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## Complementarity and the selection of nature reserves: algorithms and the origins of conservation planning, 1980–1995

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**Abstract** This paper reconstructs the history of the introduction and use of iterative algorithms in conservation biology in the 1980s and early 1990s in order to prioritize areas for protection as nature reserves. The importance of these algorithms was that they led to greater economy in spatial extent (“efficiency”) in the selection of areas to represent biological features adequately (that is, to a specified level) compared to older methods of scoring and ranking areas using criteria such as biotic “richness” (the number of features of interest). The development of these algorithms was critical to producing a research program for conservation biology that was distinct from ecology and eventually led to what came to be called systematic conservation planning. Very similar algorithmic approaches were introduced independently in the 1980–1990 period in Australia, South Africa, and (arguably) the United Kingdom. The key rules in these algorithms were the use of rarity and what came to be called complementarity (the number of new or under-represented features in an area relative to those that had already been selected). Because these algorithms were heuristic, they were not guaranteed to produce optimal (most “efficient”) solutions. However, complementarity came to be seen as a principle rather than a rule in an algorithm and its use was also advocated for the former reason. Optimal solutions could be produced by reformulating the reserve selection problem in a mathematical programming formalism and using exact algorithms developed in that context. A dispute over the relevance of full optimality arose and was never resolved. Moreover, exact algorithms could not easily incorporate criteria determining the spatial configuration of networks of selected areas, in contrast to heuristic algorithms. Meanwhile metaheuristic algorithms emerged in

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the 1990s and came to be seen as a credible more effective alternative to the heuristic algorithms. Ultimately what was important about these developments was that the reserve selection problem came to be viewed a complex optimal decision problem under uncertainty, resource, and other constraints. It was a type of problem that had no antecedent in traditional ecology.

**Keywords** Biodiversity · Complementarity · Conservation biology, history · Reserve design · Reserve selection · Systematic conservation planning

## 1 Introduction

Theoretical work in the biological sciences typically consists of constructing models and more general theories guiding model building (Sarkar 2007c). The development of (scientific) ecology during the last two decades of the twentieth century exemplifies this pattern (Sarkar 2007b). During the same period, a discipline that was widely initially regarded either as a part of ecology, conservation biology, emerged as an institutionalized discipline, initially in north America, but subsequently elsewhere.<sup>1</sup> What was unique about conservation biology in the context of the biological sciences—and only slightly less generally in the context of all the *empirical* sciences—was that theoretical innovation in several important cases consisted in the design of better *algorithms*, similar to innovation in computer science, operations research, and some of the decision sciences. This was particularly true in the sub-discipline within conservation biology that came to be known as *systematic conservation planning* (Margules and Pressey 2000). Even though there was little formal contact or collaboration between conservation biologists and operations researchers during the formative 1980–1995 period when the framework of systematic conservation planning was established (for a contrary interpretation, see Kingsland 2002), what emerged was a discipline that drew as much from operations research and other areas outside biology as from within the biological sciences.

This paper is a history of the introduction and elaboration of algorithms within conservation biology during the 1980–1995 period.<sup>2</sup> The choice of the initial date is based on it being the year the first such algorithm was developed (Kirkpatrick et al. 1980). The terminal date was selected as 1995 because a different class of algorithms (metaheuristic ones—see Sect. 6) began to be used starting 1996 (Ball 1996). What is interesting about the developments analyzed here—besides the formal issues which dominate the discussions of this paper—is the extent to which conservation biology, as it developed, departed from traditional ecology. This was also the period during which the term “biodiversity” was introduced and conservation biologists came to see their discipline as *that* which was devoted to the protection of biodiversity (Takacs 1996).

<sup>1</sup> For brief histories of these developments, see Takacs (1996) and Sarkar (1998, 2004, 2005); a detailed history is yet to be written and would not go unnoticed.

<sup>2</sup> See Justus and Sarkar (2002), Kingsland (2002), and Pressey (2002).

Throughout this period, the preferred strategy for biodiversity conservation was through the designation of nature reserves, the number of which saw a dramatic growth between 1985 and 1995 (Brockington et al. 2008). The late 1980s saw the emergence of what has since become a standard protocol for the selection of networks of such reserves (Margules and Pressey 2000), though the popularity of strict protection of habitats in reserves through human exclusion became controversial.<sup>3</sup> Much of this framework was initially developed in Australia. Even though conservation biology was at that time being institutionalized in the United States, perhaps surprisingly, the earlier framework used there, emerging mainly from island biogeography theory in the 1970s, was almost entirely rejected.

The new framework envisioned solving what was variously called the “reserve design” or “reserve selection” problem.<sup>4</sup> It was eventually conceptualized as a constrained optimization problem, the maximization of the representation of biological features (the term “biodiversity” was almost never used in this early period) in minimum area, that was supposed to be solved using formal algorithms and state-of-the-art computational tools eventually typically based on a Geographic Information System (GIS) platform. Proponents of these methods criticized earlier strategies to select protected areas (see Sect. 3) as ad hoc on the ground of sub-optimality (Pressey 1990, 1994; Pressey and Tully 1994). There was considerable argument over the algorithms to be used, a question that was never fully resolved.

## 2 Background

Two themes dominated earlier work on the design of nature reserve systems against which the new framework of conservation planning emerged: (i) that reserves should be viewed as islands surrounded by inhospitable “oceans” of developed lands; and (ii) that the conservation value of an area could be represented by a single score, typically, its species “richness,” that is, the number of species in it. Both themes will be briefly explored in this section to clarify the sense in which the new framework marked an innovative departure from past work in ecology.

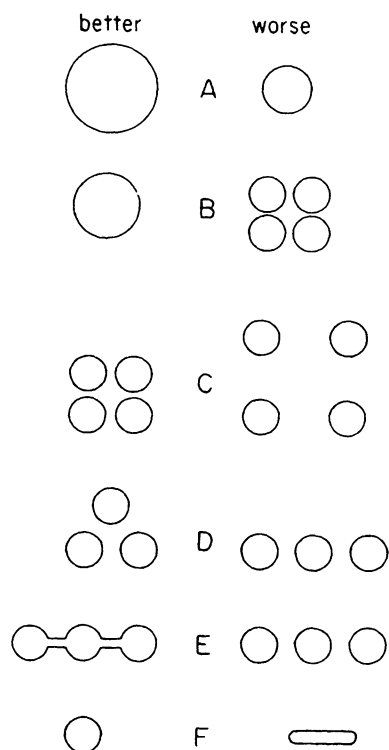
### 2.1 Reserves as islands

Though conservation biology was officially viewed as an inter-disciplinary enterprise, at least by the 1980s (Soulé 1985), its immediate historical roots lie in the ecology of the 1970s (Takacs 1996). Consequently, it is not surprising that early efforts to solve the reserve design problem invoked work in island biogeography theory which had emerged in the late 1960s as one of the more innovative developments in theoretical ecology (MacArthur and Wilson 1967). That theory attempted to predict species

<sup>3</sup> The alternative was to allow multiple use of habitats, including compatible human use (Sarkar et al. 2006; Margules and Sarkar 2007; Brockington et al. 2008).

<sup>4</sup> For “reserve design” see, e.g., Diamond (1975, 1986), Higgs (1981), Margules et al. (1988), Simberloff (1988); for “reserve selection,” see Cocks and Baird (1989), Nicholls and Margules (1993), Pressey (1994, 2002), etc.

**Fig. 1** Diamond's Rules for Reserve Design (from Diamond 1975) These six rules were supposed to have been derived from island biogeography theory. The organization is supposed to presume a homogeneous landscape. Otherwise, for instance, Rules B and C would not be applicable since several distant reserves would be needed to sample all species



richness from ecological assumptions. It predicted the richness in an island assuming an equilibrium between immigration and extinction. Relevant parameters included the size (area) of an island and its distance from the mainland. The operative model for a reserve during this period was that of a U.S.-style national park, clearly demarcated from the surrounding landscape matrix and, ideally, divorced from all non-esthetic and non-scientific human use.

It was thus perhaps natural to conceptualize such reserves as potential islands of protected areas ("refugia") surrounded by terrain that was inhospitable to biota. This was the route taken by E. O. Wilson, one of the founders of island biogeography theory. Wilson and Willis (1975) and Diamond (1975) proposed the use of the theory for the design of nature reserves (see, also, Diamond and May 1976). These rules were supposed to be based on community-level processes (that is, those that involved a suite of interacting species in the same geographical area) determining persistence (or extinction) of species. Diamond produced six geometrical rules (see Fig. 1 from Diamond 1975, p. 143):

- A Large reserves were preferable to smaller ones.
- B A single large reserve was preferable to several smaller ones adding up to the same area.
- C Reserves that were closer to each other were better than those that were not.
- D Equidistant reserves were better than those that were not.

- E Reserves connected through corridors were better than those that were not.
- F A circular reserve was better than an elongated one.

By 1980, these rules were endorsed by the World Conservation Strategy of the International Union for the Conservation of Nature [IUCN] (1980); by 1985 they found their way into textbooks (e.g., Krebs 1985; and they even received endorsement from the World Bank Simberloff 1988).

Yet, by the end of the 1980s these rules—and island biogeography theory, in general—had generally been abandoned as a guide to the design of nature reserves.<sup>5</sup> Two problems bedeviled attempts to use these rules from the beginning. The first was skepticism about the empirical status of island biogeography theory independent of conservation concerns, especially because any assumption of equilibrium in natural systems was almost never likely to be warranted (Gilbert 1980; Simberloff 1988). The second, and more important, problem was the relevance of islands to nature reserves which, according to critics, were not sufficiently analogous to islands. In particular, habitat between reserves was not typically as inhospitable to their biota as oceans were to terrestrial biota. The critics emphasized that the assumption of close analogy was an empirical claim that had not been established through appropriate experiments (Higgs 1981; Margules et al. 1982; Zimmerman and Bierregaard 1986; Simberloff and Cox 1987; Simberloff 1988). Moreover, they also pointed out that Diamond's geometric rules had not been tested in the field with any genuinely representative set of data. Meanwhile, the invocation of island biogeography theory generated a decade-long "Single Large or Several Small" (SLOSS) dispute which was finally acknowledged as having no resolution: island biogeography theory provided no unequivocal guidance (whether or not it was relevant to conservation), except for Diamond's trivial Rule A (a big protected area is better than a smaller one), and there was no non-contextual answer to the SLOSS question (Soulé and Simberloff 1986; Simberloff 1988). The only claims that were beyond dispute were that a single large reserve is better than a small one and several large reserves were better than a single one. These were hardly surprising.

## 2.2 Scoring and ranking

Island biogeography theory presumed to answer how many species could survive in a given insular habitat. But what were the species (or other biota) that should be included in a particular protected area? If island biogeography theory was equally applicable to all species under all circumstances, as its proponents at least implicitly assumed and its critics explicitly denied (see, especially, Higgs 1981), and there was no constraint on the amount of land that could be put under protection, then the question of identifying such species was moot. But, after the use of island biogeography theory was abandoned, and the stalemate in the SLOSS debate led to a recognition that strategies to ensure the persistence of biota had to be context-dependent, the question of identifying the relevant species became conceptually prior to that of devising strategies for

<sup>5</sup> Simberloff (1988) provided a comprehensive contemporary review.

their persistence. Management strategies would depend on what the biota were that were slated for protection (Margules et al. 1982).

Perhaps even more importantly, once it was realized—by the late 1970s International Union for the Conservation of Nature [IUCN] (1980)—that not all biologically interesting areas would be protected as reserves (there were other powerful demands on land, in particular, for economic development, especially in the post-colonial tropics), it became critical to determine which areas deserved protection. Though terminological usage is not entirely consistent during this period (the 1980s), there is a gradual shift from talk of “reserve design” to “reserve selection:” it mattered where reserves were to be geographically situated. Thus, the new framework of reserve selection algorithms arose from attempts to specify precise “conservation value” in the presence of an over-riding concern for what was called “efficiency” (Pressey and Nicholls 1989b). The new framework was important not as much for its rejection of the use of island biogeography theory as for its focus on the conceptually antecedent problem of identifying conservation priorities in terms of both areas and biota.

These attempts can be traced back to a paper by Ratcliffe (1971) which, for the first time, laid down explicit criteria for the selection of nature reserves. For Ratcliffe and others from that period, the goal was to make attributions of natural value less subjective; the hope was that, ultimately, if quantitative criteria could be devised, a scoring process would be repeatable. By 1977, Ratcliffe had identified ten such criteria: (i) size; (ii) diversity (interpreted as richness of communities and species); (iii) naturalness; (iv) rarity; (v) fragility; (vi) typicalness; (vii) recorded history; (viii) location in an ecological or geographical unit; (ix) potential value; and (x) intrinsic value. Between 1971 and 1978, at least seven other studies suggested richness or diversity (typically interpreted as richness); six suggested rarity; five suggested area; four suggested naturalness; and four suggested representativeness or typicalness.<sup>6</sup> Other proposed criteria included scientific, educational, or amenity value, recorded history, uniqueness, wildlife reservoir potential, and management considerations. In an influential early review (from 1981), Margules and Usher classified these criteria and clearly distinguished between those that were biological and those that were not (Margules and Usher 1981). The former were treated as more important but the latter were also considered relevant because the designation of reserves was recognized as ultimately being a political act.

The aspect of all of these scoring approaches that became a matter of controversy—and ultimately a source of innovation—was that their use was envisioned as static (a one-off step): scores were to be computed once and then areas were ranked according to these scores. The feature that was most commonly used was richness (or diversity interpreted as richness). In all such cases, as Kirkpatrick (1983, p. 128) pointed out: “A major drawback of a listing of priority areas on the basis of a single application of a 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.” For instance, the first and second areas may both have very high species richness; however, if they have many species in common,

<sup>6</sup> These developments are reconstructed in detail in Justus and Sarkar (2002).

selecting both of them may not lead to as many total species being represented as selecting the first and a more depauperate but sufficiently different third area. The problem was particularly severe if there was a constraint on how many areas could be prioritized for reservation as was always the case in practice.

Kirkpatrick's response was to develop a dynamic method, *dynamic* in the sense that it invoked an iterative process that relied on scores being updated as each area is prioritized. It was, as Pressey (2002) has pointed out, the "first reserve selection algorithm." The history of these algorithms will occupy the rest of this paper. However, it should be noted that there were at least some conservation biologists from this period who did not embrace the algorithmic approach but yet identified one feature that would recur in the algorithms: that feature was endemism. In particular, Myers (1988) began a program of designating "hot spots" on the basis of endemism and threat. Even Diamond (1986), when he proposed a network of reserves for Indonesian New Guinea (then known as Irian Jaya), relied on endemism and representativeness (and barely invoked his geometrical rules of a decade earlier). Range restriction (including endemism) was also used by Thomas and Mallorie (1985) for an area prioritization exercise for butterflies in the Atlas mountains of Morocco.

### 3 Iteration and the representation of diversity

As noted earlier, the replacement of scoring and ranking methods by iterative procedures began as early as 1980 with the work of Kirkpatrick in Tasmania (Pressey 2002). The crucial innovation of these procedures was that they were dynamic: the present conservation value of an area had to be updated relative to what areas were already selected. Variants of what is essentially the same strategy were independently introduced four times, twice in Australia, arguably once in the United Kingdom, and once in South Africa.<sup>7</sup>

#### 3.1 Endemic plants of Tasmania

Kirkpatrick prioritized areas for 25 out of 60 endemic or endangered plant species of the central east coast region of Tasmania; the other 35 were deemed to be already adequately protected in reserves. His algorithm is described in detail in Box 1.<sup>8</sup> It was first published in an obscure report in 1980 (Kirkpatrick et al. 1980) but brought to a wider audience through republication in 1983 in what was then the easily the most influential and widely read journal devoted to conservation, *Biological Conservation* in 1983 (Kirkpatrick 1983). The occurrence and abundance of the species were recorded on 460  $1 \times 1 \text{ km}^2$  grid squares. In line with earlier scoring and ranking approaches,

<sup>7</sup> A preliminary analysis of some of these algorithms is to be found in Justus and Sarkar (2002); this paper updates that account, in particular, taking into cognizance the important contributions of Kirkpatrick et al. (1980) and Margules and Nicholls (1987).

<sup>8</sup> Throughout this paper, algorithms will be reconstructed using the same notation as far as possible. The formalism will be restricted to what is necessary. When there is *any* divergence between the reconstruction and the (occasionally verbal) descriptions of the original sources, it will be explicitly noted. (Throughout " $\Rightarrow$ " is being used for "such that.")



Kirkpatrick classified the 25 species into four categories: (i) not in reserves and largely confined to the study area; (ii) poorly represented in reserves and largely confined to the study area; (iii) not in reserves and more common outside the study area; and (iv) poorly represented in reserves and more common outside the study area. He gave these four classes initial priority values ( $\pi_j$  in Box 1) of 100, 50, 25, and 10, respectively. Now, if, for each grid each grid square, the priority values of the species are added up, a conservation value ( $\kappa_i$ ) is obtained for that square. However, Kirkpatrick noticed that many of the squares with high conservation value had the same species in them.

#### Box 1

##### Kirkpatrick's 1980/1983 Algorithm

Let  $\Sigma$  be the set of areas (sites, landscape units), with  $\sigma_i \in \Sigma$ ,  $i = 1, \dots, n$ , being the individual areas. Let  $\Lambda$  be the set of species, with  $\lambda_j \in \Lambda$ ,  $j = 1, \dots, m$ , being the individual species. Let the priority value of the  $j$ th species be  $\pi_j$ . Let the conservation value of the  $i$ th area,  $\sigma_i$ , be  $\kappa_i$ ; let the minimal conservation value for a potential protected area be  $K$ . Let the conservation value of the  $j$ th species,  $\lambda_j$ , in the  $i$ th area,  $\sigma_i$ , be  $\psi_{ij}$ . Let  $\Gamma$  be the set of areas that have already been selected.

$$\text{Let } X_{ij} = \begin{cases} 1 & \text{if } \lambda_j \in \sigma_i \\ 0 & \text{if } \lambda_j \notin \sigma_i \end{cases}$$

Set  $\Gamma$  equal to the null set,  $\emptyset$ .

The algorithm consists of repeating the following four stages until  $\forall \sigma_i \in \Sigma \setminus \Gamma$ ,  $\kappa_i < K$ :

1.  $\forall \lambda_j \in \Lambda$ ,  $\sigma_i \in \Sigma \setminus \Gamma$ ,  

$$\text{set } \psi_{ij} = \begin{cases} \pi_j & \text{if } \lambda_j \text{ occurs once in } \wp(\Gamma) \\ \frac{1}{2}\pi_j & \text{if } \lambda_j \text{ occurs twice in } \wp(\Gamma) \\ 0 & \text{if } \lambda_j \text{ occurs more than twice in } \wp(\Gamma) \end{cases}$$
2.  $\forall \sigma_i \in \Sigma \setminus \Gamma$ , set  $\kappa_i = \sum_{j=1}^m X_{ij} \psi_{ij}$ .
3. Select  $\sigma_k \in \Sigma \setminus \Gamma \ni \kappa_k = \max_{\kappa_i} (\Sigma \setminus \Gamma)$ , that is, the remaining area in  $\Sigma \setminus \Gamma$  with the highest conservation value.
4. Update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ .

His response was to pick only the best of these squares (Stages 3 and 4 in Box 1). After that the conservation values of a species in a cell ( $\psi_{ij}$  in Box 1; see Stage 1) was updated by downgrading depending on the number of squares in which it already occurred. Squares continued to be selected until no remaining area had a conservation value less than a minimum ( $K$  in Box 1, set to 30 in Kirkpatrick's application). The selected squares were grouped and surrounded by 0.5km buffers to create seven nominal reserves; they were all eventually legally protected though the

process took almost 20 years. Thus, the results of the first reserve selection algorithm were fully implemented; it remains the only such case (Pressey 2002; Sarkar et al. 2006). Subsequently, Kirkpatrick and Harwood (1983) used the same algorithm to prioritize Tasmanian wetlands as well as areas in Tasmania's alpine region (Kirkpatrick 1986). A few years later, it was also used to prioritize areas for angiosperm conservation for all of Tasmania on a  $10 \times 10 \text{ km}^2$  grid with the additional constraint that each endemic species had to occur in at least two selected squares (Kirkpatrick et al. 1991).

### 3.2 Milkweed butterflies of the world

In 1984, P. R. Ackery and R. I. Vane-Wright of the Butterfly Section of the British Museum (Natural History) published a comprehensive account of the milkweed butterflies (Danainae, subfamily of the Lepidoptera, Nymphalidae) (Ackery and Vane-Wright 1984). The book was almost entirely about the cladistics and organismic biology of danaine butterflies; however, one short (three pages, pp. 156–158) section broached the problem of conservation. It is sometimes interpreted to present an algorithm for the prioritization of areas (e.g., Pressey et al. 1993; Justus and Sarkar 2002; Sarkar 2005) but this may well be only because Vane-Wright and collaborators were responsible for the introduction of the term, “complementarity” (Vane-Wright et al. 1991) and most of these algorithms came to known as complementarity-based algorithms (see Sect. 4).

#### Box 2

##### Ackery and Vane-Wright's 1984 Algorithm

Let  $\Sigma$  be the set of islands and biogeographic zones, with  $\sigma_i \in \Sigma, i = 1, \dots, n$ , being the individual units. Let  $\Lambda$  be the set of species, with  $\lambda_j \in \Lambda, j = 1, \dots, m$ , being the individual species. Let  $\Gamma$  be the set of areas that have already been selected.

Set  $X_{ij} = \begin{cases} 1 & \text{if } \lambda_j \in \sigma_i \\ 0 & \text{if } \lambda_j \notin \sigma_i \end{cases}$ .

Set  $\Gamma$  equal to the null set,  $\emptyset$ .

The algorithm consists of the following two stages:

1.  $\forall \lambda_j \in \Lambda$ , repeat:  
If  $\sum_{i=1}^n X_{ij} = 1$ , then update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$  if  $X_{jk} = 1$ .
2. Update  $\Gamma$  to  $\Gamma \cup \Omega$  where  $\Omega \subseteq \Sigma \ni$   
 $\sum_{\sigma_i \in \Gamma} X_{ij} = m$  and  $|\Omega|$  is the minimum possible.

To the extent that Ackery and Vane-Wright produced an algorithm, it is reconstructed in Box 2. They divided the world into islands and biogeographic zones in

continental landmasses. Then they prioritized each of the units that had at least one endemic species (Stage 1 in Box 2). Then they required the prioritization of the minimum number of units that would ensure full coverage of all the species (Stage 2 in Box 2). The sense in which this description is not an algorithm is that the second stage is under-specified: it stated a problem to be solved (a constrained optimization problem) but did not provide step-by-step instructions to solve it (which is what an algorithm, *by definition*, is supposed to do).

### 3.3 Minimal sets in Australia

Ackery and Vane-Wright's algorithm was an advance over Kirkpatrick's only in the very mitigated sense that it used no arbitrary scoring of species according to their presumed conservation value: all species were slated for representation at least once. However as an algorithm, it was a step backward, as noted earlier, because of under-specification. The next advances in algorithm design came from Australia in work done by Chris Margules and several collaborators, mainly at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Division of Water and Land Resources in Canberra. Four different algorithms were developed by this group, along with two relatively minor variants. Unlike Kirkpatrick's analysis, in another important innovation, these algorithms were encoded into computer programs (written in Fortran) by Nick Nicholls from CSIRO (Margules and Sarkar 2007) and were used to produce nominal reserve networks for further analysis.

In retrospect the first algorithm, from 1987, appears to have been the most conceptually innovative though it was not developed further. Unlike the later algorithms, it attempted to predict and use probabilities of occurrence of biota in habitat units (individual areas). In contrast, later algorithms assumed that a feature was definitely present at a site or that it was not: there was no option to incorporate uncertainty. The 1987 algorithm was due to Margules and Nicholls and was part of a prioritization of 101 areas (mallee patches<sup>9</sup>) by conservation value in South Australia on the basis of vegetation assemblages. (Margules and Nicholls 1987). They used a hierarchical aggregation method to classify the vegetation into six "communities." Logistic regression was then used to estimate a probability of occurrence for each community on each habitat patch.

Areas (patches) were then prioritized using the algorithm reconstructed in Box 3. This algorithm implicitly assumed that the probabilities of occurrence of communities in different areas were independent of each other. It tried to ensure a 95 % probability of occurrence of each community in at least one of the selected areas. In Stage 1, the six areas with each of the highest probabilities of occurrence for each community is selected (in Box 3, the cell with the highest  $\varpi_{ij}$ ): it is presumed that these are unique in the sense that no area has the highest probability of occurrence for more than one community. In Stage 2, areas are selected to ensure the satisfaction of the 95 % target

<sup>9</sup> These are patches with any of a large class of eucalyptus species.

for each community.<sup>10</sup> Patches are selected that contribute the highest probability for a community that is still represented at a level below the 95 % target; ties are broken using the area of the patch. The targets were all achieved with 12 patches. If the target was changed to 99 %, 17 patches were required.

### Box 3

#### Margules and Nicholls' 1987 Algorithm

Let  $\Sigma$  be the set of areas (patches), with  $\sigma_i \in \Sigma$ ,  $i = 1, \dots, n$ , being the individual units. Let  $\Lambda$  be the set of plant communities, with  $\lambda_j \in \Lambda$ ,  $j = 1, \dots, m$ , being the individual plant communities. Let  $w_{ij}$  be the probability of occurrence of the  $j$ th community,  $\lambda_j$ , in the  $i$ th patch,  $\sigma_i$ . Let  $\Gamma$  be the set of patches that have already been selected.

Set  $\Gamma$  equal to the null set,  $\emptyset$ .

The algorithm consists of the following two stages:

1.  $\forall \lambda_j \in \Lambda$ :
  - (a) Select  $\sigma_k \in \Sigma \ni w_{kj} = \max_{w_{ij}}(\Sigma)$ .
  - (b) If there are ties, select the  $\sigma_k$  with the largest area.
  - (c) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ .
2. If  $\exists \lambda_j \in \Lambda \ni \prod_{\sigma_i \in \Gamma} (1 - w_{ij}) \geq 0.05$ , for each such  $\lambda_l$ :
  - (a) Select  $\sigma_k \in \Sigma \setminus \Gamma \ni w_{kl} = \max_{w_{il}}(\Sigma)$ .
  - (b) If there are ties, select the  $\sigma_k$  with the largest area.
  - (c) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ .

The following year, Margules, Nicholls, and Bob Pressey,<sup>11</sup> presented two algorithms in perhaps the single most influential paper on reserve selection from that period. While Margules and Nicholls (1987) seem to have been unaware of Kirkpatrick's work, this paper referred to it explicitly. The aim was to prioritize a set of wetlands from a total of 432 such areas in the Macleay Valley in coastal New South Wales in Australia.

<sup>10</sup> The reconstruction in Box 3 follows Margules and Nicholls' (1987, p. 97) numerical treatment rather than their verbal description which states that Stage 2 is carried out for all communities at each stage rather than only for those that have yet to meet the target in  $\Gamma$ . This is critical because, otherwise, the algorithm would reduce to a variant of maximizing richness which was clearly not their intention (p. 87). The verbal description also does not mention that ties in maximum probabilities were supposed to be broken using the area of the patch in Stage 1.

<sup>11</sup> In contrast to Margules and Nicholls, Pressey was not from CSIRO but from the New South Wales National Parks and Wildlife Service.

## Box 4

**Margules, Nicholls, and Pressey's 1988 Algorithm I**

Let  $\Sigma$  be the set of wetlands, with  $\sigma_i \in \Sigma$ ,  $i = 1, \dots, n$ , being the individual units. Let  $\Lambda$  be the set of plant species, with  $\lambda_j \in \Lambda$ ,  $j = 1, \dots, m$ , being the individual plant species. Let  $\Gamma$  be the set of wetlands that have already been selected. Let  $\Lambda'$  be the set of species represented in  $\Gamma$ .

Let  $X_{ij} = \begin{cases} 1 & \text{if } \lambda_j \in \sigma_i \\ 0 & \text{if } \lambda_j \notin \sigma_i \end{cases}$ .

Let  $\rho_j = \frac{1}{\sum_{i=1}^n X_{ij}}$ , which measures the rarity of  $\lambda_j$ .

Let  $\phi_j = \frac{\sum_{i=1}^n X_{ij}}{\sum_{j=1}^m \sum_{i=1}^n X_{ij}}$ , which measures the frequency of  $\lambda_j$ .

Set  $\Gamma$  and  $\Lambda'$  equal to the null set,  $\emptyset$ .

The algorithm consists of the following two stages:

1.  $\forall \lambda_j \in \Lambda$ ,  $\forall \sigma_i \in \Sigma$ , if  $\exists! \sigma_k \ni X_{kj} = 1$ , update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ .
2. Repeat until  $\Lambda' = \Lambda$ :
  - (a) Select  $\lambda_p \ni \rho_p = \max_{\lambda_j} (\Lambda \setminus \Lambda')$ .
  - (b) Select  $\sigma_k \ni X_{kp} = 1$ .
  - (c) If there is a tie, select  $\sigma_q \ni \sum_{\lambda_j \in \Lambda \setminus \Lambda'} X_{qj}$  is the maximum; otherwise,  $\sigma_q = \sigma_k$ .
  - (d) If there is a tie, select  $\sigma_r \ni \sum_{\lambda_j \in \Lambda \setminus \Lambda'} X_{ij} \phi_j$  is the minimum; otherwise,  $\sigma_r = \sigma_q$ .
  - (e) If there is a tie, select  $\sigma_s$  by lexical order; otherwise,  $\sigma_s = \sigma_r$ .
  - (f) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_s\}$ .
  - (g)  $\forall \lambda_j \in \Lambda \setminus \Lambda'$ , if  $\sum_{\sigma_i \in \Gamma} X_{ij} > 0$ , update  $\Lambda'$  to  $\Lambda' \cup \{\lambda_j\}$ .

The first algorithm, reconstructed in Box 4, was designed to represent each of 118 plant species at least once in a minimal set of wetlands. In the first stage (Stage 1 of Box 4), each wetland that contained at least one species unique to it was selected. In the second iterative stage, the algorithm first tried to select a wetland with the rarest species not yet represented (in  $\Gamma$ , with rarity parameterized by  $\rho_j$ ; Steps 2(a)–(b) in Box 4). If there was a tie, the algorithm selected the wetland that contributed the highest number of unrepresented species (Step 2(c)). If a tie still remained, it selected the wetland with the least frequent group of species (with frequency measured by  $\phi_j$  in Box 4, Step 2(d)). (In retrospect, this step is problematic: a unit with a very few common species would potentially be selected over one with many rare species. This step disappears or is replaced in *all* published later variants of this algorithm.) Remaining ties were broken using the first wetland in the list. The iteration terminated when all species were represented. Twenty wetlands were required for this purpose. Straightforward modifications allowed the required representation level to be increased to  $n > 1$ .

## Box 5

**Margules, Nicholls, and Pressey's 1988 Algorithm II**

Let  $\Sigma$  be the set of wetlands, with  $\sigma_i \in \Sigma$ ,  $i = 1, \dots, n$ , being the individual units. Let  $\Lambda$  be the set of plant species, with  $\lambda_j \in \Lambda$ ,  $j = 1, \dots, m$ , being the individual plant species. Let  $\Xi$  be the set of habitat types, with  $\xi_l \in \Xi$ ,  $l = 1, \dots, p$ , being individual habitat types. Now,  $\Xi$  constitutes a partition of  $\Sigma$ : each habitat type is composed of a certain number of wetlands and no wetland belongs to more than one habitat type.

Let  $\Gamma$  be the set of wetlands that have already been selected. Let  $\Lambda'$  be the set of species represented in  $\Gamma$ .

Let  $X_{ij} = \begin{cases} 1 & \text{if } \lambda_j \in \sigma_i \\ 0 & \text{if } \lambda_j \notin \sigma_i \end{cases}$ .

Set  $\Gamma$  and  $\Lambda'$  equal to the null set,  $\emptyset$ .

Repeat the following procedure until  $\Gamma' = \Gamma$ :

1.  $\forall \xi_l \in \Xi$ , select  $\sigma_k \in \xi_l \ni \sum_{j=1}^m X_{kj}$  is the maximum.
2.  $\forall \xi_l \in \Xi$ , if  $\exists \sigma_i \in \xi_l \ni \exists \lambda_j \in \Lambda \setminus \Lambda'$  with  $X_{ij} = 1$ :
  - (a) Select  $\sigma_k \ni \sigma_k = \max_{\sigma_i \in \xi_l \cap (\Sigma \setminus \Gamma)} \sum_{\lambda_j \in \Lambda \setminus \Lambda'} X_{ij}$ .
  - (b) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ ; update  $\Lambda'$ .

The second algorithm, reconstructed in Box 5, was designed to ensure the representation of all habitat types besides species. The wetlands were classified into nine types ( $\xi_l$  in Box 5). In the first stage, the algorithm selected the wetland from each type with the highest species richness (Stage 1 of Box 5). (In retrospect this stage is problematic because it did not assay wetlands for the number of shared species, which it should have even though the similarity was likely to be small because of the difference in type.) In the second stage, until all species were represented, the algorithm continued to select one wetland from each type which maximized the number of new species (Step 2(a) of Box 5).

The first of these two algorithms (hereafter, the "MNP" algorithm, with the acronym interpreted as the algorithm without Step 2(d)) became the basis for further development by this group. In 1989, Margules (1989b) used an algorithm that replaced the problematic Step 2(d) of the MNP algorithm by a second use of rarity; it also allowed ties to be broken in favor of larger areas before invoking lexical order. Variable required levels of representation were allowed from the beginning. The algorithm was used to select reserves to include vegetation alliances in natural vegetation remnants in the mallee lands of South Australia. Because of its publication in a somewhat obscure

book Bradstock and Noble (1989), this algorithm went unnoticed even though it corrected a fairly obvious flaw of the MNP algorithm (*viz.*, Step 2(d)). Pressey and Nicholls (1989a) modified the MNP algorithm in a different way: before invoking lexical order, their algorithm encoded a preference for the smallest unit among which there was a tie. They prioritized pastoral properties in part of western New South Wales to represent all land systems. The results were interesting but what is even more important was that, by then, devising the correct algorithm had become a theoretical problem in its own right as, especially, the work of Cocks and Baird (1989), discussed below in Sect. 5, shows.

The final, much more elaborate, algorithm that emerged from these efforts was published by Nicholls and Margules (1993). Two criticisms motivated the elaboration: that there should be a premium on having less distance between reserves, and that invoking lexical order to break ties made selected sets far too dependent on the order of presentation of the data.<sup>12</sup> This algorithm is reconstructed in Box 6. It began with an option for the initialization of the set of reserves with some specified units (in set  $I$  in Box 6); this allowed the inclusion of existing reserves. The first stage (Stage 1 of Box 6) was identical to the MNP algorithm as were the first three steps (Steps 2(a)–(c)) of the second stage. If a tie still remained, the unit to be selected was the one that was closest (by  $d_{ij}$  to one of the already selected units (in  $\Gamma$ ; Step 2(d) in Box 6)). The next step (Step 2(e)) again tries to break any remaining tie by maximizing the representation of features which were yet to achieve their targeted levels.

Further ties were to be broken with two successive appeals to the representation of rarest surrogates (Steps 2(f)–(g)).<sup>13</sup> If there was still a tie, the algorithm selected the unit with the least area provided that it would enable the feature to achieve its targeted level; otherwise, it selected the unit with the largest area (Step 2(h)). Nicholls and Margules offered no justification for this rule (and, in retrospect, it is far from clear that any could be forthcoming). If there remained a tie, the unit with the largest area was selected (Step 2(i)). Further ties were resolved by lexical order (Step 2(j)).

<sup>12</sup> As Nicholls and Margules correctly argued, a third criticism, that the data used by the algorithms were inadequate, was irrelevant to the question of the performance of the algorithms.

<sup>13</sup> The reconstruction in Box 6 differs from the verbal description of Nicholls and Margules (p. 160) which makes Step 2(g) identical to Step 2(f), instead of Step 2(g) using the next rarest feature after the execution of Step 2(f) as in Box 6. Otherwise, Step 2(g) becomes redundant.

## Box 6

**Nicholls and Margules' 1993 Algorithm**

Let  $\Sigma$  be the set of units, with  $\sigma_i \in \Sigma$ ,  $i = 1, \dots, n$ , being the individual units. Let  $a_i$  be the area of the unit  $\sigma_i$ . Let  $\Lambda$  be the set of biological features, with  $\lambda_j \in \Lambda$ ,  $j = 1, \dots, m$ , being the individual features. Let  $T$  be the set of representation levels for these features, with  $\tau_j \in T$ ,  $j = 1, \dots, m$ , being the individual features

Let  $I$  be the initial set of selected reserves which may be equal to  $\emptyset$ . Let  $\Gamma$  be the set of units that have already been selected. Let  $\Lambda'$  be the set of features represented in  $\Gamma$ .

Let  $X_{ij} = \begin{cases} 1 & \text{if } \lambda_j \in \sigma_i \\ 0 & \text{if } \lambda_j \notin \sigma_i \end{cases}$ .

Let  $d_{rs}$  be the distance between units  $\sigma_r$  and  $\sigma_s$ .

Let  $\rho_j = \frac{1}{\sum_{i=1}^n X_{ij}}$ , the rarity of  $\lambda_j$ .

Set  $\Gamma$  equal to  $I$  and  $\Lambda'$  equal to the null set,  $\emptyset$ .

The algorithm consists of the following two steps:

1.  $\forall \lambda_j \in \Lambda$ ,  $\forall \sigma_i \in \Sigma$ , if  $\exists! \sigma_k \ni X_{kj} = 1$ , update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ .
2. Repeat until  $\Gamma' = \Gamma$ :
  - (a) Select  $\lambda_p \ni \rho_p = \max_{\rho_j}(\Lambda')$ .
  - (b) Select  $\sigma_k \ni X_{kp} = 1$ .
  - (c) If there is a tie, select  $\sigma_q \ni \sum_{\lambda_j \in \Lambda \setminus \Lambda'} X_{qj}$  is the maximum; otherwise,  $\sigma_q = \sigma_k$ .
  - (d) If there is a tie, select  $\sigma_r \ni \forall \sigma_e \in \Gamma$ ,  $\forall \sigma_f \in \Sigma \setminus \Gamma$ ,  $d_{ef}$  has  $d_{ek}$  as the minimum; otherwise  $\sigma_r = \sigma_q$ .
  - (e) If there is a tie, select  $\sigma_s \ni \sum_{\lambda_j \in \Lambda \setminus \Lambda'} X_{sj}$  is the maximum; otherwise  $\sigma_s = \sigma_r$ .
  - (f) If there is a tie, select  $\sigma_t \ni \rho_k = \min_{\rho_j}(\Lambda \setminus \Lambda')$  and  $\sum_{\sigma_i \in \Gamma \cup \{\sigma_t\}} X_{ik} > \tau_k$ ; otherwise  $\sigma_t = \sigma_s$ .
  - (g) If there is a tie, select  $\sigma_u \ni \rho_l = \min_{\rho_j}(\Lambda \setminus (\Lambda' \cup \{\lambda_k\}))$  and  $\sum_{\sigma_i \in \Gamma \cup \{\sigma_u\}} X_{il} > \tau_l$ ; otherwise  $\sigma_u = \sigma_t$ .
  - (h) If there is a tie, select  $\sigma_v \ni \rho_k = \min_{\rho_j}(\Lambda \setminus \Lambda') \wedge (a_v \text{ is the minimum if } \sum_{\sigma_i \in \Gamma \cup \{\sigma_v\}} X_{ik} \geq \tau_k \text{ or } a_v \text{ is the maximum if } \sum_{\sigma_i \in \Gamma \cup \{\sigma_v\}} X_{ik} < \tau_k$ ; otherwise  $\sigma_v = \sigma_u$ ;
  - (i) If there is a tie, select  $\sigma_w \in \Sigma \setminus \Gamma \ni a_w$  is the minimum; otherwise  $\sigma_w = \sigma_v$ .
  - (j) If there is a tie, select  $\sigma_z$  by lexical order; otherwise,  $\sigma_s = \sigma_w$ .
  - (k) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_z\}$ .
  - (l)  $\forall \lambda_j \in \Lambda \setminus \Lambda'$ , if  $\sum_{\sigma_i \in \Gamma} X_{ij} > \tau_j$ , update  $\Lambda'$  to  $\Lambda' \cup \{\lambda_j\}$ .

Nicholls and Margules presented an example (from south-eastern New South Wales, divided into 371 regular  $3 \times 3 \text{ km}^2$  grid cells with 31 forest tree communities). But the focus of the work was the algorithm itself. In particular, they emphasized the



contrast between results obtained with spatial distance was incorporated (Step 2(d) of Box 6) versus when it was not. Even earlier, Pressey and Nicholls (1989b) had introduced a measure for the “efficiency” of a reserve network:  $e = 1 - \frac{x}{t}$ , where  $x$  is the size of the units selected to represent biological features adequately and  $t$  is the total size of all the units.<sup>14</sup> By this measure, any of the iterative algorithms developed by this group outperformed the use of static scores to select units. Nevertheless, these algorithms were heuristic and not guaranteed to produce the most efficient solutions. Attempts to produce optimal (most “efficient” in this terminology) solutions would lead to another set of developments, also initiated at CSIRO’s Division of Wildlife and Ecology (Sect. 5).

### 3.4 Fynbos vegetation in South Africa

Iterative algorithms were also independently introduced in South Africa in 1990 to prioritize areas to protect Fynbos vegetation<sup>15</sup> in the Cape Floristic Region. (The algorithm is reconstructed in Box 7.) A. G. Rebelo and W. R. Siegfried, at the Percy Fitzpatrick Institute of African Ornithology of the University of Cape Town, used a  $12 \times 12 \text{ km}^2$  grid to map 326 taxa (species and distinct subspecies). They first distributed four intersecting transects across the study area based on richness (Rebelo and Siegfried 1990). On each transect, a grid cell (the “primary core square”; p. 20) was selected using the highest richness (Stage 1 in Box 7). At the next stage, cells (“secondary core squares”) were iteratively selected along the transect provided that they shared less than half their species with those already in the selected squares and added at least a quarter new species (Stage 2 in Box 7). Finally, cells were selected from the rest of the study area on the basis of new species that they contained (Step 3(a)); ties were broken using richness (Step 3(b)); remaining ties were broken using the amount of Fynbos vegetation in a cell (Step 3(c)). It was assumed that there would be no further ties. They found that 95 % of the species could be accommodated in 16 % of the study area. Even more importantly, they pointed out that <17 % of the existing and <50 % of the proposed protected areas were in cells with high species endemism.

For this group, too, algorithms immediately became the focus of research. In 1992, they produced two algorithms based on two rules used in the MNP algorithm (Rebelo and Siegfried 1992): (i) which cells added the most new species; and (ii) which cells added the rarest species. Their first algorithm used Rule (i) first and Rule (ii) to break ties. The second algorithm reversed this order. In both cases remaining ties were broken by a random selection of a cell. With respect to efficiency (*sensu* Pressey and Nicholls 1989b), both algorithms performed almost equally well. Strangely, they interpreted Rule (i) as being richness and explicitly, but mistakenly, disagreed with Margules et al.’s (1982) criticism of the use of richness to prioritize areas. They seemed

<sup>14</sup> Size was to be interpreted either as the number of units or their total area.

<sup>15</sup> This consists of natural shrubland or heathland vegetation which occurs in a small belt of the Western Cape of South Africa.

to have been unaware that this rule now had a name: “complementarity,” which is the focus of the next section.

### Box 7

#### Rebello and Siegfried's 1990 Algorithm

Let  $\Sigma$  be the set of areas, with  $\sigma_i \in \Sigma, i = 1, \dots, n$ , being the individual units; let  $\phi_i$  be the amount of Fynbos vegetation in each  $\sigma_i$ . Let  $\Lambda$  be the set of plant species, with  $\lambda_j \in \Lambda, j = 1, \dots, m$ , being the individual plant species. Let  $T$  be the set of richness transects, with  $\tau_l, l = 1, \dots, p$  being the individual transects. Let  $\Gamma$  be the set of areas that have already been selected. Let  $\Lambda'$  be the set of species represented in  $\Gamma$ .

$$\text{Let } X_{ij} = \begin{cases} 1 & \text{if } \lambda_j \in \sigma_i \\ 0 & \text{if } \lambda_j \notin \sigma_i \end{cases}.$$

Set  $\Gamma$  and  $\Lambda'$  equal to the null set,  $\emptyset$ .

The algorithm consists of the following stages:

1.  $\forall \tau_l \in T$ :
  - (a) Select  $\sigma_k \in \tau_l \ni \sum_{\lambda_j \in \Lambda} X_{kj}$  is the maximum.
  - (b) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ ; update  $\Lambda'$ .
2.  $\forall \tau_l \in T$ ,
  - (a)  $\forall \sigma_k \in \tau_l$ , if  $\sigma_k \in \tau_l \ni \frac{\sum_{\lambda_j \in \Gamma \cap \{\sigma_k\}} X_{kj}}{|\Lambda'|} < 0.5 \vee \frac{\sum_{\lambda_j \in \Gamma \cup \{\sigma_k\}} X_{kj}}{|\Lambda'|} > 0.25$ .
  - (b) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_k\}$ ; update  $\Lambda'$ .
3. Order the remaining areas according to the rule:
  - (a) Select  $\sigma_k \in \Sigma \setminus \Gamma \ni \sum_{\lambda_j \in \Lambda \setminus \Lambda'} X_{jk}$  is the maximum.
  - (b) If there is a tie, select  $\sigma_p \ni \sum_{\lambda_j \in \Lambda} X_{jk}$  is the maximum; otherwise  $\sigma_p = \sigma_k$ .
  - (c) If there is a tie, select  $\sigma_q \ni \phi_i$  is the maximum; otherwise  $\sigma_q = \sigma_p$ .
  - (d) Update  $\Gamma$  to  $\Gamma \cup \{\sigma_q\}$ ; update  $\Lambda'$ .

## 4 Complementarity as principle

One theme ran through the thinking of all four of these groups (from Sect. 3): that selecting reserves was best accomplished iteratively by using as one of the rules the prioritization of an area that added the most features that were not yet included in the selected set up to the required level of representation. Second, they all emphasized rarity and endemism to some extent, with the MNP algorithm and its derivatives giving rarity precedence over all other rules. By 1989, Margules had stated the constrained optimization problem that was being solved explicitly: “what is the minimum set of

sites in an ecological domain which represents all species (or other units of diversity) at least once? (Margules 1989a, p. 7).” He had gone on to note: “This minimum set ... is the smallest set of sites that are required for a reserve network if all species are to be represented. It is the bottom line; the bare minimum. Anything less would constitute an inadequate representation of biological diversity (p. 7).” Meanwhile, Pressey and Nicholls (1989b) had introduced their notion of “efficiency” to provide a quantitative measure of this optimality. In retrospect, given that they were working in the context of algorithm design, it was not the happiest of terms to use: in computer science, efficiency referred to the speed of an algorithm. But the term came to be widely used during this period.

What remained to be explicitly named was the first theme mentioned above. Vane-Wright et al. (1991) proposed a term that eventually came to be adopted by the entire community. They noted that:

“procedures [from Sects. 3.1–3.3] are based on a guiding principle—which we call *complementarity*.

In carrying out a simple critical faunas analysis (that is, representation of critical fauna in notional reserves), once the first choice has been made, all further considerations of species included with that region are eliminated. The second area is then drawn from the taxonomic complement of the first—the remaining fauna with the highest 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) (pp. 244–245; *italics in the original*).”

The choice of term was concordant with the use of “complement” in set theory. It came to dominate the field, with any algorithm that used a complementarity calculation coming to be called complementarity-based even if it not only used but gave precedence to some other rule (for instance, rarity in the case of the MNP algorithm) (Justus and Sarkar 2002).

But, was complementarity an algorithm or a principle? Vane-Wright et al. wanted it both ways. There was no obvious inconsistency there: a principle could be embedded as a rule in an algorithmic procedure. However, if it is the algorithm that mattered, it would have to be judged against other algorithms designed to solve the same (class of) problems; however, a principle was immune to such criticism because its value depended on something beyond algorithmic efficiency—these questions will occupy Sect. 5. In the early 1990s, apparently all those who were involved in the development of the iterated procedures of Sect. 3 viewed complementarity as a principle (Pressey et al. 1993; Justus and Sarkar 2002). As they increasingly demonstrated through systematic data analyses, existing reserve networks were not “efficient” but ad hoc (Pressey 1990, 1994; Pressey and Tully 1994) because they had been selected opportunistically (Pressey et al. 1993). Their alternative was to invoke complementarity as the goal of new reserves: intuitively, it captured the sense that, when it came to diversity, it is differences that matter (Vane-Wright 1996).

## 5 Heuristics and optimality

What happened if complementarity was viewed as an algorithm? It was what was known in computer science as a “greedy algorithm:” at each iteration, the best solution at that iteration is selected. Vane-Wright et al.<sup>16</sup> (1991) were aware of this and also that it did not guarantee optimal solutions but went on to argue, incorrectly, that no exact (optimal) solution may be available for large data sets:

“[These] methods proceed by choosing a single site, ideally with a maximum score, at each step. Once a step has been taken, the site is fixed, and only the distribution of the remaining ...complement is considered at the subsequent step. However, a more optimal strategy for obtaining higher average diversity scores per site is possible if multiple-site choices are considered. At the limit this involves selection in one step of a set that contains the entire complement in the smallest possible number of sites. Such multiple site-sets are much more difficult to calculate (indeed, exact methods may not be available for large data matrices, this task being a variant of the ‘traveling salesman’ problem).

What they should have said that the problem was **NP**-hard with some large data sets possibly being computationally intractable by exact methods.<sup>17</sup> More importantly, in the passage quoted in Sect. 4, Vane-Wright et al. were not thinking of the greedy algorithm when they defined complementarity: they were concerned with including both endemic species and new species, and not just the latter (as the greedy algorithm required). What they described had the same effect as a use of the greedy algorithm but that was not the expressed intent.

Exact algorithms (those guaranteed to produce optimal solutions) had already been brought into the discussion at CSIRO by Cocks and Baird (1989) who noted that the problem could be formulated and solved as a mathematical programming problem. They first showed that a relatively simple linear programming problem was relevant to reserve design. Let  $V$  be the aggregate value of a reserve system;  $V$  was then the objective function to be maximized. Let the individual sites (areas) that could be included in reserves be indexed by  $j \in \{1, 2, \dots, J\}$ . Let  $R(j)$  be the reservation value of the  $j$ th site, and let  $x(j)$  be the fraction of it which would be included in the reserve system. Then,  $J = \sum_{j=1}^J R(j)x(j)$ . Let the attributes that were to be represented in the reserve system be indexed by  $i \in \{1, 2, \dots, I\}$ , and let  $b(i)$  be a level for this attribute that must not be exceeded. Let the contribution of the  $j$ th site to the conservation of the  $i$ -attribute be  $a(i, j)$ . Then the reserve selection problem becomes:

<sup>16</sup> This was first pointed out by Underhill (1994) which will be discussed further later in this section.

<sup>17</sup> The allusion to the traveling salesman problem was also misleading; the optimization problem was the set cover problem—see below, in the text. For a discussion of complexity concepts such as **NP**-hardness tailored to this context, see Sarkar et al. (2006).

$$\begin{aligned} \text{Maximize } J &= \sum_{j=1}^J R(j)x(j) \\ \text{subject to } \sum_{j=1}^J a(i, j)x(j) &\geq b(i) \text{ with } (x(j) \geq 0).^{18} \end{aligned}$$

Cocks and Baird noted, this problem was easy to solve because the  $x(j)$  could take continuous values between 0 and 1 and was not restricted to either 0 (the site was excluded) or 1 (the site is included). This made it a linear programming problem rather than an integer programming problem and Karmakar (1984) had already shown that the former belonged in **P**.<sup>19</sup>

Once  $x(i)$  was restricted to integer values, they were faced with what they called an “integer goal programming (IGP) formulation (p. 117)” and what was usually called an integer programming problem (Underhill 1994). They provided a complex formulation of the problem to ensure flexibility so that the objective function could incorporate a wide variety of natural values relevant to conservation. All that was required was that some quantitative function (such as  $J$ ) could be devised which would measure all the natural values that were deemed worthy of protection. This formulation will not be reconstructed here because they did not provide an explicit objective function for the reserve selection problem which is the one they solved for the same data set used by Margules and Nicholls (1987, Sect. 3.3). Let  $x(j)$  be restricted to 0 or 1 as indicated earlier, with  $j \in 1, 2, \dots, J^*$ , where  $J^*$  sites were selected. Let  $p(i, j)$  be the probability of the presence of the  $i$ th community in the  $j$ th site. Cocks and Baird now conceptualized the problem to be one of minimizing the number of sites subject to the constraint.

$$\forall i, \sum_{j=1}^{J^*} 1p(i, j) + 0(1 - p(i, j)) \geq 2.$$

In this somewhat unnecessarily elaborate formulation, the values for the  $x(j)$  have been filled in and the required level of expected representation has been set to 2. Cocks and Baird observed that commercial software packages encoding exact algorithms for integer programming problems were available. When they used one of these packages to solve Margules and Nicholls’ original problem, they found 11 sites to satisfy the constraints; recall that Margules and Nicholls had found 12 (Sect. 3.3). The move to exact algorithms had not led to any spectacular improvement of optimality. But what Cocks and Baird were more interested in was the flexibility of their framework to incorporate all natural values, not only the representation of biological features.

<sup>18</sup> If, as was true for all cases discussed in Sect. 3, the level is a minimum to be achieved, the inequality in the constraint would just have to be reversed. The formula given above corrects an error on Cocks and Baird (p. 116) where the summation in the constraint relation was incorrectly taken to be over  $i$ .

<sup>19</sup> Roughly, this means that, as the size of the problem grows, the time taken to solve the problem (by an exact algorithm) would only grow as a polynomial function of the size.

Four years later, Hugh Possingham and three collaborators, also in Australia (at the University of Adelaide) provided the standard integer programming formulation of the reserve selection problem (Possingham et al. 1983). Let  $i \in 1, 2, \dots, m$  be an index running over sites and  $j \in 1, 2, \dots, n$  be the index running over species. Two control variables were introduced. Let:

$$a_{ij} = \begin{cases} 1 & \text{if species } j \text{ is present at site } i \\ 0 & \text{otherwise} \end{cases}; \text{ and}$$

$$x_i = \begin{cases} 1 & \text{if site } i \text{ is included in the reserve network} \\ 0 & \text{otherwise} \end{cases}$$

Then the “minimum set problem (p. 538)” becomes:

$$\begin{aligned} &\text{Minimize } \sum_{i=1}^m x_i \\ &\text{subject to } \left. \begin{aligned} \sum_{i=1}^m a_{ij} x_i &\geq 1 \\ x_i &\in 0, 1 \end{aligned} \right\} \quad j = 1, 2, \dots, n. \end{aligned}$$

Possingham and his collaborators showed that the use of complementarity alone or of rarity followed by complementarity did not necessarily lead to optimal solutions even with small data sets. However, instead of urging the use of exact algorithms, they explored using heuristic rules repeatedly implicitly acknowledging the power of metaheuristic algorithms (Sect. 6).

However, strong criticism of the use of heuristic algorithms came from Underhill (1994) of the University of Cape Town who noted that complementarity, interpreted as an algorithm was what computer scientists called a greedy algorithm. He, too, produced a simple example in which the use of complementarity did not lead to the optimal solution and urged the use of exact algorithms (more specifically, the “branch-and-bound” algorithm) but, because he did not analyze a single data set with field (rather than artificial) data, there was no progress on the question whether exact algorithms would prove tractable in practice. The tone of the paper was hostile, especially to Vane-Wright et al.’s (1991) elevation of complementarity to a principle. More valuably, Underhill urged a different reserve selection problem to be solved: “maximize the number of species that can be conserved within a fixed financial budget or total area (p. 86).” The importance of this problem—what should be preserved in the presence of ubiquitous budget constraints—would not be recognized in the period before 2000. Underhill also called for conservation biologists to make more use of techniques developed by decision theorists, in particular, multi-criteria analysis. Once again, this idea was not embraced at the time. Underhill had little influence, probably partly because of the hostile tone of his remarks, but more likely because he did not analyze a single field-based data set.

Underhill’s intervention provoked a response from Pressey, Possingham, and Margules whose data showed that the sub-optimality of a variety of heuristic procedures was minimal while exact algorithms became intractable quite easily (Pressey et al.

1996). Several other studies from the same period produced similar results though the extent of the intractability of exact algorithms remained inadequately delineated (Csuti et al. 1997; Pressey et al. 1997). There was no resolution of the dispute that satisfied both sides though a consensus set in that, given the complexities of reservation decisions in the field, the apparently slight loss of optimality by the use of fast heuristic algorithms was more than compensated by the flexibility of creating and exploring many scenarios. Moreover, the complexities of the factors influencing “real-world” implementation of the minimum sets produced by the algorithms made worries about limited sub-optimality seem baroque (Pressey 1998). Some of these new studies came from the United States, marking the maturation of personal and collaborative contacts that would eventually lead to a consensus framework for systematic conservation planning (Sarkar 2002).

Probably the chief factor in exact algorithms not making any headway during this period is the failure of their advocates to analyze sufficiently many “realistically complex” data sets to convince critics of their tractability. In retrospect, what is also ironic is that the proponents of the exact algorithms do not seem to have been aware that the reserve selection algorithm was one of the most-studied mathematical programming problems and was dubbed the “set covering problem” as early as 1971 (Toregas et al. 1971). Consequently, it was known exactly how sub-optimal the use of a greedy algorithm could be (Chvatal 1979): if  $m$  is the maximum richness of one of the sites in the data set, then the size of the solution produced by the greedy algorithm could potentially be more than that of the optimal solution by a multiplicative factor of  $H(m) = \sum_{i=1}^m \frac{1}{i}$ . By the time  $m$  reaches 5, that is, some unit could have as many as 5 species (or whatever biological feature is of interest), the solution produced by complementarity could potentially have twice as many units as the optimal solution. This is speculative but, had the proponents of the exact algorithms been more cognizant of ongoing research in operations research, some of the differences between them and proponents of heuristic algorithms may have been clarified and, perhaps, partially resolved.

## 6 Denouement

The next decade saw the development of a wide array of software tools implementing algorithms for reserve selection. There was also a widespread belief that the spatial configuration of reserves should be incorporated into their selection, as Nicholls and Margules (1993) had already begun to do—this point will merit further discussion in Sect. 7.2. The most important conceptual innovation was the introduction of metaheuristic algorithms which were designed to achieve a higher degree of optimality than heuristic algorithms but without sacrificing speed (as in the case of exact algorithms). Metaheuristic algorithms repeatedly applied a one-step heuristic rule (such as the greedy algorithm) to improve performance until an independent exit condition was satisfied.

In 1996, Ian Ball at the University of Adelaide produced a program called SPEX-AN (which was supposed to stand for “spatially explicit annealing”) as part of a

doctoral dissertation (Ball 1996).<sup>20</sup> It used simulated annealing to solve the representation problem while optimizing for compact shape. This was the first published use of a metaheuristic algorithm for the reserve selection problem.<sup>21</sup> The significance of simulated annealing was that it allowed for much greater control over the spatial configuration of reserves than what heuristic algorithms, such as those of Nicholls and Margules (1993), could achieve. It also remained tractable when faced with the largest data sets analyzed in the 1990s. Starting in 1997, another metaheuristic algorithm, tabu search, began to be used (Okin 1997) though, initially, without considerations of spatial design.<sup>22</sup>

Around the same time or shortly afterward, a variety of software tools for the reserve selection problem began to be developed which continued to use heuristic algorithms. These included WorldMap (which had been developed by 1991) (Vane-Wright et al. 1991), C-Plan (Pressey 1998), Target (which included cost trade-offs in a new definition of complementarity) (Walker and Faith 1998), ResNet (Kelley et al. 2002; Sarkar et al. 2002) (based on the original MNP algorithm), and Zonation (Moilanen et al. 2005). Exact algorithms continued to have advocates (Rodrigues et al. 2000; Reville et al. 2002; Rodrigues and Gaston 2002) but it became clear that complex spatial problems with large data sets could not be solved in reasonable time using exact algorithms.<sup>23</sup> To the extent that issues of spatial configuration mattered, for the decade after 1995, metaheuristic algorithms had come to stay. Shape was not the only criterion used in algorithm design; connectivity and dispersion, alignment (with habitat types or even with political units), and a variety of other spatial criteria began to be explored (Sarkar et al. 2006).

## 7 Discussion and conclusions

How important was the development of these algorithms? As far as practical conservation decisions are concerned, at least up to 2000, they were of little significance (Justus and Sarkar 2002). The only result of the algorithms that was fully implemented by on-ground protection of areas was that produced by Kirkpatrick (1983) in Tasmania with the very first use of such an algorithm as discussed earlier in this paper (Sect. 3.1). Moreover, successful implementation was a result of the political context of Tasmania—and Kirkpatrick's personal and institutional relations—rather than any recognition of the innovativeness of the method (Pressey 2002). There were some initial partial implementation in New South Wales in the mid-1990s but these efforts were subsequently abandoned (Finkel 1998a,b; Justus and Sarkar 2002). That

<sup>20</sup> SPEXAN eventually morphed into MARXAN, a widely used software package for the selection of reserve networks—see Ball et al. (2009) for this history.

<sup>21</sup> Even though the term “metaheuristic” was introduced as early as 1986 in the context of tabu search (Glover 1986), and simulated annealing is a metaheuristic algorithm, it was not used in this context until 2006 (Sarkar et al. 2006).

<sup>22</sup> For recent extensions, see Ciarleglio (2008); Ciarleglio et al. (2009).

<sup>23</sup> For a historically sophisticated scientific review of this problem, which is only slightly more optimistic about exact algorithms, see Williams et al. (2005).



situation began to change somewhat after 2000 but that story is beyond the scope of this paper (Margules and Sarkar 2007).

However, what was really important about the algorithmic turn is that it led to conservation biology embracing a distinctive set of formal theories and technical practices that were not in vogue in the ecology of that period. By the time Cocks and Baird (1989) introduced mathematical programming into the discussion, *algorithms* had become a focus of research, a development then unknown to ecology. This focus was made possible by Margules, et al.'s (1988) clear distinction between the “representativeness” problem and the “persistence” problem. The first algorithms, before spatial configuration became an issue, were only supposed to solve the former problem. The earlier attempts to use island biogeography to design reserves (recall the discussion of Sect. 2.1) were restricted to the latter.<sup>24</sup> The critical point is that the representation problem did not require biological solution: it was a formal problem to be solved using mathematical tools (albeit those from the type of applied mathematics typically studied in computer science and operations research).

However, it was not true that ecology had no theoretical tool with which representativeness could be analyzed. As Magurran (2003) has claimed, complementarity was a measure of what ecologists had long explored as  $\beta$ -diversity. Yet,  $\beta$ -diversity finds no mention in the developments discussed in this paper (though Rebelo and Siegfried (1990, p. 15) and Vane-Wright et al. (1991, p. 237) do mention it)—this issue is discussed in Sect. 7.1. What is more interesting is that the move to incorporate considerations of spatial configuration at least seems as if it is a return to the geometric rules of island biogeography theory. This issue is briefly discussed in Sect. 7.2 though a full discussion is beyond the scope of this paper because most of the relevant work comes from a later period.

### 7.1 Why Not $\beta$ -Diversity?

As early as 1960, Whittaker (1960) had distinguished between three concepts of diversity:  $\alpha$ -diversity,  $\beta$ -diversity, and  $\gamma$ -diversity. A region was supposed to be divided

<sup>24</sup> Margules et al. (1988, p. 64) explicitly note this difference in the motivations of the work in conservation biology in the late 1980s and the earlier work of the ecologists. A strangely obtuse misinterpretation of these developments has recently been provided by Linquist (2008) who criticizes these algorithms (and Margules and his collaborators explicitly) for not incorporating persistence into the original reserve selection algorithms (and, more specifically, the MNP algorithm). The criticism is bizarre: “the persistence of biological diversity in perpetuity (Margules et al. 1988, p. 64)” was supposed to be ensured through proper management of reserves after the algorithms were used to ensure that the set of reserves represented the biological features adequately; adequate representation was a “prerequisite” for measures to ensure persistence (p. 64). Rebello and Siegfried (1990, p. 24) also make this point explicitly. Linquist also seems to be entirely oblivious of the fact that what was guiding the design of these algorithms was a concern for cost, as Kirkpatrick (1983) explicitly noted, and what Pressey and others (e.g., Pressey and Nicholls 1989b; Vane-Wright et al. 1991; Rebelo and Siegfried 1992) called “efficiency” starting in the late 1980s. Island biogeography theory and reserve selection algorithms were *intended* by their proponents to solve *different* problems. Diamond explicitly noted that his rules would sometimes have to be violated to sample (that is, represent) all species adequately, for instance, on a heterogeneous landscape (Diamond 1975, p. 144). For a recent reappraisal of the relations between the two research programs, see Williams et al. (2005) which Linquist ignores.

into a set of units (areas).  $\alpha$ -diversity was supposed to measure the diversity within a unit. Over the years, a large variety of measures were proposed for it; most of these focused on species richness and evenness.<sup>25</sup> In the 1960s and 1970s, a central claim of ecology was that higher  $\alpha$ -diversity led to greater stability of ecosystems. By the 1980s attempts to establish or disprove this claim had reached an empirical and theoretical impasse (from which it is yet to recover).

In contrast,  $\beta$ -diversity was supposed to represent the diversity between units—a measure of the extent to which they were different.  $\gamma$ -diversity was supposed to measure the total diversity of a region. The former had a clear connection to complementarity: a standard measure of  $\beta$ -diversity was the ratio of shared to the total species in two units. If a set of already selected areas is taken as one unit, the new unit which would maximize this measure of  $\beta$ -diversity would be the one with the highest complementarity (as calculated, for instance, in the MNP algorithm). Yet, though Rebelo and Siegfried (1990) and Vane-Wright et al. (1991) mentioned  $\beta$ -diversity in passing, and explicitly used complementarity, they did not make that connection. Neither did anyone else throughout the 1990s.

Sarkar (2007a) has speculated that the general impasse in the diversity–stability debate led to conservation biologists ignoring all diversity measures from ecology. However, there could also have been two conceptual reasons in play: (i)  $\beta$ -diversity was usually not conceptualized as a dynamic measure to be updated iteratively. As a result, those who were developing complementarity-based algorithms did not think of complementarity as  $\beta$ -diversity. (ii) Complementarity was typically computed for a large number of small units (individual cells), and relativized to one large unit (the set of already selected cells). In contrast,  $\beta$ -diversity was thought of as more “symmetric” in the sense of quantifying a relation (of dissimilarity) between two similar units, usually with the same area. Consequently, it did not seem obvious to anyone to interpret complementarity as  $\beta$ -diversity.

## 7.2 Spatial configuration

Nicholls and Margules (1993) introduced closeness as a criterion for the selection of reserves into a network. The metaheuristic algorithms of the 1990s used shape as a criterion (Sect. 6); more recent such algorithms have introduced connectivity (and a variety of other spatial criteria) (Ciarleglio et al. 2009). Was this a return to the geometric rules produced by Diamond and others in the 1970s (Sect. 2.1) which Margules and those who followed the algorithmic tradition had once vehemently rejected?

The answer to this question is not straightforward for the period covered by this paper (and has become even less straightforward since).<sup>26</sup> In one sense, the answer is obviously “yes:” spatial criteria were being invoked to incorporate concerns about persistence as was the case in the use of island biogeography theory in the 1970s. Moreover, this was typically done with no more concern for empirical validation than with island biogeography theory in the 1970s.

<sup>25</sup> For a history of these developments, see Sarkar (2007a).

<sup>26</sup> For a recent scientific review, which has been cited earlier several times, see Williams et al. (2005).

But, in a more interesting sense, the answer is “no.” Nicholls and Margules (1993) had clearly recognized that their spatial closeness criterion was “optional.” All algorithms since (including those based on simulated annealing and other metaheuristics) have similarly left issues of spatial configuration to be decided by contextual considerations. There was no claim of universal principles of reserve design, nothing along the lines of Diamond’s (1975) Rules A–F (Fig. 1). The focus was on flexibility in the face of uncertainty. But the irony remains that, on the critical issue of persistence, the algorithms made no progress from the 1970s.

### 7.3 Concluding remarks

What is perhaps more important is that conservation biologists taking the algorithmic turn were motivated by three assumptions. The first was explicitly recognized as uncontroversial from the moment it was introduced—by Kirkpatrick (1983): that richness (or any other static measure) would not lead to “efficient” reserve network design. The influence of this recognition on the development of the field would be difficult to over-estimate. Even when optimal and metaheuristic algorithms began to compete with the complementarity-based heuristic algorithms of Sect. 3, there was no return to static measures.<sup>27</sup>

The second was the realization that conservation decisions must be made immediately with limited data. In the words of Margules and Nicholls (1987, p. 89):

“identifying suitable reserves ...should be based on information from experiments and correlational analyses but such information is rarely available, especially in the detail desired. If the problem is ignored until sufficient experimental results are available, conservation options will be severely reduced. The urgency for decisions makes it necessary to generate some minimum set of ...options.”

Rebello and Siegfried were equally explicit, claiming that their “approach [was] more than justified by the paucity of information ...and an urgent need for a strategy for maximizing the protection of Fynbos floral diversity (Rebello and Siegfried 1990, p. 16).” This realization led to many critically important decisions, especially that of basing conservation decisions on presumed (and rarely proven) surrogates for biodiversity (Sarkar and Margules 2002). This was open—and subjected—to criticism on the ground that Margules et al. (1982) used to criticize the use of island biogeography theory, that rules were being used without regard to their empirical status. Eventually, methods were developed to test the adequacy of surrogates.<sup>28</sup> In the context of this paper, the assumption of urgency led to the demand that reserve selection methods be fast and flexible.<sup>29</sup> Flexibility required speed so that a variety of alternatives could be rapidly explored. This, in turn, led to computer-aided design and thus, inexorably, to algorithms.

<sup>27</sup> Optimal and metaheuristic algorithms necessarily work by updating some function, typically an objective function. These technical issues are beyond the scope of this paper.

<sup>28</sup> This work came mainly after 2000 and is reviewed by Margules and Sarkar (2007).

<sup>29</sup> Recall the emphasis that Cocks and Baird (1989) put on flexibility (Sect. 5).

The third and, in retrospect, most important assumption was that cost was important and policies should be assayed for their economy. Richness was a poor criterion for selecting reserves because there was a limit on how many reserves a region could afford. The reserve selection problem, from the very beginning (Kirkpatrick 1983), was conceptualized as a *constrained* optimization problem with cost being a critically important constraint. Efforts to incorporate costs into reserve selection protocols using standard economic measures were already under way by the mid-1990s (Faith 1995). Multi-criteria analyses based on methods from the decision sciences eventually became routine (and were reviewed by Moffett and Sarkar 2006).

Ultimately, the use of algorithmic methods came to be definitive of what Margules and Pressey (2000) dubbed “systematic conservation planning” in 2000. It was a strategy to prioritize areas for conservation, designate “conservation areas”—which replaced “reserves”<sup>30</sup>—and then focus on questions of persistence. Systematic conservation planning eventually came to be widely embraced, particularly by Western-based large non-governmental organizations with financial resources that dominated the economies of many of the regions in which they chose to work (Dowie 2009). What—and how much—these methods contribute to the persistence of the natural features of the world remains to be seen.

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<sup>30</sup> See Sarkar (2003) for the political and ethical considerations behind this move.

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