Williams *et al* 2000) and plant and terrestrial vertebrate distributions for all of Europe (Williams *et al* 2000). However, this paper will only discuss the use of the principle in the context of formulating policy up to 2000. Almost all applications of algorithmic procedures for selecting reserve networks in this context have used complementarity-based algorithms.

3.1 *Australasia*

3.1a *Australia*: Given the extent to which the development of complementarity-based algorithms was pioneered in Australia, it should come as no surprise that the first country where the principle of complementarity had an impact on policy is Australia. In 1992, following the United Nations Conference on Environment and Development (UNCED) in Rio de Janiero (the so-called Earth Summit), the Commonwealth, State, and Territory Governments of Australia formulated a "National Forest Policy Statement" (NFPS) to ensure ecologically sustainable management of its forests (Commonwealth of Australia 1992). The objective was to help guide negotiations between state, industry, and conservation representatives to produce Regional Forest Agreements (RFAs) by formulating goal-directed criteria for creating reserve networks within each region. The NFPS document recommended reserve networks be selected according to three principles: comprehensiveness, adequacy, and representativeness. Although complementarity was not explicitly mentioned within the document, the use of representativeness implicitly suggested the use of complementarity.

The underlying intention of the 1992 NFPS was made more explicit in 1995 with the "National Forest Conservation Reserves Commonwealth Proposed Criteria" in which the reserve selection methods of Kirkpatrick (1983), Margules *et al* (1988), and Pressey and Nicholls (1989) were recommended in order to try to maximize representation of biological diversity (Commonwealth of Australia 1995). Reflecting a receptivity to emerging results within conservation biology the document noted, "[t]he belief that biological diversity is taken care of with the dedication of one or a few well chosen reserves in an ecological domain is unfounded"; "[t]he reality is that very large numbers of reserves seem necessary" (Commonwealth of Australia 1995, p. 49). A later 1997 report, "Comprehensive, Adequate, and Representative Reserve System for Forests in Australia", written by the joint Australian and New Zealand Environment and Conservation Council (ANZECC), the Ministerial Council on Forestry, Fisheries and Aquaculture (MCFFA) of Australia, and the National Forest Policy Statement Implementation Sub-committee, echoed the 1995 suggestions, and recommended the same reserve selection methods (ANZECC *et al* 1997).

Complementarity was also explicitly invoked in Australia's 1999 "International Forest Conservation: Protected Areas and Beyond" written for the Intergovernmental Forum on Forests in Lisbon:

> "When the contribution of all forest units to a regional conservation goal is estimated, some areas will be identified as making the same contribution as other areas, or the same contribution that can be made by two or more other areas, revealing scope for negotiation and choice. As planning proceeds and a network of biodiversity priority areas is built up, the relative contributions of areas not yet selected changes because some of the biodiversity values in those areas will have been represented in the priority areas already identified. The spatial context which a bioregion provides is necessary because the conservation value of any unit – its complementarity – can only be measured relative to all other units within a defined geographic region" (Commonwealth of Australia 1999, p. 42).

Beyond its invocation in policy directives, the principle of complementarity was finally used by the New South Wales State government in the late 1990s in policy decisions to formulate a prioritized list of areas for conservation. A reserve area selection program, C-Plan, developed by Pressey, Ferrier, Barrett and others at the New South Wales National Parks and Wildlife Service along with Watts at the University of New England at Armindale, was used in negotiations between seven organizations (the Resource and Conservation Assessment Council; the Forest Products Association; the Construction, Forestry, Mining and Energy Union; State Forests of New South Wales; the National Parks and Wildlife Service; conservation representatives, and the Commonwealth of Australia) regarding land conservation in an area of the eastern seaboard of NSW in 1996 (Finkel 1998a; Pressey 1998).

C-Plan uses the concept of the "irreplaceability" of a site which is defined relative to a given set of sites, a list of conservation targets, and the spatial distribution of the features referred to by the targets, usually including the representation of a given number of species or habitats. The irreplaceability of a site can be defined in two ways: "(i) the likelihood that it will be required as part of a conservation system that achieves the set of targets; and (ii) the extent to which the options for achieving the set of targets are reduced if the area is unavailable for conservation" (Ferrier *et al* 2000, p. 304). Since the irreplaceability of an area must refer to particular conservation targets, and the extent to which other areas contribute to satisfying them, complementarity is a key component of the concept of irreplaceability (Ferrier *et al* 2000; Pressey 1999). Furthermore, the irreplaceability value of an area is not binary, it will range from 1 to 0. The concept of irreplaceability was originally developed to give conservation planners a measure of the potential contribution that an unselected site (not included within the reserve network) would make to a conservation target. This is important for policy decisions because, sometimes, selected sites become unsuitable or unmanageable after a network has been established, and because of the potential time lag between many of the studies and resulting policy actions (Ferrier *et al* 2000; Pressey 1999). C-Plan enables the rapid visual display of alternative reserve networks on a map. This makes it particularly easy to use during planning.

A total of 2·4 million ha of state owned land and several million ha of private land within eastern NSW were analysed in 1996 using C-Plan. The area includes the species-rich remnants of Australia's Gondwana heritage, important to conservationists, but also covered by lucrative lumber production forests, crucial to the timber industry (Finkel 1998a; Pressey 1998). To facilitate negotiations, the total study area was divided into eleven different regions and each region was divided into approximately 250 ha cells (Pressey 1998). A large set of biodiversity surrogates (including the "pre-European" extent of selected forest types; natural rarity of forest type; past depletion and vulnerability; forest growth phase; and so on) was used in this analysis. Four conservation scenarios were distinguished which allowed logging of 100%, 70%, 50%, and 30% of the 1995 sawlog volumes that corresponded to increasing satisfaction of conservation targets (Pressey 1998). The final decision led to an agreement to establish nine new nature reserves and national parks (250,000 total ha of which 20% were cells with "high irreplaceablity") and, "816,000 ha of deferred forest, extensive new wilderness areas, and agreements on the supply of hardwood for five years" (Pressey 1998, p. 85).

Following what was judged a successful use by Pressey the year before (Finkel 1998a), in 1997, C-Plan was used to guide negotiations for 120,000 ha of the 816,000 ha that had been deferred from 1996 in southeastern New South Wales (Finkel 1998a). However, unlike 1996, when there was an agreement on pre-established conservation goals, in 1997 no such accord could be reached. The targets ultimately used differed significantly from those initially proposed. Moreover, the four strategies considered in the negotiations only met 40–50% of these targets (Finkel 1998a). Additionally, again unlike 1996, C-Plan was used with a more limited data set of surrogate distributions in the relevant areas. Consequently, the final decision made by negotiators involved a high degree of uncertainty and was unsatisfying to many stakeholders in the negotiations.

While 1996 saw a successful use of C-Plan in conservation policy, and even 1997 saw a partial success, the 1998 negotiations over 10 million ha in the northeast of New South Wales, which, along with Queensland, contains Australia's only wet subtropical ecosystem, marked a failure (Finkel 1998a). Forests in this area were better studied, and the ecological data set for the region was more reliable than those used in previous studies. As a result, "well-established" conservation targets existed for many of the surrogates that were used, such as 200 forest ecosystems, 800 endangered plant species, and 140 animal species (Finkel 1998a). However, the results of the C-Plan assessment were neglected in favour of timber industry interests. Disregarding the recommendations of conservationists, policy makers passed a bill that protected half the area that conservationists insisted was necessary to conserve biodiversity. The plan only meets 30% of the conservation targets for the species with highest conservation priority; and only a sparse 7% for the Hasting's River mouse (*Pseudomys oralis*) which is endangered (Finkel 1998b). It allowed the timber industry to continue logging with its current quota for 20 years, double of what was recommended (Finkel 1998b).

3.1b *Papua New Guinea*: The most significant application of complementarity-based algorithms in Australasia outside Australia has been in Papua New Guinea (PNG) (Faith *et al* 2001a,b,c,d). As a signatory to the UN Convention on Biological Diversity (the Rio Convention), PNG is explicitly committed to the conservation and sustainable use of biodiversity (Nix *et al* 2000). The World Bank commissioned the Papua New Guinea Biodiversity Appraisal Pilot Project to facilitate PNG's response to its commitment to the Rio Convention; it was funded through AusAID. The project was carried out between July 1997 and July 1999 by five agencies: the Centre for Resource and Environmental Studies of the Australian National University; the (Australian) Commonwealth Scientific and Industrial Research Organization (CSIRO) Division of Wildlife and Ecology; the Centre for Plant Biodiversity Research at the Australian National Herbarium; the Bishop Museum, Hawaii; and the PNG Department of Environment and Conservation (Nix *et al* 2000).

The PNG project used the BioRap Toolbox for rapid biodiversity assessment developed by the BioRap Project in Australia during 1994–1995 (Margules *et al* 1995). The BioRap Toolbox includes methods for the spatial modelling of biogeographic surrogates as well as area selection algorithms, which are slight extensions of the MNP algorithm. However, the PNG project used the

Target software (Walker and Faith 1998) which implements a complementarity-based algorithm, that significantly generalizes the original algorithms to incorporate cost considerations using trade-offs. Rapid assessment of biodiversity was supposed to be "essential for rational allocation of scarce land resources between the competing demands of agriculture, forestry and conservation" (Nix *et al* 2000, p. 1). Sociopolitical considerations were merged with scientific ones, retreating from the position that Margules and Usher (1981) had once advocated. Rapid biodiversity assessment was interpreted to imply that conservation plans had to be produced within a period of one year.

For the purpose of the analysis, PNG (462, 840 sq. km) was divided into 0·1° longitude × 0·1° latitude cells (approximately 1 km × 1 km) (Faith *et al* 2001b). This resulted in 387,109 grid cells. The biodiversity surrogates used were environmental domains, vegetation types, the distribution of 87 species that were judged to be representative, and 25 rare or threatened bird and mammal species. Targets of representation for these surrogates were determined by calculating what could be achieved if 10% of the total land area of PNG was designated for conservation without taking any other factor into account. As basic spatial units, Nix *et al* (2000) and Faith *et al* (2001c) used the Resource Map Units (RMUs), used by many government agencies in PNG; there were 4,470 of these ranging in area from 0·045 sq. km to 8,508 sq. km.

The final result was a "set of biodiversity areas . . . [which] includes all existing protected areas. . . . In addition the set minimizes foregone [sic] opportunities for timber production, avoids areas of high agricultural potential, avoids areas of high existing agricultural intensity and gives preference to areas of low human population density" (Nix *et al* 2000, p. 35; Faith *et al* 2001c). The results were presented as a detailed map. When all these other factors, not directly linked to biodiversity were taken into account, 16·8% of the land area of PNG was required to achieve the targets that had previously been set using the 10% benchmark and only biodiversity considerations (Nix *et al* 2000, p. 39; Faith *et al* 2001c). It is too early to say if this analysis will have any influence on practical legislation.

3.2 *Africa*

3.2a *South Africa*: South Africa's Succulent Karoo Desert extends over 112,000 sq. km of the Greater Cape Floristic Region. It contains 4,849 vascular plant species (1,940 endemic species; 67 endemic genera) in 12 bioregions (Cowling 1999). It is unique as the only semi-arid area that is a global hotspot of biodiversity. Many of the endemic species are extreme edaphic specialists; approximately 392 Red Data Book (RDB) highly endangered species from this region have ranges of less than 68,000 ha. Existing reserves within the Succulent Karoo do little to protect its biodiversity. Merely 2·1% (2,352 sq. km) of the area is conserved within six statutory reserves and the larger ones (> 10,000 ha) contain only 9% of its total 851 RDB species. Furthermore, immediate threats such as overgrazing, expansion of agriculture, and mining, are putting its biodiversity at increasing risk (Cowling 1999).

At least two studies of the region have been completed: one utilizing complementarity based algorithms (Lombard *et al* 1999), and another which built on this work (Cowling *et al* 1999). In the first study a place prioritization program, based on the original work of Rebelo (1989), was used to analyse a 1972 RDB database containing 221 cells of 0·25° longitude × 0·25° longitude with records of 851 surrogate vascular plant species (Lombard *et al* 1999). The RDB database was used for four reasons: (i) maps of the Succulent Karoo were too coarse-grained to represent accurately the boundaries between different habitats; (ii) the RDB classification incorporated threats to the particular floral species; (iii) the RDB data "shows very high compositional turnover along environmental and geographical gradients", and therefore, "is likely to capture a great deal of floristic diversity generally"; and (iv) the database was considered to have reliable presence-absence data (Cowling 1999, p. 21).

Targets were set to conserve each RDB species once and cells within existing reserves were exempted from selection. After assuming that species within these cells were adequately represented, the program selected 122 additional cells (56% of the possible 214) (Cowling 1999). Not surprisingly, the study revealed that the existing seven preserved cells contributed poorly to the conservation goal, containing only 80 species (9% of the RDB flora), whereas the top seven cells selected contained 314 species (37% of the RDB flora) (Cowling 1999). The 122 selected cells were prioritized using the following procedure: each species within the database was valued according to its rarity (determined by the number of cells it occupies) and its vulnerability (using a seven tier scoring system with reputedly extinct species possessing the highest score, and non-threatened ones the lowest) (Lombard *et al* 1999). This procedure was followed to try to guarantee both representation and retention (by ensuring the areas with the most at risk species be preserved first) within the minimal reserve network.

In the second study, Cowling *et al* (1999) also used a persistence criterion to analyse the 122 cells. The aim was to incorporate persistence criteria (such as the viability of populations, minimization of edge effects, maintenance of disturbance regimes, and movement patterns) into the design of reserve networks. Cowling *et al* (1999) recommended the creation of a network composed of three large reserves (265,000 ha, 175,000 ha, and 282,000 ha) covering 11 of the selected cells from Lombard *et al* (1999) and containing 139 RDB species (of the total 851). This contrasts with Lombard *et al*'s study in which the 11 highest-priority cells included 375 RDB species; 270% more species for an equal area of protection (Cowling 1999, Cowling *et al* 1999).

The South African National Parks has expressed a commitment, subject to budget constraints, to establish a system of reserves for the Succulent Karoo (Cowling 1999). Work on developing a reserve in the Vanrhynsdorp Centre, which contains hotspots of succulent, geophyte, and threatened RDB species, is under way (Lombard *et al* 1999; Cowling 1999). Preliminary planning within the Hardeveld-Kamiesberg node, identified in Lombard *et al*'s study as crucial to satisfying conservation targets, is in progress (Cowling 1999). So far four new conservation areas have been designated on the basis of these analyses; they are all sites identified by Lombard *et al* (1999) (R Cowling, personal communication).

3.3 *The Americas*

3.3a *Canada*: In 1989, in response to the continued depletion of Canada's biodiversity due to natural resource extraction, encroaching urbanization, and industrial pollution, World Wildlife Fund (WWF) Canada introduced the "Canadian Wilderness Charter" to encourage the systematic protection of biologically important areas (Sarakinos *et al* 2001). By 1992, Canada's relevant environmental ministries at both the federal and provincial levels had all signed a Statement of Commitment to an "Endangered Spaces Campaign 2000" which required that 12% of each natural region be put under protection. That same year, the Québec provincial government officially announced its intention to complete a representative network of protected areas by 2000. Yet, by 1998 only about 4·2% of the area of terrestrial Québec was under any form of protection. Moreover, much of what was protected had not been selected using biological criteria of any sort (Sarakinos *et al* 2001). In 1998 WWF-Québec published a map proposing a new set of protected areas without indicating how they had been selected; presumably it was based on local expert advice (WWF-UQCN 1998). The general strategy seems to have been to augment existing protected areas even though the latter were often known not to be relevant for biodiversity (Sarakinos *et al* 2001).

At that stage, scientists from the Redpath Museum (McGill University), in collaboration with scientists from Australia's CSIRO Division of Wildlife and Ecology, and the Biodiversity and Biocultural Conservation Laboratory at the University of Texas – Austin began framing a plan to influence area selection for Québec. For the purpose of analysis, Québec was divided into grid cells of 0·2° longitude × 0·2° latitude resulting in 21,403 cells (Sarakinos *et al* 2001). The primary biodiversity surrogates used were 346 plant and 54 animal species deemed to be at risk by the former Québec Ministry of Environment and Wildlife. For some of the analyses, this surrogate list was expanded by using game mammals, small mammals, and fish; for southern Québec, birds were also used (bird data were not available for the north). Targets of 1, 5, 10, 20 and 50 representations were set. The algorithms used were variants of the MNP algorithm.

The most important, but not unexpected, result was that the existing reserve network of Québec was largely unrepresentative of the biodiversity of the province; the sole major exceptions were reserves on the Gaspé peninsula (Sarakinos *et al* 2001). The WWF-Québec map (WWF-UQCN 1998) did not fare much better, showing the superiority of explicit algorithmic approaches to biodiversity planning even over local expert advice. Most of the results obtained by Sarakinos *et al* (2001) were promising. Even with a representation target of 50 for species at risk, less than 5·9% of the area of Québec was designated for conservation. Thus, achieving a reasonable representation of biodiversity within the 12% benchmark seems possible. However, many of the targeted areas were in southern Québec, with high human population density. This will make devising conservation plans more difficult. Later work by some members of this group and other collaborators suggests that this level of representation, without significant addition to the total area, can be achieved without this bias towards southern Québec (Garson *et al* 2002). However, the later work was not done with an explicit agenda of intervening in practical policy disputes. In the earlier work, Sarakinos *et al* (2001) also found that coastal, riparian, and wetland areas were not adequately protected.

The analysis by Sarakinos *et al* (2001) showed that two islands in the Gulf of St. Lawrence, the Île d'Anticosti and the Îles-de-la-Madeleine, were of high biodiversity priority. Neither island is densely populated. Consequently, conservation measures should be relatively easy to implement (Sarakinos *et al* 2001). In the former island, a reserve has already been designated, though because of scenic beauty rather than biodiversity value. Biodiversity considerations indicate that the proposed reserve should be expanded significantly. Finally, the analysis showed that the boreal forest in northern Québec, is of significant but not very high biodiversity value (Sarakinos *et al* 2001). There is, therefore, a reasonable option of phasing out logging over a period of several years and avoiding the social dislocation that an immediate halt to logging may create (Sarakinos *et al* 2001). These proposals were forwarded to the provincial Government of Québec in 2001. Their impact on policy remains to be seen.

3.3b *Guyana*: Guyana, with an area of 215,000 sq. km, is unique as the only country in the Americas without a system of protected areas (Richardson and Funk 1999). The human population is 800,000, with 80% distributed mostly along the coast. Guyana includes biologically diverse environments, such as white sand forests, savannah, and Amazonian rainforests that are only beginning to be exploited for their natural resources (Richardson and Funk 1999). Facing international pressure to harvest its forests and minerals in an environmentally-friendly fashion, after democratic elections in the early 1990s, the Government of Guyana ratified a National Environmental Action Plan (NEAP) in 1994 and, "agreed to take the first steps in establishing a system of protected areas that would encompass areas representative of the major ecosystems of the country" (Richardson and Funk 1999, p. 7).

As a result of their commitment to conservation, a database with 16,500 records of 312 species covering ten taxonomic groups of plants and animals was compiled in collaboration with the Smithsonian Institution (Richardson and Funk 1999). These 312 species were used as biodiversity surrogates in the analysis. Due to a lack of adequate data for the southeastern region of Guyana, caused by border disputes with Suriname, this portion of the country was not represented by the final database and analysis (Richardson and Funk 1999). Characteristic of study areas with few roads, the data set was biased around airstrips and rivers; to compensate, data were modelled to obtain both actual and predicted distributions of species (with a 95% confidence level). In the analysis, species with less than ten location points were not modeled, which may significantly bias the results against rare species (Richardson and Funk 1999).

After mapping the relevant portion of Guyana into a total of 941 16 km × 16 km cells, conservation targets corresponding to 15% of the predicted distribution area for each species in the data set, were determined (Richardson and Funk 1999). A C-Plan analysis of all 941 cells was done and 140 sites, 36 with an irreplaceability value of 1, were selected relative to the target (K S Richardson, personal communication). A vulnerability index was then calculated by determining the proximity of each cell to a forestry concession, the main threat to conservation goals (Richardson and Funk 1999). Last, a GIS overlay was then made to highlight areas of both high vulnerability and high irreplaceability (Richardson and Funk 1999). It illuminated high priority areas in the central, tall, evergreen areas of the country along with highly irreplaceable and mildly vulnerable areas around Kaieteur Falls (Richardson and Funk 1999).

Currently, Guyana has a single national park of 11 ha around Kaieteur Falls that preserves the scenic Potaro River waterfall (Richardson and Funk 1999). In 1994 the Guyana government requested assistance from the Global Environment Facility (GEF) through the World Bank to create a National Protected Areas System (NPAS). The C-Plan study of the country, which identified priority areas for conservation, was the first step towards establishing an NPAS (Richardson and Funk 1999). Based on the analysis, in 1999 the Guyana government designated two areas (the Kaieteur falls area and one within the Kanuku Mountains) to serve as its foundation and passed a bill to expand Kaieteur National Park to 580 sq. km (Richardson and Funk 1999).

Although "the results of scenarios based on irreplaceability and vulnerability . . . have been discussed with the Government", the Guyanan government has stalled on plans to develop an NPAS (Richardson and Funk 1999, p. 14). Surprisingly, the failure to act was not due to lack of funds or lack of interest by government (K S Richardson, personal communication). In fact, the GEF and other financiers were willing to procure approximately $ 9,000,000 for the realization of a NPAS and two areas around the Kaitieur Falls and the Kanuku Mountains were identified for initial funding (K S Richardson, personal communication). However, making use of the GEF funds was paralyzed by unresolved issues about the tenure rights of Amerindian communities and other political issues (K S Richardson, personal communication). Subsequently, the government of Guyana did not meet the conditions for the grant, and after a few years with no progress towards resolution, the GEF withdrew its original offer (K S Richardson, personal communication).

3.3c *United States*: In 1997, the US Fish and Wildlife Service (US-FWS) undertook a project which utilized C-Plan to plan a Grand Kankakee Marsh National Wildlife Refuge. The refuge was intended to preserve 12,140 ha within the fragmented Kankakee River Watershed wetland which, historically, ranged over 400,000 ha of northeastern Illinois and northwestern Indiana (Clark and Slusher 2000). Determining what areas should be included in the reserve network was done in two stages. The first stage was a non-quantitative process in which ecologists from the Nature Conservancy, the Illinois Department of Natural Resources, the Indiana Department of Natural Resources, the North American Waterfowl Management Plan, representatives of the Indiana GAP Analysis Project, and the Indiana University School of Public and Environmental Affairs met in workshops to determine areas of preliminary focus for the proposed reserve network (Clark and Slusher 2000). GIS satellite images were used to select twenty areas based on eight criteria: (i) inclusion of the Kankakee River corridor and corridors between existing managed areas; (ii) representation of the three primary ecosystems of the study area (prairie, wetland, and oak savanna); (iii) presence of threatened and endangered species; (iv) distance to, and connectivity between, existing managed areas; (v) overlap with federally endangered species habitat and area-sensitive migratory grassland bird habitat; (vi) anthropogenic features; (vii) threat of development; and (viii) ratio of existing to restorable habitat.

In the second stage, C-Plan was used to prioritize cells in the study area. Prioritization was based on the representation of six surrogate features that "represent the major components of biodiversity in the Kankakee River watershed in the context of FWS trust resources". These surrogates were: (i) the presence of federal endangered and threatened species; (ii) the presence of state endangered and threatened species; (iii) presence of rare community types; (iv) existence of woodland habitat (as a surrogate for existing or restorable oakland savanna); (v) existence of palustrine and restorable wetlands; and (vi) existence of habitat for the grasshopper sparrow, *Ammodramus savannarum* (used as a surrogate for grassland dependent birds) (Clark and Slusher 2000, p. 80). The targets for each feature were 100%, 75%, 50%, 5,000 ha, 5,000 ha, and 100%, respectively (Clark and Slusher 2000). Of the 1914 cells accorded an irreplaceability value of 1 by C-Plan, only 126 were included in the final twenty focus areas selected during the first stage by expert panels (Clark and Slusher 2000). This underscores the superiority of algorithmic selection procedures over intuitive ones, even if guided by local and regional expertise.

Based on these analyses 65 highly irreplaceable sites covering 4053 ha (33% of the total) that fell within two of the original focus areas of stage 1 were recommended to be reserved. After approving the forward progress of the project the US-FWS hired a refuge manager to be stationed in northern Indiana (Clark, personal communication). However, a concurrent study of the Kankakee Watershed area done by the US Army Corps of Engineers has focused more on implementing structural work in the area to solve increasing drainage problems with less emphasis on landscape-scale wetland restoration. This, combined with changes in political agendas and the enacting of conservation thwarting county ordinances, has led to a delay in the project's realization (Clark, personal communication). When the final policy considerations took place, they were predominantly divorced from C-Plan results (Clark, personal communication). No land for the refuge has yet been purchased.

4. Discussion

In spite of their increasing popularity, even among policy-makers, algorithmic methods for the design of reserve networks continue to have their critics (for a review see Cabeza and Moilenen 2001). For instance, in the 1997 edition of their guidelines for ecoregion-based conservation, *Designing a Geography of Hope*, the Nature Conservancy (US) argued that the algorithmic approaches consist of:

> "a body of mathematical models referred to as iterative reserve selection algorithms. . . . Ideally these algorithmic approaches require a healthy and consistent level of distributional information on the elements of biodiversity across a region . . . (I)terative approaches are . . . explicit, efficient, repeatable, and flexible. . . . (However, they) are 'data hungry' approaches that require substantial computing capacity and for which there are currently no commercial software packages. The quality of the analysis depends strongly on the detail, precision, and accuracy of the information being used" (Redford *et al* 1997, p. 45).

Such iterative approaches are negatively contrasted with one-shot reserve selection based on expert advice. However, the Nature Conservancy's recent strategy starts with an assessment of the viability of the relevant biotic entities, and then involves the systematic use of complementarity when new sites are selected after the selection of the first one (Groves *et al* 2000). By relying on expert advice to assess viability, the Nature Conservancy tries to combine the advantages of both practices (Groves *et al* 2000).

The criticism that algorithmic methods require unacceptably high quality data has recently been repeated by Prendergast *et al* (1999): "to work effectively, sophisticated (algorithmic) methods of site selection usually require higher-quality data than most managers can ever expect to have. . . . All reserve selection algorithms require reliable data. In their absence, the only solution is to acquire this data, often at considerable time and expense. It is a matter of judgement whether money is better spent on acquiring data or on land purchase based on imperfect (or sometimes no) data" (p. 488). Their judgement is clearly against the use of algorithms in such cases. Even when data exist, there is only reason for "modest adoption of reserve selection algorithms" (p. 488). This criticism formed part of a longer argument designed to show that "in many areas we believe that it will be sensibly targeted funding, allied with informed policy and pragmatism, rather than theoretical optimization of reserve network design, that will have the greatest immediate effect on the most pressing conservation problems" (p. 490).

In response, Pressey and Cowling (2001) pointed out: "Among the products of several decades of pragmatic conservation decisions driven by socioeconomic imperatives are extensive reserve systems whose value is overestimated by the hectares they occupy" (p. 277). This point reiterated Pressey's (1994) earlier insight that ad hoc reservation, as one would expect from decisions made with no data or with no analysis of incomplete data, has led to inefficient reserve network design, and the consequent misuse of resources. Pressey and Cowling (2001) also correctly pointed out that the problem of inadequate data plagues not only reserve selection algorithms, but any systematic approach to conservation planning. Moreover, algorithmic methods are not intended to supplant human decision-making mechanically; programs such as Target, C-Plan and ResNet are intended to be used as tools along with as much detailed local knowledge as is available. For Prendergast *et al* (1999) criticism to have force, they needed to show that the use of algorithmic methods led to error just as Sarakinos *et al* (2001) and many others have shown that ad hoc reservation leads to inadequate representation of biodiversity in existing reserve networks.

In addition, it is incorrect to argue that reserve selection algorithms require high-quality data of the kind that are not accessible to most management agencies. These algorithms can be used with very simple easy-to-acquire data sets such as geology maps and climate surfaces, to identify sets of areas that together represent the range of environments that occur in a region. Even such simple results can help guide decisions on where and how to spend scarce conservation management resources. For example, it is likely that more species will be protected over all if an area representing a climatic type and/or rock type not previously protected is added to a reserve network, rather than one representing climates or rock types already represented. Perhaps there is no need to implement computer-based algorithms to carry out such simple analyses, but the method would be utilizing a complementarity-based procedure.

As the history recounted in the last section shows, these algorithms are slowly but steadily entering into conservation planning in many areas of the world though perhaps not in the United Kingdom, to which Prendergast *et al* (1999) somewhat myopic vision seems to be restricted. In areas such as Papua New Guinea, where there are neither enough local knowledgeable experts, nor time to generate the requisite expertise before irreversible conservation decisions must be made, rational algorithmic approaches are the only alternative to ad hoc reservation with its poor record of representing biodiversity. These algorithms are here to stay and, so long as they are around, the principle of complementarity will continue to have a central role in conservation biology.

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