The selection of networks of nature reserves

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Summary

Setting aside networks of protected areas for conservation is urgently needed to counteract the current extinction crisis. Complementarity-based reserve selection algorithms have been developed in recognition that such a task needs to make the best possible use of the scarce resources available to conservation, maximising the return in terms of biodiversity protection.

This project aims to contribute to the improvement of these algorithms, particularly using optimisation methods, to make them more applicable to practical reserve selection. In pursuing this objective, a number of different approaches are adopted. Using different exemplar data sets, I (i) explore methods for the evaluation of existing networks of protected areas; (ii) develop guidelines for the selection of networks which are more robust to species temporal turnover, and present evidence that minimum complementary sets tend to select areas of ecological transition; (iii) demonstrate how optimisation tools can be applied to maximise phylogenetic diversity, and present evidence that complementary sets maximising for taxonomic richness are adequate surrogates in representing phylogenetic diversity; (iv) demonstrate how species rarity influences complementary reserve selection across geopolitical boundaries; (v) provide guidelines for the application of reserve selection algorithms in areas with poor biological data; and (vi) investigate what should be adequate conservation targets for reserve networks representing plant and vertebrate species, in the tropical rain forests and at a global scale. I then put the results obtained in this thesis and other published literature in a broader context, analysing the explanations as to why reserve selection algorithms are failing to have an impact in conservation practice.

This study demonstrates the flexibility of reserve selection algorithms as tools for the selection of complementary reserve networks, and proposes developments needed to improve their effectiveness as practical conservation planning tools.

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Declaration

This thesis includes material from ten papers (published or in press) which are jointly authored. The contributions I have made to each of these papers are detailed below.

- Rodrigues, A.S., Orestes Cerdeira, J., Gaston, K.J. 2000. Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems. *Ecography* **23**, 565-574. (Section 2.1)

Based on a joint idea by ASLR and KJG. ASLR drafted the manuscript.

- Rodrigues, A.S.L., Gaston, K.J. 2002. Optimisation in reserve selection procedures – why not? *Biological Conservation* **107**, 123-129. (Section 2.2)

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- Rodrigues, A.S.L., Tratt, R., Wheeler, B.D., Gaston, K.J. 1999. The performance of existing networks of conservation areas in representing biodiversity. *Proceedings of the Royal Society of London*, B **266**, 1453-1460. (Section 3.2)

Based on a joint idea by ASLR and KJG. ASLR did the analyses and drafted the manuscript.

- Rodrigues, A.S.L., Gaston, K.J., Gregory, R. 2000. Using presence/absence data to establish reserve selection procedures that are robust to temporal species turnover. *Proceedings of the Royal Society of London*, B **267**, 1-6. (Section 4.1)

Based on a joint idea by ASLR and KJG. ASLR did the analyses and drafted the manuscript.

- Rodrigues, A.S.L., Gregory, R., Gaston, K.J. 2000. Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London*, B **267**, 1-6. (Section 4.2)

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- Gaston, K.J., Rodrigues, A.S.L., van Rensburg, B.J., Koleff, P., Chown, S.L. 2001. Complementary representation and ecological transition. *Ecology Letters* **4**, 4-9. (Section 4.3)

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- Rodrigues, A.S.L., Gaston, K.J. 2002. Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation* **105**, 103-111. (Chapter 5)

Based on an idea by ASLR, who did the analyses and drafted the manuscript.

- Rodrigues, A.S.L., Gaston, K.J. 2002. Rarity and conservation planning across geopolitical units. *Conservation Biology* **16**, 674-682. (Chapter 6)

Based on a joint idea by ASLR and KJG. ASLR did the analyses and drafted the manuscript.

- Gaston, K.J., Rodrigues, A.S.L. in press. Reserve selection in regions with poor biological data. *Conservation Biology*. (Chapter 7)

Based on a joint idea by ASLR and KJG. ASLR did the analyses and drafted the manuscript.

- Rodrigues, A.S.L., Gaston, K.J. 2001. How large do reserve networks need to be? *Ecology Letters* **4**, 602-609. (Chapter 8)

Based on a joint idea by KJG and ASLR. ASLR collected the data, performed the analyses and drafted the manuscript.

Additionally, two further papers have been co-authored during the work for this thesis, and they are included as Appendices:

- Balmford, A., Gaston, K.J., Rodrigues, A.S.L., James, A. 2000. Integrating costs of conservation into international priority setting. *Conservation Biology* **14**, 597-605. (Appendix I)

Based on a joint idea by AB and KJG. ASLR contributed to the data analysis and interpretation of the results.

- Chown, S.L., Rodrigues, A.S.L., Gremmen, N.J.M., Gaston, K.J. 2001. World Heritage Status and conservation of Southern Ocean Islands. *Conservation Biology* **15**, 550-557. (Appendix II)

Based on a joint idea by SLC and KJG. ASLR did the data analysis, contributed to the interpretation of the results and helped draft the manuscript.

1 Introduction

1.1 Context

The twentieth century witnessed an extraordinary growth of the human world population – from 1.65 billion to 6 billion people, with almost 80% of that increase having occurred since 1950 (UN 2001). As a result, we now live in a human-dominated planet (Vitousek et al. 1997; Woodruff 2001 and references herein): our population density is now more than 30 times that predicted for an omnivorous mammal of our size; one-third to one-half of the land surface has been transformed by human action; humans use about 40% of the planet's gross terrestrial primary productivity and 8% of the primary production of the oceans (35% in temperate continental shelf systems); 66% of recognised marine fisheries are fully exploited, overexploited, or depleted; the carbon dioxide concentration in the atmosphere has increased by nearly 30% since the beginning of the industrial revolution; more atmospheric nitrogen is fixed by humanity than by all natural terrestrial sources combined; humanity uses more than half of the runoff water that is fresh and reasonably accessible (70% of this in agriculture).

As a result, biodiversity is in deep trouble. Ecosystems of all kinds are under pressure worldwide (WRI 2000 and references herein): forest cover has been reduced by at least 20% and perhaps by has much as 50%; some forest ecosystems, such as dry tropical forests of Central America, are virtually gone; more than 50% of the original mangrove area in many countries is gone; wetland area has shrunk by about half; and natural grasslands have been reduced by more than 90% in some areas. Only tundra, arctic, and deep-sea ecosystems have emerged relatively unscathed. These widespread transformations result in current species extinction rates more than 100 times greater than background extinction levels (Pimm et al. 1995; Pimm 1998), unprecedented since the last mass extinction event, 65 million years ago (see Jablonski 1995). The loss of local populations is happening at an even faster rate (Hughes et al. 1997; Ceballos and Ehrlich 2002), and the selectivity of extinction patterns for particular branches of the phylogenetic tree means a higher erosion of evolutionary history than predicted based simply on the number of species (Russell et al. 1998; Purvis et al. 2000).

The most effective way of preserving biodiversity is by maintaining native species in natural ecosystems: there is less expense and more chance of success if extinction is fought in the long term by maintaining self-sustaining populations in their habitats. Protected areas, where conservation of biodiversity is a priority over other land uses, are a fundamental strategy for *in situ* conservation (e.g., Oates 1999; Therborg 1999). However, since the amount of land that can be set aside under formal protection is limited by competition with other forms of land use (see below), protected areas need to be complemented by strategies of sustainable development which aim at preserving the natural resources in the broader landscape matrix. These are complementary, rather than opposite, strategies.

The recognition of the importance of *in situ* conservation led to an increasing investment in the creation of reserves, mainly during the last 30 years (UNEP-WCMC 1997). At the moment, most countries in the world already have protected areas (Caughley and Gunn 1996): nearly 13,000 protected areas are recognised by the United Nations, covering a total of 7.9% of the planet's land area (UNEP-WCMC 1997). This is, however, a clearly insufficient figure, even if it was unrealistically assumed that all this area was being adequately managed and protected. The IUCN and the World Commission on Environment and Development called for the near-term protection of 10-12% of the total land area in each nation or each ecosystem, but even this seems to be mainly a political target. Much higher conservation targets would be required by ecological criteria, as the species-area relationship predicts that a loss of 90% of habitat implies a loss of 50% of the species (Soulé and Sanjayan 1998).

There is an obvious need to set aside additional protected areas, but to be effective these imply restrictions to destructive human activities, and consequently this task becomes increasingly difficult as competition for land use becomes more intense (Musters et al. 2000). The human population is expected to continue growing until the end of the 21st Century (UN 2001), with recent projections indicating a peak of 9 billion people by 2070 (50% more than today), followed by a slow decrease (Lutz et al. 2001). Additionally, increase in per capita resource consumption means that pressure on natural resources will keep increasing at a rate faster than population growth. Indeed, while already one-third of the land area has been converted to agriculture and urban or built-up areas, projections suggest that an additional one-third could be converted within the next 100 years (WRI 2000).

Clearly, the designation of new protected areas is an urgent task, but also one which needs to be done as efficiently as possible, making the best possible use of the scarce resources available to conservation in order to maximise the return in terms of biodiversity conservation. Unfortunately, many currently existing protected areas have not been designated having this goal in mind, and the result is that in many regions reserve systems are highly biased towards particular subsets of natural features, usually the economically less valuable and often species poorer habitats, while leaving others inadequately protected (Pressey 1994). While it is likely that each individual reserve has significant biological value, currently existing reserve networks are often not the best approach for representing the biodiversity of particular regions. In a world of limited resources and high competition for land use, such inefficiency may come at the price that a ceiling to the total reserve area which can be acquired is attained before all features are embraced (Pressey et al. 1993). Indeed, the biological value of current reserve systems is likely to be overestimated by the hectares they occupy (Pressey and Cowling 2001).

The recognition that conservation resources are limited led to an emphasis in recent years on the development of more systematic approaches to the selection of priority areas where these resources should be invested.

1.2 Global prioritisation schemes

The results of a biased selection of the existing reserve networks are obvious at a global scale. While at least 50% of all species are predicted to exist in tropical rainforests (Wilson 1988; WCMC 1992), only 18% of the protected area worldwide is in tropical humid or dry forests, while 36% is in the species-poor tundra and warm desert/semi-desert biomes, and 12% in temperate forests (Hobbs and Lleras 1995, based on 1992 data). In relative terms, temperate grasslands – worldwide, the most productive for agriculture – are the least represented of all biomes, with only 0.8% of their area reserved (Hobbs and Lleras 1995).

Table 1.I – Main global priority systems.

Scheme	Targeted features	Selection criteria	Summary statistics
Endemic Bird Areas, BirdLife International (Stattersfield et al. 1998)	Restricted-range birds (2,451 species)	All regions with at least two restricted-range bird species (breeding range < 50,000 km²). Criteria: endemism.	218 EBAs; historical area 10% of the world land area, current area 5%; all restricted-range bird species represented (25% of all species), plus an undetermined number of other bird species.
Biodiversity Hotspots, Conservation International (Mittermeier et al. 1999; Myers et al. 2000)	Plant species	Areas having as endemics at least 1,500 plant species (0.5% of the global number of plant species), and having lost at least 70% of their natural habitat. Criteria: endemism, richness, threat.	25 Hotspots; historical area 11.8% of the world land area, current area 1.4%; 44% of all plant species and 35% of all vertebrates are endemic to the hotspots, plus an undetermined number of other species represented.
Major Tropical Wilderness Areas, Conservation International (Mittermeier et al. 1998)	Plant species	Areas having as endemics at least 1,500 plant species (0.5% of the global number of plant species), where at least 70% of the natural habitat remains. Criteria: endemism, richness, naturalness.	3 Wilderness Areas; total area 3,378,000 km² = 2.26% of the total land area.
Marine Biodiversity Hotspots, Conservation International (Roberts et al. 2002)	Species of reef fish, corals, snails, and lobsters (3,235 species)	The richest multitaxa centres of endemism (for each taxon, a centre of endemism is defined as the 10% richest cells). Criteria: endemism, richness.	18 Hotspots; total area 0.028% of the world oceans, 35.2% of the world's coral reefs; includes between 58.6 and 68.7% of restricted-range species (≤ 10 cells) from the four taxa.
Frontier Forests, World Resources Institute (Bryant et al. 1997)	Forests	Relatively undisturbed forest tracts, big enough to maintain all of their biodiversity including viable populations of the wide-ranging species; composition and structure maintained mainly by natural events. Criteria: naturalness.	40% of currently existing forest; total area 13,501,000 km² = 19.9% of the total land area; 90% of the Frontier Forest concentrated in 12 countries, and 68% in just three (Russia, Canada and Brazil).
Centres of Plant Diversity, World Wide Fund for Nature and The World Conservation Union (WWF and IUCN 1994-1997)	Plant species	Sites with ≥ 1,000 vascular plant species and ≥ 100 species endemic to their phytogeographic region or mainland sites; or with ≥ 50 endemic species or ≥ 10% endemism for islands. Criteria: endemism, richness.	234 Centres: 75 in the Americas; 102 in Asia, Australasia and the Pacific; 57 in Europe, Africa, SW Asia and the Middle East.
Global 200 Ecoregions, World Wide Fund for Nature (Olson and Dinerstein 1998*a*,*b*)	Plant species	Ecoregions within each biogeographic realm that represent the most distinctive examples of biodiversity for a given major habitat type. Main criteria: representativeness, richness, endemism, taxonomic uniqueness, unusual ecological/evolutionary phenomena, rarity of major habitat type.	233 ecoregions, 58% terrestrial, 16% freshwater, 26% marine.

A number of global priority systems have been proposed during the last decade. The main ones, by leading Non-Governmental Organisations, are listed in Table 1.I (a diversity of other priority schemes have also been published, e.g., Moran et al. 1996; Reyers et al. 1998; Balmford et al. 2000*a*; see Appendix I). The most widely used criteria are species richness and/or endemism (Endemic Bird Areas, Hotspots, Marine Hotspots, Centres of Plant Diversity, and Global 200), which naturally tend to highlight areas in tropical regions. Threat (current levels of destruction) has been used as a determinant criterion in the selection of Hotspots, while the absence of threat (i.e., current levels of naturalness) is at the basis of the selection of Wilderness Areas and Frontier Forests. An emphasis on representativeness (need to represent all major ecosystems and habitat types across the world) is central to the Global 200.

Being based on different criteria and targeting different biodiversity features, these priority schemes result in quite different maps of priority areas. They have thus been criticised for duplication of conservation effort across organisations, resulting in redundancy and generation of competing priority sets (Mace et al. 2000). Several international NGOs are currently working more closely in building consensus and cross-evaluating priority areas identified under different schemes (e.g., Brooks et al. 2001*b*; Brooks and Thompson 2001).

Despite the differences, these global priority schemes have in common the purpose of attempting to compensate for the inbalance in conservation efforts and focus on areas/ecosystems currently poorly represented. The results of several of these schemes demonstrate how highly significant fractions of biodiversity can be protected by targeting efforts at relatively small regions (e.g., Endemic Bird Areas, Hotspots and Marine Hotspots, Table 1.I). However, even if globally small, the areas identified by these schemes are usually very large in absolute area, often spanning across several countries, and therefore these are not proposals for the creation of individual reserve networks at manageable scales. Instead, they are tools aiming at focusing conservation investment in particular regions, a task at which they have had some success (e.g., the Critical Ecosystem Partnership Fund, a joint initiative of Conservation International, The Global Environment Facility, the Government of Japan, the MacArthur Foundation and The World Bank; http://www.cepf.net/; Dalton 2000).

1.3 Regional prioritisation schemes

Conflicts between conservation and other human activities can become readily apparent at large scales (e.g., Cincotta et al. 2000; Balmford et al. 2001). But most political decisions take place at the regional (usually the national) level, and it is at this scale that conservation planning needs to be particularly robust in addressing highly complex data, concerns and considerations in order to solve conflicts with human activities effectively (Brooks and Thompson 2001).

The classical approach towards systematic reserve selection at a regional level is to preserve the sites with the highest value of some index which incorporates one or several variables – what has been called the "scoring" (or "ranking") approach. The criteria most widely used in the assessment of a site's value include diversity, rarity, size, naturalness, productivity, fragility, representativeness, abundance, threat, educational or scientific value, shape and accessibility (see Margules and Usher 1981, and Smith and Theberge 1986 for reviews). These are a mixture of ecological, aesthetical, cultural and practical values that reflect the broad range of conservation goals from the preservation of rare or unique species and fragile environments to the maintenance of diversity and stability and the protection of representative samples of ecosystems (Margules and Usher 1981).

One of the prevalent scoring approaches is "hotspots analysis". Initially the term referred to areas at a global scale that simultaneously contain large concentrations of endemic species and that are facing exceptional threats of destruction (Myers 1990; see Table 1.I). Subsequently, the term has been generalised to refer to areas particularly high in one or more axes of species richness (richness or diversity hotspots), number of rare or endemic species (rarity hotspots), number of threatened species (threatspots) and intensity of threat (e.g., Prendergast et al. 1993; Williams et al. 1996*a*; Reid 1998). Currently, the most common use is with reference to regions of high species richness (Reid 1998).

Because each reserve is evaluated individually, the scoring approach doesn't seem to be appropriate when used to choose a system or set of reserves, or even a single reserve in regions where there are already other protected areas. It fails to recognise that the value attached to adding a reserve depends on the attributes of reserves already in the system, e.g., whether species/habitats in that particular reserve are already well represented. Consequently, there is no guarantee that the highest ranking sites derived from scoring might not unnecessarily duplicate some attributes (species, communities or habitats) while missing others (Kirkpatrick 1983; Pressey and Nicholls 1989*a*).

As a response to the recognition that resources for protecting biodiversity need to be allocated as efficiently as possible, other approaches for site selection have been developed based on the "complementarity principle" (Vane-Wright et al. 1991). This explicitly assumes that the aim is to produce a reserve network that, all together, can assure the preservation of a maximum of biodiversity elements or features (such as species, communities, land systems). The conservation value of any individual site is, therefore, the extent to which it complements the other sites in the network, by contributing to the achievement of the conservation goals pre-defined for the network.

At the global scale, any prioritisation scheme that focuses on the selection of areas with high numbers of endemics (Table 1.I) is implicitly addressing complementarity, as such areas will have many unique features and therefore will not be redundant in relation to any others. Schemes focusing on representativeness such as the Global 200 use complementarity in an explicit way.

The application of the complementarity principle to reserve selection at the regional scale has mainly taken place through the use of reserve selection algorithms. These are iterative procedures such that the value of each candidate for reserve selection is recalculated each time a site is added to the reserve network (Bedward et al. 1992). The first published application of a reserve selection algorithm was in 1983 (Kirkpatrick 1983), although the same idea had at least five other recorded independent origins between 1984 and 1991 (see Pressey 2002 for a review). Ever since, the increase in the popularity of reserve selection algorithms has been striking: Pressey (2002) found 245 references with publication dates up to the year 2000, and the numbers have been increasing steadily. While the first studies relied solely on the use of heuristic algorithms (e.g., Margules et al. 1988; Bedward et al. 1992; Rebelo and Siegfried 1992; Turpie 1995), it was recognised early on that complementary reserve selection problems can be stated and solved optimally by operations research techniques such as linear integer programming (e.g., Cocks and Baird 1989; Underhill 1994; Church et al. 1996).

A parallel line of application for the complementarity principle has been developed in the United States under the designation of Gap Analysis (Scott et al. 1993; Caicco et al. 1995; Kiester et al. 1996; Jennings 2000; Scott et al. 2001), and this has also been gaining popularity as a reserve planning tool outside the US (e.g., Fearnside and Ferraz 1995; Powell et al. 2000; Sierra et al. 2002; UNEP-WCMC 2002). The main focus of Gap Analysis is to find areas which fill the gaps in currently existing reserve networks, that is, to propose new reserves which are complementary to the existing ones. Taking into account existing reserves when analysing priority areas is a straightforward and very common procedure in the algorithm-based complementary methods, ever since the first application by Kirkpatrick (1983; other examples include Pressey and Nicholls 1989*b*; Rebelo and Siegfried 1992; Nantel et al. 1998; Balmford et al. 2001). The main difference between Gap Analysis and algorithm-based reserve selection has been the way additional reserves are sought: Gap Analysis has been developed from the beginning as a GIS-based tool with a higher emphasis on a landscape approach to species conservation (Burke 2000), relying more on the overlap between layers of information and visual inspection rather than on the use of specific analytical procedures. However, the boundaries between both approaches have been blurring, as algorithm-based analyses start relying more on spatial tools (e.g., CODA, Bedward et al. 1992; WORLDMAP, Williams 1996; C-Plan, Pressey 1998) and Gap Analysis starts incorporating reserve selection algorithms (e.g., Kiester et al. 1996; Clark and Slusher 2000). Although developed independently, these two complementarity-based reserve selection procedures flow naturally into one another (Pressey and Cowling 2001).

The attractiveness of complementarity-based reserve selection algorithms resides in the combination of the simplicity of the underlying idea and the power of its application, particularly because of the following traits:

1. These are tools specifically designed for taking simultaneously into account a diversity of species and/or other biodiversity features (such as habitat types). This is a fundamental trait, as the urgency of conservation action and the limits to available resources make impossible the application of species-by-species conservation planning to more than a handful of species (e.g., Oates 1999).

2. The complementarity approach aims, by definition, at maximum efficiency (Pressey and Nicholls 1989*a*) in sampling the full range of biodiversity features at a minimum cost (usually measured by total reserved area). This is very important given that in most regions there is a limit to the land or water area which can be devoted to conservation, and efficient solutions are not only more defensible they also minimise the risk of reaching a ceiling of acceptable reserve area before conservation targets are met (Pressey et al. 1993).

3. These are extremely flexible tools, with flexibility happening in two, related, ways. First, there is an unlimited number of possible adaptations that can be made to these algorithms in order to address particular conservation concerns beyond simple feature representation, such as for example species persistence (e.g., Williams and Araújo 2000), spatial configuration of the reserves (e.g., McDonnel et al. 2002), and land cost (e.g Ando et al. 1998). Second, the non-unique occurrence of many biodiversity features implies that in

most regions there are many options for combining sites to form representative networks of reserves; this variety of possible configurations gives scope for sensible resolutions of land conflicts (Pressey et al. 1993). Related to this flexibility is the concept of irreplaceability (Pressey et al. 1993; Pressey et al. 1994; Pressey 1999): the level to which a particular site can be replaced by another site or combination of other sites is variable, depending on the site's biological composition in relation to the pre-defined conservation goals. Irreplaceability provides a way of measuring the conservation value of any site, which is particularly useful when reserve acquisition needs to be scheduled in time (e.g., Pressey and Taffs 2001).

4. Complementarity-based reserve selection algorithms are highly accountable, meaning that the solutions are obtained in a transparent way, allowing others to understand why and how the result was arrived at. Reserve networks chosen explicitly can be more easily defended, which is crucial in situations of limited land resources (Nicholls and Margules 1993; Williams 1998*b*).

1.4 Objectives

The objectivity and scientific rigor of complementarity-based reserve selection procedures gives them the potential to transform the way in which land is allocated and protected for conservation (Prendergast et al. 1999). Yet, nearly 20 years after they were first published, they have had only limited application to practical conservation planning (Cabeza and Molainen 2001).

The purpose of this project is to contribute for the improvement of these tools to make them more applicable to practical reserve selection planning. In pursuing this objective, a number of different approaches were adopted, with an emphasis on tackling some of the perceived drawbacks in the way these methods have been used:

- First, the advantages of using optimisation methods have been largely neglected. Chapter 2 explores the flexibility of these methods as analytical tools in complementary reserve selection and addresses several of the misunderstandings that have been published regarding their applicability to real datasets. In an attempt to correct one of these misunderstandings, Chapter 5 demonstrates how these tools can be applied to the selection of reserve networks to maximise phylogenetic diversity.

- Second, many published studies have used minimum complementary sets in uncritical ways, presenting the results as if these correspond to ideal reserve networks. In addressing this problem, Section 3.2 investigates the risks of evaluating existing networks simply by comparing them with minimum complementary sets; Sections 4.1 and 4.2 test the effectiveness of minimum sets in retaining species over time; Section 4.3 investigates the potential bias of complementary sets for areas of ecological transition; and Section 6.1 investigates the biases resulting from considering geographic boundaries and non-target rare species in the selection of complementary sets.

- Third, there is a need for the development of general guidelines and the testing of surrogates which can be applied to practical conservation planning. Sections 4.1 and 4.2 propose guidelines for addressing species' persistence, either by using abundance or presence/absence data; Chapter 5 investigates the adequacy of using complementary sets maximising taxonomic diversity in representing phylogenetic diversity; Chapter 6 suggests ways of addressing the biases caused by geographic boundaries and species "apparent" rarity in complementary reserve selection; and Chapter 8 investigates the broader question of how large should reserve networks be in order to adequately protect species.

- Fourth, a major criticism made to the applicability of these methods is their dependence on high quality datasets. Chapter 7 investigates the value of the results obtained when complementarity-based reserve selection algorithms are applied to data obtained by low sampling effort.

In this project, a species-oriented approach to the selection of protected areas is followed. This strategy has been defended by some (e.g. Mittermeier et al. 1999) and criticised by others who suggested, for example, ecosystem-based approaches (e.g. Noss 1996, 2000). Species are only one level of the continuum of biological diversity which ranges from individual genetic diversity to the entire biota in planet earth, including the diversity of populations, species, ecosystems and the process which generate and maintain that diversity. But because they are considered the most basic, recognisable units in biodiversity, species are natural targets for systematic reserve selection. Chapter 9 discusses how other levels of biological diversity, such as habitats, ecosystems and ecological and evolutionary processes may be addressed by complementary reserve selection.

1.5 Data sets

Three very different data sets were used in the analyses performed during this research project:

- A data set on the presence/absence of wetland plant species in fens located in the central Scottish borders, some of which have been notified as Sites of Special Scientific Interest by the statutory conservation agency.
- Data on the absolute numbers (breeding couples territories) of bird species in wetland and farmland sites, obtained under the Common Birds Census (CBC) monitoring scheme run by the British Trust for Ornithology since 1964.
- A large data set on the distribution of bird species in southern Africa, obtained by the Southern African Bird Atlas Project (SAPAB), which includes information on a relative measure of abundance (reporting rates) for each species for each site. Other data also available for the same region included information on the distribution of biomes, vegetation types, land use, human density, net primary productivity and reserve boundaries.

The different properties of these datasets were explored in the analyses performed in this project. The data set on plant species in fens in the Scottish borders was used to investigate methods for assessing the performance of an existing reserve network (Section 3.2). Because the CBC data provided information on changes in species composition in each site over time, it was used to explore guidelines for the selection of reserve networks in order to make them robust to species temporal turnover, either by using abundance (Section 4.1) or presence/absence data (Section 4.2). The SABAP data and associated information were used in most of the analyses in this project, including investigating the effect of reserves in mitigating species loss (Section 3.1), the coincidence of complementary networks and zones of ecological transition (Section 4.3), the selection of complementary networks aiming at maximising representation of phylogenetic diversity (Chapter 5), the effects of geopolitical boundaries in reserve selection (Chapter 6), the application of reserve selection algorithms to data sets obtained by low sampling effort (Chapter 7), and how different characteristics of the data set influence the size of complementary networks needed to represent all species (Chapter 8).

1.6 Thesis outline

The remainder of this thesis is structured into eight main chapters (Chapters 2 to 9):

- Chapter 2 explores the advantages of mathematical programming methods as analytical tools in complementary reserve selection.
- Chapter 3 starts by addressing the value of reserves as conservation tools and then explores methods for the evaluation of existing networks of protected areas.
- Chapter 4 starts by exploring guidelines for the selection of reserve networks which are more robust to temporal turnover; it then tests if there is a tendency for the selection of areas of ecological transition using minimum complementary sets, which may help explain their ineffectiveness in ensuring species persistence.
- Chapter 5 illustrates how optimisation tools can be applied to maximise phylogenetic diversity, and assesses the surrogate value of complementary sets maximising for taxonomic richness in terms of representing phylogenetic diversity.
- Chapter 6 investigates the implications of the relative concept of species' rarity in complementary reserve selection across geopolitical boundaries.
- Chapter 7 investigates how sampling effort affects the performance of reserve networks, providing guidelines for the collection of data based on low-sampling effort.
- Chapter 8 addresses the general question of how large should reserve networks be in order to adequately represent species diversity.
- Chapter 9 puts the results obtained in this thesis, as well as the other published literature on this subject, in a broader context, analysing each one of the explanations that have been presented to why reserve selection algorithms are failing to have an impact in conservation practice.

2 Mathematical programming tools in complementary reserve selection

Flexibility, efficiency and accountability are considered key attributes of good reserve selection methods. Because of the robustness of the general integer linear model, a remarkably rich variety of problems concerning the management and efficient use of scarce resources can be represented as problems of this type. This chapter explores the use of mathematical programming methods – which will be used throughout the remainder chapters – as tools in complementary reserve selection. Section 2.1 starts by analysing a simple representation problem and then develops more general problems that can be applied to a variety of conservation planning exercises. It illustrates how high flexibility can be attained, while simultaneously addressing efficiency and accountability, by modelling reserve selection questions as integer linear problems. Section 2.2 rebuts the widespread assumptions that optimisation methods may not be able to provide solutions to more realistic problems, and that they may be too slow and therefore inadequate for interactive practical conservation planning.

2.1 Flexibility, efficiency, and accountability: adapting reserve selection algorithms to more complex conservation problems

During World War II, British military leaders asked scientists to analyze several military problems: the development of radar and the management of convoy, bombing, antisubmarine and mining operations. The application of mathematics and the scientific method to military operations was called operations research. Today, the term operations research (or, often, management science) means a scientific approach to decision making, which seeks to determine how best to design and operate a system, usually under conditions requiring the allocation of scarce resources.

Winston (1994, page 1)

2.1.1 Introduction

Flexibility, efficiency and accountability have been identified as key attributes of a good reserve selection procedure (e.g., Pressey et al. 1993; Nicholls and Margules 1993; Williams 1998*b*; see Chapter 1).

Flexibility is the ability to incorporate all the diversity of considerations, concerns and information that typically impinge on real conservation problems. This is fundamental if the particulars of any given situation are to be addressed and land use conflicts are to be effectively resolved. Flexibility can either be addressed *a priori*, when devising the problem to be solved (e.g., Cocks and Baird 1989; Nicholls and Margules 1993), or *a posteriori*, by modifying the reserve network obtained by a selection procedure (e.g., Bedward et al. 1992; Pressey et al. 1993).

High efficiency (*sensu* Pressey and Nicholls 1989*a*), the representation of the maximum diversity of the relevant features (e.g., species) at the minimum cost, is important because reserves will commonly be in direct competition with other forms of land use. Highly efficient solutions are both more defensible from a political (but not necessarily biological) viewpoint and minimise the risk that a ceiling to the reserve area which can be acquired is attained before all features are embraced (Pressey et al. 1993).

Accountability means that the solutions are obtained in a transparent way, allowing others to understand why and how the result was arrived at. Reserve networks chosen explicitly can be more easily defended, which is crucial in situations of limited land resources (Nicholls and Margules 1993; Williams 1998*b*).

This section illustrates how flexibility, efficiency and accountability can be addressed simultaneously in reserve selection procedures by modelling them as integer linear problems. For simplicity, throughout 'species' are treated as the features of interest, but most of the considerations apply equally to other features, such as 'land types' (Pressey et al. 1996*a*, 1997), 'plant communities' (Cocks and Baird 1989; Bedward et al. 1992; Nicholls and Margules 1993) and 'environmental domains' (Bedward et al. 1992; Pressey and Tully 1994).

2.1.2 Addressing flexibility

Integer linear programming deals with problems of maximising or minimising a linear function of variables subject to inequality and/or equality constraints and integrality restrictions on some or all of the variables. Because of the robustness of the general model, a remarkably rich variety of problems concerning the management and efficient use of scarce resources can be represented as linear integer problems (Nemhauser and Wolsey 1988).

<u>The basic problem: to represent each species at least once in the minimum number of sites</u>

Representing each species at least once in the minimum number of sites is the conservation planning problem addressed most frequently in the literature (e.g., Sætersdal et al. 1993; Kershaw et al. 1994; Margules et al. 1994*b*; Lombard et al. 1995; Castro Parga et al. 1996; Williams et al. 1996*b*; Csuti et al. 1997; Pressey et al. 1997; Hacker et al. 1998; Nantel et al. 1998). This is a well known 0/1 linear programming problem: the *set covering problem* (Padberg 1979; Balas 1980; Balas and Ho 1980; Underhill 1994; Ando et al. 1998) and can be written as:

$$\text{Minimise } \sum_{j=1}^{n} x_j \qquad \text{(I)}$$

Subject to:

$$\sum_{j=1}^{n} a_{ij} x_j \geq 1, \qquad i = 1, 2, \ldots, m \qquad \text{(II)}$$

$$x_j \in \{0,1\} \qquad j = 1, 2, \ldots, n \qquad \text{(III)}$$

where n is the number of sites, m is the number of species, a_{ij} is 1 if species i is present in site j and 0 otherwise, and variable x_j is 1 if and only if site j is selected.

The objective function (I) is to minimise the number of sites selected. Inequalities (II) ensure that each of the m species must be present at least once. The integrality restrictions (III) state that each variable x_j is either 0 or 1, forcing each site to be treated as an indivisible unit (thereby avoiding solutions that would select fractions of each site).

Defining a higher representation target: represent each species at least *b* times in the minimum number of sites

Typically, representation in just one site will clearly be insufficient to ensure the long-term persistence of all species in a reserve network (Rodrigues et al. 2000*a,b*; see Sections 4.1, 4.2). It is possible to set a higher representation target by changing the restrictions represented by inequalities (II). When the target is to represent each species at least $b \geq 1$ times (e.g., Margules et al. 1988; Pressey and Nicholls 1989*a,b*; Rebelo and Siegfried 1992; Williams et al. 1996*a*; Willis et al. 1996; Freitag et al. 1998*b*), the restrictions are:

$$\text{Subject to } \sum_{j=1}^{n} a_{ij} x_j \geq b, \qquad i = 1, 2, \ldots, m \qquad \text{(II')}$$

Note that it may not be possible to find a minimum set for the each-species-once target among the subsets of a minimum set for higher representation targets. In addition, and this is perhaps more disappointing, it may happen that no minimum set satisfying constraints (II') is obtained by adding sites to an optimal solution of the each-species-once problem. Consider the following matrix $[a_{ij}]$, describing which species 1, 2, 3 are present in each site s_1, s_2, s_3, s_4.

$$\begin{array}{c} \\ 1 \\ 2 \\ 3 \end{array} \begin{array}{c} \begin{array}{cccc} s_1 & s_2 & s_3 & s_4 \end{array} \\ \begin{bmatrix} 1 & 0 & 1 & 0 \\ 1 & 0 & 0 & 1 \\ 0 & 1 & 1 & 1 \end{bmatrix} \end{array}$$

All three species do not occur simultaneously in one single site. Since all occur in $\{s_1, s_2\}$, this is an optimal set of sites for the each-species-once problem. If we want to obtain a solution for the each-species-twice by adding sites to $\{s_1, s_2\}$, we are forced to use the two remain sites s_3 and s_4. Yet, each species is present twice in $\{s_1, s_3, s_4\}$.

Thus, whilst it has been argued that a method which identifies a network that represents each species at least once provides a core of areas that can subsequently be expanded (e.g., Nicholls and Margules 1993; Margules et al. 1994*b*), the set which results if this is done may not necessarily be the most efficient network for attaining a higher target.

When sites have different sizes: represent each species at least once in the minimum area

Thus far it was assumed that all sites are equally relevant, i.e., the coefficient of every variable x_j in the objective function (I) is equal to 1. This is often the case, since many analyses are based on occupancy data mapped on grids, all grid cells have the same area and are considered to have the same cost of acquisition (e.g., Rebelo and Siegfried 1992; Lombard et al. 1995; Castro Parga et al. 1996; Williams et al. 1996*a,b*; Willis et al. 1996; Freitag et al. 1997; Hacker et al. 1998; Nantel et al. 1998). However, it may be desirable to consider the implications of differences in the cost of different networks, for example when sites are of different sizes (e.g., Pressey and Nicholls 1989*b*; Bedward et al. 1992; Sætersdal et al. 1993; Margules et al. 1994*b*; Turpie 1995; Pressey et al. 1997) and/or when sites differ in monetary value (e.g., Ando et al. 1998). In this set covering problem, the objective function (I) is replaced by:

$$\text{Minimise } \sum_{j=1}^{n} c_j x_j \,, \qquad \text{(I')}$$

where c_j is the cost of site j (usually, but not necessarily, the area).

Assigning different targets to species: represent each species i at least b_i times in the minimum area

The reserve selection problems considered thus far, like most addressed in the literature, assume that all species should receive the same investment. Several heuristic algorithms do deal with species weighted differently. Examples are rarity-based algorithms (e.g., Pressey and Nicholls 1989*b*; Rebelo and Siegfried 1992; Kershaw et al. 1994; Castro Parga et al. 1996), those that take taxonomic distinctiveness into account (e.g., Vane-Wright et al. 1991; Kershaw et al. 1994), and the algorithm applied by Freitag et al. (1997) which uses a ranking of species according to their conservation importance (Freitag and van Jaarsveld 1997). However, these weightings influence only the order in which sites are selected (by resolving ties), with those sites containing priority species tending to be selected first. The final representation target is generally the same (usually each species once) for all species, which means that the integer linear formulation is the same as without species weighting.

Species prioritisation makes sense if used to allocate limited conservation resources to the features that most need protection. This can easily be achieved by setting higher representation targets for priority species (as in Kirkpatrick 1983). Ideally, such targets are an expression of the level of representation required in the reserve network for the long-term persistence of each species (Bedward et al. 1992). The priority value for each species can be determined using single (e.g., rarity, taxonomic distinctiveness) or multi-criteria evaluation systems (e.g., Freitag and van Jaarsveld 1997), or by existing classifications such as the IUCN Red List categories (Anon. 1994). When working with other biodiversity features, such as plant communities or environmental domains, priority can be determined in terms of rarity (e.g., inversely related to the frequency of occurrence or total extent in the region) or threat (e.g., a measure of fragility or risk of short-term destruction).

For the problem where each species is represented a predefined number of times according to its priority, inequalities (II) must be modified to:

$$\sum_{j=1}^{n} a_{ij} x_j \geq b_i, \qquad i = 1, 2, \ldots, m \qquad \text{(II'')}$$

which states that the number of selected sites in which each species i must be represented is at least b_i.

Problem (I′) subject to (II″),(III) is called the *multicovering problem* (Hall and Hochbaum 1992), a generalisation of the set covering problem.

Giving sites different values: represent each species in at least a given percentage of its range in the minimum area

When working with sites with different areas, a target of representing each species a given number of times may be misleading. By requiring a species to be present once, for example, no distinction is made between selecting a large site comprising most of its geographical range or a small one comprising only a small proportion. Indeed, since we aim at a minimum area, the tendency is to select the smallest possible sites. Assuming a homogenous density across the range of a species, a larger site will contain a higher proportion of its population, and will therefore, all else being equal, make a higher contribution to its conservation in the long-term. As a first approximation, the relative importance of a site to the persistence of a species may therefore be expressed in terms of the fraction of its range contained in the site.

The problem of representing each species in at least a given percentage, b_i%, of its range in the minimum area can be expressed as (I′) subject to (II″), (III):

$$\text{Minimise } \sum_{j=1}^{n} c_j x_j , \qquad \text{(I′)}$$

Subject to

$$\sum_{j=1}^{n} a_{ij} x_j \geq b_i , \qquad i = 1, 2, \ldots, m \qquad \text{(II″)}$$

$$x_j \in \{0,1\} \qquad j = 1, 2, \ldots, n. \qquad \text{(III)}$$

but now a_{ij} is the percentage of the range of species i in site j, and not, as before, a binary value of presence or absence. This is a general 0/1 linear programming problem.

Defining the same target for all species in terms of percentage of range (e.g., Nicholls and Margules 1993; Kirkpatrick and Brown 1994; Pressey and Tully 1994; Pressey et al. 1997) may be a bad strategy in conservation terms. In practice, it means that the absolute target for a rarer species is lower than for a common one (30% of a small range is less than 30% of a large one), meaning that a higher conservation investment is being made in relatively unimportant species. Therefore, when using a percentage of range as a target, it is advisable to establish different values for each biodiversity feature (as in Lombard et al. 1997), ideally proportional to the conservation investment we want to allocate them. A very rare species (e.g., a narrow endemic) may require protection in 100% of its range, while a species that has declined greatly and has at the present non-viable populations may require more than 100% of its range reserved (e.g., for habitat restoration and reintroduction).

Working with densities: represent at least a given percentage of the population of each species in the minimum area

The ranges of species are typically not homogenous in terms of ensuring their long-term persistence, some areas being more important than others. When density data are available, and assuming that species tend to be more abundant in sites which are more important for their survival, these provide an objective measure of the importance of each site. Ideally, a system of reserves should capture the sites with higher densities (see Sections 4.1 and 7.1; Rodrigues et al. 2000*b*; Gaston and Rodrigues in press), or eventually compensate for the selection of less adequate sites by selecting a larger area.

One possible approach is that followed by Kershaw et al. (1994) and Turpie (1995), who for the purposes of area selection considered species to be present in a site only when they occurred there in substantial populations. But this implies a loss of information, since it results in the deletion of real occurrences (those below the population threshold) from the database. It also means that each site is either considered sufficient for the persistence of the species or totally irrelevant, which often is not the case. A more useful approach is to incorporate a continuous measure of the importance of sites, based on the continuous values of density.

Assuming that each species is homogeneously distributed across each site in which it occurs, the population size of each species in each site is obtained simply by multiplying the site's area by the local density of the species. The total population is the sum of these values for all sites. The fraction of the overall population in each site may be used as a measure of the importance of the site to the species.

The problem of representing each species by at least b_i % of its population in the minimum area can be expressed in the same way as the previous problem ((I′) subject to (II″), (III)). But a_{ij} is now the percentage of total population of species i in site j, while the target b_i is the minimum percentage of the population of species i that must be protected in the selected set of reserves.

If the population size of each species in each site is known, then the target for each species can also be defined in terms of a minimum number of individuals (as in Nicholls 1998). However, to address the problem of representing at least a given percentage of the population of each species it is not essential to know absolute densities or number of individuals. Any abundance values can be used if given on a linear interval scale (i.e., doubling the relative abundance corresponds to a doubling of the real density). Also, values do not need to be comparable between species (only between sites for the same species), thereby avoiding the problem that values may be better reflections of absolute density for some species (e.g., those that are more conspicuous) than for others.

Instead of abundance, other measures of the importance of sites to each species can be used if the assumption is met that doubling the value means doubling the importance. For example, for a bird it may perhaps be considered that the nesting sites are five times more important than the foraging areas. Another possibility is to use as measures of importance the values derived from models of the probability of occurrence of a species at different sites (Williams 1998*b*), or priority may be given to sites in the core of a species' range (Nicholls 1998). When working with biodiversity features other than species, the importance of each site for each feature may, for example, be measured as the percentage of the range of each feature that exists in each site or by an index of its relative conservation status in each site.

Further flexibility

All reserve selection problems presented thus far are particular cases of the general 0/1 linear programming problem ((I′) subject to (II″), (III)). Despite its simplicity and conciseness, this is a sufficiently flexible model to include a variety of other requirements which may be desirable to consider in the context of reserve selection (see also Cocks and Baird 1989; Possingham et al. 1993; Church et al. 1996). For example:

1) If m_j is the monetary value of site j, the constraint stating that the total monetary cost should not exceed a certain amount M is:

$$\sum_{j=1}^{n} m_j x_j \leq M .$$

2) If S is a given subset of sites (say, for instance, owned by the state), the imposition that at least a fraction p of the total area should belong to S is attained with the inequality:

$$\sum_{j \in S} c_j x_j \geq p \sum_{j=1}^{n} c_j x_j ,$$

which, in the format of the inequality constraints (II′) can be equivalently rewritten as:

$$\sum_{j=1}^{n} a_j x_j \geq 0, \text{ where } a_j = \begin{cases} (1-p)c_j & \text{if } j \in S \\ -pc_j & \text{if } j \notin S \end{cases}$$

3) Since each species is represented by an independent set of restrictions, not only different targets but also different levels of information can be used for different species. For a threatened species with no abundance data, the target may be to be represented in 80% of its range, for a species with good census data, the target may be of at least 1000 individuals, a value that may even have been obtained from population viability analysis, as suggested by Nicholls (1998).

4) For more complex integer linear problems it is unlikely that several optimal solutions exist, but it may be possible to explore the flexibility of reserve networks (in the sense

given by Pressey et al. 1993) by obtaining near-optimal solutions. It is possible to prevent a given set S of s sites from being selected by adding a restriction that explicitly excludes it:

$$\sum_{j \in S} x_j \le s - 1 .$$

When an optimal solution of a specific problem is excluded, the algorithm will find another optimal solution, if it exists, or else the second best result. By successively adding a restriction that excludes the previous solution, a sequence of different networks with costs equal or near to the optimal value is obtained. This diversity of solutions can afterwards be explored in order to address concerns that were difficult to include in the formal model, such as connectivity or specific land use conflicts.

As Nicholls (1998) concluded, it is more likely that the future of area-based selection methods is limited by lack of data than by our ingenuity to interface the data with the methods. Where possible, future fieldwork must be directed towards collecting useful data for conservation planning.

2.1.3 Addressing efficiency: optimal and heuristic solutions

Efficiency is the attribute of a good reserve selection procedure to which reference is most frequently made (e.g., Bedward et al. 1992; Rebelo and Siegfried 1992; Sætersdal et al. 1993; Lombard et al. 1995; Kershaw et al. 1994; Castro Parga et al. 1996; Willis et al. 1996; Ando et al. 1998; Freitag et al. 1998*b*; Haecker et al. 1998; Nantel et al. 1998). Maximum efficiency can only be achieved by using algorithms that guarantee the attainment of optimal solutions. Since the set of solutions is finite, one could think of finding the optimum by simply enumerating all the possible solutions. However, even for moderate sized problems, enumerating is completely impractical. On a 40 MIPS computer, enumerating all the 2^n subsets of $\{1, 2, \ldots, n\}$ (assuming that each subset requires no more than one single instruction) takes about 14 minutes for $n = 15$ and about seven hours for $n = 20$. But for $n = 30$ it would take more than 800 years.

Mathematical Programming gives the proper tools for dealing with integer linear programming problems. Unfortunately, for many integer problems, such as the ones presented above and even for the particular case of set covering (I)-(III), there is little hope that algorithms which always perform better than complete enumeration can be designed (these problems are proved to be NP-hard, which is widely assumed to mean that their computational time increases exponentially with the size of the input, see Garey and Jonhson 1979).

In most situations, a considerable reduction in the size of the data set may result from applying some simple pre-processing rules (Nemhauser and Wolsey 1988). Some rules were suggested by Possingham et al. (1993) and Camm et al. (1996) for the problem of representing each species once in the minimum number of sites. A more general set of rules that can be applied to any of the problems referred to above is:

1. To identify the irreplaceable sites: look for all the sites such that if removed from the analysis at least one of the species would exist in the remaining area below its required target. Irreplaceable sites are selected and excluded from the analysis, and the targets for all species occurring in those places must be updated. All species whose targets become zero or negative must be excluded.

2. To identify the redundant sites: some sites may contain only species that have been eliminated in the previous step. These are sites that make no contribution to the representation of the remaining species, and can therefore be excluded from the analysis.

These simple rules can permit a substantial reduction in the size of a data set. For example, when applied to the problem of representing 125 wetland plant species (including 25 considered rare) in 68 fens in the Scottish Borders (Rodrigues et al. 1999; see Section 3.2), they reduced the data matrix to: 16 species and 45 sites for the problem of representing each species once in the minimum area; 9 species and 24 sites for the problem of representing each of the rare species four times and each of the others once in the minimum area; 11 species and 37 sites for the problem of representing each of the rare species in 60% and each of the others in 10% of its range in the minimum area.

Reduction is normally effective because there is usually some degree of coincidence between sites with the rarer species, those with high diversity and those with high abundances (these are often the well preserved habitats, with less human interference). The irreplaceable sites, which usually depend on the presence of rarer species, are often sufficient also to fulfil the representation targets for many of the most widespread species, resulting in several species being removed from the analysis. Other sites that contain only those same widespread species become redundant and can be ignored. This outcome is more marked when the conservation targets are higher for the rare species (see example above), since it tends to increase the number of irreplaceable sites.

When, despite pre-processing, problems are too large to be solved in a reasonable time period by algorithms which guarantee an optimal solution, heuristics may be the only sensible option. Their ability to produce quick answers as part of interactive systems, such as CODA (Bedward et al. 1992) and WORLDMAP (Williams 1996), may be important for real-time evaluation of different reserve networks (but see Section 2.2; Rodrigues and Gaston 2002*b*).

However, heuristics such as the ones that have been commonly used in conservation literature may not be the most appropriate from an efficiency perspective. These algorithms consist of stepwise procedures and comprise more or less intuitive rules to decide which site to add at each step (e.g., Margules et al. 1988; Nicholls and Margules 1993; Csuti et al. 1997; Pressey et al. 1997). It is generally stated that some of these are 'good' heuristics that produce results that are only slightly sub-optimal (e.g., Pressey et al. 1996*b*; Csuti et al. 1997; Nantel et al. 1998; Williams 1998*b*). However, the degree of sub-optimality has been reported to vary widely (see Table 2.I), from heuristics that found the exact minimum (Willis et al. 1996) to situations where heuristic algorithms have produced grossly sub-optimal solutions (Sætersdal et al. 1993; Csuti et al. 1997; Pressey et al. 1997). The drawback of these particular heuristic methods is that although in some cases they can produce very good results, or even the optimal solution, there is no certainty that they will always perform well. The fact that one heuristic achieved a good result in a specific situation is not a guarantee of its efficiency in all cases (one good result does not make a 'good' heuristic), since this is highly dependent on particulars of data structure (Willis et al. 1996; Pressey et al. 1996*b*). For example, Sætersdal et al. (1993) applied the same heuristic to two distinct datasets and obtained a large discrepancy in the degree of sub-optimality of the results: 5% extra area for plants, and 43.3% for birds (Table 2.I).

The only way to know exactly how sub-optimal is the result obtained by an heuristic in a given situation is to assess it against the optimal result. Naturally, when this is possible there is no need for the heuristic in the first place. However, it is possible to evaluate the quality of the solutions (of a minimisation problem) produced by an heuristic by comparing it with a *lower bound* – a value that is known to be below or equal to the true (unknown) optimal value. The difference between the value of the heuristic solution and the lower bound is an upper bound of the distance between the heuristic solution and the optimal value, and therefore a measure of its quality (see Figure 2.1, Section 2.2).

Table 2.I – Summary of the results of examples of published studies that assessed the efficiency of heuristic algorithms by comparing them with optimal solutions (partially adapted from Pressey et al. 1996*b*). In the two last examples, the optimal solution was not found but results are given to illustrate the variability of solutions obtained by the heuristics. In the analysis by Csuti et al. (1997) and Pressey et al. (1997), the values for heuristics correspond to the best results out of 100 runs for each algorithm, and not to the average result.

Study	**Objective**	**Results**
Sætersdal et al. (1993), Norway	To represent each of 321 plant species at least once in the minimum number of woods (out of 60).	Optimal: 71.4% of total area Heuristic: 'nearly 75%' of total area The heuristic found 5% more area than the optimal solution
Sætersdal et al. (1993), Norway	To represent each of 47 bird species at least once in the minimum number of woods (out of 60).	Optimal: 27.9% of total area Heuristic: 40% of total area The heuristic found 43.4% more area than the optimal solution
Willis et al. (1996), South Africa	To represent each of 110 plant species at least once in the minimum number of grid cells (out of 53).	Optimal: 13 cells Heuristics: 13 cells The heuristics found the optimal solution (n = 2)
Csuti et al. (1997), USA	To represent each of 426 terrestrial vertebrates at least once in the minimum number of hexagons (out of 441).	Optimal: 23 sites Heuristics: between 24 and 29 sites The heuristics found between 4.4% and 26.1% more sites than the optimal solution (μ = 9.2%; σ = 6.1%; n = 18)
Pressey et al. (1997), Australia	To represent each of 248 land system at least once in the minimum number of pastoral holdings (out of 1885).	Optimal: 54 sites Heuristics: between 57 and 81 sites The heuristics found between 5.6% and 50% more sites than the optimal solution (μ = 19.4%; σ = 15.2%; n = 12)
Pressey et al. (1997), Australia	To represent each of 248 land system at least once in the minimum area of pastoral holdings (out of 1885).	Optimal: 12084.50 km² Heuristics: between 13359.75 and 16958.25 km² The heuristics found between 10.6% and 40.3% more area than the optimal solution (μ = 21.6%; σ = 10.0%; n = 12)
Pressey et al. (1997), Australia	To represent at least 5% of the total regional extent of each of 248 land system in the minimum number of pastoral holdings (out of 1885).	Optimal: not found Heuristics: between 123 and 157 sites The worst heuristic found 27.6% more sites than the best one (μ = 7.2%; σ = 8.0%; n = 18)
Pressey et al. (1997), Australia	To represent at least 5% of the total regional extent of each of 248 land system in the minimum area of pastoral holdings (out of 1885).	Optimal: not found Heuristics: between 25887.5 and 30756.25 km² The worst heuristic found 18.8% more area than the best one (μ = 8.3%; σ = 4.9%; n = 18)

Methods for obtaining good lower bounds (near the optimal) are fundamental in Mathematical Programming, not only for evaluating the quality of heuristic solutions but also for obtaining optimal solutions. Exact methods for the resolution of hard integer problems are essentially variations of the well-known enumerative 'branch-and-bound' method, and their efficacy results mainly from the ability to find good lower bounds (for more details see Nemhauser and Wolsey 1988).

A way of obtaining a lower bound to the optimal value of a (minimisation) problem is by solving some easy *relaxation*, i.e., a new problem that contains all the solutions of the initial one. A continuous linear relaxation of a 0/1 linear problem is the one obtained when replacing the integrality constraints $x_j \in \{0,1\}$ by $0 \leq x_j \leq 1$. The new problem is a standard *linear programming problem*, for which an optimal solution can be quickly obtained. Usually, this is not a 0/1 solution (if it were, then it would be an optimal solution of the integer problem), but its value is surely a lower bound to the 0/1 optimal value. However, the bounds thus obtained are normally far from the optimal value, which means that they are not good bounds.

It can be proven that given a solution R of a relaxation which is not a solution of the original linear problem, there is always some linear inequality which 'cuts' R, i.e., a new restriction that is violated by R but verified by all the solutions of the original integer problem. The new problem obtained by adding this new inequality to the current relaxation is still a relaxation (again an easy linear programming problem) of the original problem, whose optimal solution is a better (or equal) lower bound than the previous one. Proceeding in this way a sequence of non-decreasing lower bounds to the optimal solution of the integer problem is obtained. This general procedure is called a cutting-plane algorithm (see for example Nemhauser and Wolsey 1988). Its efficacy depends on the ability to find suitable cuts. Nemhauser and Wolsey (1988) describe a family of cuts (strong cover inequalities) which produces excellent lower bounds.

'Intuitive' heuristic algorithms, such as many of those that have been used in the conservation literature, have the advantage of being easy to understand and to program. But for increasingly complicated problems they become more difficult to create. For example, where representation targets for different species are measured in different units, because of differences in the information available, (e.g., percentage of range, percentage of population, number of individuals), it is not straightforward to create a 'good' heuristic. In these situations, it is also more likely that simple intuitive heuristics will perform poorly in terms of efficiency. Therefore, although for these more complex (more realistic) problems the processing time increases, it may very well be that here particularly the need to apply optimisation tools becomes more imperative.

Fortunately, Mathematical Programming is providing improved optimisation programmes, some of which are capable of dealing with large data sets and making use of approximation tools to reach the optimal solution faster. Also, they can be used as heuristic algorithms to obtain a sub-optimal solution. If processing time extends beyond reasonable limits, the programme can be interrupted and the best solution obtained meanwhile can be considered to be a heuristic result. Most optimisation programmes will also give the value of the best lower bound obtained so far, therefore providing a good measure of the degree of sub-optimality of this solution. One possible strategy may be to consider to be satisfactory any solution which has a maximum degree of sub-optimality of, say, 5% and interrupt processing as soon as it is obtained.

Many programmes also accept as input the value of a known feasible solution that is an upper bound of the optimal value. This can reduce considerably the processing time by eliminating *a priori* the more expensive solutions. The solution obtained by an heuristic (including an 'intuitive' one) can therefore be used as an initial upper bound, and the result obtained after some processing time is never worse than the initial one. In this way, optimisation programmes can be used to improve the result obtained by a heuristic.

The decision about how to obtain a solution for a specific situation will depend mainly on the reserve selection problem in hand. In some situations, an assumedly non-optimal solution might be all that it is possible to attain, but if so a measure of sub-optimality should be provided. For most problems, however, an optimal solution should probably be possible to obtain in a reasonable time (see Section 2.2; Rodrigues and Gaston 2002*b*). How long is 'reasonable' is variable and mainly a trade-off between the importance of having a quick result versus having an exact solution. In real conservation problems, where the cost associated with a worse solution is a real concern, it might be worth waiting for some days to obtain a cheaper result.

This focus on obtaining more efficient solutions does not mean that concern about cost should be the priority when addressing real conservation planning problems. As far as possible, the first step must be to decide what should be the problem that is to be solved (i.e., determine the ecological constraints) and then make the best possible use of optimisation techniques to look for the less costly solutions. The purpose of applying these methods to conservation planning is not that less money is invested in the acquisition of reserves, but that the amount available is invested in a more effective way.

2.1.4 Addressing accountability

Modelling reserve selection questions as integer linear problems by using Mathematical Programming tools can bring substantial advantages in terms of the accountability of the results.

The formal writing of integer linear problems requires that conservationists make very explicit the goals to be achieved by a reserve network. The objective function clearly states what is the variable that should be optimised (usually a measure of cost) and the restrictions identify the constraints that must be imposed on the network. Potentially subjective values, such as the investment to be allocated to each species or the relative importance of each site, are necessarily made explicit. In this way, an integer linear problem expresses unequivocally the problem being solved, resulting in more explicit solutions. This is particularly relevant in more complex situations, where it becomes more difficult to devise appropriate 'intuitive' heuristics that correspond to the problem in hand. For example, Pressey et al. (1997) did not develop specific heuristics for each of the problems of minimising the total area in a network and of minimising the total number of sites. Instead, they used the same algorithms for both, therefore obtaining necessarily identical solutions.

Furthermore, by solving a formally written problem there is a guarantee that all the concerns addressed are taken into account in the result. With 'intuitive' heuristics, however, there is less clarity in this regard. Issues such as valuing species differently (Freitag et al. 1997) or minimising the total area rather than the total number of sites (e.g., Pressey et al. 1997), have been incorporated into heuristic approaches in the form of rules to solve ties. This assumes that ties will occur, but in more complex problems this may not happen. When ties exist, it is unpredictable how each concern will really influence the final result, because it depends on the frequency of ties, on the 'hierarchy' of each concern in the tie-resolving rules and often on random decisions.

Finally, the optimality of the solution is itself a guarantee of more transparency in the results. For example, when adding a new constraint to a *minimisation* problem, the new optimal solution is never less costly than the original one, which allows an exact measure of the cost associated with a specific constraint. The sub-optimality of heuristics brings uncertainty to detailed comparative analyses of efficiency, because variance obtained in the costs of the solutions of two problems does not necessarily reflect real differences in cost. The higher the degree of sub-optimality of the solution obtained by the heuristic the more serious this problem can be, and in extreme situations, it may even lead to an inversion of the expected results (e.g., in Pressey and Tully 1994). Even in the situations where an optimal solution is not achieved, it is useful to have a measure of the quality of the solution obtained (a lower bound), in order to assess the reliability of the conclusions taken from the result.

2.1.5 Conclusions

Most reserve selection exercises reported in the literature have focused on relatively simple problems, such as that of representing each species once or a fixed number of times. However, most real conservation scenarios are likely to be considerably more complex, in order to reconcile all of the concerns prevailing and to use all the relevant information available. In order to ensure the long-term effectiveness of reserve networks, it is essential that considerations arising from ecological theory, at the population, community or landscape levels, are integrated in selection algorithms (Nicholls 1998), including issues such as viability and threat (Williams 1998*b*). Otherwise, reserve selection procedures will inevitably result in approaches that are too simplistic from the perspective of the conservation agencies, compromising their credibility as valuable tools for application in real-life conservation problems.

This section illustrates how a wide diversity of considerations and information can easily be integrated in reserve selection procedures when they are modelled as integer linear problems. Many of the issues discussed, such as valuing species and sites differently, do not presuppose the existence of higher levels of information than those commonly available in real situations. Indeed, in most regions where detailed information on the distribution of species exists (enough for the application of the classical complementarity methods), other relevant data is also accessible but has usually been ignored. For example, most countries have Red Data books before they have distribution atlases, and at least for some species there is information on the most relevant sites for their conservation, sometimes resulting from population viability analysis. Therefore, the higher complexity advocated in this section does not correspond in most situations to a need to obtain more information, but to make the best use of the available data when selecting a network of reserves.

More complexity implies more difficulty in creating adequate 'intuitive' heuristics for the specific problem in hand, therefore risking an even higher level of sub-optimality and reducing the explicitness of the results. Mathematical Programming techniques provide a more effective way of improving the flexibility of reserve selection algorithms without compromising the efficiency and accountability of the results.

2.2 Tractability and speed of optimal reserve selection procedures

Methods for the selection of priority areas for conservation based on the complementarity principle (Vane-Wright et al. 1991) have been receiving extensive interest in the conservation literature (e.g., Pressey et al. 1993; Dobson et al. 1997; Ando et al. 1998; Howard et al. 1998; Margules and Pressey 2000). These methods have been proposed in response to the acknowledgement that resources available for conservation purposes are scarce and should therefore be employed in efficient ways that maximize the diversity of biological features benefited (Pressey and Nicholls 1989*a*; Pressey et al. 1993; Scott et al. 1993).

The first papers on this subject (e.g., Kirkpatrick 1983; Margules et al. 1988; Pressey and Nicholls 1989*a,b*; Bedward et al. 1992; Nicholls and Margules 1993; Pressey et al. 1993) stressed the efficiency of these methods in relation to previously more popular scoring procedures. Efficiency (*sensu* Pressey and Nicholls 1989*a*) has been defined as being inversely related to the cost needed to acquire a reserve network which achieves a given conservation target (such as representing all species at least a given number of times), and has been widely considered to be an important attribute of a good reserve selection procedure (e.g., Bedward et al. 1992; Rebelo and Siegfried 1992; Sætersdal et al. 1993; Lombard et al. 1995; Kershaw et al. 1994; Castro Parga et al. 1996; Willis et al. 1996; Ando et al. 1998; Freitag et al. 1998*b*; Hacker et al. 1998; Nantel et al. 1998).

Those first papers also presented the basic heuristic algorithms which (in their original or modified form) subsequently became popular in the conservation literature. However, it was observed early on that reserve selection problems can be solved optimally (i.e., with maximum efficiency) by application of a standard operations research technique, namely integer linear programming (e.g., Cocks and Baird 1989; Underhill 1994; Church et al. 1996). The use of intuitive heuristics that cannot guarantee the optimality of the solutions found has therefore been criticised (Underhill 1994). In response to these criticisms, two subsequent papers (Pressey et al. 1996*b*, 1997) defended the importance of heuristics in 'real-world conservation planning', with three main arguments:

1. That 'good' heuristics provide results which are only slightly sub-optimal.

2. That optimisation methods may not be able to provide solutions to more realistic problems. Pressey et al. (1996*b*, 1997) reported being unable to obtain an optimal solution for the problem of finding the minimum set of sites (or the minimum area) representing at least 5% of the area of each of 248 land types (distributed across 1885 pastoral holdings): using standard optimisation packages, the problem ran for weeks without finding solutions.

3. That optimisation methods may be too slow and therefore inadequate for interactive practical conservation planning (where managers and politicians may be waiting to see the results). Pressey et al. (1996*b*, 1997) reported long processing times (days or, in a more recent version of the software, 10 hours) for the problem of finding the minimum number of sites needed to represent each of 248 land types on 1885 pastoral holdings.

The large majority of subsequent papers about complementarity-based methods for reserve selection have persisted in the use of intuitive heuristics, often justifying their application by quoting the three arguments presented by Pressey et al. (1996*b*, 1997): that the results are expected to be similar (e.g., Howard et al. 1998; Williams et al. 1996*a*,*b*; Williams 1998*b*); that optimisation methods are unable to solve some more realistic problems (e.g., Lombard et al. 1997; Pressey and Logan 1998; Williams 1998*b*; Polasky et al. 2001*b*); and/or that optimal solutions would take too long to obtain (e.g., Erasmus et al. 1999; Lombard et al. 1997; Williams et al. 1996*a*,*b*; Williams 1998*b*).

In a previous study (Rodrigues et al. 2000*c*; see Section 2.1), it has been argued that intuitive heuristics cannot offer guarantees of providing good solutions to reserve selection problems. Here, the focus is on rebutting the other two arguments, concerning the tractability and speed of problem resolution using optimisation methods. I argue that, given the capability of currently existing software and computers, these are no longer a real obstacle to the use of optimisation procedures for most of the reserve selection problems being published in the literature.

Table 2.II presents a list of published studies which used complementarity-based methods for the selection of sets of priority sites. This provides an overview of the size (number of biodiversity features, such as species, and number of selection units) and type of problems most frequently addressed in the literature.

Table 2.II – Summary of examples of published studies which used complementarity-based methods for the selection of networks of priority areas for conservation. * refers to studies that used optimisation procedures (sometimes alongside heuristics); others only used heuristic approaches.

Reference	**Data**	**No. features**	**No. sites**	**Problem**
1. Rebelo and Siegfried 1992	Plants, South Africa	332	550	Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, 5× and 10×
2. Sætersdal et al. 1993 *	Plants and birds, Norway	321, 47	60	Find a set with minimum number of sites representing all species at least once
3. Kershaw et al. 1994	Antelopes, Africa	99	249	Find a set with minimum number of sites representing all species at least once
4. Margules et al. 1994*b*	Plants, U.K.	50	77	Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, and 5×
5. Lombard et al. 1995	Snakes, South Africa	122	~ 1900	Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, and 5×
6. Turpie 1995	Birds, South Africa	88	42	Find a set with minimum number of sites representing all species at least once
7. Castro Parga et al. 1996	Plants, Iberian Peninsula	801 2133	5184 259	Find a set with minimum number of sites representing all species at least once
8. Church et al. 1996 *	Vertebrates, U.S.A.	333	280	Find a set which maximises the number of species that can be represented within a given number of sites
9. Williams et al. 1996*b*	Plants, Neotropics	729	1751	Find a set which maximises the number of species that can be represented within a given number of sites
10. Williams et al. 1996*a*	Birds, U.K.	218	2827	Find a set with minimum number of sites representing all species at least once
11. Willis et al. 1996 *	Plants, South Africa	110	53	Find a set with minimum number of sites representing all species at least 1×, 2×, 3×, 4×, and 5×
12. Dobson et al. 1997	Endangered species, U.S.A.	924, 503, 107, 84, 72, 58, 57, 43	2858	Find a set with minimum number of sites representing all species at least once
13. Lombard et al. 1997	Vegetation types and plant species, South Africa	97 species + 11 veg. types	193	Find a set with minimum number of sites representing all plant species and a target % of area of each vegetation type
14. Muriuki et al. 1997	Birds, Kenya	970	210	Find a set with minimum number of sites representing all species at least once
15. Pressey et al. 1997 *	Land systems, Australia	248	1885	Find a set with minimum number of sites representing all land systems at least once
16. Pressey et al. 1997 *	Land systems, Australia	248	1885	Find a set with minimum area which represents all land systems at least once

Table 2.II (cont.)

Reference	Data	No. features	No. sites	Problem
17. Pressey et al. 1997	Land systems, Australia	248	1885	Find a set with minimum number of sites which represents each land system by at least 5% of its regional extent
18. Pressey et al. 1997	Land systems, Australia	248	1885	Find set with minimum area which represents each land system by at least 5% of its regional extent
19. Stokland 1997	Birds and insects, Norway	32, 309	40, 17	Find a set which maximises the number of species that can be represented within a given number of sites
20. Ando et al. 1998*	Endangered taxa, U.S.A.	911	2851	Find a set which maximises the number of taxa that can be represented in a given number of sites or in at set with a given acquisition cost.
21. Freitag and van Jaarsveld 1998	Mammals, South Africa	192	474	Find a set with minimum number of sites representing all species at least once
22. Hacker et al. 1998	Primates, Africa and Madagascar	205	1825	Find a set with minimum number of sites representing all species at least once
23. Howard et al. 1998	Plants and animals, Uganda	2452 (and subsets of variable size)	50	Find a set which maximises the number of species that can be represented within a given number of sites
24. Nantel et al. 1998	Plants, Canada	244	456	Find a set with minimum number of sites representing all species at least once
25. Pressey and Logan 1998 *	Land systems, Australia	248	1885, 5278, 247	Find a set with minimum area such that each land system is represented in a given percentage of area target
26. Lombard et al. 1999	Plants, South Africa	851, 771	197, 188	Find a set with minimum number of sites representing all species at least once
27. Virolainen et al. 1999	Plants, Finland	32	25	Find a set with minimum number of sites representing all species at least once
28. Araújo and Williams 2000	Trees, Europe	174	4419	Find a set which maximises the number of species that can be represented within a given number of sites
29. Fjeldså and Rahbek 1998	Birds, South America	~ 1700	913, 118, 226, 456, 540	Find a set with minimum number of sites representing all species at least 3×
30. Reyers et al. 2000	Plants and animals, South Africa	1588, 574, 328, 214, 427	215	Find a set with minimum number of sites representing all species at least once
31. Williams et al. 2000*c*	Plants and vertebrates, Europe	2435	3143	Find a set which maximises the number of species that can be represented within a given number of sites
32. Polasky et al. 2001*b*	Birds, U.S.A.	167	1223	Find a set which maximises the number of genera that can be represented within a given number of sites

Table 2.III – Processing times needed to solve a diversity of linear integer problems using the C-PLEX software (ILOG 1999) on a Pentium II processor with 128.0 MB RAM.

References	**Data**	**No. species**	**No. sites**	**Problem**	**Processing time**
1. Harrison et al. 1997	Birds, Southern Africa	852	3885	Find a set with minimum number of sites representing each species at least once	4.71 seconds
2. Harrison et al. 1997	Birds, Southern Africa	852	3885	Find a set with minimum number of sites representing each species at least five times	1.58 seconds
3. Harrison et al. 1997	Birds, Southern Africa	852	3885	Find a set which maximises the number of species that can be represented within 10 sites	92,911 seconds (~26 hours)
4. Harrison et al. 1997	Birds, Southern Africa	852	3885	Find a set with minimum area such that each species is represented within at least 5% of its range (variation in the size of the selection units was simulated by attributing to each cell an area obtained as a random integer number between 1 and 10)	103,404 seconds (~ 29 hours)
5. Harrison et al. 1997; Gaston et al. 2001	Birds, South Africa and Lesotho	651	1858	Find a set with minimum number of sites representing each species at least once	1.79 seconds
6. Harrison et al. 1997	Birds, South Africa and Lesotho	651	1858	Find a set which maximises the number of species that can be represented within 20 sites	18.08 seconds
7. Balmford et al. 2000*a*; Mace and Balmford 2000	Mammals, World	4228	111	Find a set with minimum number of sites representing each species at least once	0.11 seconds
8. Balmford et al. 2000*a*; Mace and Balmford 2000	Mammals, World	4228	111	Find a set which maximises the number of species that can be represented at a cost of 50% of the minimum needed to represent all species	90.13 seconds
9. Murray et al. 1998	Birds, Scotland	138	1756	Find a set with minimum number of sites representing each species at least once	1.80 seconds
10. Murray et al. 1998	Birds, Scotland	138	1756	Find a set which maximises the number of species that can be represented within 4 sites	3.34 seconds
11. Sawford 1987	Butterflies, United Kingdom	45	496	Find a set with minimum number of sites representing each species at least once	0.06 seconds
12. Sawford 1987	Butterflies, United Kingdom	45	496	Find a set which maximises the number of species that can be represented within 4 sites	151.25 seconds

Table 2.III presents the processing times I have recorded for reserve selection problems of sizes and types that embrace this variation. All problems were tractable and could be solved exactly using the C-PLEX software (ILOG 1999) on a Pentium II processor with 128.0 MB RAM. Most problems, even some of the larger ones, took just a few seconds to solve. It is likely that this would also be the case with the majority of problems addressed in the literature (Table 2.II). Indeed, Ando et al. (1998), working with a large data set (see problem 20 in Table 2.II) did not report any difficulty in obtaining optimal solutions and Church et al. (1996), working with a medium sized problem (number 8 in Table 2.II), reported an average processing time of 2.9 seconds (9 seconds maximum).

Two of the largest problems explored did take significant time to solve (problems 3 and 4 in Table 2.III, which took 26 and 29 hours, respectively). However, in both cases, the optimisation software found relatively good solutions to the problems after just a few minutes. During processing, C-PLEX continuously calculates lower bounds to the solutions to minimisation problems (Figure 2.1*a*), i.e., values that are known to be below or equal to the true, unknown, optimal value (in maximisation problems, upper bounds are calculated). Using these lower bounds, C-PLEX obtains an estimate of the sub-optimality of the best solution found at any given time; this is defined as the gap, which is given by the difference between the lower bound and the best solution found in relation to the value of the best solution (Figure 2.1*b*). Even when the total processing times (needed to find the true optimal solution) are very long, optimisation software may find good solutions quite fast. In problem 3, a solution reported to have a gap of ≤ 7.42% was found after just 7 minutes, while after 21 minutes the level of sub-optimality was known to be ≤ 4.90%. Twenty-five out of the 26 hours of processing time were consumed in improving a solution with a known sub-optimality ≤ 4%. In problem 4, the gap after 6 minutes processing was ≤ 1.50%, which had dropped to ≤ 0.92% after 26 minutes (Figure 2.1). Twenty-seven out of 29 hours of processing time were spent finding solutions with a gap ≤ 0.33%.

These levels of sub-optimality are better than the average figures reported for intuitive heuristics (Rodrigues et al. 2000*b*; see Table 2.I in Section 2.1). Therefore, optimisation software may also be used to obtain good solutions (even if not optimal) for more complex problems in a reasonable processing time. The main advantage of the solutions obtained in this way is that an estimate of the level of sub-optimality is known, and there is always an option to extend the processing time in order to improve the result. Solutions obtained by intuitive heuristics have a substantial risk of being grossly sub-optimal, and having previously obtained a good result with a given heuristic cannot guarantee its efficiency for all data sets (see Section 2.1; Rodrigues et al. 2000*b*).

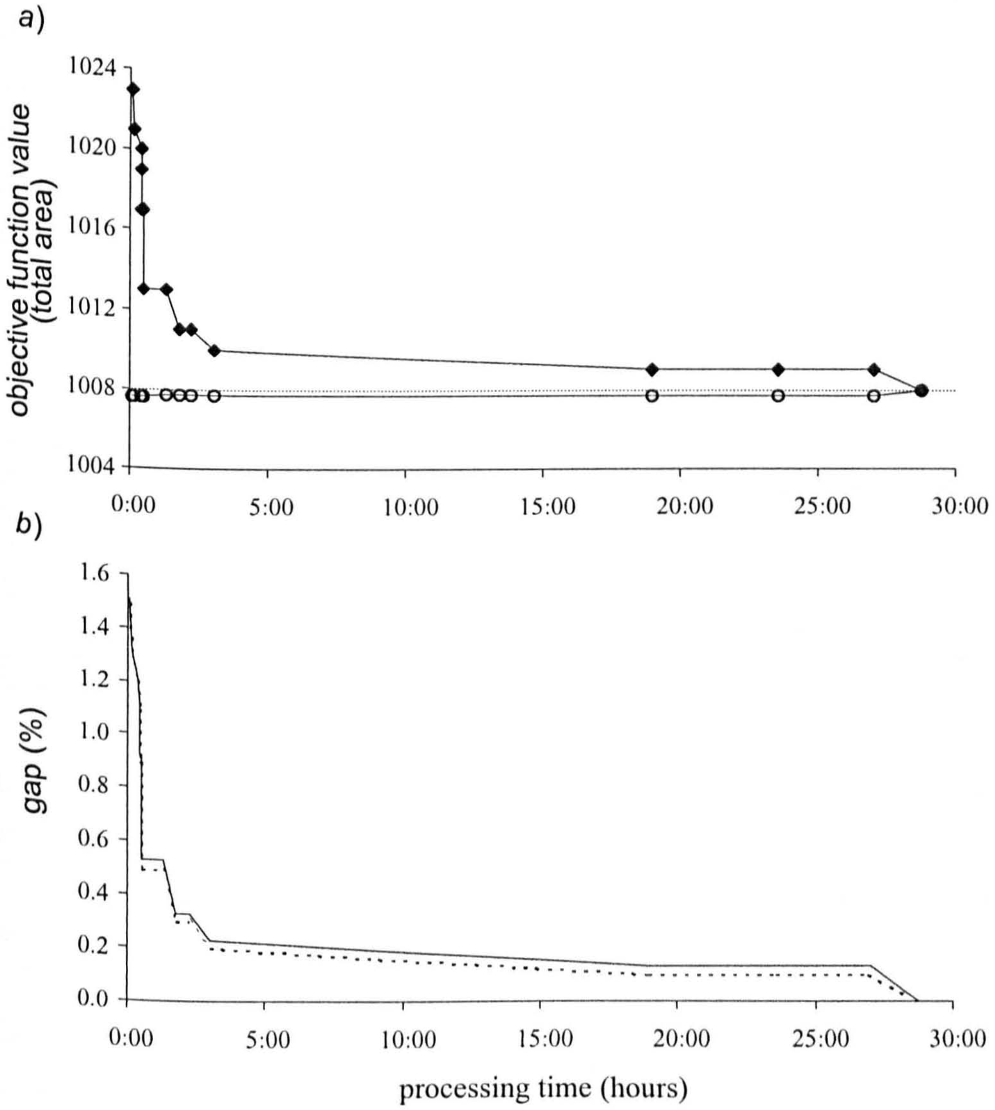

Figure 2.1 – Values provided by C-Plex (ILOG 1999) during processing of problem 4 in Table 2.III. *a*) Trend in the values of the objective function (total area) for the best solution found (dark diamonds) and for the best lower bound obtained (open circles). The horizontal broken line indicates the position of the true optimal solution (only known at the end of processing, when the best integer and the best lower bound coincide). *b*) Trend in the values of the known gap (solid line) and the true gap (broken line). The known gap is given by the difference between the values of the best solution and the best lower bound in relation to the value of the best solution, and this is an upper bound of the true gap (calculated in relation to the true optimal instead of the best known solution), providing an over-estimate of the degree of sub-optimality of each solution found.

Problem 4 differs from the others in Table 2.III by having non-integer values in the restriction inequalities (corresponding to the values of the percentage of the range of each species located within each site). The number of decimal places chosen makes a significant difference to processing time. The results referred to above and in Table 2.III (~29 hours processing time) were obtained for four decimal places (i.e., the minimum unit was 0.0001%). Setting the number of decimal places to eight (i.e., up to 0.00000001 %) the problem takes about 7 days to solve – but a solution with ≤ 3.13% gap is found after one hour, and after 20 hours the solution has ≤ 0.16% gap. Nevertheless, this difference in processing time (as well as the evolution of computers and software) may also help to explain why, for example, Pressey et al. (1997) failed to find an optimal solution to an equivalent problem (problem 18 in Table 2.II) despite working with a smaller data set.

There are certainly situations where reserve selection problems cannot be solved by the straightforward application of linear programming. This is, of course, particularly true of non-linear problems (e.g., Polasky et al. 2000; Williams and Araújo 2000). It is also possible that extremely large problems may exceed the computational capacity of currently existing software and computers (although these are continuously improving). But to date I have not encountered such problems, and for the large majority of the problems found in the literature (Table 2.II) there is really no good reason why optimisation approaches cannot be used.

On the other hand, there are several good reasons why optimisation should be used. Not only are the solutions found expected to be more efficient, there is also great flexibility in the type of data and concerns that can be integrated in linear integer problems, while retaining the accountability of the decision process (see Section 2.1; Rodrigues et al. 2000*b*).

The use of optimisation techniques implemented by software such as C-PLEX does not require expert programming skills. Actually, it requires less programming than needed to solve most 'intuitive' heuristics when applied to moderate-sized data sets, because the solving procedure itself is comprised of existing routines (such as branch-and-bound) already incorporated in the software. The fundamental step is being able to convert the selection problem in hand into a linear programming one, which can be done for most selection problems with only basic knowledge of operations research theory (see for example Winston 1994). Rodrigues et al. (2000*c*) explain in detail how problems such as the ones in Table 2.II can be represented as integer linear problems (see Section 2.1).

3 Evaluating the performance of existing reserve networks

Protected areas are central to strategies for the long-term maintenance of biodiversity. This chapter addresses the effectiveness of existing networks in fulfilling this role. Section 3.1 addresses the general issue of whether protected areas are useful conservation tools, by investigating the extent to which protected areas in southern Africa are mitigating local species' extinction. Section 3.2 assesses the performance of the system of Sites of Special Scientific Interest in representing the diversity of wetland plants in fen sites in the Scottish Borders as a case-study to explore methods for the evaluation of networks of protected areas.

3.1 Protected areas and the mitigation of local species extinction

3.1.1 Introduction

Protected areas are seen as central to strategies for the long-term maintenance of biodiversity (Convention on Biological Diversity 1992). How effective existing networks are in fulfilling this role remains poorly understood. Whilst there are many studies documenting the ecological degradation of existing reserves (Ferreira et al. 1999; IUCN 1999; Singh 1999; Liu et al. 2001; Rao et al. 2002), there is nevertheless evidence that such areas have a significant effect in mitigating levels of land clearance and other pressures (Sánchez-Azofeifa et al. 1999; Bruner et al. 2001*a*). Moreover, while there are many case studies demonstrating the inefficiency of reserve networks in representing biodiversity features (e.g., Pressey and Tully 1994; Jaffre et al. 1998; Nantel et al. 1998) and the inability of individual reserves to retain all of the species present when they were established (Newmark 1987, 1996; Nicholls et al. 1996; Gurd and Nudds 1999; Rivard et al. 2000), little attention has been given to the role of protected areas in preserving overall local species richness.

A strong positive relationship between net primary productivity (NPP) and the number of bird species has been demonstrated previously for South Africa (van Rensburg et al. 2002). While local NPP is likely to not have been significantly affected by human influence, local species richness is known to be sensitive to human activities. Here, I analyse how the relationship bewteen these two variables is influenced by the extent of reserved area, to investigate the extent to which protected areas are having an effect in mitigating local species' extinction.

3.1.2 Data

The Southern African Bird Atlas Project (SABAP; Harrison et al., 1997) has provided the most comprehensive information currently available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana. Observers visiting each cell recorded the presence of identified species on checklists, breeding and non-breeding records being considered equivalent. A variable number of checklists has been submitted for each cell. In this study, I have used presence/absence data for 651 bird species in South Africa and Lesotho, converted to half-degree scale to match the scale of the available NPP data. To reduce biases, cells expected to have very incomplete species lists due to insufficient sampling effort were excluded. Hence, only the 369 half-degree cells which had on average ten checklists (across each of the component quarter-degree cells) have been considered. The relationship between sampling effort and percentage of protected area is only very weak and with little predictive power (p = 0.04; r = 0.11; n = 369).

Restricted-range species were defined as the 25% species with smaller range size in the study area, measured as the number of occupied half-degree cells (Gaston 1994). Net Primary Productivity data (NPP; g C m^{-2} yr^{-1}) were obtained at the half-degree scale based on outputs from the SDGVM model (Woodward et al. 2001). The boundaries of two-hundred and sixty-four protected areas, listed on the 1997 United Nations list of protected areas for South Africa (WCMC 1997), were mapped using ArcView GIS (ESR I Inc. 1998).

3.1.3 Analyses

In South Africa and Lesotho, bird species richness has a strong positive relationship with NPP (Figure 3.1; Table 3.I; van Rensburg et al. 2002). Although weaker, this relationship is also highly statistically significant when only restricted-range species are considered. For both sets of species, but particularly for the latter, the fitted least-square regressions tend to predict higher values of species richness for a given NPP when subsets of cells with increasing percentages of protected area are considered (Figure 3.2; Table 3.I). Indeed, controlling for NPP, the mean residual species richness of cells containing no protected areas is negative for all species (μ = -22.2 ± 6.4; throughout, values indicated after ± refer to the 95% confidence interval) as well as for restricted-range ones (μ = -3.3 ± 0.9), while the mean residual richness of cells including protected areas is positive and significantly larger (for all species μ = 20.2 ± 6.5; for restricted range species μ = 3.0 ±1.9). Additionally, the mean residual richness tends to increase for subsets of cells with increasing percentages of protected area (Figure 3.3), so that, for example, cells with 5 to 10% of their area preserved have on average 43 additional species, including 3 restricted-range ones, than cells without any level of protection, while cells with 20 to 30% reserved area have on average 69 additional species, including 20 restricted-range ones.

Assuming that, in general, species composition inside protected areas is closer to the natural undisturbed situation than in areas without formal protection, these results indicate that reserves are making a considerable difference in retaining the species richness of the areas in which they are located. Furthermore, the larger the percentage of protected area, the more species are being retained. Proportionally, this effect is more pronounced for restricted-range species (Figure 3.2; Figure 3.3). For example, cells with 5 to 10% reserved area have on average 20% more species and 80% more restricted-range species, while cells with 20 to 30% reserved area have on average 33% more species and 515% more restricted-range species than non-reserved cells (percentages are in relation to the mean for non-reserved cells: $\mu = 208.5 \pm 8.1$ for all species; $\mu = 3.8 \pm 0.7$ for restricted range species). This agrees with the known higher susceptibility of restricted-range species to local extinction. Indeed, species of restricted distribution tend to have lower local abundances (Brown 1984; Gaston 1994; Gaston et al. 1997), and as a result their populations inside a given protected area tend to be smaller, and the probability of extinction higher, than those of widespread species.

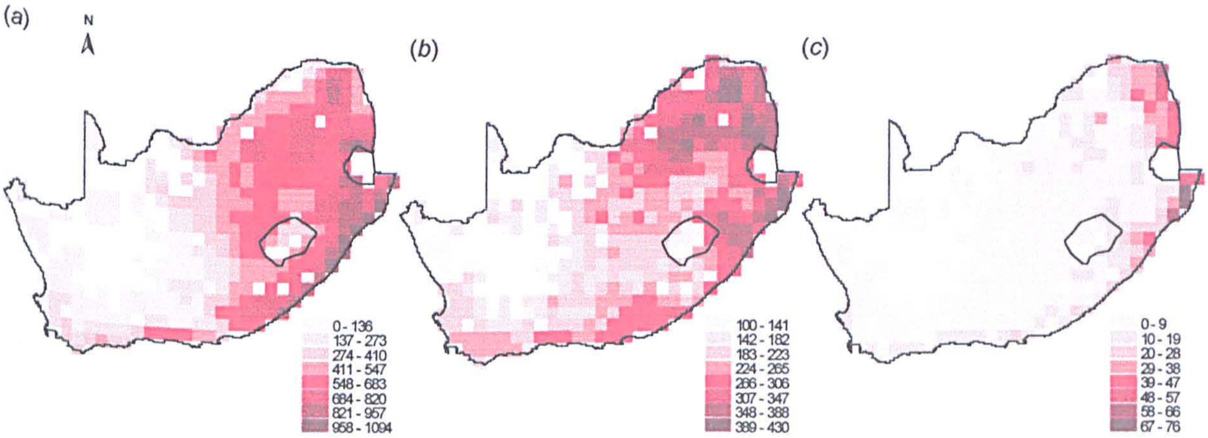

Figure 3.1 – Maps of (a) NPP (g C M^{-2} Yr^{-1}), (b) bird species richness (number of species), and (c) restricted-range bird species richness (number of species), in South Africa and Lesotho at half-degree scale. Shades of red are based on eight equal interval classes, darker colours corresponding to higher values. Cells in white were not included in the analyses.

Despite the mismatch between cell and reserve boundaries, smaller percentages of protected area in a given cell tend to be associated with smaller reserves and, conversely, larger percentages are a result of the presence of larger reserves. The fact that the positive effect on species richness is noticeable even for small percentages of protected area (Figure 3.2; Figure 3.3) indicates that even small reserves are contributing towards protecting local diversity. However, this effect is considerably weaker for the restricted-range species, for which more substantial differences in species richness in relation to non-reserved cells are associated with percentages of protected area above 20% (Figure 3.2; Figure 3.3). This indicates that while smaller reserves have a non-negligible role in retaining species diversity, they may be retaining a species community composed mainly of widespread species, often the ones less in need of immediate conservation action.

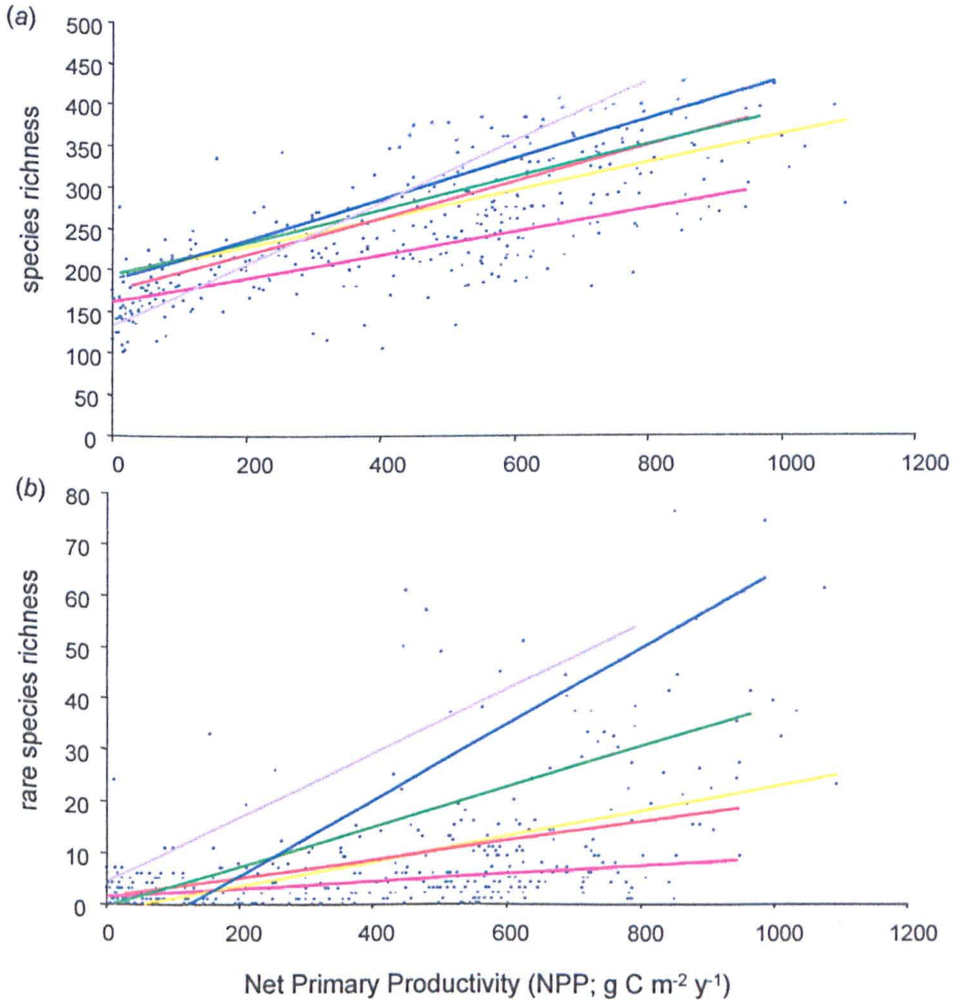

Figure 3.2 – Relationship between NPP and (a) species richness and (b) restricted-range species richness for cells with different percentages of protected area. There is a tendency for increasing slopes in regression lines for higher percentages of protected area. Pink: cells without reserves (n = 176); yellow: cells with]0, 5] % protected area (n = 117); red: cells with]5, 10] % protected area (n = 29); green: cells with]10, 20] % protected area (n = 22); blue: cells with]20, 30] % protected area (n = 11); violet: cells with > 30% protected area (n = 14). All regressions highly significant (Table 3.I).

Table 3.I – Simple linear least squares regressions of NPP against species diversity for cells with different percentages of protected area; *n* – number of data points; *a* – intercept; *b* – regression coefficient (slope); *r* – correlation coefficient; * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$. Interpretation of significance values should be made cautiously (spatial autocorrelation implies that the points are not fully independent) but the values of regression coefficients (slopes in Figure 3.2) are not affected.

	all species				**restricted-range species**			
	n	*a*	*b*	*r*	*n*	*a*	*b*	*r*
all data	369	163.7	0.200	0.74***	369	-0.26	0.022	0.49***
non-reserved	176	160.2	0.144	0.66***	176	1.42	0.007	0.37***
0 - 5% reserved	117	194.5	0.170	0.70***	117	-1.30	0.024	0.51***
5 - 10% reserved	29	174.7	0.221	0.84***	29	1.43	0.018	0.51*
10 - 20% reserved	22	194.1	0.199	0.85***	22	-0.29	0.038	0.74**
20 - 30% reserved	11	187.3	0.246	0.93***	11	-9.20	0.073	0.84*
> 30% reserved	14	132.4	0.373	0.88***	14	4.44	0.062	0.70*

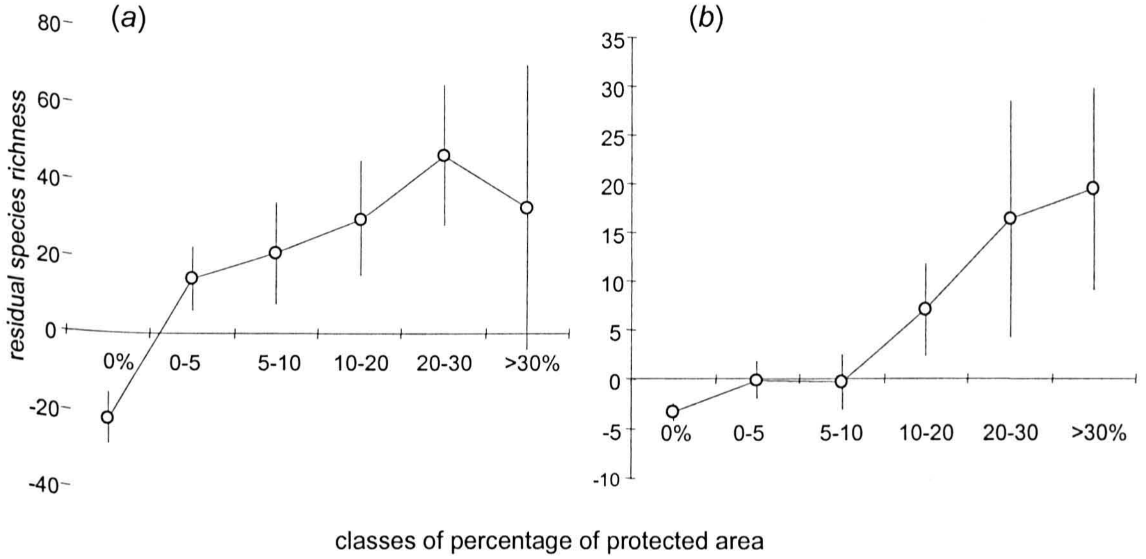

Figure 3.3 – Mean residual species richness for (a) all species and (b) restricted-range species when controlling for NPP, for subsets of cells with variable percentage of protected area. Residuals were obtained from the simple linear regressions of NPP against richness of all species and richness of restricted-range species, respectively (see Table 3.I for values of intercept and slope used). Circles indicate mean values while vertical lines indicate the limits of the respective 95% confidence intervals. A tendency for increasing width in confidence intervals for larger percentages of protected area is at least partially a result of a decrease in sample size (see Table 3.I for values of *n* in each class).

If species composition inside larger protected areas is closer to the natural situation, then the relationship between NPP and species richness for these areas is a better predictor of what is the potential species richness of each cell given its productivity. Comparison between this and current richness values then provides an estimate of the impact of human activities on local avifaunas. To investigate this, a scenario was selected in which 20% to 30% of each cell is protected (Table 3.I). This is a conservative scenario, selected for being such that records (n=11) span a diversity of NPP values (0 to 945 g C m^{-2} y^{-1}) not much narrower than the observed values for all cells (0 to 1094 g C m^{-2} y^{-1}). In relation to this scenario, each half-degree cell in the study area is predicted to have lost on average 43.4 ± 5.2 species (equivalent to 15% of their predicted species richness), with a maximum value of 184 species (Figure 3.4). Regarding restricted-range species, it is estimated that on average 12.9 ± 1.8, maximum 52, have been lost (58% of their predicted richness in restricted-range species). Equivalently, this corresponds to an estimated reduction of 15% of all occurrence records for all species and of 58% of occurrence records for restricted-range species.

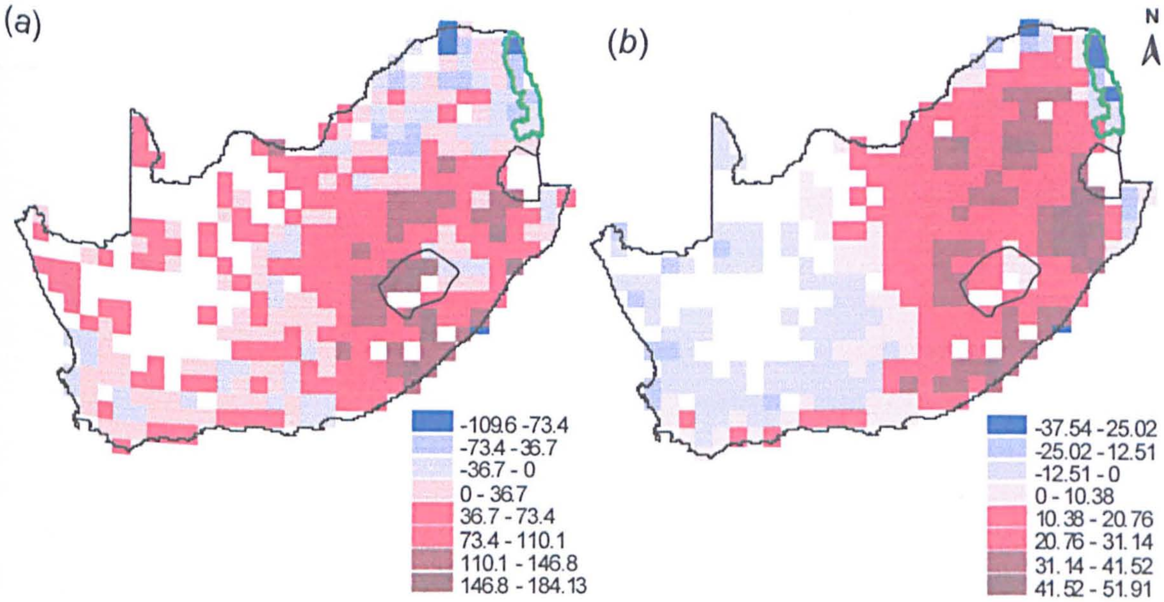

Figure 3.4 – Maps of (a) predicted number of bird species lost, and (b) predicted number of restricted-range bird species lost, in South Africa and Lesotho at half-degree scale. Predicted losses are the difference between number of expected species if each cell had 20 to 30% of its area reserved and the number of species actually recorded. Darker red colours correspond to higher positive values and darker blue colours to lower negative values. Cells in white were not included in the analyses. The polygon in green corresponds to the boundaries of Kruger National Park.

If the assumptions are correct, these values are likely to be underestimates of the real numbers of bird species that have been lost from each cell as a consequence of human activities. First, slopes in the relationship between NPP and species richness get even steeper for cells with more than 30% protected area than for the considered 20%-30% scenario (Figure 3.2; Table 3.I). Second, there are cells for which current species richness is above the predicted values. The six cells overlapping at least 50% with Kruger National Park, for example, have, on average, 54 additional species (including 22 restricted-range ones) than would be predicted from their NPP. While human practices can increase local species richness (e.g., by increasing local habitat diversity or water availability; Fairbanks et al. 2002), it is unlikely that this can explain such situations where protection for bird species is essentially through the protection of natural habitat.

3.1.4 Discussion

These results provide mixed news for conservation. The bad news is that levels of estimated local avian extinction in South Africa and Lesotho are considerable (even when based on a conservative scenario), with restricted-range species being proportionally more affected. A high proportion of this region may now comprise highly depauperate avifaunas. The good news is that protected areas make a substantial difference in limiting that extinction process. Although these results indicate that even small percentages of protected area make a difference (Figure 3.2; Figure 3.3), they agree with both theoretical predictions (Rosenzweig 1995) and previous empirical analyses (Newmark 1987; Newmark 1996; Gurd and Nudds 1999; Rivard et al. 2000) in that larger reserves are more robust to local species extinction, especially for restricted-range species. Smaller reserves face the double jeopardy of their size and a tendency to be located in more adverse surrounds (Harcourt et al. 2001; Parks and Harcourt 2002).

The findings in this study support the valuable role of protected areas in mitigating biodiversity loss, reinforcing their importance as conservation tools (Bruner et al. 2001*a*). However, existing networks of protected areas are known to have serious gaps in biodiversity representation (Pressey and Tully 1994; Jaffre et al. 1998; Nantel et al. 1998), and their effectiveness in retaining their biological value is known to correlate not only with area but also with levels of human activity both inside and outside the protected areas (Woodroffe and Ginsberg 1998; Gascon et al. 2000; Rivard et al. 2000; Brashares et al. 2001; Parks and Harcourt 2002). Indeed, even protected areas as large as Kruger National Park are known to be vulnerable to species extinction (Nicholls et al. 1996). Existing reserve networks need therefore to be expanded in efficient ways that make the best use of scarce conservation resources, and maximise the probability of species persistence inside designated reserves, a particularly urgent task given the increasing pressure over natural resources (Musters et al. 2000; Sizer and Plouvier 2000).

3.2 The performance of existing networks of conservation areas in representing biodiversity

3.2.1 Introduction

The establishment of networks of protected areas for conservation is an obligation placed on parties to the Convention on Biological Diversity, the Ramsar Convention on Wetlands, the Bern Convention on the conservation of European wildlife and natural habitats, the OSPAR Convention for the protection of marine environments of the North-Atlantic, and on all members of the European Union (committed to the Birds and Habitats Directives). Most regions already have some system of protected areas in place, although obviously incipient in many cases. This begs the question of how well such networks already perform, particularly in terms of representing biodiversity. Simple representation is, in essence, the common initial goal in establishing networks of protected areas under many of these agreements, albeit of itself not sufficient to ensure long-term conservation objectives.

There have been a number of attempts to measure the performance of existing protected area networks (Table 3.II). Most conclude that they are woefully inadequate. This outcome is expected in regions with less of a tradition of formal conservation, and hence where reserve systems are still poorly developed, such as India (Khan et al. 1997) and New Caledonia (Jaffre et al. 1998). However, this is perhaps a rather more surprising conclusion for other regions, such as parts of Europe (Williams et al. 1996*a*; Castro Parga et al. 1996), Canada (Nantel et al. 1998), South Africa (Rebelo and Siegfried 1992; Freitag et al. 1998*b*) and Australia (Pressey et al. 1996*a*). Indeed, the growing number of studies reporting similar conclusions has led to a belief in some quarters that existing reserve networks in general are inherently poor. It has frequently been stated that they have been chosen in an *ad hoc* fashion (e.g., Pressey and Tully 1994; Pressey 1994; Lombard et al. 1995; Freitag et al. 1998*b*) and in some situations existing networks have been regarded by some as a heavy burden to efficient conservation (e.g., Pressey and Tully 1994). Some authors have even found that existing reserves perform no better than a random choice of areas (Rebelo and Siegfried 1992). Indeed, this idea has become sufficiently well established that when Kershaw et al. (1994) used random sets of areas to simulate the effect of having sites already set aside for conservation Pressey et al. (1996*a*) cited this analysis as an example of how existing reserves lower the efficiency of the area selection procedure.

Table 3.II – Summary of the results of examples of published studies of the performance of existing nature reserves. ([1]Pressey and Nicholls 1989*b*; [2]Rebelo and Siegfried 1992; [3]Sætersdal et al. 1993; [4]Lombard et al. 1995; [5]Castro Parga et al. 1996; [6]Pressey et al. 1996*a*; [7]Williams et al. 1996*a*; [8]Khan et al. 1997; [9]Freitag et al. 1998*b*; [10]Jaffre et al. 1998 and [11]Nantel et al. 1998)

Study	**Features (no.)**	**Selection units (no.)**	**Geographic region**	**Result**
1	Land systems (128)	cadastral units (1026)	New South Wales, Australia	The near-minimum area to represent each land system once is 5.7% of the study area. Starting with the existing reserves (3.3% of total area) 8.3% is needed.
2	Plants (332)	12×13 km cells	Cape Region, South Africa	Existing reserves (66 cells) contain no more species than predicted by a null model. 32 more sites are necessary to represent each species at least once. Only 16 cells of the 53 near-minimum set are reserves.
3	Plants (321) Birds (47)	woods of different sizes (60)	Western Norway	The 12 reserves contain 78% of plant species and 66% of bird species. 37 additional woods are necessary to include all plants. In a set of 12 sites it is possible to represent 87% of plants, or 83% of birds.
4	Snakes (122)	25′×25′ cells	South Africa	In near-minimum sets, between 63 and 78% of the selected cells contain existing reserves.
5	Plants (801)	10×10 km cells (6330)	Iberian Peninsula	97 extra squares must be added to the reserve system (415 squares) to represent each species at least once. The near-minimum set requires 140 squares.
6	Land types (248)	pastoral holdings (1885)	New South Wales, Australia	It is necessary to expand the existing reserve system at least 79% to represent each land type at least once.
7	Birds (218)	10×10 km cells (2576)	Britain	The system of protected areas (65 cells) excludes 31 species. 20 additional cells are necessary to represent each species at least once, including 16 additional cells to represent all red data species.
8	Plants (3331)	-	Meghalaya State, NE India	Reserves (1.43% of the area) are insufficient to protect the high diversity of plants, e.g., 17.15% of the state endemic species occur only above 1500m, where there are no protected areas.
9	Mammals (192)	15′×15′ cells (474)	Transvaal, South Africa	Considering a cell reserved if > 50% of its area is formally protected, it would be necessary to add 9 cells to the existing 36 reserves to protect each species once. The near-minimum set requires 12 cells.
10	Plants (3063)	-	New Caledonia	83% of the 447 threatened species do not occur in a protected area. At least 5-9 times the current protected area is estimated to be needed.
11	Rare plants (244)	1×1 km cells (456)	New-foundland, Canada	43% of species are outside protected areas (113 cells). In a near-minimum set of 78 cells to protect all species at least once, only 13 are already reserves.

Even ignoring the fact that existing conservation networks were often chosen for reasons other than simply the representation of biodiversity, including other conservation objectives as well as political and financial constraints, it seems unlikely that they would almost without exception fail to some marked degree to attain the goal of embracing much of the richness of the group(s) of interest. There are two possible explanations for why they appear to perform so poorly.

First, in many published studies there is a mismatch between the actual units of conservation, which are natural and geopolitical units of land, and those units on which optimal conservation networks are determined, which are commonly grid cells for which data on the geographic occurrences of species have been mapped (e.g., Rebelo and Siegfried 1992; Lombard et al. 1995; Williams et al. 1996*a,b*; Nantel et al. 1998). To deal with this problem, most authors consider a grid cell as already conserved if more than a certain percentage of its area coincides with an existing reserve (e.g., 55% in Rebelo and Siegfried 1992; 50% in Williams et al. 1996*a*). A cell in which a reserve occupies less than this percentage is not considered to contain a reserve, although the species regarded as occurring in that cell will probably include all those that occur in this area of a reserve. This may distort the results of analyses of the performance of existing reserve systems. Williams et al. (1996*a*) noticed this when analysing the occurrences of bird species and Sites of Special Scientific Interest (SSSIs) in 10×10 km grid cells across Britain. In exploring methods for identifying additions to the network of existing conservation areas, they observed that the existing SSSI network did not embrace the occurrences of 31 bird species and that 20 additional cells would be necessary to fill the gap. However, they also found that at least 16 cells (the ones needed to fill the gap for Red Data species) already enjoyed limited SSSI cover (but this was insufficient for those cells to be scored as reserves), which means that some of the 31 species considered excluded from the SSSI system may not have been so.

A second possible explanation for why existing conservation networks appear to perform so poorly is that their performance has mainly been evaluated using measures of *efficiency* (*sensu* Pressey and Nichols 1989*a*). This is a measure of how good is a system of reserves in harbouring the maximum diversity (all the conservation features) in the minimum number of sites or total area (throughout this section, 'efficiency' is used in this strict sense). This approach is founded on the recognition that competition between conservation and other forms of land use will often be intense, and therefore that networks of protected areas should be as small as it is possible for them to be whilst still attaining their objectives. Efficiency is evaluated in a relative way, and the performance of a network has usually been assessed in terms of similarity with the minimum set of sites that represents each species in the region at least once. This approach largely ignores how close the reserve network comes to attaining the general conservation objective of representing the diversity of the group(s) of interest in the study region, which is probably a more important question when evaluating their performance.

In this section, I use an exemplar data set for plants in fens in the Scottish borders to examine the performance of a designated set of reserves using the efficiency-based approach and a novel alternative method. The occurrence data are derived for 'natural' areas, thereby avoiding the problem of mismatches of units of analysis and of conservation. I illustrate how misleading efficiency-based approaches may sometimes prove.

3.2.2 Data and Methods

These analyses are based on the occurrence of wetland plant species in a nationally important series of fens located in the central Scottish borders, a region located approximately 50 km south of Edinburgh at the eastern extremity of the southern Uplands, and bounded in the north and northeast by the Moorfoot and Lammermuir Hills and in the south by the Cheviots. Here, within an area of about 30km^2, there are almost 100 separate, small (mostly < 5ha) fen sites, occupying discrete waterlogged basins within a predominantly agricultural landscape. Sixty-eight of these sites (those which were accessible and which have not been badly damaged) have received a comprehensive botanical survey (for details, see Tratt 1997); of these, sixteen have been notified as SSSIs by the statutory conservation agency. The presence or absence of a total of 125 wetland plant species was recorded at each site surveyed, of which 25 are nationally rare by the criteria of Wheeler (1988).

Following previous analyses, I examine the performance of the existing protected area network (the SSSIs) in terms of capturing the biodiversity of wetland plants as represented by the 125 species occurring across all the surveyed fen sites, accepting that these protected areas may have been designated for a variety of reasons, of which this is but one (albeit an important goal). As such, and again following previous analyses, the objective is to examine how well the protected areas perform in this regard, not how well they meet the objectives of those individuals who actually designated them.

Throughout, unless otherwise stated, optimal solutions to network design problems were determined through linear integer programming using LINDO (LINDO Systems, Inc. 1996), rather than the heuristic ('near-minimum') methods more typically adopted in such analyses.

3.2.3 The 'efficiency' approach

The efficiency of the SSSI system was first assessed by the common approach of comparison with the minimum set of areas (the minimum network) which represents each species at least once. The exact minimum set was determined by solving the integer problem

$$\text{minimise } \sum_{j=1}^{n} x_j$$

subject to

$$\sum_{j=1}^{n} a_{ij} x_j \geq 1, \qquad i = 1, 2, \ldots, m$$

$$x_j \in \{0,1\},$$

where m is the total number of species, n is the total number of sites, a_{ij} is 1 if species i is present in site j and 0 otherwise, and x_j is 1 if site j has been selected and 0 otherwise. This is known as the *set covering problem* (Balas and Ho 1980; Camm et al. 1996; see Chapter 2). Given that the SSSI system does not represent all species at least once (see below), the minimum set of extra sites needed to fill this gap was determined in the same way, but excluding from the analysis those areas which are SSSIs and all species that occur within them.

The selection units (sites) have different sizes, therefore I looked also for the solution of the problem of minimising the total area needed to represent each species at least once. This is the problem

$$\text{minimise } \sum_{j=1}^{n} c_j x_j$$

subject to

$$\sum_{j=1}^{n} a_{ij} x_j \geq 1, \qquad i = 1, 2, \ldots, m$$

$$x_j \in \{0,1\},$$

where c_j is the area of site *j*. As before, the minimum extra area needed to fill the representation gap in the SSSI system was also determined. Finally, all four of these analyses were repeated using only the rare species.

Table 3.III – Performance of the SSSI system when compared with optimal minimum sets of sites.

Problem	No. of sites	No. of sites classified as SSSI	% total area	% total area classified as SSSI
Existing SSSI system	16	-	45.8	-
Min. no. of sites to represent each species at least once	13	5	30.5	21.0
Min. no. of sites to complete the SSSI system to represent each of the 8 uncovered species at least once	7	-	9.6	-
Min. area to represent each species at least once	15	4	23.4	13.2
Min. area to complete the SSSI system to represent each of the 8 uncovered species at least once	7	-	9.2	-
Min. no. of sites to represent each rare species at least once	6	5	14.7	14.4
Min. no. of sites to complete the SSSI system to represent each of the 2 uncovered rare species at least once	1	-	0.2	-
Min. area to represent each rare species at least once	7	4	14.0	13.2
Min. area to complete the SSSI system to represent each of the 2 uncovered rare species at least once	1	-	0.2	-

The results obtained from these analyses sustain the usual conclusions found in the literature about the poor performance of existing networks of protected areas in representing the diversity of biological attributes in a region (Table 1.I). First, the SSSI system does not cover all the species; eight are not represented, including two rare ones. Second, although the SSSI system already occupies 16 sites and 45.8% of the study area, it would be possible to preserve each species once in only 13 sites or 23.4% of the area and to represent each rare species in only 6 sites or 14.0% of the area. Third, in order to fill the gaps in the SSSI system it would be necessary to add extra sites, which implies another loss in efficiency. At least seven extra sites or an additional 9.2% of the total area are required to represent each species at least once and at least one extra site or an additional 0.2% of the area to represent each rare species once. Finally, there is a poor match between SSSIs and the optimal set of sites needed to represent each species at least once. Only five of the 13 sites in the minimum set are SSSIs, and only 13.2% of the 23.4% minimum area is classified as SSSIs.

Since problems for minimising the number of sites may have several equally optimal solutions, I have tested the possibility of obtaining a better match between the SSSI system and a minimum set of sites. It is not possible to obtain any other set of 13 sites covering each species at least once that includes more than five SSSIs nor is it possible to obtain another set of six sites that represents each rare species at least once that included more than five SSSIs. For problems that minimise the area, it is highly unlikely that different equally optimal solutions exist, since the coefficients in the objective function are continuous.

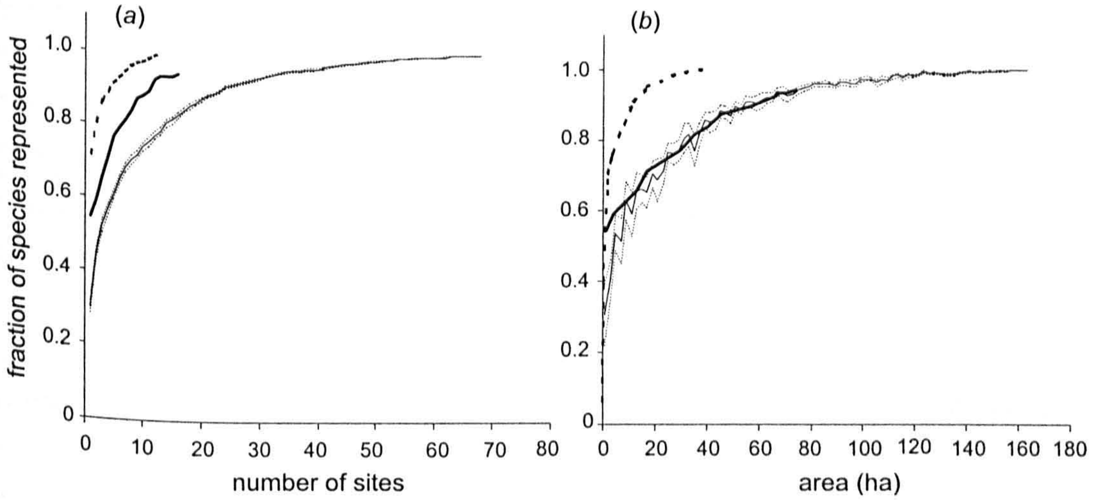

Figure 3.5 – Performance of the SSSI system (thick continuous line) in terms of the cumulative representation of species with (*a*) increasing total number of sites and (*b*) increasing total area, when compared with the correspondent random model (thin continuous line) and an optimal set (thick dashed line). Random models consist of 30 replicates (thin dashed lines are the limits of the 95% confidence interval) and in (*b*) data were classed in area steps of 2 ha.

The efficiency of the SSSIs can also be analysed with regard to the chronological sequence in which they were selected, because the date of each site's designation as an SSSI is known. I compared the cumulative number of species represented as the number of sites or the overall area of SSSIs progressively increased with time with the maximal number that could have been represented (resulting in an optimal set) and with the expectation from choosing areas at random (Figure 3.5; for a similar type of analysis see Rebelo and Siegfried 1992). The random selection was repeated 30 times. The results of this analysis again support the conclusion that the designation of SSSIs was not efficient, this time with reference to the purpose of representing all species in the region at the fastest rate. The actual trajectory of the cumulative number of species represented in the SSSIs with increasing numbers of sites (Figure 3.5*a*) lies between that of the random model and that of the exact solution. The actual trajectory for species represented in SSSIs with increasing total area (Figure 3.5*b*) is indistinguishable from the performance of the random model, and again noticeably poorer than the performance of the exact solution.

3.2.4 The 'effectiveness' approach

The efficiency approach to determining the performance of conservation networks focuses on the comparison between the area/number of sites occupied by the existing system and that occupied by the minimum set that represents each species once (or some other specified target). Although it is implicit that the minimum set is not necessarily a definitive system of reserves, but a basic network of sites on which other considerations can be superimposed (e.g., Pressey and Nicholls 1989*b*), in many studies it is in practice treated as the 'ideal' set. As a result, all dissimilarities between it and existing reserves are considered to be a demonstration of the poor performance of the existing network.

I propose that as well as considering their efficiency, the performance of existing reserve systems should be assessed in terms of what I shall call their *effectiveness* in attaining a defined representation target for the region (Figure 3.6). The extent of this attainment is probably the more relevant issue, if only because regardless of their dissimilarity or otherwise to an optimal set, existing protected areas will provide the nucleus of any future developments of conservation networks (there is little likelihood of them being traded for a set of options closer to the optimum, although some have suggested this might be done; Margules et al. 1994*b*).

I define the gap, gap_i, in the representation of a particular species, i, in a reserve network as

$$Max\left[0, \frac{RT_{total,i} - RT_{reserves,i}}{RT_{total,i}}\right],$$

where $RT_{total,i}$ is the total representation target required for the species i, and $RT_{reserves,i}$ is the representation reached in the reserve system for that species. The representation target for each species can be defined in numerous ways. Usually it has been defined as being represented once, but it can be for example to be represented 5 times, in 25% of its range in the study area, by 1000 individuals or by 10% of its population. Different targets can be assigned to different species, a higher target meaning a higher conservation investment to be made in the species when creating a reserve network.

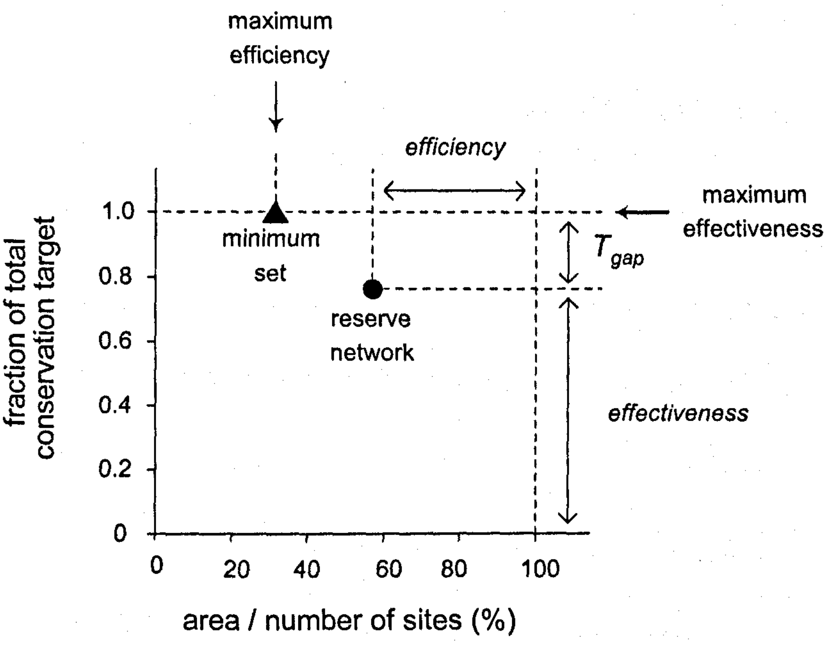

Figure 3.6 – Illustration of the concepts of *efficiency* and *effectiveness*. *Efficiency* is larger when the area or number of sites occupied by a reserve network is smaller. Maximum possible efficiency is the one obtained by the minimum set that attains the total representation target (note that this corresponds to the minimum set that represent each species once only when considering that specific target). *Effectiveness* is larger when the reserve is closer to attaining the total representation target, i.e., when T_{gap} is smaller. Maximum possible effectiveness is reached by a set of reserves with $T_{gap} = 0$. Therefore, while efficiency is a measure based on the size of the reserve system (*y* axis), effectiveness is a measure based on its performance in terms of achieving a predetermined representation target (*x* axis).

The *total gap*, T_{gap}, of a reserve system is a value between 0 (all species reached RT_{total}) and 1 (all species totally unprotected) measured as

$$\frac{\sum_{i=1}^{m} gap_i}{m}.$$

Effectiveness is then 1 - T_{gap} (Figure 3.6).

It is not the aim of this study to determine what would be an adequate representation target for each species in the fen sites, something that should be based on a more detailed analysis of the conservation needs of each species in the region and on viability considerations (Williams 1998*b*). As an explorative exercise, however, I have considered several very different representation targets and evaluated how well the fen SSSI network performs with regard to each. T_{gap} was calculated for the targets of representing (*a*) all species at least once, (*b*) each rare species at least once, (*c*) common species at least once, rare species at least twice (or the maximum possible), (*d*) common species at least twice, rare species at least four times (or the maximum possible), (*e*) common species at least 1% of range (total area of sites occupied) in the study area, rare species at least 60%, (*f*) common species at least 10% of range, rare species at least 60%, and (*g*) common species at least 10% of range, rare species at least 90% (Figure 3.7*a*,*b*).

The total gap of a reserve system measures how far the system is from attaining the global representation target that is the main purpose (or one of them) for the creation of the reserves. It is not, however, a measure of how well the existing reserves have been selected. A large gap may be due to an ineffective choice but also to the fact that the representation target may be impossible to attain in a reserve system of the size of the existing one. In fact, regarding the SSSIs, the minimum sets for the more demanding targets are larger than the existing system of 16 sites and 45.8% of the total area (74.49 ha). Using the same notation as above, these minimum sets comprise (*c*) 17 sites, (*d*) 22 sites, (*e*) 27 sites, (*f*) 50.0% of the total area, (*g*) 50.1% of the total area, and (*h*) 71.3% of the total area. In these cases, even if the SSSIs had been created with the explicit purpose of minimising the total area or number of sites, it would have been impossible to reach the required representation targets in a system of the same size.

To adequately evaluate the effectiveness of a reserve system in terms of a defined representation target, we need to know what would be the minimum possible total gap (M_{gap}) that could exist in a system of the same size. Therefore, what I shall term the *real gap* (R_{gap}) of a reserve network is $T_{gap} - M_{gap}$.

Calculating M_{gap} in a system the size of the SSSI network corresponds to the problem of maximising the effectiveness (or equivalently minimising T_{gap}, Figure 3.6) subject either to selecting ≤ 16 sites, or to selecting a total area ≤ 74.49 ha. This is the integer programming problem known as the *maximal covering location problem* (Church and ReVelle 1974; Church et al. 1996). However, since the objective function is not linear (because of the function *Max*), I use an approximation obtained by a simple greedy heuristic that in each iteration selected the site that allowed for a maximum reduction in the total gap. I estimated M_{gap} of the SSSI system for each of the above mentioned targets (Figure 3.7*a*,*b*). I have also considered two random models (iterated 100 times), one selecting sets of 16 sites (Figure 3.7*a*), the other sets of approximately 74.49 ha (Figure 3.7*b*). While M_{gap} corresponds to the maximum possible effectiveness that can be attained by a system with the same efficiency (same size) as the SSSI network, the random models give an indication of the expected effectiveness that would be attained if a set of sites with the same efficiency was selected randomly.

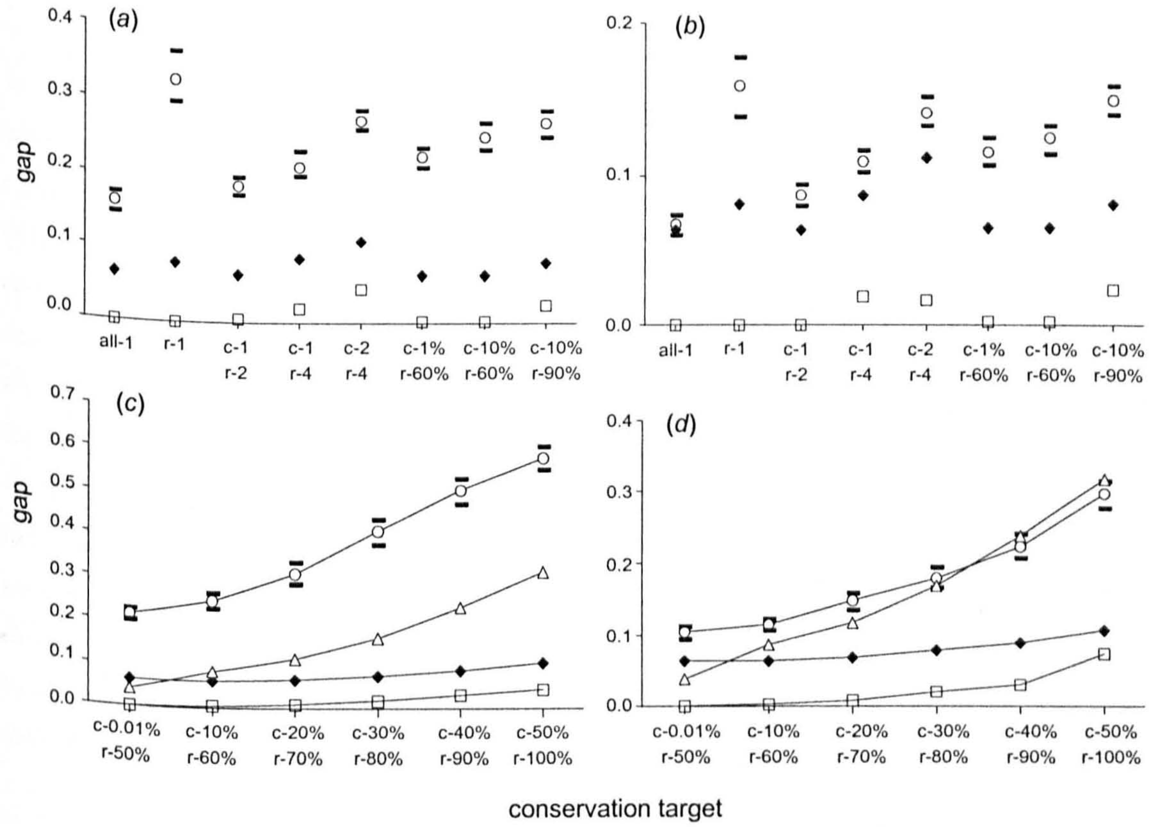

Figure 3.7 – Performance of the SSSI system in terms of its effectiveness when evaluated according to different representation targets. In (*a*) and (*b*) the representation targets are the number of times or the percentage of range required for each species (all – all species; r – rare species; c – common species). In (*c*) and (*d*) an increasingly demanding series of targets is illustrated, expressed in terms of the relative percentage of range required for common and rare species. (*a*) and (*c*) refer to analysis of the performance of the SSSI system as a network of 16 sites, while (*b*) and (*d*) refer to a system of 74.49 ha. For each target T_{gap} (diamonds) and M_{gap} (squares) were calculated for the SSSI system, as well as the T_{gap} of the corresponding random model (circles indicate averages and horizontal marks indicate the limits of the 95% confidence interval, n = 100). The real gap, R_{gap}, is T_{gap} - M_{gap}. In (*c*) and (*d*), the T_{gap} is also given for the minimum set of sites (with minimum area) that represents each species at least once (triangles).

As already concluded (Figure 3.5*b*), the SSSI system is indistinguishable from a random selection of ≈74.49 ha when the representation target is to protect each species at least once (Figure 3.7*b*). However, in all other situations, the SSSI system performs considerably better than any of the random models (Figure 3.7*a*,*b*). In the situations where T_{gap} is higher, so is M_{gap}, resulting in a remarkably constant R_{gap} either considering a system of 16 protected areas (Figure 3.7*a*) or a system no larger than 74.49ha (Figure 3.7*b*): the values are always between 0.054 and 0.095. In fact, the relative performance tends to increase for more demanding representation targets (a trend also found by Pressey et al. 1989b; Pressey and Tully 1994; and Freitag et al. 1998*b*) and when disproportionate representation of rare species is required compared with common ones.

To further investigate how the performance of the SSSI network changes with more demanding representation targets I considered the series of targets (percentage of range, based on the area of the sites in which they occur) for common and rare species, respectively: 0.01% (≈0)-50%; 10%-60%; 20%-70%; 30%-80%; 40%-90%; and 50%-100%. For each scenario, I calculated T_{gap} and M_{gap}, considering a system of 16 sites (Figure 3.7*c*) and a system not larger than 74.49 ha (Figure 3.7*d*). Again, R_{gap} is low and remarkably stable, between 0.033 and 0.064, and with a tendency to decrease. Since the gap for two random models, constructed as before, tends to increase faster than T_{gap}, the relative performance of the SSSI system is better for more demanding representation targets (Figure 3.7*c*,*d*). I also measured T_{gap} for the optimum minimum set (minimum area) for representing each species once, the 'ideal' system when considering efficiency. In this case, the system performance becomes poorer for more demanding representation targets. According to this analysis, this set is only better than the existing system in the 0.01%-50% scenario. In the most demanding scenario, its gap exceeds 0.30, three times more than T_{gap} for the SSSI network (Figure 3.7*c*,*d*).

3.2.5 Conclusions

As judged in terms of its efficiency, the performance of the SSSI network in representing wetland plant species of fens in the central Scottish borders region is rather poor (Figure 3.5, Table 3.III). All 125 species, or just the rare species, can be represented at least once in notably fewer sites and in a markedly smaller area than have been designated as SSSIs, and one to seven sites would be needed in addition to the present network to attain these ends (Table 3.III). Likewise, the cumulative number of species represented in the SSSI network has increased more slowly with the increasing number of sites and area than could have been attained by a choice of a different set of sites and an alternative sequence of designation as protected areas (Figure 3.5). These results would appear to confirm the general contention that conservation networks are rather poor at representing biodiversity, even in regions with better networks (Table 3.II).

This conclusion might reasonably be argued to reflect the fact that, in common with most existing networks of protected areas, a variety of criteria contributed to the designation or otherwise as SSSIs of fen sites in the central Scottish borders region, of which the representation of plant diversity was only one. Nonetheless, when the SSSI network is considered in terms simply of its effectiveness, rather than its efficiency, in representing the plant species of the region, it performs rather well. Indeed, this conclusion is upheld when the network is evaluated according to very different representation targets. The gap between the representation achieved by the SSSI network and that potentially achievable in the same number of sites or area ranges only between 3.3-9.5% of the target, for a wide variety of representation targets (Figure 3.7). In fact, that the gap is so small is perhaps surprising given the diversity of other criteria involved in the actual designation of the sites.

The poor performance of the minimum set of areas necessary to represent each species once with regard to other representation targets is a good example of the fact that what constitutes a set of sites that is optimal, or close to so being, depends on which question is asked. Although optimal in terms of efficiency and with maximum effectiveness in representing each species once, this system performs worse than the SSSI system when considering more demanding representation targets (Figure 3.7*c*,*d*).

The contrast between results of analyses of the SSSI network based on efficiency and effectiveness suggests that more care is needed when evaluating the performance of existing networks of conservation areas. Different approaches to the same data can lead to significantly different conclusions. Efficiency is an important attribute of reserve systems. But a system should not be regarded as inherently poor solely because it does not closely match the most efficient solution to the problem of representing each species once, or the solutions to closely related problems of efficiency. Neither should the failure of a close match necessarily be interpreted as suggesting that the composition of a conservation network reflects an opportunistic approach to the acquisition of protected areas. In the data for fens, all the SSSIs are among the sites with higher species richness (e.g., nine of the ten richest sites are SSSIs) and the mean area of an SSSI is almost three times that of all the other sites. Clearly, they were chosen mainly from amongst the richest and the largest fen sites in the region, two of the most widely used criteria in conservation evaluation (Margules and Usher 1981; Smith and Theberge 1986). This approach plainly served to generate an SSSI network which is highly effective when judged against a variety of representation targets.

4 Addressing species persistence

Complementarity-based algorithms for the selection of reserve networks emphasise the need to represent species efficiently, but this may not be sufficient to ensure their persistence in the long-term. The first two sections of this chapter use the results of the Common Birds Census in Britain as an exemplar data set to explore how to incorporate the concern for species persistence in the selection of reserve networks. Guidelines are suggested for the selection of reserve networks which are more robust to temporal turnover in features, either based on abundance (Section 4.1) or presence-absence data (Section 4.2). Section 4.3 uses data on the distributions of birds in South Africa and Lesotho to test the hypothesis that minimum complementary sets preferentially select sites in areas of ecological transition, with a bias towards the representation of species at marginal areas within their ranges. This is presented as a possible explanation for the ineffectiveness of minimum complementary sets in ensuring species persistence.

4.1 Robustness of reserve selection procedures under temporal species turnover

4.1.1 Introduction

The prime purpose of establishing a network of protected areas for conservation is the long-term maintenance of the biological diversity of the region in question. An essential pre-requisite is that biological diversity is appropriately represented in the network in the first place (Margules et al. 1988; Pressey et al. 1993). This need for representation has been strongly emphasised in recent literature on methods for the selection of reserve networks. Furthermore, it has been recognised that reserves are economically costly and consequently will be in direct competition with more destructive forms of land use (e.g., Bedward et al. 1992; Pressey et al. 1993). This has resulted in the development of procedures that aim at high efficiency (*sensu* Pressey and Nicholls 1989*a*) by representing the biodiversity attributes of interest in a minimum area, generally called complementarity-based methods (e.g., Bedward et al. 1992; Rebelo and Siegfried 1992; Williams et al. 1996*a*; Csuti et al. 1997).

However, *representation* is only the first step towards achieving the final purpose of *maintaining* biodiversity in the long-term (Williams 1998*b*). These are not equivalent because species distribution patterns change over time, and reserve networks may not necessarily continue to serve the purpose of their declaration some years afterwards (Margules et al. 1994*b*). It can be argued that once a reserve network which represents all features of interest has been established, it is a matter of adequate management to ensure those features are retained. Nevertheless, the success of management efforts and the cost of management actions may be influenced strongly by the quality of the sites which are selected in the first place. It is expected that a more robust network of protected areas would result from selecting areas less subject to the 'natural' local extinction of features, independently of subsequent management practices.

In this section, I ask (a) how effective is a simple representation strategy (minimum set) in maintaining feature diversity over time?; and (b) is it possible to predict *a priori* which sites should be selected in order to obtain a reserve network that is robust to temporal turnover in features? Although previous studies (Margules et al. 1994*b*; Virolainen et al. 1999) addressed the first question, they did not provide many clues to the answer of the second. Nicholls (1998) and Williams (1998*b*) proposed strategies for improving the robustness of networks, the first by establishing a minimum population size as a required representation target for each species and the second by targeting core populations using niche-based modelling of habitat suitability, but their effectiveness in ensuring the long term persistence of species has not yet been tested.

In this section, I consider the case of species as features of biodiversity, and use data from the Common Birds Census to explore the influence of temporal turnover in their occurrence for reserve selection procedures. First, I determine which variables had more influence on rates of local species extinction. Then I use this information to propose selection guidelines that aim to produce reserve networks that are more robust to such turnover.

4.1.2 Data

The Common Birds Census (CBC), run by the British Trust for Ornithology, has been the main scheme by which populations of common breeding birds have been monitored in the United Kingdom (for a comprehensive description of the history and methodology of CBC, see Marchant et al. 1990). Since 1964, a mapping census technique (see Bibby et al. 1992) has been employed that provides a very accurate measure of the number of territories occupied by each species in each site during a breeding season.

In this analysis, I have used the CBC data collected for 113 species between 1974 and 1991 in a variable number of farmland and woodland sites. I considered eight pairs of years with years in each pair separated by a 10-year interval (1974-1984 through 1981-1991), and analysed only those sites with good quality information in both years of a pair. Only those species for which presence/absence had been recorded in both years of each pair were considered. In order to obtain a final matrix with a territory count for each species for all sites: (i) where a species was seen but the territory count on a site in a given year was zero, the species was assumed not to be breeding but to be casually using or moving through an area; (ii) where nest counts were available instead of territory counts these were considered to be equivalent; (iii) three very common species (Woodpigeon *Columba palumbus*, Starling *Sturnus vulgaris*, and House Sparrow *Passer domesticus*) were eliminated from the analysis, because they often were not counted systematically (and are of minimal interest here); and (iv) where any other species was thought to have held territory but for some reason was not counted (less than 1% of the total presence records) a density value was extrapolated from the average territory density of the respective species in the other occupied sites of the same habitat type.

The CBC data is used here as an exemplar data set to explore general reserve selection strategies, and therefore the results should not be interpreted as an attempt to propose a new reserve network in Britain.

4.1.3 Extinction patterns

I used the 1981-1991 data set (97 species in 56 sites) to explore variables that influenced the temporal patterns of species turnover. Applying logistic regression models, I analysed the relationships between extinction (throughout, 'extinction' is used to refer to a situation when a species was present in a given year and absent 10 years afterwards) and site species richness, species frequency (number of sites where the species occurs) and local abundance.

No significant relationship was found between the species richness of sites and the extinction rates suffered (Table 4.I). These results do not support a simple hotspot strategy, based on the selection of the sites with higher species richness (e.g., Prendergast et al. 1993; Williams et al. 1996*a*), as a method for obtaining reserve networks that are more robust to temporal species turnover.

Table 4.I – Relationship between extinction patterns in the 1981-1991 period and site species richness, species frequency (number of sites at which the species occurs) and local abundance. A logistic regression was applied to analyse each relationship. Results were interpreted using a likelihood ratio test (χ^2-test).

predictor variable	**response variable**	***n***	**results**
site species richness	extinction rate(1)	56	non significant (χ^2-test = 0.001)
species' frequency(2)	extinction rate(3)	94	highly significant negative relationship (χ^2-test = 12.088; $p < 0.001$)
site number of territories(4)	extinction probability(5)	1858	highly significant negative relationship (χ^2-test = 292.177; $p < 0.001$)
site density(6)	extinction probability(5)	1858	highly significant negative relationship (χ^2-test = 224.863; $p < 0.001$)

(1) Fraction of species that occurred in the site in 1981 but not in 1991 in relation to the number of species in the site in 1981.

(2) Number of sites where the species occurred in 1981.

(3) Fraction of the sites from where the species disappeared between 1981 and 1991 in relation to its frequency in 1981.

(4) For a given species, the number of territories at a given site in 1981.

(5) Binary variable indicating whether the species disappeared form the site between 1981 and 1991 (1) or not (0).

(6) For a given species, number of territories per unit area at a given site in 1981.

Highly significant negative relationships between species frequency and local extinction rates were found (Table 4.I; Figure 4.1*a*). The observation that rare species are more prone to local extinction agrees with established ideas in this regard (Gaston 1994) and with previous results (Margules et al. 1994*b*). The implication in terms of reserve selection strategies is that the occurrence of common species is more predictable than the occurrence of rare ones (in the absence of appropriate management). This means that a higher investment may be needed in order to ensure the persistence of rarer species, which may imply targeting those as priorities when allocating conservation resources. And, indeed, the presence of rare species is one of the most frequent criteria for the selection of protected areas (Margules and Usher 1981; Smith and Theberge 1986).

There was also a highly significant negative relationship between local abundance, expressed either as the number of territories or as the density of a given species in a site, and the probability of extinction (Table 4.I; Figure 4.1*b*,*c*). These results indicate that species are more likely to disappear from the sites where they are locally rarer. Again, this is an expected result, since smaller populations are known to be more prone to local extinction, due to demographic and environmental stochasticity and reduction in genetic variation (Caughley and Gunn 1996). Although for these data it is unlikely that genetic considerations play a significant role, the other two processes may have been important in determining extinction. The implication of these results for reserve selection procedures is that it may be possible to obtain more robust networks if species are represented in the sites where they occur in higher abundance.

The 'abundance-occupancy' relationship, a widespread attribute of species assemblages in which locally rare species tend be of restricted distribution and locally abundant ones tend to be widespread (Hanski 1982; Brown 1984; Gaston 1994; Gaston et al. 1997), implies that the negative relationships between both frequency and local abundance and probability of extinction are connected (the *'double jeopardy'* of Lawton 1993). Those species that occur in fewer sites in the study area may be more prone to extinction simply because being locally more scarce they suffer a higher probability of local extinction.

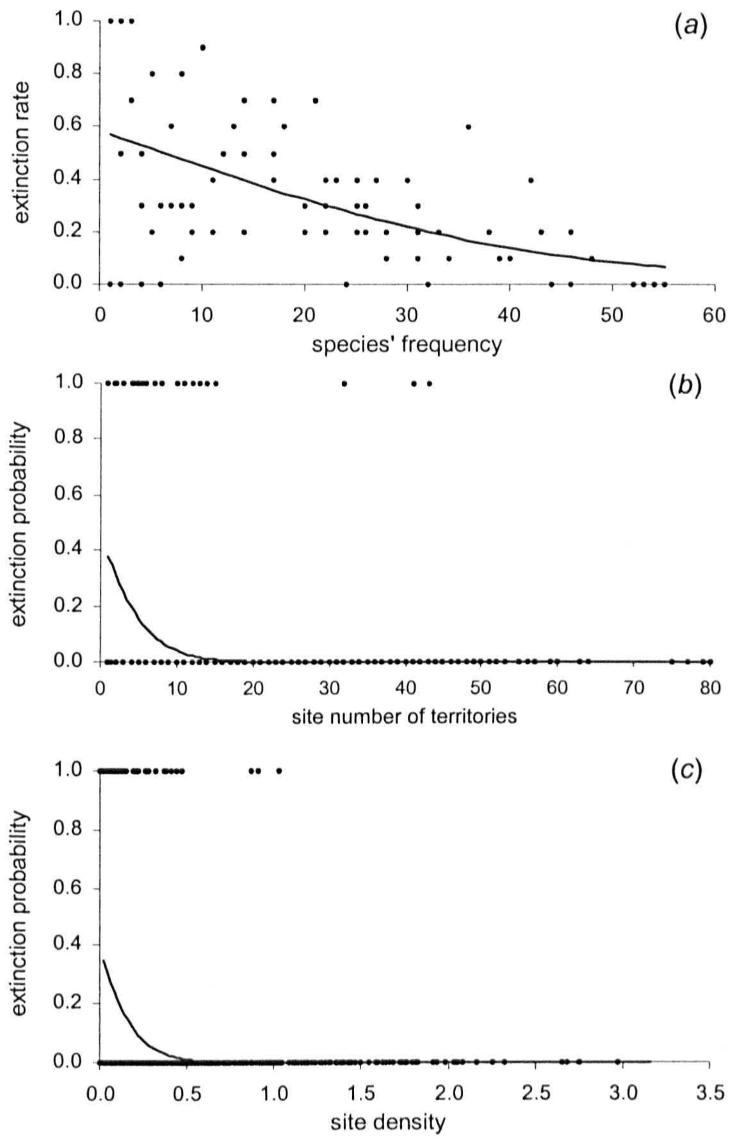

Figure 4.1 – Extinction patterns for the 1981-1991 pair of years: (*a*) relationship between species frequency (number of sites where the species occurs) and extinction rate (fraction of sites from where the species disappeared between 1981 and 1991 in relation to its frequency in 1981); (*b*) relationship between the number of territories in a site for a given species and the extinction probability (the probability of the species becoming extinct in that site); (*c*) relationship between the site density (number of territories per hectare at a site) for a given species and the extinction probability. The relationships were analysed using logistic regressions (for more details see Table 4.I).

The selection units considered in this section are census plots (average area ≈ 47 ha), much smaller than most nature reserves (average area of Special Protection Areas for birds classified until March 1998 in the UK ≈ 6020 ha; English Nature 1998). It is therefore likely that the turnover rates observed here are considerably faster than the ones occurring in reserves. In compensation, turnover is known to increase over time (Russell et al. 1995), and reserves are expected to prevail far longer than the 10-year intervals considered in this study. I assume that the turnover rates observed within 10-year intervals in the CBC plots exhibit similar patterns to the ones observed in larger areas over longer periods and can be used to infer about the relative performance of different reserve selection strategies. This assumption is supported by the fact that the same patterns explored in this study (rarer species tend to be more prone to local extinction and species are more likely to persist in sites with higher local abundance) agree with previous studies (see references above).

4.1.4 Reserve selection strategies

Using the information obtained in the previous analyses, several reserve selection strategies were proposed and tested, using data on the eight pairs of years corresponding to a 10-year interval. In each pair, the first year's data were used to select a reserve network following a specific strategy, and the last year's data to assess the results in terms of *efficiency* (Pressey and Nicholls 1989*a*) and *effectiveness* (see Section 3.2; Rodrigues et al. 1999). Efficiency is higher when the total area occupied by the network is smaller. Effectiveness is higher when the fraction of species absent from the network (the *representation gap*) is smaller.

For each pair of years, the average efficiency and effectiveness were also determined for 100 randomly selected networks of (approximately) a pre-defined area. This was done by selecting sites randomly, without replacement, until the total area was approximately that desired. I applied this procedure to a wide range of areas to establish a null relationship between efficiency and effectiveness (random model).

Five reserve selection strategies were tested:

1) Select the minimum area such that each species is represented in at least one site.

2) Select the minimum area such that each species is represented at least by the site where it occurs in higher abundance in terms of number of territories.

3) Select the minimum area such that each species is represented at least by the site where it occurs in higher abundance in terms of density.

The following strategies 4 and 5 are a relaxation of strategy 3, in the sense that species must be represented by the best sites where they occur in terms of density. But instead of requiring that the best site is selected for each species, a higher flexibility is given in the choice for the most common species. If a species has a flexibility value of *n*, it means that the site selected to represent it can be chosen among the *n* top sites in terms of density.

4) Species are classified into three classes according to their frequency (number of sites in which they occur) in the data set – less than 15, between 16 and 30, and more than 31 – with flexibility values respectively of 1, 2 and 3 (Figure 4.2).

5) Species have flexibility values between 1 (the rarest species) and 25 (the most frequent). These were obtained according to the curve represented in Figure 4.2, which gives low flexibility to species with low and medium frequencies and high flexibility only to the most common ones. The maximum flexibility of 25 corresponds to approximately half of the frequency of the most common species (which means that for this species the selected site can be any among the top half best ones).

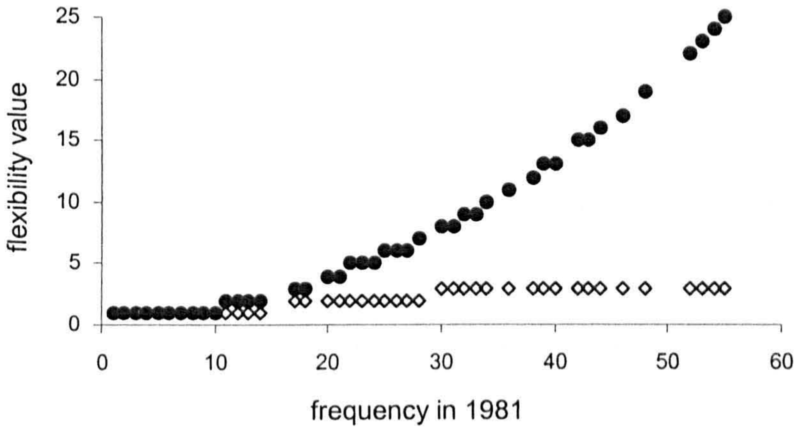

Figure 4.2 – Conversion between the frequency of a species (number of sites occupied) and the flexibility values applied in strategies 4 (white diamonds) and 5 (black circles), here illustrated for the 1981-1991 pair of years. The curve for strategy 5 was obtained by transforming the frequency values, f_i, of each species *i* using the equation $y_i = 2f_i + f_i^2$, then scaling the resultant y_i to a [1, 25] interval and rounding the values obtained to the nearest integer to get a flexibility value for *i*.

All minimisation problems were solved exactly as integer linear programming problems using LINDO (LINDO Systems, Inc. 1996; see Chapter 2). In each case only one optimal solution was found (which is not unexpected since sites have different areas and there is a low probability that the exact minimum is obtained by different sets of sites).

4.1.5 Results of the reserve selection strategies

The random models (Figure 4.3) reveal an intrinsic trade-off between the efficiency and the effectiveness of a reserve network: the larger the area covered, the more likely it is to have a lower representation gap 10 years afterwards. A possible strategy in terms of obtaining robust reserve networks could therefore be simply to select as much area as possible. In the limit, however, only by selecting the entire area could a maximum effectiveness be guaranteed *a priori*, which is obviously unrealistic.

In general, all five strategies tested performed considerably better than a random selection in terms of both effectiveness and efficiency.

Strategy 1 aims explicitly at maximising the efficiency of a reserve network and corresponds to the most popular complementarity-based approach in the recent conservation literature (e.g., Rebelo and Siegfried 1992; Williams et al. 1996*a*; Csuti et al. 1997). However, it always resulted in a significantly larger representation gap than the other strategies (Figure 4.3), demonstrating that it was not possible simultaneously to maximise efficiency and effectiveness using this approach.

All strategies excluding strategy 1 addressed the lower probability of extinction in the best sites where a species occurs. Selecting the best sites in terms of number of territories (strategy 2) means selecting a larger fraction of each species' population, which makes sense in terms of long-term persistence, as reflected by the generally small representation gap obtained. However, because a high number of territories in one site is often a reflection of a larger area, this strategy tends to select larger sites, and indeed in all situations except one this was the least efficient strategy (Figure 4.3).

Selecting the best site in terms of density (strategy 3) may imply that very small sites are selected (Gaston et al. 1999), but a high density may be associated with high habitat quality and may be a good predictor of the probability of persistence in the site. As expected, this strategy produced networks that were generally more efficient than those selected by strategy 2, but always less efficient than the minimum set. Furthermore, their effectiveness was usually high, indicating that this may provide a good compromise between efficiency and effectiveness.

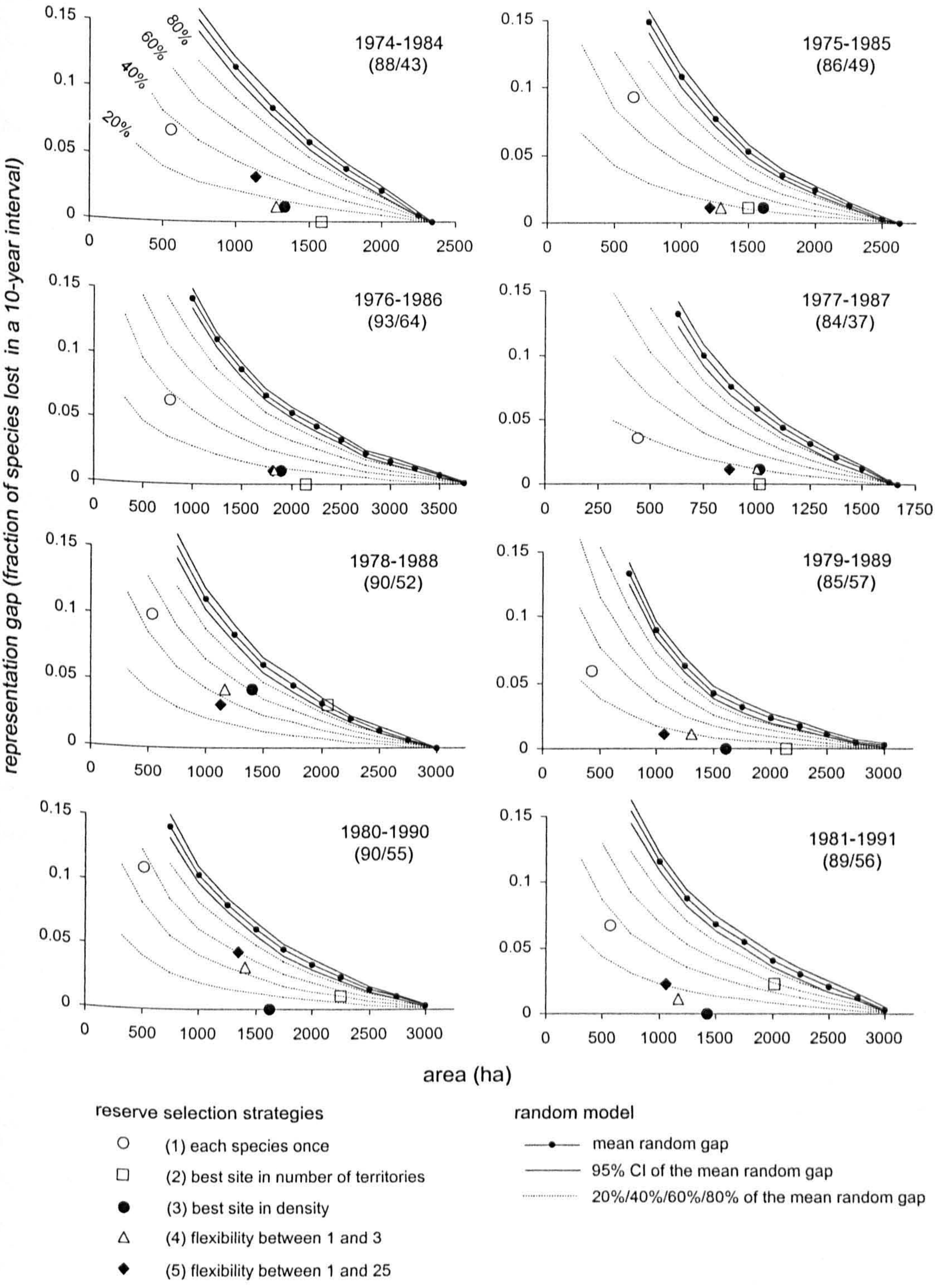

Figure 4.3 – Results obtained for each of the reserve selection strategies tested, for each of the eight pairs of 10-year interval considered, compared with the respective random models. For each reserve selection strategy, the data point indicates the total area occupied by the correspondent network (the smaller the area the higher the efficiency, *x* axis) and the representation gap (the lower the gap the higher the effectivenessm, *y* axis). Mean gap values and the 95% confidence intervals were obtained from 100 randomly selected sites for each area. The values in parentheses refer to the number of species/number of sites.

Strategies 4 and 5 addressed the lower probability of local extinction of more common species to increase the flexibility of choice in those species. As expected, this always resulted in a higher efficiency of the reserve networks in relation to strategy 3, although sometimes it incurred a larger representation gap (Figure 4.3). Because of its higher flexibility, this pattern was more evident for strategy 5.

4.1.6 Discussion

The results obtained in this study suggest that, in spite of its popularity in recent conservation literature, a minimum set strategy to selecting reserve networks may not be sufficient if the role of a network is to *maintain* species in the long-term rather than simply to *represent* them in the present (Williams 1998*b*). This is consistent with the results obtained by Margules et al. (1994*b*; 36% species lost during a 11-year interval from the minimum set of limestone pavements that represented each plant species once, U.K.) and Virolainen et al. (1999; 16% species lost during a 63-year interval from the minimum set of lakes that represented each plant species once, Finland).

The results accomplished using the other selection strategies indicate that it is possible to obtain reserve networks that are more robust to temporal turnover if species are represented in the sites where they are more likely to persist in the long-term. All strategies that used this basic rule performed significantly better in terms of effectiveness than the minimum representation set (Figure 4.3). When a higher flexibility in the selection of the best sites was allowed for the most common species (which corresponds to giving priority to the rarer species in the selection procedures), it was possible to improve efficiency, although often by compromising some effectiveness.

Naturally, it should not be concluded from this exercise that to select the single best site is sufficient to ensure the long-term maintenance of most species. Nevertheless, I believe that the two major guidelines presented here are of general application: species must be protected in the best sites where they occur (those that offer better chances of long-term persistence) and the rarest species should receive a higher conservation investment. Although crude, these allow for a simultaneous integration of viability and threat concerns in complementarity reserve selection procedures (Nicholls 1998; Williams 1998*b*).

Unsurprisingly, these two guidelines are not new in practical reserve selection exercises (see Thomas 1991). For example, the EU Birds Directive (Council Directive 79/409/EEC of 2 April

1979) gives priority to the most vulnerable species (listed in Annex I) and establishes that the 'most suitable territories' for those species should be classified as Special Protection Areas. Accordingly, the EU Habitats Directive (Council Directive 92/43/EEC of 21 May 1992) considers two levels of important species (the ones listed in Annex II, and among those the ones classified as 'priority') and establishes that in the classification of Special Conservation Areas the density and dimension of the population of the species in each site must be taken into account. More or less systematically, conservation agencies have always been struggling to protect the best sites for the most threatened species, but there are practical constraints to be considered at the same time (Thomas 1991).

However, such a strategy is more costly than one aiming at simple representation (Figure 4.3). This may provide an additional explanation for the observation that existing reserve networks are less efficient in representing biodiversity features than a minimum set (e.g., Rebelo and Siegfried 1992; Castro Parga et al. 1996), which has been interpreted as demonstrating that reserve networks have been selected in an *ad hoc* fashion (e.g., Pressey and Tully 1994; see Section 2.2 for a critique). Less efficiency may also be a consequence of incorporating in the reserve selection procedures a concern for the long-term maintenance of the biodiversity features of interest.

The results presented in this study also demonstrate that there is a trade-off between effectiveness and efficiency, and that maximising both simultaneously is unlikely to be possible. The fact that conservation planners have been emphasising the former while scientists working in conservation research have been mainly concerned with the latter may help to explain the gap between theory and practice in reserve selection procedures (Prendergast et al. 1999). Effectiveness has mainly been addressed by focusing on some target species or ecosystems and selecting networks of reserves that aim at maintaining them. On the other hand, complementarity-based algorithms have been aiming at maximising efficiency by looking for minimum sets that represent all features. There are dangers in both approaches: the first results in a biased and inefficient distribution of the conservation resources among biodiversity features, some being highly protected while others are totally unrepresented; the latter may result in reserve networks that are not robust over time, and it may be sending, albeit unwittingly, the message that a minimum set is sufficient to maintain diversity when in fact it is not.

Here I have illustrated how it is possible to achieve a compromise between efficiency and effectiveness if the concerns about viability and threat are embedded in complementarity-based algorithms. This does not imply a need to hold such detailed data as the CBC, but does imply a need to make the best use of all the relevant information available. Indeed, it is often the case that when the detailed distribution data required to apply complementarity-based algorithms are available, so is other relevant information that has been overlooked in simply searching for minimum representation. This includes, for example, Red Data books, which can be used to establish priorities in terms of conservation investment, and information on the location of the best sites for at least some species, even if established qualitatively in terms of habitat quality or availability.

Reducing the gap between theory and practice in reserve selection procedures (Prendergast et al. 1999) will require that scientists working in conservation research give to conservation planners the tools that allow them to integrate the concerns and information that they consider to be relevant.

4.2 Using presence/absence data to establish reserve selection procedures that are robust to temporal species turnover

4.2.1 Introduction

Maintaining the diversity of biological features in a given region over the long term is the prime objective in the establishment of a network of nature reserves. Indeed, concern about the likely persistence of features in reserves has always been a feature of practical reserve selection exercises. Often this has been expressed by focusing resources on a few target species, frequently the most endangered ones (e.g., Thomas 1991; Madsen et al. 1998), with the expectation that in maintaining them other features of interest will be preserved as well. However, it has been demonstrated that in some situations, at least, this approach may not be effective in conserving non-target species (e.g., Kerr 1997).

One approach to addressing simultaneous concerns about persistence and about the conservation of a multitude of species has been to use reserve selection procedures that select the best sites on the basis of an index that incorporates one or several variables thought to be of importance (so-called scoring procedures). The appeal of such indices is that they can easily integrate a diversity of concerns, including biological, social and economic ones. The long-term persistence of features has usually been addressed by valuing sites with more threatened species and/or sites with higher value for wildlife (frequently those with higher abundance of the species of interest; e.g., Götmark et al. 1986; Brown et al. 1995*a*; Turpie 1995). The drawback of these procedures is the risk that the areas selected are unnecessarily duplicating some attributes, while leaving other features of interest totally unrepresented in the reserve network (Pressey and Nicholls 1989*a*).

Reserve selection strategies based on the complementarity principle (Vane-Wright et al. 1991) have been developed as a response to the recognition that resources for the protection of biodiversity will always be limited. These aim at a high efficiency (*sensu* Pressey and Nicholls 1989*a*) in the representation of all biodiversity features of interest with the minimum cost. The most commonly used of these procedures searches for the minimum area such that all features are represented at least once in the reserve network (e.g., Margules et al. 1988; Sætersdal et al. 1993; Csuti et al. 1997; Pressey et al. 1997; Howard et al. 1998). The underlying rationale is that features cannot be protected by reserves if they do not occur in the network in the first place (Margules et al. 1988).

However, this simple representation strategy may not be sufficient to assure the long-term persistence of features in the network. Indeed, previous studies have found that minimum sets failed to retain all the species that justified their selection some years afterwards (Margules et al. 1994*b* – 36% species lost during a 11-year interval from the minimum set of limestone pavements that represented each plant species once, U.K.; Virolainen et al. 1999 – 16% species lost during a 63-year interval from the minimum set of lakes that represented each plant species once, Finland; Rodrigues et al. 2000*b* – average 8% species loss during ten-year intervals from the minimum number of census plots that represented each bird species once, United Kingdom, see Section 4.1).

Different strategies have been suggested in the literature to improve the robustness of complementarity-based reserve selection procedures. Making use of abundance data, Kershaw et al. (1994) and Turpie (1995) proposed that only those sites where species occur above a certain abundance value should be considered for selection, while Nicholls (1998) proposed the establishment of a minimum population size as a required representation target for each species. Furthermore, the results obtained in Section 4.1 (Rodrigues et al. 2000*b*) suggest that more robust networks can be obtained by selecting the sites at which each species occurs at relatively high local abundance. Strategies based on presence/absence data that have been proposed include multiple representations (e.g., Pressey and Nicholls 1989*b*; Lombard et al. 1995; Williams et al. 1996*a*) and representation of all species in a minimum fraction of their range in the study area (e.g., Nicholls and Margules 1993; Pressey and Tully 1994; Pressey et al. 1997). A more elaborate approach proposed by Williams (1998*b*), consists of excluding records for particular species in areas where their viability seems likely to be poor as assessed using niche-based modelling of the local habitat suitability.

Here I consider three families of reserve selection strategies based on presence/absence data: multiple representations, selecting an increasing percentage of each species' range, and selecting the sites where species exhibited a higher permanence rate in the past. Considering species as features of biodiversity, I use data from the Common Birds Census in the United Kingdom to examine how these strategies affect the efficiency and the effectiveness (a measure inversely related to the gap between the representation target required and the one attained by the network; see Section 3.2 and Rodrigues et al. 1999) of reserve networks in maintaining species over time in comparison with a single representation strategy.

4.2.2 Data and methods

The Common Birds Census (CBC), run by the British Trust for Ornithology, has been the primary scheme by which populations of common breeding birds have been monitored in the United Kingdom (for a comprehensive description of the history and methodology of CBC, see Marchant et al. 1990). Although it provides information on the abundance of each species in each site, in this analysis I used presence/absence data only.

I used the CBC data collected between 1976 and 1991 in a variable number of farmland and woodland sites. I considered six pairs of years with a ten-year interval in between: 1976-1986 through 1981-1991. For each pair, I analysed only those sites with good quality information in both years and that had been visited at least twice in the previous five years. Only those species for which presence/absence had been recorded in all years (77 species) were considered.

Three families of reserve selection strategies were tested.

1) **Single and multiple representations. Single representation**: select the minimum area such that each species is represented in at least one site (*a*). This corresponds to the most commonly used complementarity-based approach in the recent reserve selection literature. **Multiple representations**: select the minimum area such that each species is represented in at least n sites (or the maximum number of sites where the species occurs, if less than n): (*b*) $n = 2$; (*c*) $n = 3$; (*d*) $n = 4$; (*e*) $n = 5$.

2) **Percentage of range.** Select the minimum area such that each species is represented in at least a p percentage of its range in the study area: (*a*) $p = 10\%$; (*b*) $p = 20\%$; (*c*) $p = 30\%$; (*d*) $p = 40\%$; (*e*) $p = 50\%$. As an approximation, the range of each species was given by the total area of sites where the species occurs.

3) **Permanence rate.** A *permanence rate* is calculated for each species in each site, given by the fraction of years in which the species was recorded at the site in relation to the total number of years in which the site was visited in the period between five years before and the first year of a pair of years separated by a ten-year interval (e.g., for the 1976-86 interval, the permanence rate for each species in each site is given by the number of times the species was recorded at the site from 1971 to 1976 in relation to the total number of

visits in those years). Select the minimum area such that each species is represented at least at the site, or one of the sites, where it has the higher permanence rate registered.

In each pair of years, the first year's data were used to select a reserve network following a specific strategy. The network was then evaluated according to: a) its efficiency (Pressey and Nicholls 1989*a*), which is higher when the total area occupied is smaller; b) its effectiveness (see Section 3.2; Rodrigues et al. 1999) over time, which is higher when the fraction of species absent from the network ten years afterwards (the *representation gap*) is smaller (throughout this section, I use 'effectiveness' in this sense).

The optimal solution was found in each case and then four near-optimal solutions. This was done by first determining the optimal solution and then solving the problem after adding an additional constraint that excludes the optimal solution previously found (Camm et al. 1996; Rodrigues et al. 2000*c*; see Section 2.1). In this way, the optimisation algorithm finds another optimum (if it exists) or the nearest best solution. By repeating this procedure, a sequence of five solutions with non-decreasing areas (but all close to the minimum) was obtained for each problem. The average area and average representation gap of those five solutions was obtained. The average area is still very close to the optimal value while the average effectiveness is a value that is more representative of the performance of a given strategy and less likely to have been determined by chance.

For each pair of years, the average efficiency and effectiveness were also determined for 100 randomly selected networks of (approximately) a pre-defined area. This was done by selecting sites randomly, without replacement, until the total area was approximately that pre-defined (obviously, given variability in the areas of sites random networks will seldom be precisely this area). I applied this procedure to a wide range of areas to establish a null relationship between efficiency and effectiveness (random model).

All minimisation problems were solved exactly as integer linear programming problems (see Section 2.1; Rodrigues et al. 2000*c*) using CPLEX (ILOG 1999).

The selection units considered in this section are census plots, much smaller than most nature reserves. Although this implies that the turnover rates observed are probably much faster than the ones occurring in reserves during a ten-year interval, turnover is also known to increase over time (Russell et al. 1995) and reserves are expected to prevail far longer than ten years. It was assumed that the turnover rates observed within ten-year intervals in the CBC plots exhibit similar patterns to the ones observed in reserves over longer periods (see Section 4.1; Rodrigues et al. 2000*b*).

Although the CBC concerns species that are "common" in the UK, many are rare in this data set (for example, in 1981 nearly 40% of the species had a range of less than a quarter of the total study area). The CBC data are used here as an exemplar data set to explore general reserve selection strategies, and therefore the results should not be interpreted as an attempt to propose a new reserve network in the United Kingdom.

4.2.3 Results

For each pair of years, the corresponding random model illustrates what is the expected effectiveness of a network of a given area selected randomly (Figure 4.4). As predicted, the larger the area, the lower the representation gap ten years afterwards (in the limit, when all sites are selected a representation gap of zero is obtained). This has consequences for the interpretation of the results of the strategies tested – just by increasing the area (lowering the efficiency) of a network a higher effectiveness is anticipated.

By definition, maximum efficiency in a reserve network is achieved by the minimum set that represents every species at least once (single representation strategy, 1*a*). However, this strategy always resulted in large representation gaps (Figure 4.4). Increasing the minimum number of representations required for each species (strategies 1*b*, 1*c*, 1*d* and 1*e*) always required the selection of a larger reserve network area but resulted generally in a considerably higher effectiveness of the networks obtained (Figure 4.4). In particular, increasing the number of representations from one to two resulted always in a reduction of the gap to less than half its initial value (although requiring on average more than twice the area).

The general pattern of results obtained for the family of strategies involving the selection of some percentage of the range of each species is similar to that of the single and multiple representation family – a higher representation target corresponds always to a lower efficiency and generally to a higher effectiveness (Figure 4.4). However, in some cases an inversion was obtained in the pattern of decreasing effectiveness, i.e., an increasing representation gap in spite of the larger area (Figure 4.4*a,c,e,f*).

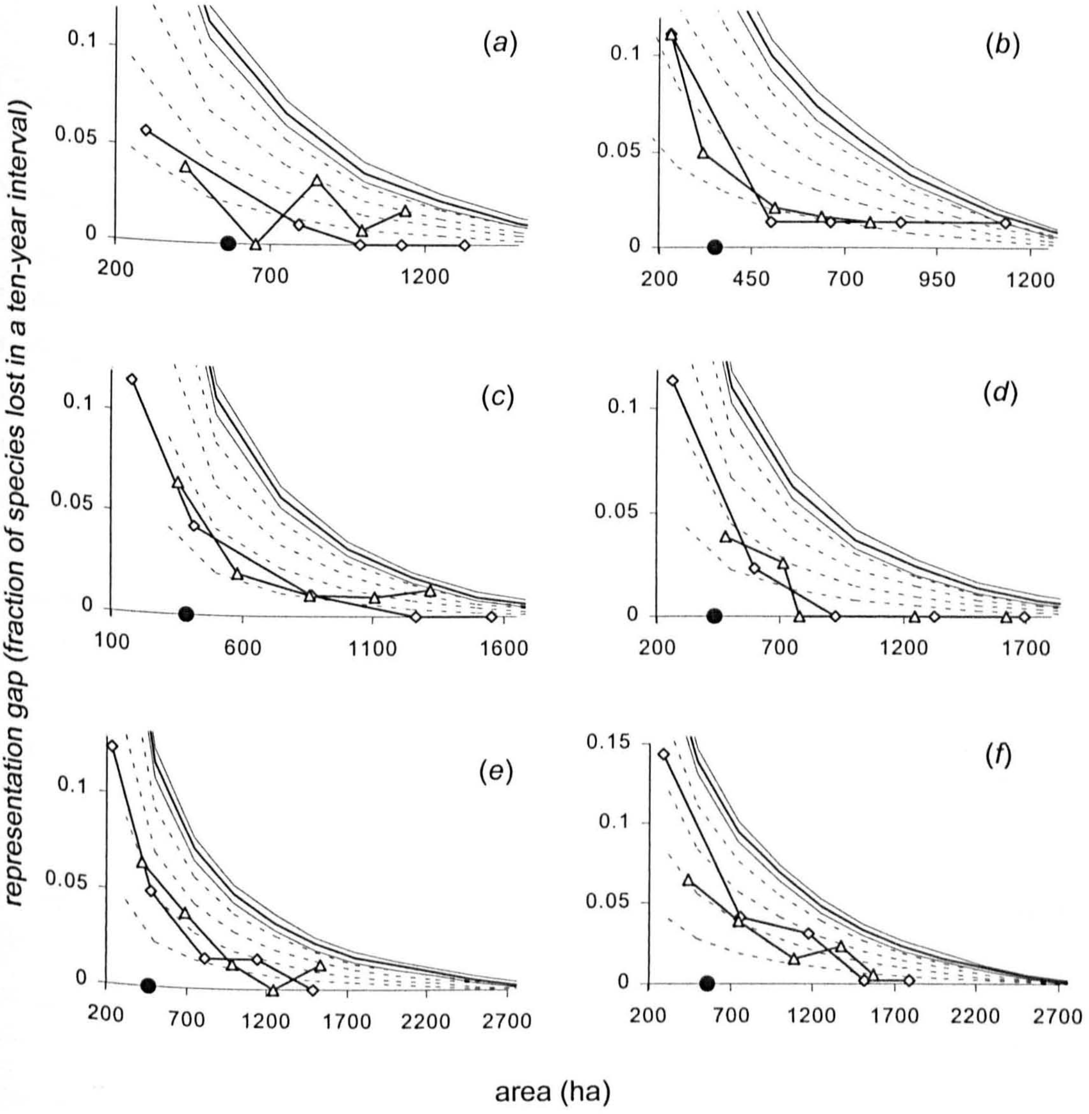

Figure 4.4 – Results obtained for each of the reserve selection strategies tested, for each of the six pairs of ten-year interval considered, compared with the respective random models. Results for random models were obtained for 100 replicates and are given by the thick continuous lines (mean random gap), the thin continuous lines (limits of the 95% confidence interval) and thin broken lines (20%, 40%, 60%, and 80% of the mean random gap). Diamonds correspond to the single and multiple representation family of strategies (from left to right, $n = 1$; $n = 2$; $n = 3$; $n = 4$; $n = 5$), triangles to the percentage of range family (from left to right, $p = 10\%$; $p = 20\%$; $p = 30\%$; $p = 40\%$; $p = 50\%$), and black circles to the strategy based on permanence rate. For each reserve selection strategy, a data point indicates the average total area and average representation gap of the optimal correspondent network and another four near-optimal solutions. The smaller the area (*x* axis) the higher the efficiency, and the lower the gap (*y* axis) the higher the effectiveness. (*a*) 1976-1986 (42), (*b*) 1977-1987 (41), (*c*) 1978-1988 (58), (*d*) 1979-1989 (65), (*e*) 1980-1990 (67), (*f*) 1981-1991 (64). The values in parentheses refer to the number of sites (number of species is 77 in all cases).

Selecting sites with a high permanence rate resulted consistently in networks with maximum effectiveness (zero representation gap) and a high efficiency (always higher than the one obtained by the strategy of representing each species twice; Figure 4.4).

4.2.4 Discussion

The results obtained in this study are consistent with previous findings (see Section 4.1; Margules et al. 1994*b*; Virolainen et al. 1999; Rodrigues et al. 2000*b*) in suggesting that a single representation strategy to selecting reserve networks is not sufficient to ensure the maintenance of species over the long-term. A high level of efficiency is attained at the cost of low effectiveness. However, the results obtained using the three families of strategies tested indicate that by compromising some efficiency it is possible to obtain reserve networks that are more robust to species temporal turnover.

A multiple representation strategy seems to be a safer investment than one based on a percentage of area. The results in the first case – a general tendency to a decrease in the representation gap when the target is increased (Figure 4.4) – are as expected, since by requiring multiple representations there is a higher probability that each of the species will persist over a ten-year period in at least one of the sites selected. On the other hand, some of the results found in the percentage of range family of strategies are apparently counter-intuitive, as they suggest a significant risk of obtaining a simultaneously less efficient and less effective network when increasing the representation target (Figure 4.4*a,c,e,f*). These contrasting results are probably a consequence of the fact that the first family of strategies gives more emphasis to rare species while the second in fact gives priority to the most widespread ones. For a multiple representation strategy, a target of $n = 3$ sites, for example, means selecting all of the sites which are occupied by species which occur in a total of three or fewer sites, and a decreasing proportion of the total number of sites occupied by each of the more widespread species as this number increases. On the contrary, a target of $p = 30\%$ for a percentage of range strategy means requiring very large areas for very widespread species and very small areas for very rare ones. When the goal is to generate networks that are robust to temporal species turnover, the first approach is expected to perform better, since rare species are known to be more prone to local extinction (Section 4.1; Gaston 1994; Rodrigues et al. 2000*b*), and may therefore require a higher investment in order to persist in a reserve network. The inversions observed in the results for a percentage of range strategy (Figure 4.4*a,c,e,f*) follow perhaps from a reduction of total area allocated to some of the rarer species when increasing the required representation target. For a small target (say, 10%), only one or two sites at which they occur need to be included for both rare and common species to be sufficiently represented. For increasing targets, most of the sites added are likely to be required to meet the target for the most common species, as the rare ones will still achieve the percentage of area required with representation at only one site. If when increasing the target some sites that contain rare species but that are unnecessary to achieve their representation target (that happened to have been selected previously) are replaced by others that contribute only to representing more common species, the probability of extinction of these rare species in the network increases and may result in a lower effectiveness despite the larger area being selected.

A practical problem when using the multiple representation strategy is to know what is the adequate degree of replication needed in order to attain a high effectiveness without unnecessarily compromising the efficiency of the network. In practice, the adequate target for each species may have to be decided on a case-by-case basis, according to the available information and the specific goals established for the network.

A drawback of the multiple representation strategy is that it considers all sites where a species is present to have the same value for its persistence. Although the risk is lower when setting higher representation targets, there is a danger in this approach that all sites of a network where the species is represented are inadequate for its long-term survival while the best sites are left unprotected (Turpie 1995). Strategies that target sites where species are more likely to persist are therefore expected to perform better in terms of long-term effectiveness (Williams 1998*b*). Indeed, in this data set the strategy based on permanence was the most effective (Figure 4.4), which can be explained by a lower local extinction probability in the sites with higher permanence rate (Figure 4.5).

Deciding which sites should preferentially be selected for each species can be based on abundance data, as in Section 4.1 (Rodrigues et al. 2000*b*), or on presence/absence information about species persistence over time, as here. Both types of information are often unavailable to planners and can be expensive to obtain. Obtaining an accurate estimate of the abundance of each species in each site at a given time requires a substantial investment when compared with the one needed to obtain presence/absence data. For example, the time input required for a full CBC analysis to obtain the number of breeding pairs of each species in each plot is estimated to be at least 3.5 times that of presence/absence data (14 versus 4 days per plot per year to carry out fieldwork and analysis; presence/absence could be obtained with less investment, but with greater uncertainty about which species use a site). In a related study, Gregory et al. (1994) estimated the time input required for a full CBC to be 6.9 times that of using point counts (55 versus 8 hours per plot per year).

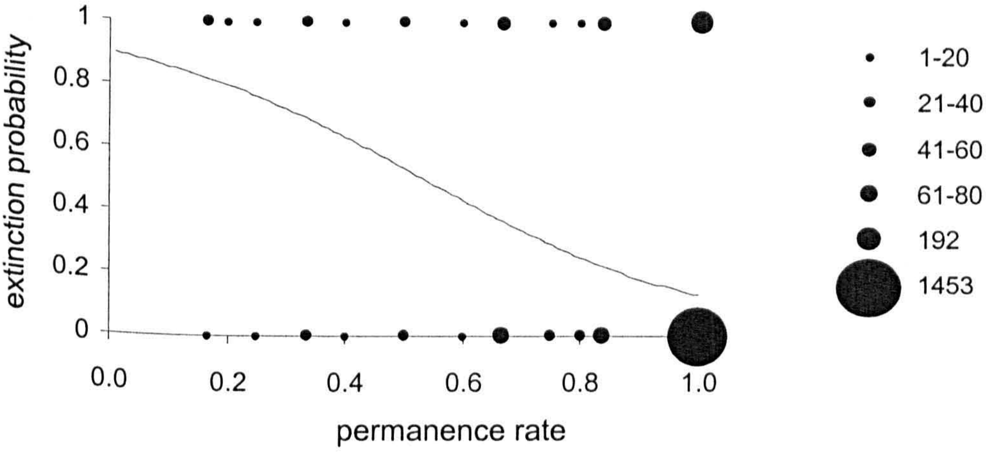

Figure 4.5 – Relationship between the local permanence rate (fraction of years in which a species was recorded at the site in relation to the total number of years in which the site was visited between 1976 and 1981) and the subsequent extinction probability (the probability of the species becoming extinct in that site between 1981-1991). Likelihood ratio test (χ^2-test): $n= 2205$; $\chi^2\text{-test} = 304.661$; $p < 0.001$. Dot sizes refer to the number of correspondent data values (as there is only a small number of possible values for the permanence rate). Only data on the 1981-91 pair of years has been used to prevent non-independence caused by overlapping time-series.

Permanence rates require having information on the presence/absence of species in each of the sites in a series of years, which involves a period of monitoring before deciding which reserves to select. Nevertheless, the collection of presence/absence data requires less expertise and may be more attractive to volunteers (Bart and Klosiewski 1989). And it may be easier to recruit volunteers to work less intensively over some years than to concentrate the same investment in a short period in order to collect abundance data.

Either by using abundance or time series of presence/absence data, there is an additional cost attached to directing surveys at obtaining information about the best sites for the conservation of each species, over and above that of simply determining the spatial occurrence of species. But including this information in the reserve selection procedures may result both in a higher effectiveness and in a higher efficiency (i.e., lower cost) in the implementation of the network. And indeed, in these analyses I found that it was a better strategy to select the best site for each species than to invest in multiple, but blind, redundancy (Figure 4.4). In practical reserve selection exercises, the gain from using more information is avoiding the cost of acquiring unnecessarily large reserve systems and may well compensate for the resources invested in the monitoring schemes needed to acquire that information (Balmford and Gaston 1999).

4.3 Complementary representation and zones of ecological transition

4.3.1 Introduction

The methods by which priority areas for conservation should be identified have been much debated (e.g., Diamond 1975; Smith and Theberge 1986; Shafer 1991; Scott et al. 1993; Mittermeier et al. 1998; Schwartz 1999; Myers et al. 2000). Those approaches based on the complementarity principle (Vane-Wright et al. 1991) are becoming increasingly popular in the conservation literature (e.g., Pressey et al. 1993; Williams et al. 1996*a*; Csuti et al. 1997; Howard et al. 1998). Most commonly, these methods look for a set of sites such that all species of concern are represented in the minimum possible total area.

One potential drawback of such minimum sets is that some species may be represented at sites that are inadequate for their long-term persistence in the final conservation network (Harrison and Martínez 1995; Turpie 1995). For example, Branch et al. (1995) found that seven of the eight sites selected to represent all species of land tortoises and terrapins in southern Africa were inadequate for the protection of the species that justified their selection. Likewise, Nicholls (1998) found that in a near-minimum set selected to represent species of snakes in South Africa, most species were mainly represented in grid cells covering the periphery of their spatial distributions. This might explain the finding by other studies that minimum sets are ineffective in maintaining species over time (see Sections 4.1 and 4.2; Margules et al. 1994*b*; Virolainen et al. 1999; Rodrigues et al. 2000*a*,*b*).

To date, there has been no investigation of whether there is reason to suspect an inherent tendency in minimum complementary sets to select sites that are of marginal value for the conservation of species. The high efficiency of minimum sets (i.e., the ability to represent a maximum of diversity in the minimum number of sites; Pressey and Nicholls 1989*a*) is their most acclaimed trait, and derives from the selection of sites that are highly complementary in terms of species composition. It is implicitly assumed that this complementarity is obtained by selecting sites representative of different ecological regions, which therefore have species assemblages that complement each other. However, it can be envisaged that an even more efficient way of representing all species would be to select areas in the transition between ecological regions, with species assemblages resultant from a mixture of floras or faunas, which would allow the simultaneous representation of species belonging to different ecological regions (Figure 4.6). If so, then the high efficiency of minimum sets may be attained at the cost of a preferential selection of sites which are not truly representative of any ecological region and where species are represented at marginal sites within their ranges.

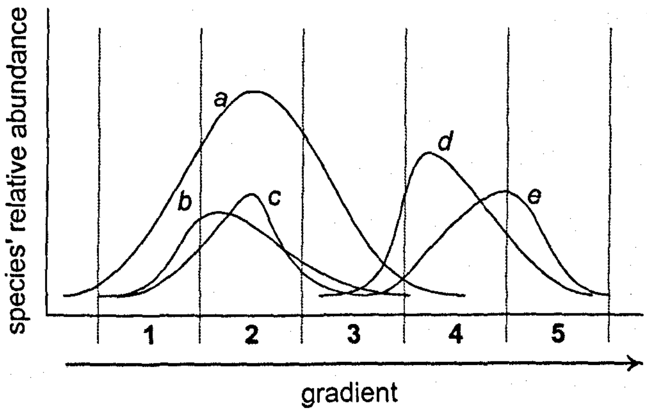

Figure 4.6 – Hypothetical distribution of five species (*a, b, c, d, e*) across an environmental gradient. All species might be represented at the core of their ranges by two sites (2 and 4) or by a minimum set of just one site (3) in the transition between different species assemblages.

In this section, I use data on the distribution of birds in South Africa and Lesotho to test this idea. First, I determine if a minimum complementary set provides an adequate representation of species. Then, I explore whether this method tends to select sites in areas of ecological transition.

4.3.2 Data

The Southern African Bird Atlas Project (SABAP; Harrison et al. 1997) has provided the most comprehensive information currently available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana. Observers visiting each cell recorded the presence of identified species on checklists, breeding and non-breeding records being considered equivalent. A total of 909 species were recorded. Based on these data, reporting rates were calculated for each species in each cell as the proportion of checklists submitted for that cell on which the species was recorded (for a more detailed description of the methods used in the SABAP, see Harrison et al. 1997).

In this section, I used the presence/absence data for South Africa and Lesotho (1858 grid cells), excluding marine, vagrant, marginal and escaped species from the analysis (651 species were analysed). Following Gaston (1994), species in the lower range size (the number of cells occupied) quartile were considered as rare (163 species).

For these rare species, I also used the printed maps in Harrison et al. (1997) to obtain information on reporting rates across their ranges. Reporting rates are represented as, usually four, classes (two for species with few records). For cells falling in the class of lowest reporting rate, less than 2% of checklists submitted recorded the presence of a given species, but cut-off values for other classes vary greatly between species.

Seven biomes were defined within the study area: Desert, Succulent Karoo, Nama Karoo, Fynbos, Grassland, Woodland (Savanna and thicket biomes combined) and Forest (see Rutherford and Westfall 1994; Low and Rebelo 1996 for descriptions). The percentage of each cell occupied by each biome was calculated by digitising Low and Rebelo's (1996) map of the biomes, replotting it in ArcInfo, and using this software to calculate percentage coverage of each cell by each biome type.

In addition, I used two classification systems of vegetation types for the study area: that into sixteen types by Harrison et al. (1997), who provided corresponding distribution maps; and a finer classification into sixty-eight types by Low and Rebelo (1996) for which only the number of types present in each cell were known.

4.3.3 Are species adequately represented by a minimum complementary set?

Thirty complementary sets were obtained that represent all 651 bird species in South Africa and Lesotho by solving the integer linear problem of minimising the number of grid cells such that each species is represented at least once (Underhill 1994; see Chapter 2). The problem was solved using the CPLEX optimisation software (ILOG 1999), and the minimum number of cells needed to represent all species was 19. Because numerous equally optimal solutions exist for this problem, the specific solution found depends on the order in which variables (sites) are introduced. In order to obtain 30 representatives of the entire set of optimal solutions, the problem was solved 30 times after re-ordering the data set randomly. To avoid repeated selection of the same solutions, each time one was sought an additional restriction was added to the problem that excluded the solution previously found (see Section 2.1; Rodrigues et al. 2000c). This procedure obtains a random set of optimal solutions without replacement.

I have considered that sites at which species occur at lower abundance, at the periphery of their ranges, or that do not correspond to their preferred vegetation type, are not adequate for the species' conservation, or at least would not provide the best basis for such action (throughout this section, I use the term 'adequate' and its derivatives in this sense). Therefore, in order to determine whether bird species were adequately represented in reserve networks corresponding to each of the complementary sets identified, I have performed three analyses. First, for the rare species only, I determined the quality of the sites selected in terms of reporting rates, by overlaying the sites selected by each of the complementary solutions on the distribution maps in Harrison et al. (1997). The eight species that had only one class of reporting rate in the study area were excluded from this analysis. Within each species' range, the reporting rates were assumed to increase in a broadly monotonic manner with increasing density (Robertson et al. 1995; Harrison et al. 1997), therefore providing a measure of relative abundance. Across the 30 complementary solutions, between 36.1% and 40.0% (mean 38.2%) of the rare species analysed were represented in the complementary sets by sites other than those from the best class of reporting rates found in the study area, while 18.1% to 21.9% (mean 20.1%) were represented only by sites from the worst class.

Second, I determined the quality of sites selected in terms of their spatial positions in the ranges of the species. I considered a cell to be at the edge of a species' range if the species is present in that cell but not in at least one of its neighbours (the eight surrounding cells). Species whose ranges are so fragmented that they consist of edge cells alone (92 species) were excluded from this analysis. Between 23.4% and 28.3% (mean 24.4%) of the species analysed were represented in the complementary sets solely by edge cells.

Third, I used the 16 vegetation types of Harrison et al. (1997) to determine the quality of the complementary sets in relation to each species' preferred type. Overlaying each species' range with the vegetation distribution maps, the preferred type was defined as that in which the highest percentage of the species' range falls. Species whose ranges fall entirely inside the preferred vegetation type (26 species) were excluded from this analysis. Between 6.2% and

14.4% (mean 11.7%) of the species analysed were represented in the complementary sets only by cells that do not correspond to the preferred vegetation type.

The results of all three of the above analyses demonstrate that a large to moderate fraction of the bird species in South Africa and Lesotho are inadequately represented in a complementary set of sites that represents all species at least once.

4.3.4 Are complementary sets prone to selecting sites in areas of ecological transition?

Five measures were considered that are expected to reflect the location of areas of ecological transition and used to determine whether complementary sets for the birds of South Africa and Lesotho tend to select higher values of these measures than expected by chance. This was done by calculating the mean value for each measure across the cells in each complementary set and counting the number of occasions on which this value falls within the 5% upper tail (i.e., a one-tailed test) of a random distribution of means obtained by selecting 10,000 random sets of 19 cells each. For each of the measures, I also compared the mean frequency distribution of values obtained for the cells selected by complementarity to the frequency distribution for all the 1858 cells in the study area (see legend to Figure 4.9 for an explanation).

First, I determined whether complementary sets tend to select areas at the edge of vegetation types. A cell was considered to be at the edge of a given type if it belongs to that type but at least one of its neighbours does not (Figure 4.7*a*). Whilst the fraction of all cells in the study area which are edge cells was 0.51, a mean of 0.74 (minimum 0.63, maximum 0.84) of the cells selected by complementarity were edges (Figure 4.7*b*-*i*). The mean fraction of edge cells in each of the 30 complementary sets always fell within the 5% upper tail of a random distribution.

Second, I determined whether complementary sets tend to select areas of high biome heterogeneity. For each grid cell, a biome heterogeneity measure was obtained using Simpson's index of diversity (Krebs 1999):

$$1 - \mathrm{Sum}\,(p_i)^2$$

where p_i is the fraction of the grid cell's area occupied by biome i (Figure 4.8*a*). This index ranges from zero, when only one biome is present in the cell, to 0.86 when all seven biomes are present in the same proportions. This measure is expected to reach high values in areas of transition between biomes. The values recorded ranged between zero and 0.76. The mean biome heterogeneity value of complementary sets fell within the 5% upper tail of a random distribution in 18 of the 30 cases (binomial test = 0.18, n.s.). The frequency distribution for the complementary sets was slightly skewed to the right in relation to the general frequency distribution (Figure 4.9*a*).

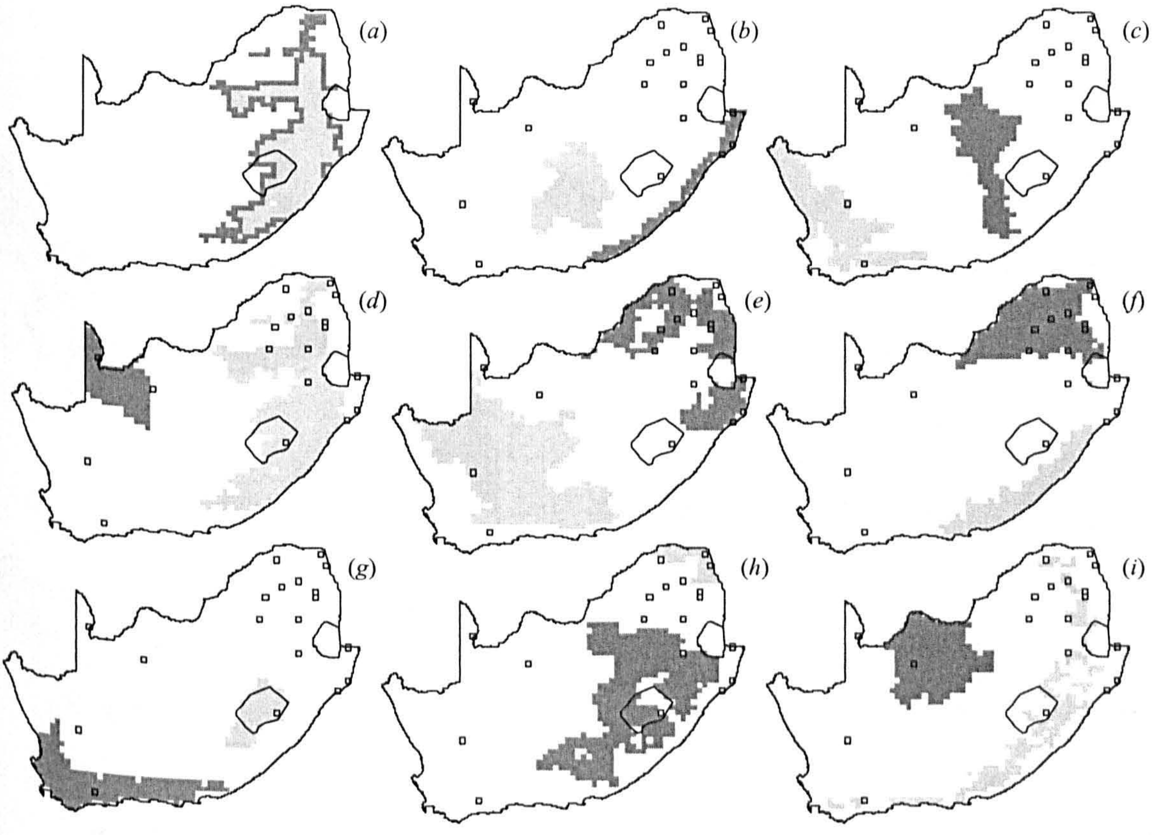

Figure 4.7 – (*a*) Illustration of the definition of edge cells (dark grey), as opposed to core cells (light grey), exemplified for the Sour Grasslands vegetation type. Position of cells selected by complementarity (open squares; here illustrated for one of the 30 complementary solutions found) in relation to the edges of vegetation types: (*b*) Grassy Karoo (light grey) and East Coast Littoral (dark grey); (*c*) Succulent Karoo (light) and Sweet Grasslands (dark); (*d*) Sour Grasslands (light) and Southern Kalahari (dark); (*e*) Nama Karoo (light) and Arid Woodland (dark); (*f*) Valley Bushveld (light) and Moist Woodland (dark); (*g*) Alpine Grasslands (light) and Fynbos (dark); (*h*) Mopane (light) and Mixed Grasslands (dark); and (*i*) Afromontane Forest (light) and Central Kalahari (dark).

Third, I used as a measure of ecological transition the number of vegetation types recorded for each grid cell, out of the sixty-eight types defined by Low and Rebelo (1996) (Figure 4.8*b*). This is expected to be higher in areas of transition between different vegetation compositions. The values recorded ranged between one and eight. The mean number of vegetation types in each of the complementary sets always fell within the 5% upper tail of a random distribution. The frequency distribution for these 30 sets showed a marked displacement to the right (Figure 4.9*b*).

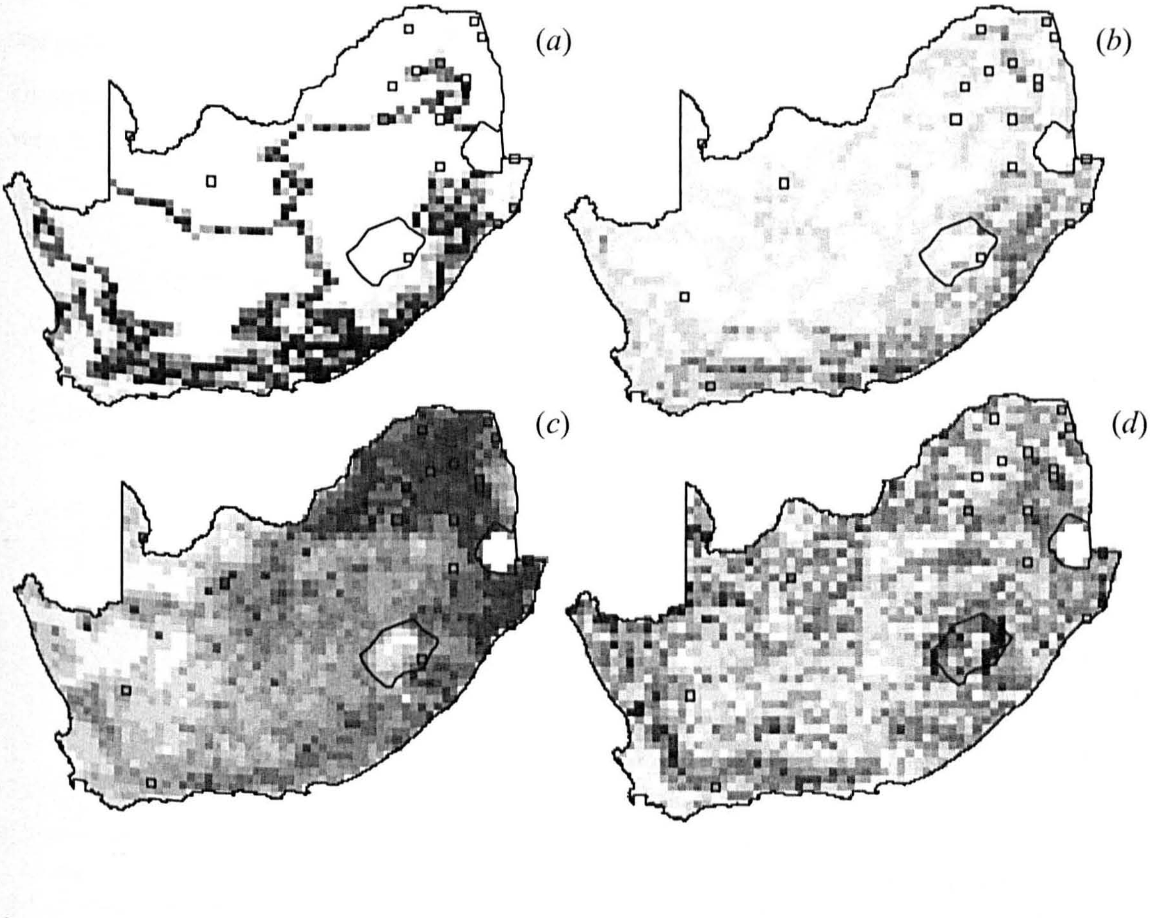

Figure 4.8 – Values of (*a*) biome heterogeneity, (*b*) number of vegetation types, (*c*) bird composition heterogeneity, and (*d*) β_g across South Africa and Lesotho. Darker colours correspond to higher values. White is absence of data. The cells outlined in black correspond to one of the complementary solutions found.

Fourth, using the presence/absence data for each bird species in each grid cell, a dissimilarity measure was obtained for each pair of cells using the complement of the simple matching coefficient (Krebs 1999):

$$1 - (a + d)/(a + b + c + d)$$

where a is the number of species occurring in both cells (A and B) of a pair, b is the number of species occurring in A but not in B, c is the number of species occurring in B but not in A, and d is the number of species absent from both cells. For each cell, the value of bird composition heterogeneity was obtained by calculating the average dissimilarity between the cell and each of its neighbours (Figure 4.8*c*). This index ranges between zero, when the cell has the same species composition as all of its neighbours, and one, when it does not share any species with its neighbours. This measure is expected to capture the transition between areas of different species composition. The values recorded ranged from 0.03 to 0.26. For all of the complementary sets, the mean value of bird composition heterogeneity always fell within the 5% upper tail of a random distribution. The frequency distribution for these sets showed a very clear displacement to the right (Figure 4.9*c*).

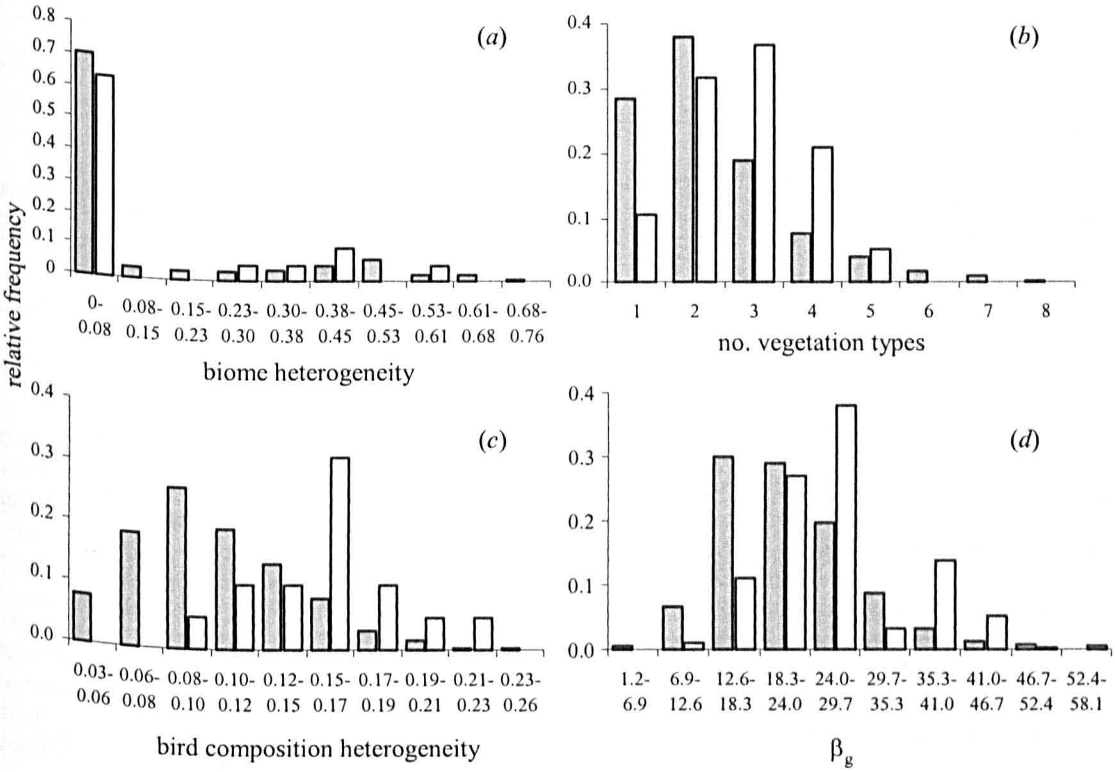

Figure 4.9 – Comparison between the frequency distributions obtained for all grid cells in the study area (grey bars) and the mean frequency distributions of the 30 complementary sets (white bars), for each of the measures: (*a*) biome heterogeneity, (*b*) number of vegetation types, (*c*) bird composition heterogeneity, and (*d*) β_g. In each histogram, ten (eight in *b*) equal width classes were considered between the minimum and the maximum values recorded in all cells. The frequency distribution for all cells was obtained by computing the fraction of all cells in the study area whose values fall within each class (relative frequency). The mean frequency distribution for the complementarity sets was obtained by calculating the mean relative frequency in each of those classes for the 30 complementary sets.

Finally, I tested if complementary sets tend to fall into areas of high species spatial turnover, a notion that has been associated with the concept of β diversity (e.g., Blackburn and Gaston 1996). I developed a measure of β diversity based on the rate of species replacement across multidirectional gradients (β_g; see Figure 4.10 for an explanation; Figure 4.8*d*). As with the previous measure, this is expected to highlight transition areas between different species assemblages, but it is more effective in capturing directional gradients in composition. It is also less sensitive to fragmentation, whether real or artificially imposed on the data set by uneven sampling effort (a potential limitation associated with neighbourhood indices; Williams et al. 1999) and to local species richness. The values recorded ranged between 1.2% and 58.1%. The mean β_g in each of the complementary sets always fell within the 5% upper tail of a random distribution. Accordingly, the frequency distribution for these sets showed a marked displacement to the right when compared with the distribution for the entire data set (Figure 4.9*d*).

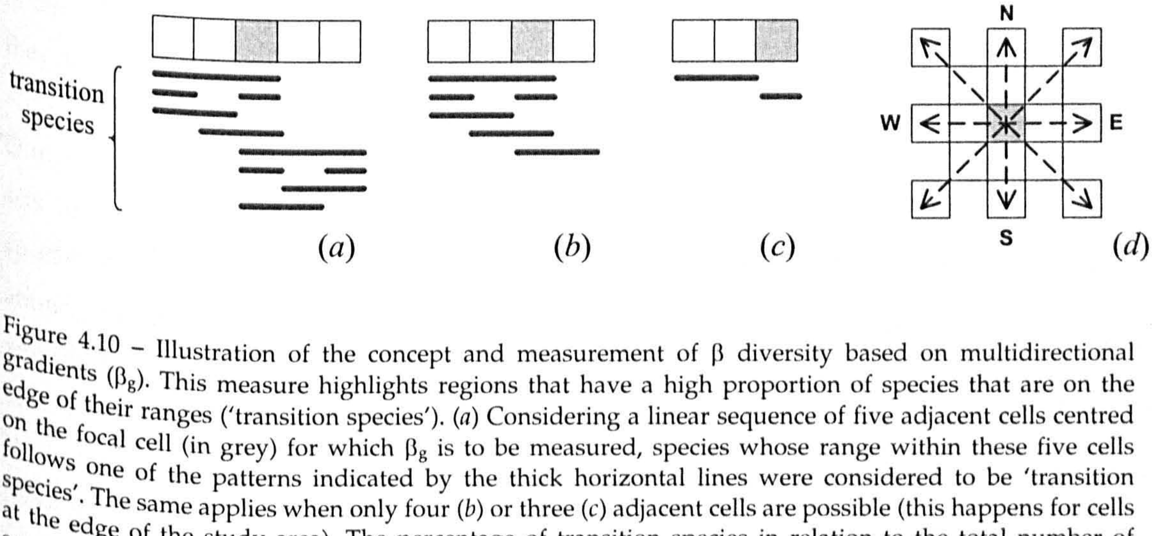

Figure 4.10 – Illustration of the concept and measurement of β diversity based on multidirectional gradients (β_g). This measure highlights regions that have a high proportion of species that are on the edge of their ranges ('transition species'). (*a*) Considering a linear sequence of five adjacent cells centred on the focal cell (in grey) for which β_g is to be measured, species whose range within these five cells follows one of the patterns indicated by the thick horizontal lines were considered to be 'transition species'. The same applies when only four (*b*) or three (*c*) adjacent cells are possible (this happens for cells at the edge of the study area). The percentage of transition species in relation to the total number of species found in the sequence of adjacent cells measures the intensity of species replacement across that direction. (*d*) The intensity of species replacement is measured across four directions (dashed arrows): West-East (horizontal), North-South (vertical), NW-SE and NE-SW (two diagonals). The final β_g value is the maximum of these values.

Overall, these results suggest a marked tendency for minimum sets for birds in South Africa and Lesotho to coincide with areas of ecological transition, an outcome that was consistent for four of the five measures of transition considered. Only for the biome heterogeneity measure was there no significant difference between minimum sets and areas chosen at random, but this is likely to be the least sensitive of the measures, since being based on seven biomes only it overlooks transition areas within biome classes.

4.3.5 Discussion

The simplicity of minimum sets as a way of representing a maximum of biodiversity features at minimum cost makes them extremely appealing for conservation planning. In practice, of course, few proponents of complementarity-based methods would argue that representing each species only once in a conservation network is a sensible planning strategy (although several published studies have actually used this simple representation target in analysing methods for the definition of priority areas for conservation; e.g., Sætersdal et al. 1993; Castro Parga et al. 1996; Howard et al. 1998; Nantel et al. 1998). Nevertheless, it has been advocated that these minimum sets can constitute a nominal core reserve network and the starting point for the development of regional conservation programs (Nicholls and Margules 1993; Margules et al. 1994*b*). However, even this approach may be inadequate if these minimum set nodes form a poor or unsuitable basis for reserves aimed at the conservation of the species that they are supposed to represent (Branch et al. 1995; van Jaarsveld 1995).

Our results for birds in South Africa and Lesotho confirm that there is a risk that minimum sets representing each species once may not be sufficient to represent adequately all the species of concern. A large to moderate fraction of species was represented by sites of lower abundance, at the periphery of their ranges, or sites that do not correspond to the preferred vegetation type. Furthermore, I found a tendency for these minimum sets to coincide with areas of ecological transition. If, as seems likely commonly to be the case, the high efficiency of minimum complementary sets is obtained by a preferential selection of transition areas, then these results may not be exclusive to this particular data set, and may translate into a more general tendency for representing species at peripheral areas within their ranges (see also Harrison and Martínez 1995). Without denying the potential importance of peripheral populations for the conservation of species (Lesica and Allendorf 1995; Channell and Lomolino 2000*a*,*b*), it may be a questionable strategy to select preferentially these areas, where species are expected to exhibit lower abundance (Maurer and Brown 1989; Lawton 1993; Brown 1995) and therefore be more vulnerable to local extinction. A reserve network built on these sites is likely to be very ineffective in ensuring the maintenance of species over time. Nevertheless, there is some evidence that areas of ecological transition (ecotones) may be important over the longer term for the maintenance of evolutionary processes (see Chapter 9).

These results do not refute the value of applying complementarity-based methods to the selection of networks of nature reserves. They are a powerful and flexible tool that allows the integration of a wide range of concerns in the simultaneous evaluation of many sites for the conservation of many species, and that can be used in much more sophisticated ways than simply looking for minimum representation sets (see Section 2.1; Rodrigues et al. 2000*c*). Indeed, methods have already been proposed that are expected to reduce the probability that sites of marginal interest in the conservation of individual species are selected, thereby increasing the long-term effectiveness of complementary sets. Examples applicable to presence/absence data include the suggestion by Branch et al. (1995) that all marginal locality records be excluded from the database, and Nicholls' (1998) proposal to alter selection algorithms to select preferentially grid cells from the core of species' spatial distributions. Williams (1998*b*) went further and suggested the use of probability models based on environmental variables to seek 'viability centres' within the niche space of each species, followed by the exclusion of areas below a threshold probability of occurrence. Finally, the results in Section 4.2 (Rodrigues et al. 2000*a*) suggested that if data were available on the presence/absence of species over time, then sites where species had higher persistence rates in the past should be targeted. When data on the relative abundance of a species across its range are available, records may be pre-filtered to exclude those corresponding to populations that are unlikely to be viable. Kershaw et al. (1994), for example, included in their analysis only the species occurring in substantial populations in each site, while Turpie (1995) considered species to be present only at the three sites where they were most abundant or those with at least 10% of the total population. The results in Section 4.1 (Rodrigues et al. 2000*b*) suggested targeting higher density sites within each species' range.

On the other hand, seeking multiple representations of each species within the reserve network (e.g., Rebelo and Siegfried 1992; Williams et al. 1996*a*) is unlikely to be a very effective strategy for reducing the probability that sites of marginal conservation value are included. Although this procedure is expected to decrease the extinction probability of species in the network (the higher the number of sites at which a species is represented, the lower the probability that it will go extinct from all of them; see Section 4.2), it is likely to maintain the tendency for the selection of sites in areas of ecological transition. Indeed, using the data for birds in South Africa and Lesotho I found similar results for complementary sets that represent each species twice as for those based on a single representation: for all measures reflecting ecological transition, except for biome heterogeneity, the mean value for the 30 complementary sets always fell within the 5% upper tail of a random distribution of means.

Reserve networks obtained by methods that take viability concerns into account are expected to be significantly more costly than those obtained by minimum representation sets (see Sections 4.1 and 4.2; Nicholls 1998; Rodrigues et al. 2000*a*,*b*). Nonetheless, they should be preferred to the latter, as they are likely to perform considerably better in achieving long-term conservation, the reason for the designation of reserves in the first place.

5 Beyond species: representing evolutionary history

Most studies on complementary reserve selection aim at maximising species diversity as a surrogate for the broader biological diversity that ought to be protected. However, species have different value in terms of their evolutionary history, depending on whether they are more or less closely related to any other living ones. Phylogenetic diversity (PD) is a biodiversity measure that takes account of phylogenetic relationships (hence evolutionary history) between taxa. It may therefore provide a better currency for conservation evaluation than taxonomic richness. This chapter illustrates how optimisation tools can be used to maximise PD in the context of complementary reserve selection. A case study using data on bird genera in northwest South Africa is then used to compare the results obtained in the selection of complementary networks maximising for taxonomic richness and for phylogenetic diversity, in order to test the adequacy of the former measure of biodiversity as a surrogate for the latter.

5.1 Maximising phylogenetic diversity in the selection of networks of conservation areas

5.1.1 Introduction

The most effective way of preserving biodiversity is by maintaining self-sustaining populations of native species in their natural ecosystems. This often requires the designation of "nature reserves", areas where conservation of biodiversity is a priority over other forms of land use. However, because maintaining the integrity of these areas often imposes restrictions to other economically and/or socially important human activities, there will always be limitations to the total amount of land that can be set aside for conservation purposes (Vane-Wright et al. 1991).

Methods for the selection of reserve networks based on the complementarity principle (Vane-Wright et al. 1991) have been proposed as a response to these concerns. They look for sets of sites which are highly complementary, in order to improve the efficiency of reserve selection (Pressey and Nicholls 1989*a*) by maximising the overall amount of biodiversity that can be preserved with the existing limited resources. Most commonly, published studies applying these methods aim at maximising species diversity as a surrogate for the broader biological diversity that ought to be protected (e.g., Williams et al. 1996*a*; Howard et al. 1998; Rodrigues et al. 2000*a*). However, species richness may not be an ideal measure of biodiversity, as it assumes that all species have *a priori* the same value as conservation units (May 1990; Vane-Wright et al. 1991; Faith 1992). Indeed, the extinction of species not closely related to any other living ones (such as the tuataras and the *Welwitshia*) would represent a disproportionate loss of evolutionary history and genetic diversity, much greater than the extinction of other individual species which have many close relatives (such as species of grass snake and *Taraxacum*; May 1990; Vane-Wright et al. 1991). Those taxonomically distinct species, and the places where they occur, should therefore be given priority in the allocation of conservation resources. This can be achieved if, instead of species richness, a currency of biological diversity which takes the phylogenetic relationship between species (hence evolutionary history) into account (taxonomic distinctness, May 1990, Vane-Wright et al. 1991, Humphries et al. 1991; phylogenetic diversity, Faith 1992, 1994, Polasky et al. 2001*b*; or character diversity, Williams et al. 1994; Hacker et al. 1998) is maximised in the selection of networks of reserves.

Unfortunately, data on the phylogenetic relationships between species are often scarce and very incomplete, hindering the possibility of their widespread application to reserve planning (Polasky et al. 2001*b*). In this case, it is pertinent to ask if the results of analyses using such data where they are available are significantly different from those obtained using simple species richness (see also Williams and Humphries 1996).

In a recent issue of *Biological Conservation*, Polasky et al. (2001*b*) have used data on the distribution of 167 bird genera in North America, for which the phylogenetic tree was known, to address this question. Phylogenetic relationships between genera, rather than species, were used because interspecific distances within genera were not available for most species. Their purpose was therefore to determine if generic diversity is an adequate surrogate of phylogenetic diversity (PD). They measured the PD of a given set of genera as the branch length of the phylogenetic tree that includes only those genera. Using heuristic iterative algorithms, they found a set of sites that maximises PD and a set that maximises genus diversity. The use of optimisation algorithms to solve the same problems was rejected because of concern about computational difficulties. The study found that the sets of sites obtained when maximum genus richness or maximum PD were represented followed a very similar spatial pattern, and that the pattern of increase of the two measures of diversity with increasing number of sites was also similar. Based on these two observations, the authors concluded that taxonomic richness is likely to be a good proxy for phylogenetic diversity for the purpose of choosing reserve sites.

This section has three purposes:

1) To challenge the notions that optimisation tools are too complex, that they cannot be used for solving this type of reserve selection problem, and that heuristic algorithms provide nearly as good results (a widespread belief after the papers by Csuti et al. 1997; Pressey et al. 1996*b*; 1997).

2) To demonstrate that the interpretation of their results made by Polasky et al. (2001*b*) is partially incorrect, in that the spatial overlap between the sets of sites obtained when maximising genus diversity and PD cannot be used as evidence that the first measure is a good surrogate for the second.

3) To report the results of a new analysis addressing the question of whether taxonomic diversity (here, genus diversity) is a good surrogate for phylogenetic diversity in the selection of complementary networks of priority areas for conservation.

5.1.2 How to maximise phylogenetic diversity – an illustrative example

Measuring phylogenetic diversity

Consider the phylogenetic tree for six hypothetical genera (g1 to g6) represented in Figure 5.1*a*. The phylogenetic diversity (PD) of a group of taxa has been defined as the branch length of the phylogenetic tree which includes only those taxa (Faith 1994; Polasky et al. 2001*b*; Figure 5.1*b*). It is not clear in this definition what happens to basal branches that are common to all the taxa considered. In the original definition of PD (Faith 1992) and in several subsequent studies (e.g., Faith 1994; Williams et al. 1994; Polasky et al. 2001*b*) the option followed was not to consider them in the calculation of PD (Figure 5.1*c*; PD defined as the length of the minimum spanning path). Here, I decided to include them (Figure 5.1*d*,*e*), which confers important advantages (see below). The rationale for this decision was that each branch in the phylogenetic tree refers to the accumulation of features or characters over a given evolutionary period; therefore, it is logical to consider as part of the PD of a group of taxa also those features which they have in common, represented by the correspondent basal branches. That is, the amount of evolutionary history accumulated by one particular taxon includes also the fraction of that history that it has in common with its relatives. Otherwise, a set consisting of one genus only (as in Figure 5.1*e*), would have the rather counter-intuitive zero phylogenetic diversity. Note that the purpose here is to measure the PD contained in a set of taxa, not to make comparisons about their relative PD. In my definition of PD, all taxa considered in isolation have the same PD (in this case, PD = 7; Figure 5.1*e*) and therefore all sites containing only one genus are *a priori* equivalent in terms of conservation priorities. Differences only arise when sets of sites with different generic composition are considered.

Including the basal branches in the calculation of PD agrees with the procedure adopted by several previous studies which analysed the amount of PD lost when a given number of taxa goes extinct (e.g., Nee and May 1997; Heard and Mooers 2000). In the phylogenetic tree represented in Figure 5.1*a*, for example, the total PD lost when genera g5 and g6 disappear is B+I+J. This would be higher than the total PD contained in both genera under the definition that excludes the basal branches. In the measure that includes these branches, the PD lost when a set of genera disappears corresponds to the part of the tree that is unique to those taxa and is always ≤ their total PD.

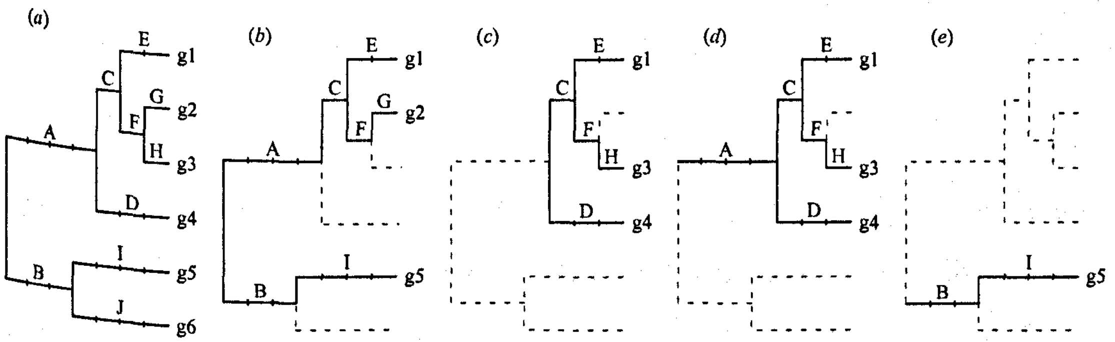

Figure 5.1 – Phylogenetic tree for six hypothetical genera (g1 to g6). The phylogenetic diversity (PD) of a group of taxa is the branch length of the phylogenetic tree which includes only those taxa. The length of each branch (A to J) is given by the number of intervals represented (for example, G has length 1; A has length 4). (a) Tree for all taxa; PD = 24. (b) Sub-tree for taxa g1, g2 and g5; PD = 16. (c) Sub-tree for taxa g1, g3 and g4, excluding the basal branch A; PD = 8. (d) Sub-tree for taxa g1, g3 and g4, including the basal branch A; PD = 12. (e) Sub-tree for taxa g5, including the basal branches; PD = 7. See text for details.

A potential problem with this definition of PD is where to draw the limits of the phylogenetic tree, which, in principle, could go back to the origin of life. In practice, it makes no difference if the calculation of PD is based on the tree for only the set of taxa being analysed (say, species within class Aves), or on an expanded tree relating these to other taxonomic groups (say, subphylum Vertebrata, phylum Chordata,...). Expanding the phylogenetic tree would result in a common set of additional branches being added to all taxa. This would increase the values of PD in each cell (the equivalent to the total length of that common set of branches), but not the results of reserve selection, because those branches would be present in all cells. The sensible option in reserve selection is therefore to calculate PD based on a phylogenetic tree of only those taxa that were considered in the analysis.

In practice, the difference between the two ways of measuring PD did not affect the results obtained in this study (see below), and it is most unlikely to affect any result of complementary reserve selection aimed at maximising PD. This is because, in order to maximise PD for any phylogenetic tree, it is necessary to select at least two of the most distinct taxa (i.e., to include the most basal node of the tree; see Nee and May 1997). In the tree represented in Figure 5.1, this would mean selecting at least one genus from g1, g2, g3 and g4, and another one from g5 and g6, requiring the inclusion of branches A and B regardless of the type of PD measure applied. However, including the basal branches in the phylogenetic tree brings considerable computational advantages for calculating the PD of a set of taxa or of a set of sites (Figure 5.2 illustrates how this can be done using simple linear algebra), allowing the use of integer linear programming to obtain optimal solutions to reserve selection problems.

Maximising phylogenetic diversity in reserve selection

The solution to the problem of obtaining the minimum set such that the maximum PD is represented (equivalent to requiring that all branches are represented) can be obtained by solving the following set covering problem (see Section 2.1; Underhill 1994; Rodrigues et al. 2000*c*):

$$\text{Minimise } \sum_{j=1}^{n} x_j \qquad \text{(I)}$$

$$\text{Subject to } \sum_{j=1}^{n} a_{ij} x_j \geq 1, \qquad i = 1, 2, \ldots, m \qquad \text{(II)}$$

$$x_j \in \{0,1\} \qquad j = 1, 2, \ldots, n \qquad \text{(III)}$$

where n is the number of sites, m is the number of branches, a_{ij} is one if branch i is present in site j and zero otherwise (i corresponds to the rows and j to the columns in matrix $\mathbf{BS}_{0/1}$, Figure 5.2), and variable x_j is one if and only if site j is selected. The objective function (I) is to minimise the number of sites selected. Inequalities (II) ensure that each of the m branches must be represented at least once. The integrality restrictions (III) state that each site j is an indivisible unit (see Section 2.1, Rodrigues et al. 2000*c*).

The solution to the problem of minimising the number of sites such that all genera are covered is represented in exactly the same way, but now m is the number of genera and a_{ij} is one if genus i is present in site j and zero otherwise (i corresponds to the rows and j to the columns in matrix **GS**, Figure 5.1).

(*a*)

$$\mathbf{BG} = \left[\begin{array}{c|cccccc} & g1 & g2 & g3 & g4 & g5 & g6 \\ \hline A & 1 & 1 & 1 & 1 & 0 & 0 \\ B & 0 & 0 & 0 & 0 & 1 & 1 \\ C & 1 & 1 & 1 & 0 & 0 & 0 \\ D & 0 & 0 & 0 & 1 & 0 & 0 \\ E & 1 & 0 & 0 & 0 & 0 & 0 \\ F & 0 & 1 & 1 & 0 & 0 & 0 \\ G & 0 & 1 & 0 & 0 & 0 & 0 \\ H & 0 & 0 & 1 & 0 & 0 & 0 \\ I & 0 & 0 & 0 & 0 & 1 & 0 \\ J & 0 & 0 & 0 & 0 & 0 & 1 \end{array}\right] \quad \mathbf{l} = \left[\begin{array}{c|c} A & 4 \\ B & 3 \\ C & 1 \\ D & 3 \\ E & 2 \\ F & 1 \\ G & 1 \\ H & 1 \\ I & 4 \\ J & 4 \end{array}\right] \quad \mathbf{GS} = \left[\begin{array}{c|cccc} & s1 & s2 & s3 & s4 \\ \hline g1 & 1 & 1 & 1 & 0 \\ g2 & 1 & 0 & 0 & 1 \\ g3 & 1 & 0 & 0 & 1 \\ g4 & 1 & 0 & 1 & 0 \\ g5 & 0 & 0 & 1 & 0 \\ g6 & 0 & 1 & 0 & 1 \end{array}\right]$$

$$\mathbf{BS} = \left[\begin{array}{c|cccc} & s1 & s2 & s3 & s4 \\ \hline A & 4 & 1 & 2 & 2 \\ B & 0 & 1 & 1 & 1 \\ C & 3 & 1 & 1 & 2 \\ D & 1 & 0 & 1 & 0 \\ E & 1 & 1 & 1 & 0 \\ F & 2 & 0 & 0 & 2 \\ G & 1 & 0 & 0 & 1 \\ H & 1 & 0 & 0 & 1 \\ I & 0 & 0 & 1 & 0 \\ J & 0 & 1 & 0 & 1 \end{array}\right] \quad \mathbf{BS}_{0/1} = \left[\begin{array}{c|cccc} & s1 & s2 & s3 & s4 \\ \hline A & 1 & 1 & 1 & 1 \\ B & 0 & 1 & 1 & 1 \\ C & 1 & 1 & 1 & 0 \\ D & 1 & 0 & 1 & 0 \\ E & 1 & 1 & 1 & 0 \\ F & 1 & 0 & 0 & 1 \\ G & 1 & 0 & 0 & 1 \\ H & 1 & 0 & 0 & 1 \\ I & 0 & 0 & 1 & 0 \\ J & 0 & 1 & 0 & 1 \end{array}\right]$$

(*b*)

$$\mathbf{subBG} = \left[\begin{array}{c|ccc} & g1 & g2 & g5 \\ \hline A & 1 & 1 & 0 \\ B & 0 & 0 & 1 \\ C & 1 & 1 & 0 \\ D & 0 & 0 & 0 \\ E & 1 & 0 & 0 \\ F & 0 & 1 & 0 \\ G & 0 & 1 & 0 \\ H & 0 & 0 & 0 \\ I & 0 & 0 & 1 \\ J & 0 & 0 & 0 \end{array}\right] \quad \mathbf{a} = \left[\begin{array}{c|c} A & 2 \\ B & 1 \\ C & 2 \\ D & 0 \\ E & 1 \\ F & 1 \\ G & 1 \\ H & 0 \\ I & 1 \\ J & 0 \end{array}\right] \quad \mathbf{a}_{0/1} = \left[\begin{array}{c|c} A & 1 \\ B & 1 \\ C & 1 \\ D & 0 \\ E & 1 \\ F & 1 \\ G & 1 \\ H & 0 \\ I & 1 \\ J & 0 \end{array}\right]$$

$$\mathrm{PD} = \mathbf{a}_{0/1}{}^{\mathrm{T}} . \mathbf{l} = \begin{bmatrix} 1 & 1 & 1 & 0 & 1 & 1 & 1 & 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} 4 \\ 3 \\ 1 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \\ 4 \\ 4 \end{bmatrix} = 16$$

(*c*)

$$\mathbf{subBS} = \left[\begin{array}{c|cc} & s1 & s4 \\ \hline A & 1 & 1 \\ B & 0 & 1 \\ C & 1 & 0 \\ D & 1 & 0 \\ E & 1 & 0 \\ F & 1 & 1 \\ G & 1 & 1 \\ H & 1 & 1 \\ I & 0 & 0 \\ J & 0 & 1 \end{array}\right] \quad \mathbf{b} = \left[\begin{array}{c|c} A & 2 \\ B & 1 \\ C & 1 \\ D & 1 \\ E & 1 \\ F & 2 \\ G & 2 \\ H & 2 \\ I & 0 \\ J & 1 \end{array}\right] \quad \mathbf{b}_{0/1} = \left[\begin{array}{c|c} A & 1 \\ B & 1 \\ C & 1 \\ D & 1 \\ E & 1 \\ F & 1 \\ G & 1 \\ H & 1 \\ I & 0 \\ J & 1 \end{array}\right]$$

$$\mathrm{PD} = \mathbf{b}_{0/1}{}^{\mathrm{T}} . \mathbf{l} = \begin{bmatrix} 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 0 & 1 \end{bmatrix} \begin{bmatrix} 4 \\ 3 \\ 1 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \\ 4 \\ 4 \end{bmatrix} = 20$$

Figure 5.2 – Measuring phylogenetic distance (PD) for a data set. (*a*) Data matrices for the phylogenetic tree represented in Figure 5.1*a*. Matrix **BG** corresponds to the distribution of branches (A to J) in each genus (g1 to g6). Vector **l** corresponds to the length of each branch. Together, **BG** and **l** have *all* the information of the phylogenetic tree represented in Figure 5.1*a*. Matrix **GS** represents the distribution of each genus in each of four sites considered (s1 to s4). The product of matrix **BG** (dimensions 10 × 6) by matrix **GS** (6 × 4) results in matrix **BS** (10 × 4), which indicates the number of times each branch is represented in each site. Converting this to a 0/1 matrix, matrix $\mathbf{BS}_{0/1}$ is obtained, providing the distribution of each branch in each site. (*b*) Computation of PD for a set of genera. Matrix **subBG** corresponds to a submatrix of **BG** considering only genera g1, g2 and g5 (as in Figure 5.1*b*). Vector **a** is the sum of the columns of **subBG**; converted into the 0/1 $\mathbf{a}_{0/1}$ vector, this indicates which branches are present in the tree which includes only these genera (Figure 5.1*b*). PD for the three genera is then given by the multiplication of the transposed vector $\mathbf{a}_{0/1}{}^{\mathrm{T}}$ by the vector **l**. (*c*) Computation of PD for a set of sites. Matrix **subBS** corresponds to a submatrix of **BS** considering only sites s1 and s4. Vector **b** is the sum of the columns of **subBS**, subsequently converted into the 0/1 $\mathbf{b}_{0/1}$ vector. PD for the two sites is then given by the multiplication of the transposed vector $\mathbf{b}_{0/1}{}^{\mathrm{T}}$ by the vector **l**. This is equivalent to calculating the PD for the taxa present in sites s1 and s2 (all genera except g5). This way of measuring PD can be applied if, instead of a phylogenetic tree, the relationships between taxa are represented by a cladogram of features or characters (e.g., Faith 1992; Williams and Humphries 1996). In that case, matrix **BG** would represent the distribution of features/characters in each taxon, and vector **l** would be a column of 1's (unless different characters were given different weights).

For the data matrices represented in Figure 5.2, the optimal solution for both problems is to select sites s3 and s4. It is not a coincidence that the same result is found in both cases. Because the maximum PD (in this case, equal to 24) can only be obtained by representing all of the branches, and because all taxa have one unique branch, the maximum PD is only obtained by having all the genera represented. Consequently, the problem of representing the maximum PD in the minimum number of sites is equivalent to the problem of representing all genera in the minimum number of sites. It would therefore be expected that Polasky et al. (2001*b*) should obtain the same result when prioritising for PD or for the diversity of genera (Figure 5 in Polasky et al. 2001*b*).

What may be surprising is that Polasky et al. (2001*b*) did not obtain *exactly* the same results to the problems of obtaining the minimum sets that maximise PD or cover all genera. There are two explanations. First, most set-covering problems have a diversity of equally optimal solutions (see below). The results presented in the two maps in Figure 5 of Polasky et al. (2001*b*), presented as solutions respectively to each of the two problems, are therefore two of the possible solutions to the same problem. Second, the problems were not solved optimally, and this, as the authors acknowledge, explains why sets of different sizes were found (15 areas in one case, 16 in the other). The use of sub-optimal algorithms has been justified by arguing that "optimisation algorithms can present computational difficulties" and that "in particular, it is difficult to solve optimisation algorithms when the objective is to maximise a diversity measure based on the branch lengths of the phylogenetic tree for species represented in the set of chosen sites" (Polasky et al. 2001*b*). Here, I have demonstrated that the problem of representing the maximum PD is also a set-covering problem, and that it can be solved as easily as the problem of representing maximum taxonomic richness.

Finding that the solutions to the problems of representing the maximum PD and all genera are similar or identical is not sufficient evidence that taxon diversity is a good surrogate for PD. What needs to be investigated is what happens when there are limited resources and not all genera can be represented. The analysis in Figure 5 of Polasky et al. (2001*b*) indicates little agreement in the order in which sites were selected in each case. However, more important than establishing if the geographical location of the sites is the same, is to assess how well sets of sites selected to maximise genus richness perform in terms of representing PD, when it is not possible to select a sufficient number of sites to represent all genera or the maximum PD. In Polasky et al. (2001*b*), this corresponds to comparing the curves for the accumulation of PD when prioritising for genus diversity (their Figure 3) and when prioritising for PD (their

Figure 2). The similarity of these two curves is the best indication given in this study that generic diversity performs quite well in representing PD.

The problem of maximising the PD in a given set of sites can be formulated as the maximal covering location problem (MCLP, Church *et. al.* 1996):

$$\text{Maximise } \sum_{i=1}^{m} l_i y_i \qquad \text{(IV)}$$

Subject to

$$\sum_{j=1}^{n} a_{ij} x_j \geq y_i, \qquad i = 1, 2, \ldots, m \qquad \text{(V)}$$

$$\sum_{j=1}^{n} x_j \leq k, \qquad \text{(VI)}$$

$$x_j \in \{0,1\} \qquad j = 1, 2, \ldots, n \qquad \text{(III)}$$

$$y_i \in \{0,1\} \qquad i = 1, 2, \ldots, m \qquad \text{(VII)}$$

where l_i is the length of branch i, y_i is one if branch i is covered and zero otherwise, k is the maximum number of sites that can be represented and all the other variables are as before.

The objective function (IV) maximises the total PD (sum of the length of all branches represented). Each one of the restrictions (V) indicates that the branch i cannot be counted as preserved if none of the sites where it exists is selected. Restriction (VI) ensures that the total number of sites does not exceeds k. Restrictions (III) and (VII) state that both sites and branches are indivisible units.

The problem of representing the maximum number of genera in k sites can be formulated in an equivalent way, but replacing the objective function by:

$$\text{Maximise } \sum_{i=1}^{m} y_i \qquad \text{(VIII)}$$

where y_i refers to genus i; a_{ij} (in restrictions V) is now one if genus i is present in site j and zero otherwise.

These two problems represent two different ways of maximising biodiversity in a given set of sites: in the first, the unit of biodiversity is one unit of branch length, each one considered to have the same value; in the second one, the biodiversity units are the number of genera, all genera considered to be of equal value.

Unlike the set-covering problem, there is no reason why the results for these two MCLP should be the same (for *k* less than the minimum number of sites needed to represent all genera or all branches). For example, for the data represented in Figure 5.2, the results of maximising PD in one site (site s3; PD = 17, no. of genera = 3) are different from those of maximising number of genera (site s1; no. of genera = 4, PD = 13). It may therefore happen that, for limited resources, maximising taxon diversity does not provide an adequate surrogate for maximising PD. I used a data set on the distribution of birds in South Africa to explore this further. These data are used here as an exemplary set and, therefore, these results should not be interpreted as an attempt to propose a new reserve network in South Africa.

5.1.3 Application to the birds of South Africa

The Southern African Bird Atlas Project (SABAP; Harrison et al. 1997) has provided the most comprehensive information currently available on the distribution of birds in southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana (for a detailed description of the methods used in the SABAP, see Harrison et al. 1997). In this study, I used the presence/absence data for 166 genera in the South African provinces of Gauteng, Mpumalanga and Northern Province (319 quarter-degree grid cells). As in Polasky et al. (2001*b*), I used data on the phylogenetic relationships between genera, rather than species, because data on the interspecific distances within each genus were not available for most species. The taxonomy of each genus followed Sibley and Monroe (1990) and was not always coincident with the one used in Harrison et al. (1997).

As in Polasky et al. (2001*b*), the phylogenetic relationships between genera were obtained from the phylogenetic tree published by Sibley and Ahlquist (1990; pp. 838-870), who obtained phylogenetic distances between genera by average linkage (UPGMA) clustering of DNA-DNA hybridisation distances ($\Delta T_{50}H$). The phylogenetic tree for this data set had 326 branches and a total PD = 1582.1 $\Delta T_{50}H$. The 166 genera analysed covered 73% of the total of 589 species found in the study area.

The minimum set found to be needed to represent all genera or maximum PD had seven sites. This problem had several optimal solutions, and 10 of these (selected randomly and without replacement from the set of optimal solutions – see Section 2.1, Rodrigues et al. 2000*c*; and Section 4.3, Gaston et al. 2001) were obtained. By mapping them (Figure 5.3), I found that some particular sites tend to be selected more often (Figure 5.3*a*) but that different solutions may look quite distinct in terms of the spatial location of particular sites (Figure 5.3*b*,*c*).

Solving the corresponding MCLPs, sets of sites were obtained which represent the maximum number of genera or the maximum PD within a number of sites $k \leq 7$. Most of these problems had more than one equally optimal solution. In that case, 10 solutions or the total number of existing ones, if ≤ 10, were obtained. The average PD and average number of genera across all replicates were calculated in each case.

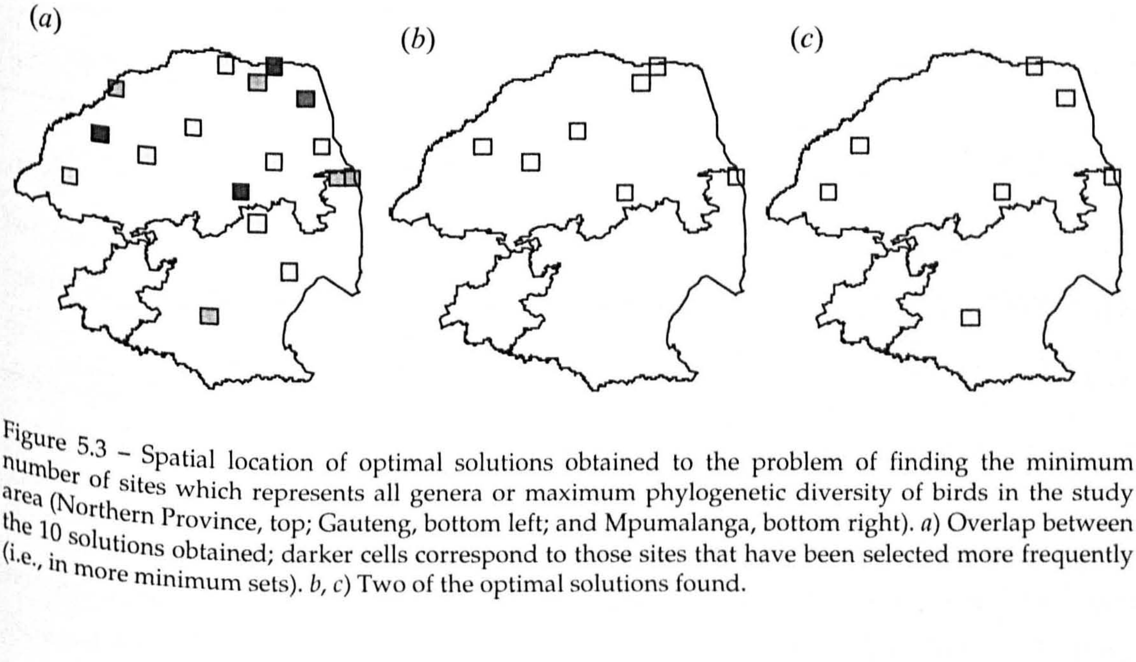

Figure 5.3 – Spatial location of optimal solutions obtained to the problem of finding the minimum number of sites which represents all genera or maximum phylogenetic diversity of birds in the study area (Northern Province, top; Gauteng, bottom left; and Mpumalanga, bottom right). *a*) Overlap between the 10 solutions obtained; darker cells correspond to those sites that have been selected more frequently (i.e., in more minimum sets). *b*, *c*) Two of the optimal solutions found.

I found that the solutions obtained by maximising the number of genera represented in a given set of sites $k \leq 7$ are very similar to the ones obtained by maximising the PD in the same number of sites (Table 5.I). More specifically, I found that when maximising for PD, the optimal solutions obtained were always optimal solutions to the problem of maximising the number of genera in the same number of sites. And that when maximising for number of genera, some of the optimal solutions found were also optimal solutions to the problem of maximising PD or else they had a value of PD very close to the one obtained by maximising PD in the same number of sites.

Table 5.I – Results of maximal covering location problems (MCLP) maximising the number of genera and maximising the phylogenetic diversity (PD) that can be represented in a given number of sites (between one and seven). For each problem, the average number of genera, the average PD and the number of optimal solutions found are presented.

No. of sites	Maximise for No. genera			Maximise for PD		
	Average No. genera	Average PD	No. of solutions	Average No. genera	Average PD	No. of solutions
1	142	1413.6	1	142	1413.6	1
2	158	1541.25	2	158	1542.5	1
3	161	1555.82	6	161	1558.4	2
4	163	1568.6	≥ 10	163	1568.6	≥ 10
5	164	1571.3	≥ 10	164	1575.4	≥ 10
6	165	1577.26	≥ 10	165	1579.4	≥ 10
7	166	1582.1	≥ 10	166	1582.1	≥ 10

For comparative purposes, I also obtained near-minimum sets representing all genera and maximum PD using the greedy heuristic algorithms described by Polasky et al. (2001*b*). The near-minimum number of sites needed to represent all genera was eight and the near-minimum number of sites needed to represent maximum PD was nine. These correspond to an extra cost of 14% and 29% in relation to the minimum set of seven sites.

As expected, these results have not been affected by the measure of PD applied, as the first site selected in any case (both in the optimisation and the heuristic approaches) was one which included the basal branches of the phylogenetic tree (i.e., a site which had members of both the Eoaves and Neoaves Infraclasses).

5.1.4 Discussion

This study illustrates how reserve selection problems aiming at maximising phylogenetic diversity can be formally represented and solved optimally as integer linear programming problems. Using the C-Plex software (ILOG 1999) on a Pentium II PC (128 MB RAM), all the problems presented in this analysis were solved in less than three seconds. Indeed, my experience in previous studies using other data sets indicates that large set-covering problems can be solved very quickly (for example, the problem of finding the minimum set representing 651 bird species in 1858 grid cells in South Africa is solved in 2.2 seconds; see also Table 2.III in Section 2.2; Rodrigues and Gaston 2002*b*). On the other hand, using greedy heuristic algorithms gives no guarantee that an optimal solution can be obtained. Although the one or two additional sites selected in the present case may seem negligible in terms of the efficiency of the algorithms, the additional 14% and 29% costs in reserve acquisition would be highly significant if this was an application to a real life problem with a limited budget. This illustrates the point that, contrary to widespread belief (e.g., Pressey et al. 1996*b*, 1997; Csuti et al. 1997; Howard et al. 1998; Williams 1998*b*; Polasky et al. 2001*b*), these heuristic approaches do not necessarily provide solutions which are optimal or only slightly sub-optimal (see also Table 2.I in Section 2.1; Rodrigues et al. 2000*c*).

Perhaps more important than the optimality of the solution obtained, the main advantage of using optimisation tools is the flexibility of situations that can be represented and solved as linear integer programming problems (see Section 2.1, Rodrigues et al. 2000*c*). As measured in this study, PD is just another possible currency of biodiversity, which (as long as the phylogenetic data are available) can easily be integrated in a diversity of problems and situations. For example, an MCLP problem aiming at maximising PD in *k* sites, may be subjected to a diversity of additional restrictions, such as: that at least 25% of those *k* sites selected need to be owned by the State; that a given species *i* needs to be reserved in at least 50 % of its range; or that the set of sites selected must have a human population < 1,000,000. The possibilities are numerous, and can be solved exactly if stated as integer problems. However, it would not be obvious how to formulate an "intuitive" heuristic which could satisfactorily solve these more complex problems.

Complementarity-based reserve selection problems typically have several optimal solutions (e.g., Arthur et al. 1997; Csuti et al. 1997; Williams et al. 2000*a*; Gaston et al. 2001; see also Table 5.I), and these may look quite distinct in terms of the spatial position of individual sites (Figure 5.3). This is why the comparison between results to the problems of maximising PD or the number of genera cannot rely on the spatial overlap between solutions (as in Polasky et al. 2001*b*) and should instead be made in terms of their relative performance in diversity (PD or genera) representation (Table 5.I). This is also true of other comparative reserve selection analyses, and studies which based their conclusions on the analysis of spatial overlap between solutions may need revision (e.g., Lombard 1995; Freitag and van Jaarsveld 1998; van Jaarsveld et al. 1998; Erasmus et al. 1999; see also Reyers and van Jaarsveld 2000).

When evaluated in terms of the effectiveness in maximising the PD of those areas selected to maximise generic richness (Table 5.I), the results for birds in South Africa support the assertion by Polasky et al. (2001*b*) that taxon diversity may be a good surrogate for phylogenetic diversity. This is likely to be the result of a highly significant positive relationship between the values of both measures of diversity in each site (Figure 5.4), a result which agrees with previous findings (Williams and Humphries 1996; Hacker et al. 1998).

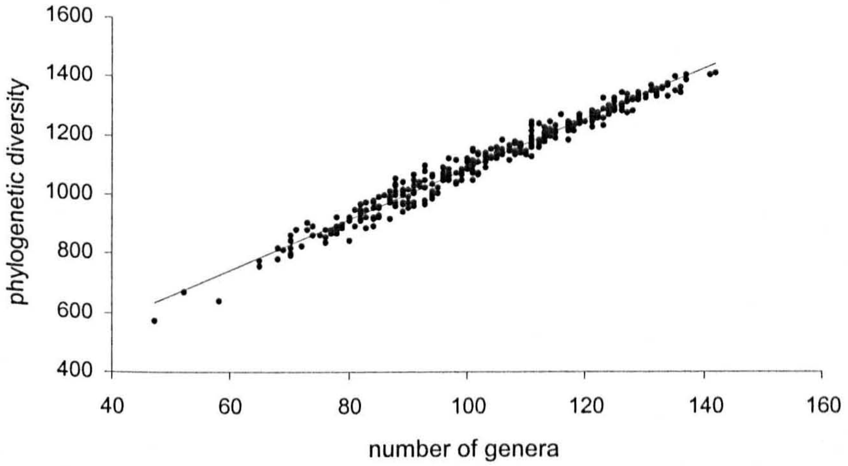

Figure 5.4 – Relationship between the number of genera and the phylogenetic diversity in each cell (r^2 = 0.97; n = 319; $p < 0.0001$).

I believe that it is likely that these findings can be generalised, and that, in practice, taxonomic richness (usually, species richness) can continue to be safely used as a surrogate for phylogenetic diversity within the same taxonomic group. However, it may be instructive to consider those situations in which this may not be the case: if the phylogenetic tree is highly unbalanced, with some of the branches being very ramified while others correspond to monophyletic taxa, *and* if there is a spatial segregation between the sites where these two types of branches occur. In this case, it is possible that reserve selection based on taxonomic richness tends to select sites with many closely related species while selection based on PD will tend to select sites with monophyletic taxa. This is what happens in the example represented in Figure 5.1 and Figure 5.2: site s1 is the richest in taxa, but its four genera are taxonomically close; site s2 has only two genera, but these are taxonomically quite distinct, and therefore s2 has higher PD than s1 (14 instead of 13). In this example, the relationship between number of genera and PD at each site is not only very weak (R^2 = 0.057, p-value = 0.76) but it actually has also a negative slope (*b* = -0.5). A parallel situation may occur in practice if the study area includes sites with very marked differences in taxonomic structure (Gaston 2000). Insular biotas, for example, such as isolated islands and lakes, may have suffered evolutionary radiations which resulted in the separate evolution of particular branches of the phylogenetic tree, for example, the radiation of Lemurs in Madagascar. It may also be the case with the bumble bees of the sibiricus-group used in WORLDMAP (2000), which have a higher species richness in South America and a higher PD in Asia. This effect is likely to be more noticeable at the species, rather than at the generic, level.

6 Conservation planning across geopolitical units

Conservation planning is usually made within geopolitical units which tend to encompass only part of the geographic range of most species. Consequently, the relative rarity of a species within the study area considered does not necessarily reflect its relative global rarity or its conservation relevance. However, complementarity methods make no distinction between "true" (narrow endemics) and "apparent" rarities (e.g., vagrants), both having a disproportionate influence on the results. This chapter investigates the implications of species' rarity in complementary reserve selection across geopolitical boundaries, based on data on the distribution of birds in southern Africa.

6.1 Rarity and conservation planning across geopolitical units

6.1.1 Introduction

Complementarity-based methods are receiving increasing support as tools for conservation planning (e.g., Pressey et al. 1993; Dobson et al. 1997; Howard et al. 1998; Margules and Pressey 2000). Acknowledging that resources available for conservation purposes are limited, these methods aim at a high efficiency (sensu Pressey and Nicholls 1989*a*) in the representation of biodiversity at the minimum cost (usually, in the minimum area) by identifying sets of sites that are complementary in terms of their biological composition.

The essential purpose of complementarity-based methods is to ensure that each one of the species (or other features) considered is represented in the selected reserve network by at least some predefined number of occurrences. But species do not all have the same influence on the results (Willis et al. 1996; Pressey et al. 1999; Ferrier et al. 2000). At one extreme, a species that occurs everywhere is neutral in terms of the sites selected (any site selected will represent it); at the other extreme, a species with a single occurrence imposes the selection of the particular site where it has been recorded (which is therefore irreplaceable in the sense that it cannot be substituted by any other site or combination of sites; Williams et al. 1996*a*; Ferrier et al. 2000). In general, the rarer the species the higher tends to be its influence on the sites selected (throughout, rarity refers to area of occupancy of range [*sensu* Gaston 1991, 1994], as inversely related to the number of sites in which a given species has been recorded).

Conservation planning is usually conducted within geopolitical units, such as nations, states and counties, because these are the units within which macroeconomic and administrative decisions are made (Hunter and Hutchinson 1994). These tend to encompass only part of the geographic range of most species, particularly in geopolitically complex regions. Consequently, the relative rarity of a species within the study area considered in a given reserve selection exercise does not necessarily reflect its relative global rarity or its conservation relevancy. Carried to the extreme, species with very restricted ranges in a data set may be of two types: "truly rare" species, such as narrow endemics, which are of major conservation concern, and species which are "apparently rare" in the study area (but common else where), such as vagrants, species very marginal to their range or introduced, which are largely irrelevant for conservation planning in a region.

Previous work has provided evidence that species' rarity has an effect on the results of complementary reserve selection exercises (e.g., Pressey and Nicholls 1989*b*; Lombard et al. 1995; Willis et al. 1996; Pressey et al. 1999). Also, it has been demonstrated that the sub-division of a study area increases the total area required for complementary representation (Pressey and Nicholls 1989*b*; Erasmus et al. 1999). In this study, I investigated the relationship between these two effects based on data on the distribution of birds in southern Africa. First, I clarify the mechanism by which restricted-range species influence the areas selected by complementarity, providing additional evidence that they have a disproportionate effect not only on the number but also on the identity of sites selected. Then, I illustrate how this affects the results of reserve planning across geopolitical boundaries. Finally, I discuss the implications of these results for reserve planning.

6.1.2 Data

The southern African Bird Atlas Project (SABAP; Harrison et al. 1997) has provided the most comprehensive information currently available on the distribution of birds in southern Africa. Data were collected mainly between 1987 and 1992 at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland, and Zimbabwe and on a half-degree grid for Botswana. Observers visiting each cell recorded the presence of identified species on checklists, breeding and non-breeding records being considered equivalent. A total of 909 species were recorded. Based on these data, reporting rates were calculated for each species in each cell as the proportion of checklists submitted for that cell on which the species was recorded (for a more detailed description of the methodology used in the SABAP, see Harrison et al. 1997). I used the SABAP data for South Africa and Lesotho (1858 grid cells), excluding marine species from the analysis (690 species were analyzed).

As with any data collected at a coarse scale by a large number of observers with a range of bird identification skills, this data set has potential problems that would have to be taken into account in any application to a real reserve planning exercise. However, the SABAP data are here used only as an exemplary data set, and the results should not be interpreted as an attempt to propose a new reserve network to South Africa and Lesotho. It is assumed that the data correspond to the "reality" of species distribution in the study area, and its limitations are not expected to have an influence on the conclusions obtained.

6.1.3 Influence of restricted-range species

To evaluate the effect of species' rarity on the sites selected by complementarity analyses, I solved consecutive maximal covering location problems (Church et al. 1996) that obtain the maximum number of species that can be represented by a given number of cells (up to 31 cells, the minimum number required to represent all 690 species in this data set). The problems were solved optimally using the *CPLEX* software (ILOG 1999).

The maximum number of species that could be represented by a given number of cells rose quickly at first with increasing number of cells and then flattened (Figure 6.1). This result implies that most species can be represented in a fraction of the 31 cells necessary to represent all species; for example, 92% of the species can be represented in only 6 cells. Thus, many of the sites selected are required to represent just a few species. Indeed, the last 15 cells were added to represent a single additional species each.

The mean range size of the species not represented by a reserve network composed of a given number of cells demonstrates that the uncovered species were progressively rarer as the number of selected cells increased (Figure 6.1). That is, the most common species were rapidly covered by the selection of just a few cells, whereas the rarest ones required the selection of additional sites. In particular, each of the last 6 cells added to the minimum set of 31 is required to represent a single species occurring in just one cell.

Fifteen irreplaceable cells (containing at least one species which occurs only there), existed in the data set, accounting for nearly half of the minimum set of 31 cells required to represent all species. Most of these were within the last sites selected, with 9 out of the last 10 cells being irreplaceable (Figure 6.1).

These results support previous findings that species' rarity has an influence on the results of complementary reserve selection (e.g., Pressey and Nicholls 1989*b*; Lombard et al. 1995; Willis et al. 1996; Pressey et al. 1999), and demonstrate that the restricted-range species (in particular, those that occur in only a few cells) have a disproportionate effect on the number and identity of the cells selected by complementarity. A significant fraction of these (many of them irreplaceable) was required because of just a few, very rare, species.

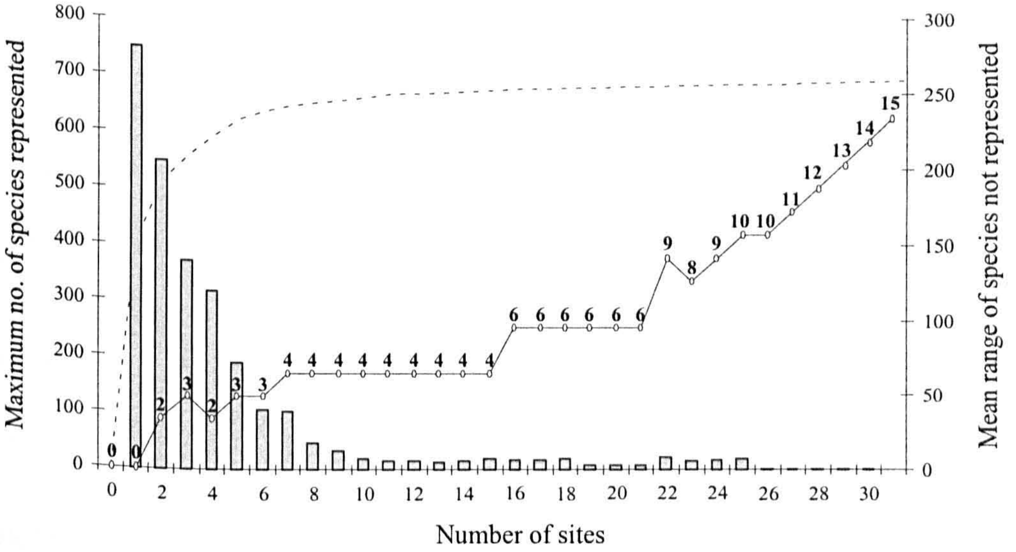

Figure 6.1 – The influence of restricted-range species on the results of complementarity-based methods for reserve selection based on data on the distribution of 690 bird species in South Africa and Lesotho. The dashed line represents the maximum number of species (left *y* axis) that can be represented in a given number of sites. Bars are the mean range size (in number of sites, right *y* axis) of the species not represented by a reserve network composed of a given number of sites (e.g., a maximum of 622 species can be represented within 5 sites, and the remaining 68 species have an average range occupying 72 grid cells). Open circles represent the number of irreplaceable sites (out of 15) selected in each case (values presented over the circles).

Not all of these restricted-range species are truly rare. Out of the 23 species that had just one presence record in South Africa and Lesotho, 17 were "apparent rarities" in the data set because they are vagrants, very marginal to their range, or have been introduced (e.g., the European Turtle Dove [*Streptopelia turtur*], the Lesser Golden Plover [*Pluvialis fulva*], the Eurasian Redstart [*Phoenichurus phoenichurus*] and the Spotted Redshank [*Tringa erythropus*]), which accounts for 10 of the 15 irreplaceable cells selected. To evaluate the effect of these non target species, I eliminated from the data set vagrant, marginal (here considering just extreme cases of species with just one occurrence in the study area and a substantial population outside of it, for example the Angola Pitta [*Pitta angolensis*]), and escaped/introduced species (39 species total). Nineteen cells (5 irreplaceable) were required to represent the 651 target species, as opposed to the 31 cells (15 irreplaceable) required to cover the initial 690 species (Figure 6.2). Removing the 39 non target species resulted therefore in a substantial improvement in the efficiency (i.e., a reduction in the area) of the reserve network. This was largely a result of the elimination of 10 out of the initial 15 irreplaceable cells from the minimum set.

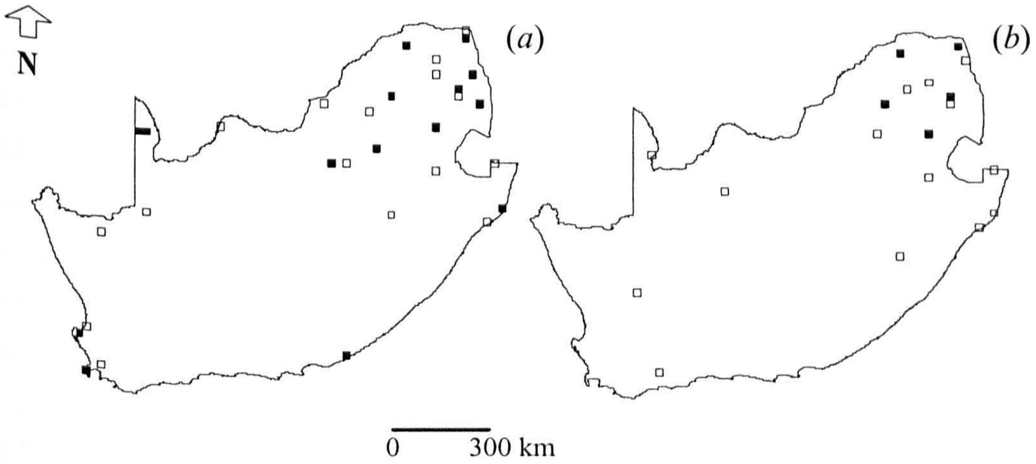

Figure 6.2 – Minimum set representing all bird species at least once in South Africa and Lesotho: (a) for all 690 species (31 sites); and (b) for target species (651 species, after excluding vagrants, marginal, and introduced species; 19 sites). Black squares are irreplaceable cells, and open squares are flexible sites.

6.1.4 Implications for reserve selection across geopolitical units

The non target species eliminated above are extreme cases. But various other levels of species' "vagrancy" or "marginality" exist, still making many species rare (and therefore highly influential in complementarity analyses) but not necessarily excludable from reserve selection analyses. Species such as the Tropical Boubou (*Laniarius aethiopicus*), the Longtailed Starling (*Lamprotornis mevesii*), and the Yellow White-Eye (*Zosterops senegalensis*) have very restricted ranges in South Africa and Lesotho (≤ 30 cells) but occur widely outside this region. From a global perspective, they could be better preserved somewhere else, and the tip of their ranges falling within South Africa would probably not be considered a priority for their conservation. But in practice conservation decisions are usually made within geopolitical units (Hunter and Hutchinson 1994; Erasmus et al. 1999).

Because of the influence of species' rarity, adding political boundaries has a profound effect on the sites selected by complementarity analyses. I tested that effect by subdividing the study area into 10 geopolitical units: Lesotho and the South African provinces of Northern Cape, Western Cape, Northwest, Free State, Eastern Cape, Northern Province, Mpumalanga, Gauteng, and KwaZulu/Natal. For each unit separately, and considering just the 651 target species, I determined the minimum number of cells required to represent each bird species at least once. These problems were solved optimally with *CPLEX* software (ILOG 1999).

The total number of cells required to represent all species occurring within each unit was 221 (Figure 6.3*a*), more than 10 times the 19 cells required when no political boundaries were considered (Figure 6.2*b*). The loss in overall efficiency (i.e., increase in the cost of the minimum set) when a region is subdivided into geopolitical units has been demonstrated before (Pressey and Nicholls 1989*b*; Erasmus et al. 1999), and it is an expected result because, for all the species whose range extends beyond more than one unit, multiple representations become required. However, this alone could only account for a maximum of a tenfold increase in the number of cells required (and only in the extreme situation of all species occurring in each one of the 10 geopolitical units, which is not the case). The loss in efficiency is also a consequence of many species that are widespread across the entire region being rare in some of the units, therefore requiring the designation of additional sites.

One first inference from the increase in the number of cells selected when geopolitical boundaries were added is that geopolitical coordination in complementary reserve selection results in a significantly higher efficiency in relation to a parochial approach, a considerable advantage if the resources available for land acquisition in the region are scarce. However, it is likely that a larger reserve network, and one where species are represented multiple times, is more effective in maintaining species over time (see Section 4.2; Rodrigues et al. 2000*a*). Furthermore, the multiple representations for species occurring in more than one unit are necessarily spread across the species' range, which has advantages in terms of preserving intraspecific genetic diversity.

With geopolitical coordination, however, it would be possible to devise perhaps more effective reserve networks, at an equivalent or even lower cost. For example, it would require 200 cells to ensure that each species is represented in at least 10 cells across South Africa and Lesotho (or the maximum possible for species whose range occupies less than 10 cells; Figure 6.3*b*). Although this network does not guarantee that widespread species are represented across their ranges, it has the advantage of giving higher relative protection to species that are rare across the entire region, because it means all species occurring in ≤ 10 cells are protected in all of their range (which explains the cell clustering in Figure 6.3*b*), with the proportion of the range protected for other species being higher for the least widespread (see Section 4.2; Rodrigues et al. 2000*a*). In the network representing each species once within each geopolitical unit (Figure 6.3*a*), the reverse may happen, because the number of representations required for each species depends essentially on the number of units covered by its range, with very rare species that occur in only one unit being represented once and widespread species occurring throughout the study area being represented 10 times.

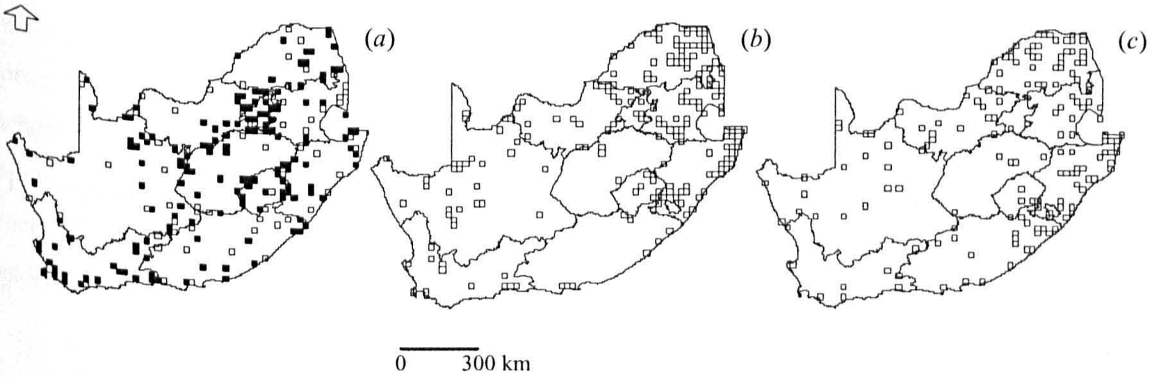

Figure 6.3 – Minimum set representing bird species in South Africa and Lesotho: (*a*) each species at least once in each of the 10 geopolitical units (221 sites; black squares are irreplaceable cells, open squares are flexible sites); (*b*) each species at least 10 times (or the maximum possible, for ranges occupying < 10 cells; 200 sites); and (*c*) each species in at least one of the sites where it occurs at a reporting rate over 90% of the maximum value registered for the species (160 sites).

Another possible strategy for selecting a more effective network in retaining species diversity is to target cells where species have a higher likelihood of persistence over time. I assumed that the reporting rates recorded for each species in each cell are a relative measure of the species abundance in the cell (Robertson et al. 1995; Harrison et al. 1997) and that a species has a lower probability of local extinction in cells where it is more abundant (see Section 4.1; Rodrigues et al. 2000*b*). A minimum set such that each species is represented by at least one of the cells where higher reporting rates have been recorded (defined as those cells with a reporting rate above 90% of the maximum value recorded for the species) occupied 160 cells (Figure 6.3*c*).

When dividing a region into geopolitical units, the problems associated with the disproportionate influence of restricted-range species on the number and identity of the cells selected are multiplied. For example, in the Northern Cape province 31 out of the 542 species present there occurred in only one cell. As a result, 28 irreplaceable cells were imposed on the minimum set of 42 cells representing each species at least once in the province. None of these 31 species is typical of the Karoo or Kalahari habitats characteristic of the Northern Cape province. They are mainly species whose range is very peripheral to the province, but often widespread elsewhere in South Africa (Figure 6.4). The end result was that within each geopolitical unit a high investment ended up being made in species atypical of that unit and that could hence be better protected elsewhere. Therefore, many of these species ended up receiving more attention at the edge of their ranges than at the center (Hunter and Hutchinson 1994; Erasmus et al. 1999). For example, the Barred Warbler (*Calamonastes fasciolatus*) is widespread and abundant in two units (Northwest and Northern Province), but it becomes a priority in four other provinces (Northern Cape, Free State, Gauteng, and Mpumalanga), where it is at the periphery of its range and less abundant (Figure 6.5). This is reflected in the spatial configuration of the cells selected when geopolitical boundaries are considered, which tend to be abnormally concentrated at the periphery of the units (compare Figure 6.3*a*, especially the irreplaceable cells, with *b* and *c*).

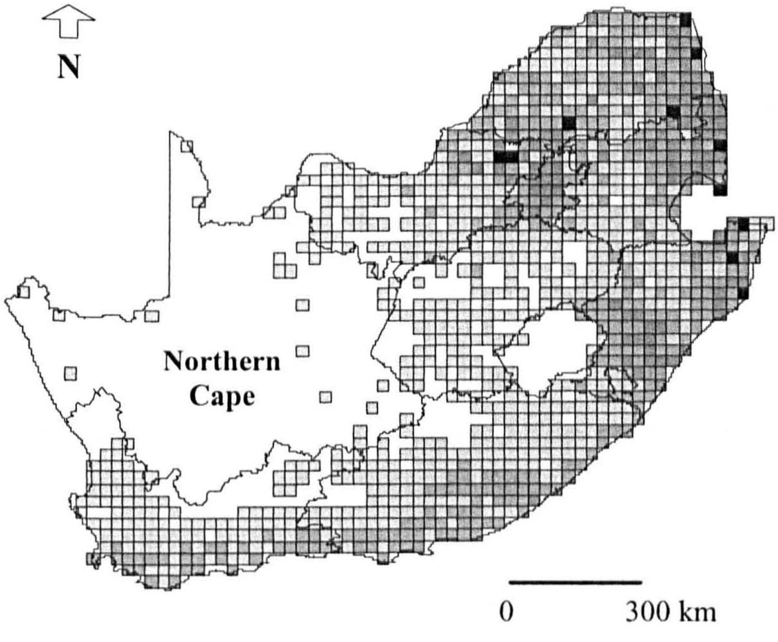

Figure 6.4 – Species richness of the 31 species represented in the Northern Cape unit by only one cell. Darker shading corresponds to higher values of species richness.

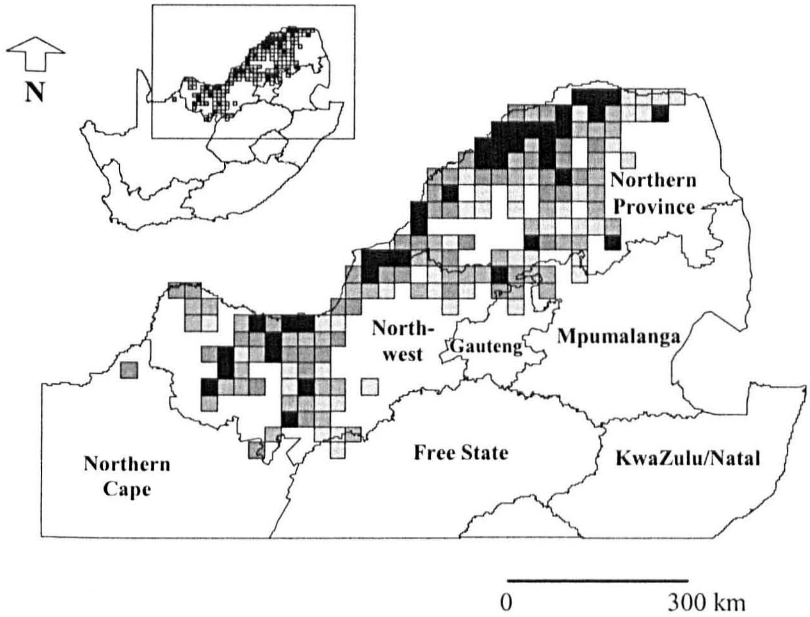

Figure 6.5 – Distribution of the Barred Warbler (*Calamonastes fasciolatus*) in South Africa. Darker shading corresponds to higher values of reporting rates.

6.1.5 Discussion

Species rarity is highly valued in reserve selection procedures (e.g., Margules and Usher 1981; Smith and Theberge 1986; Stattersfield et al. 1998), an emphasis justified by the acknowledgement that rare species have a greater likelihood of local extinction (Gaston 1994; Caughley and Gunn 1996) and are therefore in need of higher conservation investment. The results of complementarity-based methods are intrinsically influenced by species with restricted ranges. This is a desirable property if relative rarity provides an accurate measure of the relative conservation significance of each species. Sometimes, however, this condition is not met, particularly when conservation planning is made within geopolitical units unrelated to biogeographical boundaries. In these situations, having a restricted range in a given region is not necessarily an indication of high conservation concern if the species does not truly belong to the region's biota: if it is a vagrant, if its distribution extends only very marginally to the region, or if the species is introduced.

Complementarity methods make no distinction between "true" and "apparent" rarities, both having a disproportionate influence on the results. In fact, it is likely that apparent rarities may have an even stronger effect. The occurrence of a truly rare species may be an indication of the presence of a high-quality habitat (maybe a more pristine one), which may be suitable for a number of other species and therefore a good choice in a complementary set irrespective of the presence of the rare species. Records of apparent rarities, on the other hand, may be more correlated with areas better prospected by skillful observers or to regions geographically more prone to the presence of vagrants, such as some coastal regions for birds. If so, then the presence of such rarities may not be an indication of the site's value despite still imposing its selection as part of the complementary set. This may be the case in these analyses, where I found that the irreplaceable cells selected because of the presence of apparent rarities tend to be near the coast (Figure 6.2*a*) and have lower species richness than irreplaceable cells containing true rarities (on average 72 less species), despite having had a higher sampling effort (on average 209 more submitted lists). This situation will particularly be a problem for data sets based on presence-absence data only and for regions where the true status of species (e.g., breeding or not) is not well understood.

I found that, in this data set, including non target species (< 6% of all species, most of them being apparent rarities) in the reserve selection resulted in a 63% increase in the area required by the minimum complementary set (from 19 to 31 cells). When efficiency is among the most valued properties of a reserve system (e.g., Pressey and Nicholls 1989*a*; Pressey et al. 1993; Csuti et al. 1997; Ando et al. 1998), this effect can hardly be ignored.

The most extreme effect of apparent rarities, reflected in both the number and identity of the cells selected, occurs when they impose the selection of irreplaceable cells. Although considered here a binary property (a site is irreplaceable if and only if it contains unique species), the irreplaceability of a site has also been defined as a continuous measure between 0 and 100% of (1) the potential contribution of a site to a reservation goal and (2) the extent to which the options for reservation are lost if the site is lost (Pressey et al. 1993). Irreplaceability has been receiving increasing support as a useful tool in assisting managers in practical conservation planning, with 100% irreplaceable cells being considered the nodes of reserve systems (Pressey et al. 1993, 1994; Ferrier et al. 2000). But irrespective of the definition or method of calculation, species with very restricted ranges in the study area will significantly amplify the level of irreplaceability of the cells where they occur. Therefore, particular attention must be taken to ensure that the irreplaceability of a site does not result from the presence of unimportant (in terms of conservation action) species. In these analyses, 10 out of 15 irreplaceable cells derived from the presence of apparent rarities. This means that if a simple complementarity-based approach had been applied to the data set, nearly one-third of all cells needed to represent each of the 690 bird species at least once in South Africa and

Lesotho might have been classified incorrectly as priority areas for bird conservation. This illustrates one of the dangers in considering minimum sets for one representation as ideal reserve systems against which existing reserves must be compared (e.g., Rebelo and Siegfried 1992; Castro Parga et al. 1996; Nantel et al. 1998; see also Section 3.2 [and Rodrigues et al. 1999] for a critique).

It may therefore be advisable to initially filter those species that are relatively unimportant but are expected to have a substantial influence on the results (i.e., non target species with just a few occurrences). This initial step is particularly needed for taxa with high mobility, where vagrancy is more likely (in insect communities in tropical rain forests, for example, "tourists" constituted 20% of the total species found at given sites and were often collected as single individuals; Novotný and Basset 2000).

When dividing a region into geopolitical units, the issues associated with the disproportionate influence of restricted-range species on the number and identity of the cells selected are multiplied. This results in many more cells being required to represent each species within each unit than across the entire region (Figure 6.2*b* and Figure 6.3*a*). This is not in itself a disadvantage if each geopolitical unit is willing (and can afford) to create a representative reserve system within its boundaries. Larger reserve systems are obtained, with species whose ranges cross more than one unit receiving increasing protection by being represented multiple times. There is a risk, however, that species atypical of each unit (which could be better protected somewhere else) become a priority. From a regional perspective, the result is an artificial concentration of reserves at the periphery of the geopolitical units, where most vagrant and marginal species occur (Figure 6.3*a*). In addition, several species will end up receiving more attention at the edge of their ranges (in geopolitical units in which they are rare) than at the center (in units where they are common; Figure 6.5). Although it is generally expected that species exhibit lower abundance at the edges of their ranges (Maurer and Brown 1989; Lawton 1993; Brown 1995), and are therefore more likely to suffer local extinction there (but see Channell and Lomolino 2000*a*,*b*), there are three main reasons peripheral populations may nevertheless be considered a priority. One is their potential importance for maintaining and generating intraspecific genetic diversity (Hunter and Hutchinson 1994; Lesica and Allendorf 1995). The second is the value given by local people to species that are rare in the regions where they live, even though they may be common elsewhere (Hunter and Hutchinson 1994). The third is that if countries where the core of some species' ranges fall do not have adequate legislation for their protection, then the burden of conservation falls to the neighboring countries who do have such legislation, even if only peripheral populations occur there (Abbitt et al. 2000). The point, however, is not that populations at the edges should be ignored by conservation networks, but rather that if resources are scarce (which is the basic premise of complementary selection) then these populations may not be a first priority. The advantages of geopolitical coordination in conservation planning may therefore be not only an improved overall efficiency but also a better allocation of resources which gives priority to species that are rare across the entire region (Figure 6.3*b*) or to the sites where each species is expected to present a higher probability of long-term persistence (Figure 6.3*c*).

The analysis presented in this study draws attention to a broader question in reserve planning – before applying any area-selection method, planners need to clearly define objectives and set targets, and that often requires making decisions about what is the conservation investment to be made in particular species. Deciding to exclude the obvious non-target species is easy, but deciding what to do with the not-so-obvious marginal species may prove harder. It is possible that no clear solution exists, and that it will have to be solved on a case-by-case basis, making the best use of the available information and including some judgement in the decision process. Complementarity-based methods do provide sufficient flexibility for this (see Section 2.1; Rodrigues et al. 2000*c*). For example, one way to alter the relative influence of species on the results is to weight species according to their importance by setting higher representation targets for priority species (as in Kirkpatrick 1983; Rodrigues et al. 2000*c*; see Section 2.1,). This may translate, for example, into requiring that priority species be represented in more sites than those of least concern or that species be represented by a fraction of their range that is inversely proportional to their importance. The priority value for each species should reflect its relative conservation concern by integrating aspects such as its international conservation status, the fraction of its population inside each unit (Avery et al. 1994; Warren et al. 1997), and the status of each species in the study area (for example, breeding or non-breeding), besides the range extent within a given study area to which complementarity-based methods are so sensitive. This would not only allow a reduction of emphasis on the "apparently rare" species (e.g., marginal ones), it would also give a higher value to those species which are "apparently common" (species which are widely distributed but locally rare because of, for example, narrow habitat requirements, for example the Cinnamon-breasted Warbler [*Euryptila subcinnamomea*]).

7 Conservation planning with poor biological data

Complementarity-based approaches for the identification of priority areas for conservation are gaining popularity for their efficiency in maximizing species representation. However, their dependence on detailed distributional data severely hinders their application to regions where such information is limited, although these are commonly also the regions where conservation planning and action are most urgently required. In this chapter, exemplar data on the distribution of Southern African birds is used to investigate how sampling effort affects the performance of reserve networks selected by complementarity-based methods. It then provides guidelines for the collection of data based on low-sampling effort that can provide highly valuable information for reserve selection. This can be particularly useful for application to countries where exhaustive inventories are not immediately possible.

7.1 Reserve selection in regions with poor biological data

7.1.1 Introduction

Most conservation planning involving the selection of reserves is based on single or only a few species (Simberloff 1988), often the most charismatic ones and/or those considered umbrella, indicator, flagship, or keystone species (Caro and O'Doherty 1999). However, reserve networks selected in this way may be ineffective for the conservation of other, non-target, species (Pimm and Gittleman 1992; Andelman and Fagan 2000; Williams et al. 2000*b*).

Complementarity-based methods for reserve selection have been proposed in response to the acknowledgement that resources available for conservation purposes are limited and should therefore be employed in ways that maximize the diversity of biological features (such as populations, species, land systems) which are benefited (Pressey and Nicholls 1989*a*; Pressey et al. 1993; Scott et al. 1993). These methods are becoming increasingly popular as tools for conservation planning (Pressey et al. 1993; Dobson et al. 1997; Ando et al. 1998; Howard et al. 1998; Margules and Pressey 2000), and the complementarity principle is now commonly applied in practical reserve selection exercises, including the U.S. Gap Analysis Program (Scott et al. 1993; Kiester et al. 1996).

The efficiency of complementarity-based methods is obtained by identifying sets of sites that are highly complementary in terms of their biological composition. To identify the sets, these methods rely on high-quality information on the spatial distribution of all species of concern. However, regions with such data are often in developed countries where reserve networks are already well established. The scarcity of distributional data restricts the possibility of applying these approaches to regions where it would be more relevant, such as poor tropical countries with high biodiversity levels and incipient reserve systems (Pimm 2000). Ideally, investment should be made in obtaining distributional data for these countries (Balmford and Gaston 1999), but many lack the time, personnel, and financial resources to do so (Ehrlich 1992), and increasing rates of habitat destruction make reserve selection and conservation action an urgent task.

Complementarity-based methods have also emphasized the representation of species in reserve networks. However, this does not ensure species' persistence over time (see Sections

4.1, 4.2; Margules et al. 1994*b*; Virolainen et al. 1999; Rodrigues et al. 2000*a*,*b*) because they may be represented in sites that are inadequate for their long-term viability (see Section 4.3; Gaston et al. 2001). The abundance pattern of most species over their geographic range is characterized by the existence of many sites of low abundance and just a few peaks where abundance can be orders of magnitude higher (Gaston 1994; Brown et al. 1995*b*). The long-term effectiveness of reserve networks in retaining species can on average be improved by targeting these peaks of abundance for inclusion (see Section 4.1; Rodrigues et al. 2000*b*), but to locate these for each species of concern would require a still higher investment in sampling effort from those countries with poor biological data.

Restricted-range species, commonly considered priority targets for conservation investment because of their higher vulnerability to extinction (Stattersfield et al. 1998; Myers et al. 2000), present an even more challenging case. Because there is a widespread positive relationship between occupancy and local abundance, restricted-range species also tend to be locally rare (Gaston et al. 2000). Therefore, they typically require a substantial sampling effort even to be detected, let alone for obtaining data on relative abundances across their range.

Ideally, complementary reserve selection should be based on the best possible data, obtained through sufficient sampling effort to detect the rarest species and to obtain information on the location of species' peaks of abundance. However, it remains unclear how the quality of the networks selected changes with the quality of the data used, and, in particular, how well do networks based on data obtained from low sampling effort perform.

Freitag and van Jaarsveld (1998) evaluated the sensitivity of selection procedures for conservation areas to survey intensity, survey extent and taxonomic diversity by randomly deleting records, grid cells and species from their data set on mammals in South Africa. In this study I am concerned about the effects of survey intensity (sampling effort) across all cells. Freitag and van Jaarsveld's (1998) study has a number of weaknesses in this regard. First, the approach to data degradation (by deleting records at random) does not simulate a realistic situation of lower sampling effort across all cells, as it assumes that all records have the same probability of occurrence (for example, a record where a species has been seen in 90% of visits or in just 1% of them). As a result, a species' range in the degraded data is made of a random selection of grid cells from the original range. In a low-sampling effort situation, the most natural outcome would be a reduced range such that the species tends to have been recorded in those sites where it is more abundant. Second, the performance of the reserves obtained using the degraded data was assessed mainly by measures of spatial congruence between sites selected. However, there is often a large diversity of possible solutions to each complementary reserve selection problem (e.g., Arthur et al. 1997), often differing considerably in terms of the identity of the sites selected (see Chapter 5; Rodrigues and Gaston 2002*a*). Third, viability considerations were not taken into account in the evaluation of the performance of reserve networks obtained from degraded data sets.

Here, I use exemplar data on the distribution and reporting rates of bird species in South Africa and Lesotho (Harrison et al. 1997) to assess how the effectiveness (see Section 3.2; Rodrigues et al. 1999) and efficiency (Pressey and Nicholls 1989*a*) of reserve networks obtained by complementary reserve selection are affected by the intensity of sampling effort.

I am concerned about the variation in the sampling effort across all candidate sites for reserve selection. This study does not address situations where low sampling effort consists of a fraction of sites being well studied while for others there is no data. For these, the solution probably involves some form of data interpolation techniques, and the main issue then becomes to evaluate the effectiveness of such techniques.

7.1.2 Data and Methods

The Southern African Bird Atlas Project (Harrison et al. 1997) has provided the most comprehensive information currently available on the distribution of birds in Southern Africa. Several previous studies have used this data set as a basis for planning studies (e.g., Allan et al. 1997; Reyers et al. 2000; Fairbanks et al. 2001). Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland, and Zimbabwe and on a half-degree grid for Botswana. Observers visiting each cell recorded the presence of identified species on checklists, and breeding and non breeding records were considered equivalent. A variable number of checklists has been submitted for each cell ($\mu = 39$, $\sigma = 88.0$). A total of 909 species were recorded. Based on these data, reporting rates were calculated for each species in each cell as the proportion of checklists submitted for that cell on which the species was recorded. I used the data for South Africa and Lesotho (1858 cells), excluding marine, vagrant, marginal and introduced or escaped species from the analysis (total of 651 species).

For each species, peaks of reporting rates were defined as cells with reporting rates ≥ 80% of the maximum value observed for that species, and I assumed these peaks of reporting rates correspond to peaks of abundance. This assumption was based on the positive association between abundance and reporting rates found by Robertson et al. (1995), and it is expected to be robust because it refers only to intra species relative abundance (thereby avoiding bias related to the species' different levels of conspicuousness). These peaks of abundance correspond on average to 5.8% of the total number of records for each species.

I considered the efficiency of a reserve network to be inversely related to the percentage of total area that it occupies (a first approximation to its relative cost; Pressey and Nicholls 1989*a*). Effectiveness in species representation was evaluated using four different measures. First, I determined the percentage of the overall number of species represented (out of 651) in each reserve network. This is the most traditional measure of effectiveness (see Section 3.2; Rodrigues et al. 1999), but it may be misleading if the species are only represented at sites that are inadequate to ensure their persistence. As a second measure of effectiveness, I determined the percentage of species represented in at least one of their respective peaks of abundance. The third and fourth measures of effectiveness refer to the representation of restricted-range species, here after considered the 25% of species with the smallest ranges in the study area (those present in < 8.8% of the 1858 grid cells; Gaston 1994). I determined the percentage of restricted-range species represented at least once and the percentage of these represented in at least one of their peaks of abundance.

Four scenarios of data availability resulting from different levels of sampling effort were derived from the initial data set on the reporting rates of each of the 651 species in each of the 1858 grid cells: abundance, presence/absence, low sampling effort, and absence of data.

In the first scenario, the location of the peaks of abundance for each species was known. Reserve networks of variable total area that maximized the number of species that could be represented in at least one of their peaks of abundance were obtained.

In the second scenario, I used data on the presence/absence of each species in each cell to obtain reserve networks of variable total area that maximize the number of species represented at least once. This is the most common scenario in the literature, with most reserve selection exercises being based on presence/absence data, which can potentially be obtained with less sampling effort than abundance data (see Section 4.2; Rodrigues et al. 2000*a*).

For both the abundance and presence/absence scenarios, I assumed for the purpose of these analyses that the data correspond to "the truth" of species distribution and location of peaks of abundance.

In the third scenario, I used the original information on reporting rates to simulate a situation in which very low sampling effort – two visits – was applied across all cells. A visit to a given cell was reproduced by randomly re-sampling that cell such that the probability of each species being observed during the visit is given by the reporting rate for that species in the cell (i.e., each species has an associated binomial distribution of parameters $\beta(1, p)$, where p is the reporting rate for that species in the cell). Ten replicates of this scenario were conducted. The presence/absence matrices obtained retained, across the entire grid, on average 95.9% of the initial 651 species, but the species richness sampled in each cell was much reduced (on average each cell had 42.6% of the original species richness). This reduction in species richness is the result of species with lower reporting rates in each cell being missed when low sampling effort was applied (Figure 7.1). These matrices were therefore highly biased toward retaining information about those species that are locally more abundant. These low sampling effort presence/absence matrices were then used to obtain reserve networks of variable area that maximize the number of species represented.

In the fourth scenario, I assumed a total absence of information on the distribution of species in the study area. This was simulated by randomly selecting sets of cells of variable total area.

The problem of finding the maximum number of species represented without exceeding a given area is a maximal covering location problem (Church et al. 1996), represented as

$$\text{maximize} \sum_{i=1}^{m} y_i$$

subject to

$$\sum_{j=1_i}^{n} a_{ij} x_j \geq y_i, \qquad i = 1, 2, \ldots, m$$

$$\sum_{j=1}^{n} x_j \leq k,$$

$$x_j \in \{0,1\} \qquad j = 1, 2, \ldots, n$$

$$y_i \in \{0,1\} \qquad i = 1, 2, \ldots, m$$

where m is the total number of species, n is the total number of sites, k is the maximum number of sites to be selected, y_i is 1 if species i is represented in at least one of the sites selected and 0 otherwise, x_j is 1 if site j has been selected and 0 otherwise, and a_{ij} is 1 if species i

is present in site *j* and 0 otherwise (in the abundance data scenario, being present refers to having a peak of abundance at site *j*). For each one of the first three scenarios, maximal covering location problems were solved for values of *k* ranging between 1 and 80 (or until the minimum number of sites needed to represent all species was reached if < 80). All problems were solved optimally with C-PLEX software (ILOG 1999).

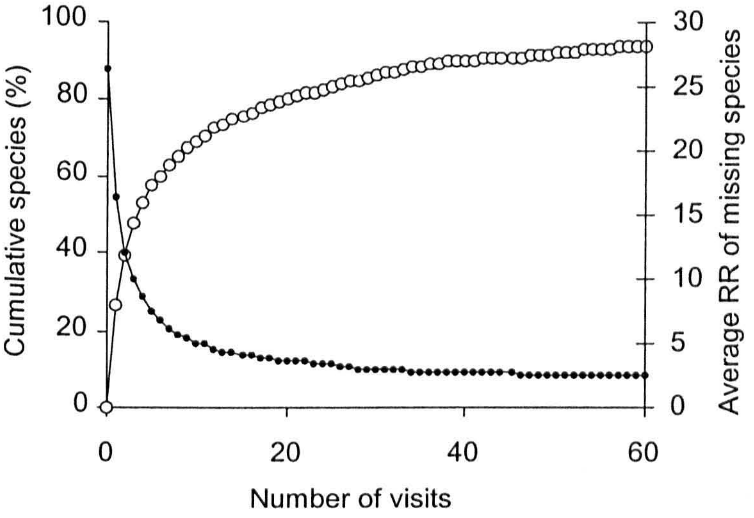

Figure 7.1 – Species accumulation curve for a cell in the study area (open circles) and average reporting rate (RR) in the cell of the species not yet represented (closed circles) after a given number of simulated visits to the cell. The figure corresponds to the mean result for 10 sequences of 60 visits to a particular cell (2528CB, randomly selected), but represents the typical shape of species accumulation curves that can be obtained for different cells in the study area and indeed for different geographic regions and taxonomic groups (e.g., in Gentry 1990). On average, 39.3% of all species were sampled within the first two visits to this particular cell. Species with higher local reporting rates tend to be sampled first.

7.1.3 Results

A significantly larger reserve network was required if the purpose was to obtain networks where species are represented at peaks of abundance rather than simply represented anywhere within their ranges (Figure 7.2). Indeed, I found that the area needed was more than six times larger if the purpose was to represent species in peaks of abundance (6.4% of the total area instead of 1.0%).

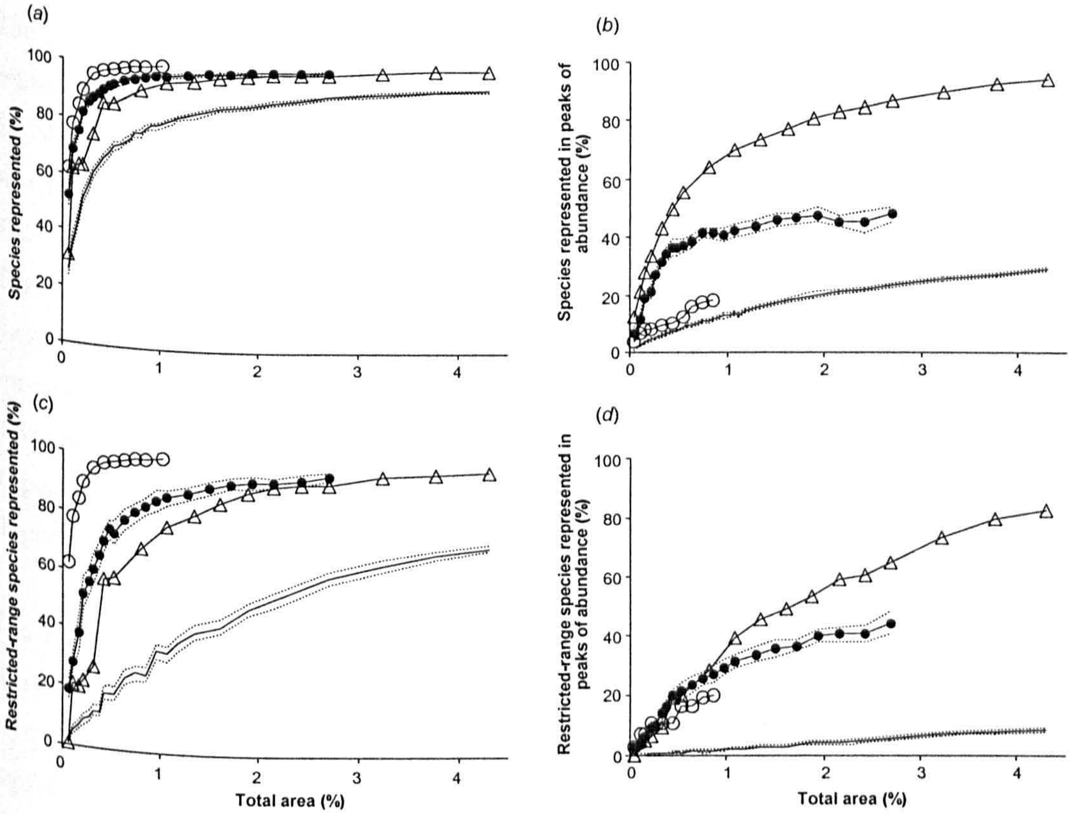

Figure 7.2 – Effectiveness and efficiency of reserves selected for four different scenarios of data quality: 1) knowing the location of the peaks of abundance for each species (triangles); 2) having presence/absence data for each species in each cell (open circles); 3) using data obtained from very low sampling effort (filled circles represent the mean value across 10 replicates, dashed lines represent the limits of the 95% confidence interval); and 4) having no data on the species' distribution (continuous lines represent the mean value across 100 replicates, dashed lines represent the limits of the 95% confidence interval). The efficiency of reserve networks is inversely related to the percentage of total area selected (*x* axis). The effectiveness has been assessed in four ways, corresponding to the *y* axes in (*a*), (*b*), (*c*) and (*d*). Each data point corresponds to the solution of one maximal covering location problem. For the data on the location of the peaks of abundance for each species (triangles), 100% of species representation is achieved by selecting 6.4% of the total area (not represented).

The reserve networks obtained in the absence-of-data scenario always (as expected) performed worst in terms of their efficiency and effectiveness (Figure 7.2). But whereas relatively high percentages of species could be represented by selecting sites at random (Figure 7.2*a*), it was much more difficult to represent them in peaks of abundance (Figure 7.2*b*), especially for the restricted-range species (Figure 7.2*c*, *d*). For example, 79% of all species were represented in randomly selected networks occupying 1% of the total area (Figure 7.2*a*), but only 13% of all species were represented in peaks of abundance (Figure 7.2*b*). Regarding the restricted-range species, 34% of these were represented at least once in a network of the same size (Figure 7.2*c*) but only 2% were represented in peaks of abundance (Figure 7.2*d*).

The networks obtained in the presence/absence-data scenario were the most effective in representing species at least once within a given area (100% of all species represented within 1% of the total area [Figure 7.2*a*,*c*]), but their performance declined dramatically if the purpose was to represent species in their respective peaks of abundance (21.7% of all species [Figure 7.2*b*] and 21.5% of restricted-range species [Figure 7.2*d*] represented in 1% of the total area). The networks obtained in the abundance data scenario (with knowledge of the location of these peaks) were not as effective in terms of simple species' representation (97.7% of all species [Figure 7.2*a*] and 77.3% of restricted-range species [Figure 7.2*c*] represented within 1% of the area), but they were (as expected) the ones that performed better in representing species at peaks of abundance (70% of all species [Figure 7.2*b*] and 39.3% of restricted-range species [Figure 7.2*d*] represented in 1% of the area).

The most surprising results came from the performance of the networks obtained in the scenario of low sampling effort. They always performed much better than a random selection of sites, indicating that the results obtained cannot be explained by accidental species representation with the selection of increasingly large areas. In terms of species representation, either for all (Figure 7.2*a*) or for just the restricted-range species (Figure 7.2*c*), they performed better than the networks obtained in the abundance-data scenario (95% and 85%, respectively, in 1% of the area). They were not as good in representing species at their peaks of abundance (41% of all species [Figure 7.2*b*] and 30% of restricted-range species [Figure 7.2*d*] represented in 1% of the area), but in terms of these measures of effectiveness they performed much better than the networks obtained in the presence/absence-data scenario.

7.1.4 Discussion

The result that a significantly larger reserve network was required if the purpose was to obtain networks that improve the probability of maintaining species over time (by representing them at peaks of abundance), rather than simply those in which they are represented (Figure 7.2), agrees with previous results (e.g., see Sections 4.1, 4.2; Araújo and Williams 2000; Rodrigues et al. 2000*a*,*b*). The six-fold difference between the areas needed in the two cases is likely to arise because the occurrences of different species coincide much more frequently than do their peaks of abundance. But even these larger areas required are unlikely to be sufficient for establishing a network that retains all the species over the long-term because reserves of the size of the units I considered (~ 650 km²) may not be sufficient for the maintenance of viable populations (e.g., Mattson and Reid 1991; Nicholls et al. 1996; Manne et al. 1999). Nevertheless, I expect that the results for the different scenarios explored will generalize to more demanding levels of representation of occurrence and of peaks of abundance.

The performance of networks based on low sampling effort was never optimal (i.e., the maximum values of species representation that could be obtained for a given area were never reached), either in terms of species representation (which, by definition, was obtained by the networks based on presence/absence data; Figure 7.2*a,c*) or of representation of species in their peaks of abundance (which, by definition, was obtained by the networks based on abundance data; Figure 7.2*b,d*). But it was generally good, well above the results of a random selection and sometimes close to the optimal. This suggests that the data on which basis these networks were chosen still retain useful information for identifying areas that are highly complementary in terms of species representation and in terms of their representation in peaks of abundance.

The high effectiveness of these networks in terms of species representation (Figure 7.2*a,c*) was likely a direct consequence of the effectiveness of the low sampling effort in recording at least some information on the distribution of most of the species in the original data set. Indeed, despite an average reduction of 39% in the total number of records, the large majority (on average 95.9%) of all species were recorded in at least one site by the low sampling effort. Their recorded mean range size was much reduced (on average, to 28.6% of the original), but complementary networks obtained from the low-sampling-effort data still represented these species because some information existed regarding their location in the study area. The decrease in the efficiency of these networks compared with the ones obtained using the original presence/absence data was an expected result from the increase in the species' rarity in the data set (e.g., see Chapters 6 and 8; Lombard et al. 1995; Willis et al. 1996; Pressey et al. 1999; Rodrigues and Gaston 2001, 2002*c*).

In terms of absolute numbers, the performance of the networks obtained using data resulting from low sampling effort is considerably worse when the purpose is to represent species in their peaks of abundance (Figure 7.2*b,d*) rather than simple species representation (Figure 7.2*a,c*). However, their performance is actually quite good compared with the optimal values that can be obtained (i.e., the values achieved by the networks based on abundance data) and values obtained by random selection of the same percentage of total area. Despite being a more reduced presence/absence data set than the original one, they performed better than reserves selected using the more complete original data (Figure 7.2*b*,*d*). In the latter, most records correspond to sites where species exist at very low abundance (Figure 7.3), having only been detected after considerable sampling effort. These sites are likely to be less adequate in maintaining species over time and are therefore relatively uninteresting with regard to the selection of priority areas for conservation. However, these records contribute much to improve the efficiency (i.e., to reduce the area needed) of complementary sets in representing all species. In an extreme situation, after enough sampling effort has been applied, the recorded range of most species will have been substantially expanded by the detection of vagrant individuals. The minimum reserve networks needed to represent all species will then be tiny (very efficient), but highly ineffective in ensuring species' persistence over time (see Sections 4.1, 4.2; Rodrigues et al. 2000*a*,*b*). In the low-sampling-effort scenario, the probability of a species being recorded in a given cell is directly related to its reporting rate in that cell. Although this means locally rarer species are likely to be missed, it also results in a bias toward the inclusion of records that correspond to peaks of abundance (Figure 7.3). Indeed, the reduction in the number of data records in the low sampling scenario (as referred to above, each species' recorded range was on mean reduced to 28.6% of the original) was made chiefly by the deletion of low local abundance records, whereas most (81.3%, on mean) of the peaks of abundance have been retained. Therefore, there is a higher probability that reserve networks selected using the low sampling effort data include those sites within species ranges where they are locally more abundant. This result does not mean data become less adequate for reserve selection when higher sampling effort is invested. Without high sampling effort, it is unlikely that the rarest species – the ones requiring higher conservation investment – are ever detected. But it does demonstrate that, in complementary reserve selection, using too much indiscriminate data is not necessarily better than using less data. In most sampling schemes designed to obtain presence-absence data across a given region, it should be possible to extract additional information on the location of the peaks of abundance of most species if information on the sampling effort involved in obtaining each record is retained (as in Harrison et al. 1997).

All of the species missing from the low-sampling-data matrices were restricted-range ones. However, compared with the optimal values that can be obtained and with values obtained by random selection of the same percentage of total area, the relative performance of reserve networks based on these data was actually better in terms of representation of the restricted-range species at their peaks of abundance (Figure 7.2*d*) than in the representation of all species (Figure 7.2*b*). This is because the bias in the data obtained by low sampling effort toward the selection of records that correspond to peaks of abundance is stronger for the restricted-range species. Indeed, although the mean number of these records in the low sampling matrices is of 21.7% for restricted-range species, the corresponding value for the remaining species is only 8.4%. This means that when selecting a complementary data set based on presence/absence data obtained by low sampling effort there is a higher probability that the peaks of abundance of the restricted range species will be captured than the peaks of abundance of the more common species.

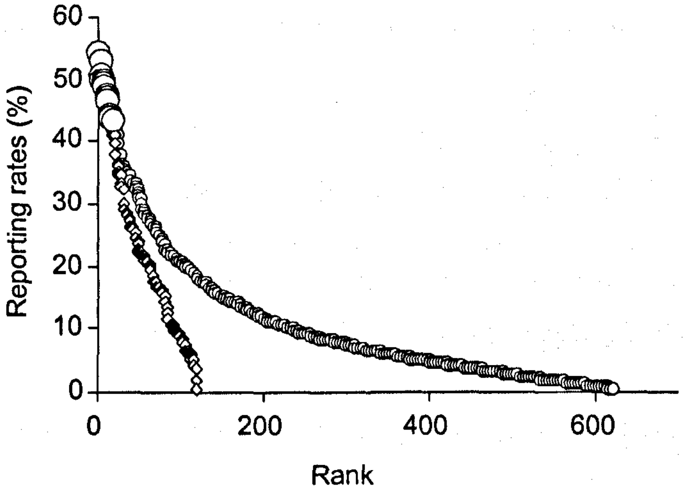

Figure 7.3 – Distribution of the values of reporting rates with the rank of each site (in descending order of reporting rates) in the original presence/absence scenario (shallower curve) and in the low-sampling-effort scenario (steeper curve). The values are for the Ovambo Sparrowhawk (*Accipiter ovampensis*, randomly selected) but are representative of the overall result. Although the number of records has been substantially reduced in the low sampling effort data (from 624 to 120), this has been mainly a result of the selective deletion of records with low reporting rates, and most of the peaks of abundance (13 out of 16; larger circles) have been retained.

Naturally, the best results in terms of representing species having viability concerns into account were obtained using the data set with more complete information about the location of the peaks of abundance for each species. However, these results demonstrate that even distributional data obtained through low sampling effort may be valuable for the application of complementary approaches for the selection of priority areas for conservation. Although more empirical testing is needed, including for data on other taxonomic groups with finer-scale distributions, this suggests that these approaches can also be valuable tools in regions with poor biological data. They may be used as an initial coarse approach for the selection of a coherent network of reserves, based on data from low-intensity-sampling schemes such as

Conservation International's Rapid Assessment Program (Conservation International 2001). This is good news at a time when the pressure on natural resources requires "quick-and-dirty" methods of evaluating natural ecosystems and designing reserves to protect them (Ehrlich 1992).

8 Global conservation targets – how much is enough?

An extensive literature exists on the required size of individual reserves, but to date there has been little investigation regarding the appropriate size of entire networks. IUCN's proposal that 10% of each nation be reserved is often presented as a desirable target, but concerns have been raised that this is insufficient and dictated primarily by considerations of feasibility and politics. This chapter integrates the results of a number of published complementarity-based analyses to investigate which variables control the percentage of area that needs to be reserved in order to represent each species. It then builds on that information to predict how large reserve networks need to be in order to represent plant and vertebrate species, in the tropical rain forests and at a global scale.

8.1 How large do reserve networks need to be?

8.1.1 Introduction

Article 8 of the Convention on Biological Diversity (http://www.biodiv.org/) obliges contracting parties to establish networks of protected areas for conservation. As these areas cannot be expected to protect what they do not contain in the first place, the initial minimum requirement of such networks is that they represent all the species that are to be conserved. IUCN – The World Conservation Union advocates that at least 10% of the land area of each nation be set aside for this purpose (IUCN 1993). But although achieving this target would require nearly doubling the currently protected land area (Hobbs and Lleras 1995), recent concerns have been raised that even this is woefully insufficient and dictated more by considerations of feasibility and politics than of biology (Soulé and Sanjayan 1998). However, to date there has been little investigation of what would be an appropriate target from a biological perspective.

Complementarity-based methods provide a way to integrate political and biological considerations in the selection of networks of protected areas. They have been proposed in acknowledgement of the fact that resources available for conservation purposes are limited and should therefore be employed in efficient ways that maximise the diversity of biological features benefited (Pressey and Nicholls 1989*a*; Pressey et al. 1993). When data on the distribution of all the species within a region are available, this is achieved by selecting areas that complement one another to the fullest possible extent in terms of their species composition. In the most widespread type of analyses applying these methods, minimum sets (i.e., sets of sites with minimum total area) are obtained which represent all of the target species at least once. These minimum networks are unlikely to be sufficient for ensuring the long-term persistence of the species represented (see Sections 4.1, 4.2; Rodrigues et al. 2000*a*,*b*), but they provide a lower bound to the size of an adequate network for conserving those species. These methods are therefore particularly suitable tools for determining the *minimum* percentage of a given region that needs to be reserved in order to ensure the representation of its species diversity.

In this study, complementary-based methods are used as a tool to explore the issue of how large reserve networks need to be. First, I examine patterns of variation in the sizes of minimum networks for a variety of assemblages. Second, I test predictions for these patterns. Third, I analyse the implications of the patterns for conservation planning.

8.1.2 Predictions from previous complementarity studies

I analysed 21 published and unpublished studies that found the minimum or near-minimum percentages of area required to represent each species in a region at least once (published studies: Rebelo and Siegfried 1992; Lombard et al. 1995; Castro Parga et al. 1996; Church et al. 1996; Freitag et al. 1996; Williams et al. 1996*a,b*; Willis et al. 1996; Csuti et al. 1997; Muriuki et al. 1997; Hacker et al. 1998; Nantel et al. 1998; Araújo 1999; Humphries et al. 1999; Lombard et al. 1999; Reyers et al. 2000; Williams et al. 2000*a,b*; unpublished studies: near-minimum area to represent plant species in the Northern Province of South Africa provided by B. Reyers, *pers. comm.*; minimum area to represent bird species in South Africa and Lesotho and in south-east Scotland calculated from data provided in published atlases – Harrison et al. 1997; Murray et al. 1998). These studies concern a diversity of geographic regions (in Europe, North America, Africa, and the Neotropics), with scales varying from regional analyses (456 km^2) to entire continents (Africa, ~ 20 million km^2) and with selection units sized between 1 km^2 and 1 degree grid cells (~ 12,000 km^2). In all cases, analyses were based on contiguous equal-sized selection units (grid cells, hexagons or rectangles), so that the solution to the problem of obtaining the minimum number of sites such that each species is represented at least once is equivalent to the problem of minimising the area.

The mean value of the minimum percentage of the area needed to represent all species in these studies is 13.6%, not far from the IUCN recommendation that 10% of land area be set aside for conservation, however the range is very wide (0.3-66.0%). I tested a diversity of logistic regression models to look for the most parsimonious explanation of this variation. I found that the combined influences of the number of species considered in each study and the number of contiguous sites into which the study area was divided, expressed as a ratio of species per site, explains a highly significant part of this variation. This ratio is positively correlated with the minimum percentage of area required to represent all species (Figure 8.1); this does not result from an intrinsic relationship between the number of species and the number of sites (r^2 = 0.017; p = 0.57). Moreover, a substantial proportion of the variability of the results seams to be explained by the nature of the biodiversity features considered: studies on plants and vertebrates lead to substantially different logistic regression curves when considered separately (Figure 8.1).

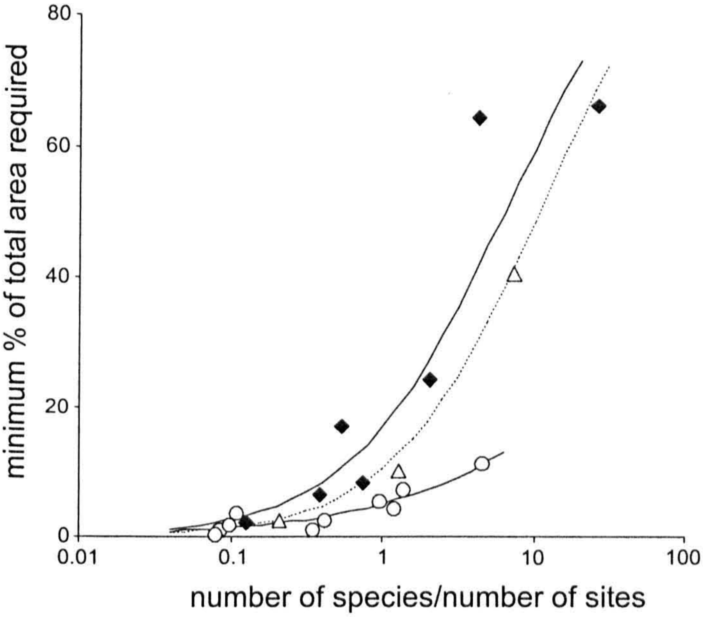

Figure 8.1 – Relationship between the ratio of the number of species analysed to the number of sites into which the region has been divided and the minimum percentage of total area required to represent each species at least once (see text for details). The values were obtained from 21 published and unpublished studies that found the minimum (or near-minimum) percentage of area required to represent each species at least once. Logistic regression models were applied to determine the relationships for all studies (dashed line) and separately for plants (black diamonds, upper continuous line) and vertebrates (open circles, lower continuous line). Highly significant relationships ($p < 0.001$) were obtained in all cases (all data: χ^2-test = 410.69, n = 21; plants: χ^2-test = 227.29, n = 8; vertebrates: χ^2-test = 20.71, n = 10). Open triangles refer to studies based on multiple higher taxa (including plants and vertebrates).

These results suggest three mechanisms by which intrinsic properties of the data set affect the minimum percentage of area needed to represent all species within a region. First, everything else being equal (i.e., for the same geographic area and considering the same selection units), as more species are included in a reserve planning exercise, the minimum percentage of total area needed to ensure representation of all of those species will increase.

Second, an increase in the size of the selection units should result in an increase in the minimum percentage of the area required for representation of all species (see also Pressey and Logan 1998; Pressey et al. 1999).

Third, it seems probable that the different relationships for plants and vertebrates between the ratio of the number of species to the number of sites and the minimum percentage of total area required to represent each species at least once are derived from the larger mean geographic range sizes and greater distributional overlap of vertebrates compared to plants. If this is a general rule, then taxa that have higher levels of local endemism are expected to require higher percentages of area in order to be fully represented (see also Soulé and Sanjayan 1998; Pressey et al. 1999).

Whilst logical and possibly obvious, these predictions have received little testing. This can be done by manipulating data sets in order to vary each one of the three variables mentioned (number of species, size of selection units and level of endemism) while controlling for the remaining ones. I used data on the distribution of birds in Southern Africa to perform these tests.

8.1.3 Test of the predictions

The Southern African Bird Atlas Project (Harrison et al. 1997) provides the most comprehensive information currently available on the distribution of birds in Southern Africa. Data were mainly collected between 1987 and 1992, at a spatial resolution of a quarter-degree grid for Lesotho, Namibia, South Africa, Swaziland and Zimbabwe, and on a half-degree grid for Botswana. Observers visiting each cell recorded the presence of identified species on checklists. A total of 909 species were recorded (for a more detailed description of the methodology used, see Harrison et al. 1997).

In this study, I used presence-absence data collected for South Africa and Lesotho (1858 quarter-degree grid cells), and excluded marine, vagrant, marginal and escaped species from the analysis (651 species were analysed). I manipulated the data properties in order to test each one of the predictions presented above. All optimisation problems referred to below have been solved optimally using *CPLEX* software (ILOG 1999; see Chapter 2).

Prediction 1. An increase in the number of species should result in an increase in the minimum percentage of area required

This prediction was tested using data subsets for Lesotho (329 species, 46 quarter-degree grid cells) and for the South African provinces of Northern Cape (401 bird species, 542 cells), Northern Province (555 species, 174 cells) and Mpumalanga (561 species, 118 cells). These were used rather than the entire data set in order to obtain *a priori* higher values for the ratio between the number of species and the number of sites.

For each political unit separately, data subsets were created with variable numbers of species while keeping the number of sites constant (for example, for Lesotho, subsets were obtained with 10, 30, 50, 100, 150, 200, 250 and 300 species, all with 46 cells). In this way, a wide range of values for the ratio between the number of species and the number of sites was obtained, which was necessary to cover the variability (across the *x* axis) of the data points plotted in Figure 8.1.

The species included in each subset were selected randomly, and ten replicates with the same number of species were created in each case. For each subset, the minimum percentage of area needed to represent each species at least once was obtained, and the average values across the ten replicates were then calculated.

The results support the first prediction. For each unit separately, the minimum percentage of total area needed to represent all species increased steadily for increasing numbers of species (Figure 8.2*a*). The values obtained are very accurately described by logistic regression curves (Figure 8.2*a*).

Prediction 2. An increase in the size of the selection units considered should result in an increase in the minimum percentage of area required

Using the entire data set on the distribution of bird species in South Africa and Lesotho I manipulated the size of the selection units while keeping the number of species constant (651 species) by re-sampling the data at different spatial resolutions. Unit sizes employed were of 1×1 (the original 1858 quarter-degree grid cells), 2×2 (498 half-degree cells), 3×3 (240 cells), 4×4 (139 one-degree cells), 5×5 (95 cells), 6×6 (68 cells), 7×7 (54 cells) and 8×8 (44 two-degree cells) grid cells. A species was considered to be present in a given cell at a given resolution if it occurred in at least one of the quarter-degree grid cells that composes the larger cell. For each unit size, the minimum percentage of area needed to represent each species at least once was obtained.

The results support the second prediction, as the minimum percentage of total area needed to represent all species increased steadily with increasing size of the unit (Figure 8.2*b*). The values obtained are again very accurately described by a logistic regression curve.

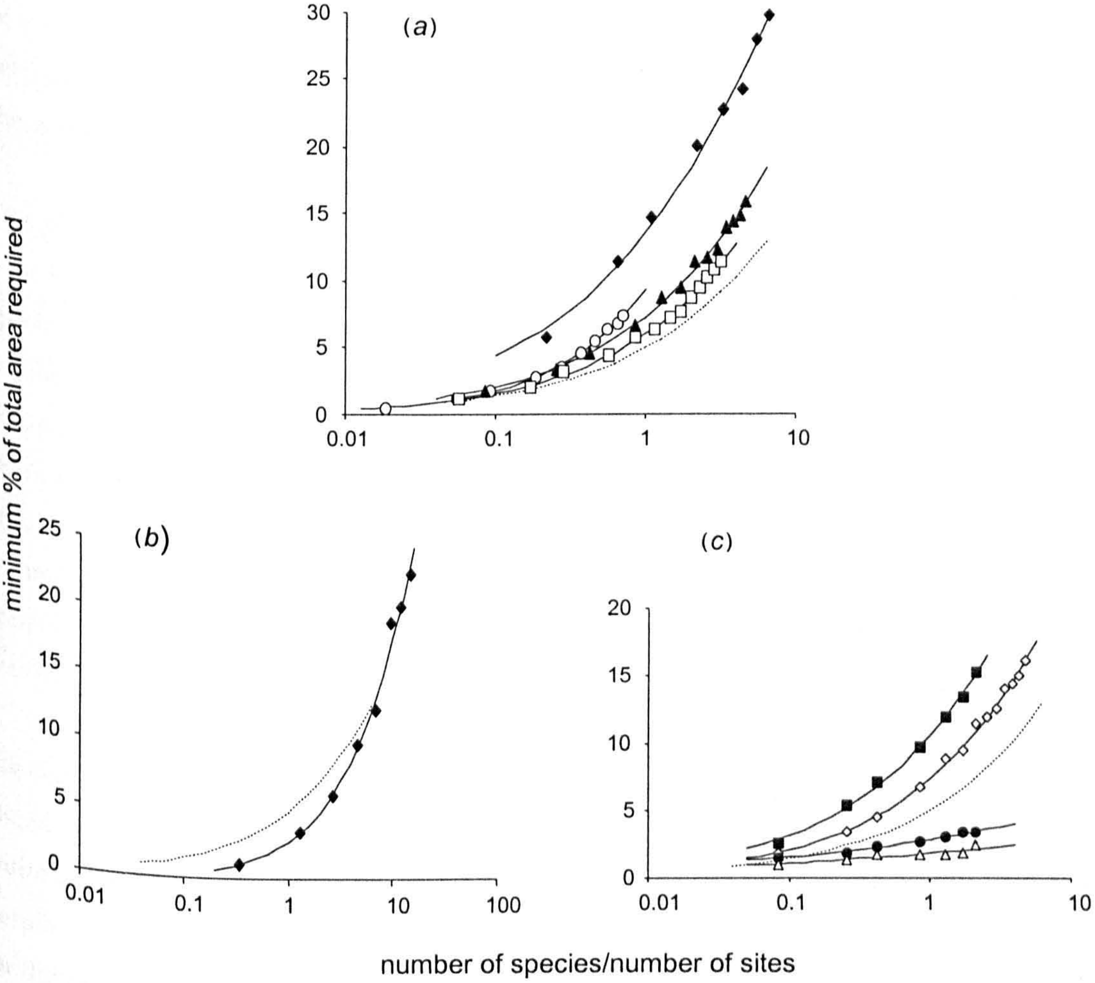

Figure 8.2 – Variation in the minimum percentage of total area required to represent all species when data are manipulated to vary *(a)* the number of species, *(b)* the spatial resolution, and *(c)* the level of endemism (see text for details). For reference, the dashed line is that obtained for studies on vertebrates, as plotted in Figure 8.1. *(a)* Variation in the minimum percentage of total area required as the number of bird species increases in Lesotho (black diamonds), Northern Cape (open circles), Mpumalanga (black triangles), and the Northern Province (open squares). Each data point corresponds to the average minimum percentage of area obtained across ten replicates. All relationships are well described ($p<0.001$) by logistic regression models (Lesotho: χ^2-test = 33.6, n = 8; N. Cape: χ^2-test = 16.1, n = 10; Mpumalanga: χ^2-test = 33.1, n = 13; N. Province: χ^2-test = 24.6, n = 13). *(b)* Variation in the minimum percentage of total area required to represent all species as size of selection units increases for data in South Africa and Lesotho. The leftmost data point corresponds to the smallest selection units (quarter-degree grid cells) and the rightmost to the largest (two-degree grid cells). The relationship is well described by a logistic regression model (χ^2-test = 50.2, n = 8, $p<0.001$). *(c)* Variation in the slopes of the relationship between the ratio of the number of species to the number of sites and the minimum percentage of total area needed to represent all species for four levels of endemism: *(i)* all species (open diamonds); *(ii)* the 50% most common species (open triangles); *(iii)* the 50% rarest species (black diamonds); and *(iv)* the 50% "middle" species (black circles). Highly significant relationships ($p<0.001$) were found in *(i)* (χ^2-test = 33.1, n = 13) and *(iii)* (χ^2-test = 15.8; n = 7). The lack of significant relationships in *(ii)* and *(iv)* reflects the limited variation in the minimum percentage of total area required in these cases.

Prediction 3. Steeper slopes are expected for taxa with higher levels of endemism

One way of measuring the level of endemism in a data set is by calculating the average range of the species, which can be presented in a standardised way (comparable across different data sets) as the average percentage of sites in the study area occupied by each species. The smaller the average range, the higher the level of endemism.

This prediction was tested using data for the Mpumalanga province (561 species, 118 cells). Four levels of endemism were analysed by creating data subsets with a variable number of species randomly extracted from: (*i*) all the 561 species (average range 43% of the total area); (*ii*) the 50% most common species in terms of range size (measured as the number of cells occupied by a given species; average range 69%); (*iii*) the 50% rarest species (average range 18%); and (*iv*) the 50% "middle" species (excluding the 25% rarest and the 25% most common species; average range 40%). Ten replicates were obtained for each number of species (between 10 and 550 in (*i*) and between 10 and 250 in (*ii*), (*iii*) and (*iv*)) and each of the four levels of endemism. The minimum percentage of area needed to represent each species at least once was found for each subset, and average values were calculated across the ten replicates.

The results support the third prediction, as steeper slopes are obtained for increasing levels of endemism (Figure 8.2*c*). However, the curves for the levels obtained by selection from the entire set of 561 species (*i*) and from the "middle" species (*iv*) have quite different slopes, despite having similar average range sizes. The first one is much closer to the level obtained for the rare species (*iii*), while the second is closer to the level for the common species (*ii*). This is likely due to the disproportionate influence of the very rare species (excluded from level (*iv*) but still present in level (*i*)) on the number of sites selected (see Chapter 6; Rodrigues and Gaston 2002*c*). If so, then the average range size may not be the most adequate measure of the data property that is influencing the slope of the regression curves obtained. A more sensitive measure of the influence of very rare species is the average range size for the 10% rarest species amongst the ones considered in each data set. The corresponding values for the different levels are: (*i*) 1.9%; (*ii*) 42.4%; (*iii*) 1.1%; and (*iv*) 19.3%. These are more consistent with the relative position of the curves in Figure 8.2*c*.

The relative position of the curves in Figure 8.2*a* also supports the prediction that higher levels of endemism result in higher slopes when the measure of endemism is the average range size for the 10% rarest species (Lesotho: 0.85%; N. Cape 1.04%; Mpumalanga: 1.88%; N. Province: 2.27%), but not when the measure is the average range for all species (Lesotho: 30%; N. Cape:

22%; Mpumalanga: 43%; N. Province: 40%). These results support the idea that it is the range of the rarest species that determines the slope of the relationship between the ratio of the number of species to the number of sites and the minimum percentage of total area needed to represent all species.

8.1.4 Implications for conservation planning

Our results demonstrate that the minimum percentage of area that would need to be reserved simply in order to represent all species within a region is highly variable and depends upon the diversity and endemism of the taxa of concern, and on the size of the selection units considered. This is supported by the analyses of data from various taxa and geographic regions (Figure 8.1), as well as by analyses manipulating data on the distribution of birds in Southern Africa (Figure 8.2).

Plainly, conservation requires *more* than just representation, however, these results have three important implications for practical conservation planning. First of all, they demonstrate that no single universal target for the minimum percentage of area that should be reserved (such as the 10% proposed by IUCN) can be appropriate. Instead, ecosystems or nations with higher species diversity and/or higher levels of endemism, such as the tropical ones, are expected to require substantially larger fractions of their areas to be reserved. This need is acknowledged in the main proposals of priority areas for global conservation (16 out of the 25 biodiversity hotspots, comprising 75% of the overall area proposed, include tropical biomes: Mittermeier et al. 1999; Meyers et al. 2000; and 76% of all Endemic Bird Areas are in the tropics: ICBP 1992; Stattersfield et al. 1998), but, unfortunately, is the opposite of the current situation (Pimm and Lawton 1998). For example, a higher percentage of the area of the species-poor tundra communities (7.5%) or mixed mountain systems (8.0%) is protected than of the rich tropical humid forests (5.1%), tropical dry forests/woodlands (4.7%) or tropical grasslands/savannahs (5.5%) (Hobbs and Lleras 1995).

Second, these results confirm that a minimum conservation network sufficient to capture the diversity of vertebrates will not be an effective umbrella for biodiversity in general (Kerr 1997; Howard et al. 1998), because many other more diverse groups with higher levels of local endemism (including plants and many groups of invertebrates) are expected to require considerably larger areas to be fully represented. Since in practice it is unlikely that data on the distribution of all species of concern in a given region will be available in the near future, this provides another reason why reserve networks must not be based solely on a minimum representation target of the well-studied species. The finding that higher levels of endemism result in the need to select larger areas supports the emphasis given by international conservation organisations to areas of exceptional concentrations of endemic species (as in the biodiversity hotspots, Mittermeier et al. 1999; Meyers et al. 2000; and in the Endemic Bird Areas, ICBP 1992; Stattersfield et al. 1998).

The third implication of these results is that considerable variation in the minimum percentage of the area required for representation of all species results from changing the size of the selection units. Conservation plans that consider the smallest possible selection units would greatly reduce the minimum percentage of area needed to *represent* all species: carried to an absurd extreme, the cheapest reserve network would adopt a Noah's Ark approach, by reserving only a few square meters to represent one pair of each species (Pimm and Lawton 1998). However, representation is not the same as conservation, and in order to ensure that the reserve networks selected fulfil their role of maintaining biodiversity over time, the size of selection units must be one at which the populations of species are likely to persist (recognising that for many species more than one unit in which they occur will be selected, which may be adjacent or not). This reinforces both the need for caution in the interpretation and implementation of the results obtained when selecting minimum complementary sets, and the belief that complementary reserve planning must take viability considerations into account (e.g., Chapter 4; Rodrigues et al. 2000*a,b*; Gaston et al. 2001; see also Fahrig 2001).

Treating the relationships in Figure 8.1 as representative, they can be used to predict what would be the minimum percentage of land area required to represent each species of terrestrial plant and higher vertebrate in a global or a tropical rain forest conservation network considering selection units of different sizes (Figure 8.3). In order to do so, the parameters of the corresponding logistic model obtained from the empirical data (Figure 8.1) have been used, and it was assumed that 24,500 higher vertebrates (mammals, birds, reptiles and amphibians) and 240,000 seed plants have been described (WCMC 1992), that at least 50% of all species exist in tropical rain forests (WCMC 1992; Wilson 1988), and that the area of land surface on earth (excluding Antarctica) is 133,149,000 km^2 (Good 1974) and of the remaining rain forest is c. 12,008,000 km^2 (WCMC 1992).

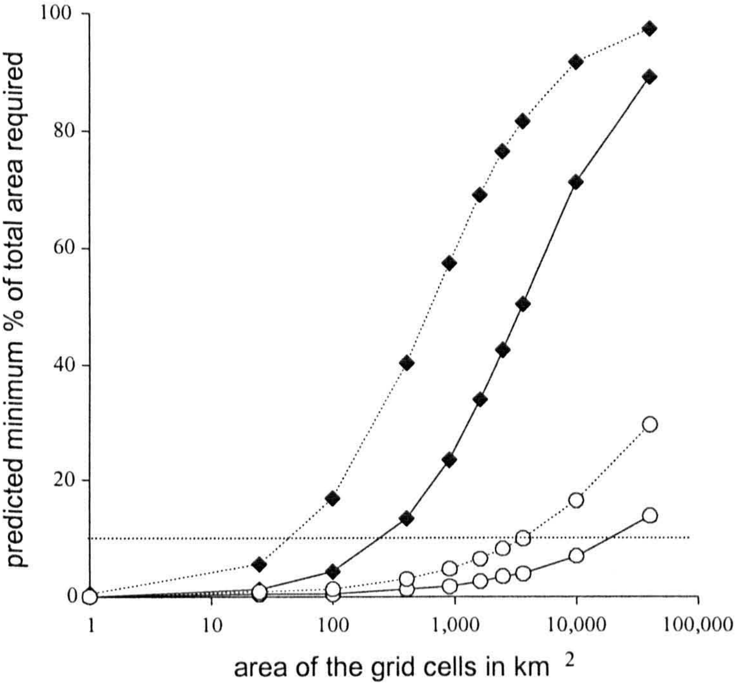

Figure 8.3 – Relationship between the size of the selection units and the predicted minimum percentage of area required to represent each species at least once, for seed plants (black diamonds) and higher vertebrates (open circles), at a global scale (continuous lines) or in the tropical rain forest (dashed lines; see text for details). The dashed horizontal line indicates IUCN's proposed 10% target.

Considering selection units of 1°×1° (c. 12000 km²), the finest resolution that has been considered practical for mapping bird species (the best known group) across an entire continent spanning the tropical zone (Fjeldså and Rahbek 1998), it is predicted that 74.3% of the global land area and 92.7% of the tropical rain forests would be required to represent every plant species once, and 7.7% and 17.8% for higher vertebrates (Figure 8.3). Although the values obtained for plants may seem high, they simply mean that, for example, in 92.7% of all 1°×1° cells across the tropical rain forest it is expected that at least one plant species exists that requires that cell or part of it to be selected. This may not be unrealistic given that high percentages of the tropical plant species described are known from single localities (e.g., 33.8% of neotropical plants in Andersen et al. 1997). The values obtained for the higher vertebrates are probably underestimated. The sites selected by complementarity tend to be highly scattered (e.g., Lombard 1995), and therefore isolated, and even reserves of this size (1°×1°) may not be sufficiently large for maintaining viable populations of many species. For example, even very large reserves such as Kruger National Park in South Africa (19,485 km²) and

Yellowstone in the United States (8,992 km^2) have lost or are in danger of losing some of their mammal species (e.g.Mattson and Reid 1991; Newmark 1987, 1996; Nicholls et al. 1996); and Manne et al. (1999) showed that a high percentage of American bird species with range of the size of a 1°×1° cell are threatened with imminent extinction.

Conversely, if the target was to reserve 10% of the total area, as suggested by the IUCN guidelines, selection units of 16.5×16.5 km for the world, or of 7.0×7.0 km for the tropical rain forest, would have to be considered to represent all plant species. Reserves of this size would undoubtedly be inadequate for maintaining viable populations of many (probably most) species, demonstrating that 10% of land area is indeed an insufficient target. Especially for species-rich areas with high levels of endemism, such as the tropical rain forest, a much larger fraction of the total area is needed if a significant fraction of species diversity is to be conserved into the future.

Further empirical data are needed to test how realistic the values obtained in this study are. But, meanwhile, these results reinforce the need for urgent conservation action, particularly in the tropical regions, where the protected area network needs to be large, little biological data exist to support decisions about the appropriate location of sites, little national political will and economic resources exist to invest in reserve acquisition and which continue to suffer high rates of habitat destruction.

9 Reserve selection algorithms in context

When this PhD research project started, it was already obvious the wide gap between the theoretical developments in complementary-based reserve selection algorithms and the practice of reserve planning. The purpose of this project was to contribute to reducing this gap by improving these tools in order to make them more applicable in practical terms (see Chapter 1). The emphasis was on exploring the flexibility of these methods for addressing a diversity of concerns of potential interest in practical applications (such as guidelines for addressing species persistence, Chapter 4; and for reserve selection in regions with poor biological data, Chapter 7), on drawing attention for limitations of complementary sets when used uncritically (such as potential biases, Sections 4.3 and 6.1; limitations in terms of ensuring species presistence, Sections 4.1 and 4.2) and test of surrogates (taxonomic diversity in representing evolutionary species, Section 5.1). Yet, after four years, although I believe that this research project provided valuable methodological developments, it did not contribute significantly to reducing the gap between the theory and practice of reserve planning.

The purpose of this final chapter is not to discuss the relevance of the findings in each of the previous chapters, which has been done at length elsewhere. Instead, its purpose is to try to shed some light on why the research made during this PhD, as well as that published in a few hundreds of other studies, is not being routinely applied to real-life reserve planning. It does so by analysing each one of the explanations that have been presented to why reserve selection algorithms are failing to have an impact in conservation practice, hoping that understanding these may perhaps help to reduce the gap between theory and practice.

9.1 Reserve selection algorithms: promises and problems

9.1.1 Introduction

Setting aside protected areas for conservation is urgently needed to counteract the current extinction crisis (e.g., Oates 1999; Terborgh 1999). Complementary-based reserve selection algorithms have been developed in recognition that such task needs to be done in ways which make the best possible use of the scarce resources available to conservation, maximising the return in terms of biodiversity conservation (see Chapter 1). Since they were first published (Kirkpatrick 1983), these methods have been increasing in popularity in the conservation literature (Pressey 2002). Their objectivity and scientific rigor gives them the potential to transform the way in which land is allocated and protected for conservation (Prendergast et al. 1999). And yet, despite holding such promise, they have had only limited application to practical conservation planning (Prendergast et al. 1999; Cabeza and Molainen 2001).

A number of explanations have been presented as to why reserve selection algorithms are failing to have an impact in conservation practice, and these fall into five general categories:

Explanation 1 – Reserve selection algorithms cannot be applied to regions where they are most needed (tropical countries with high diversity and archaic reserve networks).

Explanation 2 - Reserve selection algorithms are useless in those countries where they could be most applicable (developed countries with good biological data).

Explanation 3 - Reserve selection algorithms focus on representation of pattern, ignoring the processes that create and sustain biodiversity.

Explanation 4 - Reserve selection algorithms are too simplistic and do not account for all the social, economic, and political aspects of real-life planning.

Explanation 5 - Reserve selection algorithms are not easily accessible to conservation practitioners.

Here, I analyse each one of these explanations, review the published literature on reserve selection algorithms to understand how they have addressed the problems identified, and suggest developments needed to improve the utility and applicability of these methods as decision-making tools in practical conservation planning.

9.1.2 Explanation 1 - Reserve selection algorithms cannot be applied to regions where they are most needed (tropical countries with high diversity and archaic reserve networks)

Given the urgency of the current biodiversity crisis, in most parts of the world conservation planning requires 'quick and dirty' methods (Ehrlich 1992). Perhaps the most commonly observed limitation of reserve selection algorithms is that they are data hungry, requiring massive high-quality data on species ranges (Prendergast et al. 1999; Pimm 2000; Cabeza and Moilanen 2001; Peres 2002). This seriously limits the possibility of their application to those parts of the world where they are most urgently needed, and where there is higher scope for their application (Pimm 2000; Ferrier 2002): biologically rich tropical countries, many with still archaic reserve networks (Balmford and Long 1995), where existing biological information is highly biased and fragmented (e.g., Patton et al. 1997; Kress et al. 1998), and where current threats mean that habitats will be lost before we even glimpse what taxa they contain, let alone map them (Pimm 2000). Authors have therefore called for "new approaches that build on data currently available, rather than on idealised comprehensive knowledge" (Peres 2002).

While any conservation evaluation of tropical regions will be limited by the availability of quality data, it is commonly assumed that this is a particularly serious problem for complementary-based reserve selection algorithms. This is probably because they have been developed in countries where such resources tend not to be a critical issue (Prendergast et al. 1999), and because the majority of the published analyses use quite impressive data sets, mainly from developed countries (e.g., Williams et al. 1996*a*; Csuti et al. 1997; Howard et al. 1998; Rodrigues et al. 2000*a,b*; Williams et al. 2000*c*; Araújo et al. 2001; Brooks et al. 2001*a*; Gaston et al. 2001; Pressey and Taffs 2001; all datasets used in this thesis). That most published papers in international journals originate from developed countries is, of course, not exclusive to reserve planning algorithms (e.g., 83% of the papers submitted to *Conservation Biology* in 2000 were from authors based in the U.S., Europe or Australia, despite explicit intentions of the editorial board to invert this tendency; Meffe 1998*a*; Meffe 2001). Not only do authors from these countries generally have better conditions in which to perform high-quality research, the very nature of scientific publishing means that analyses based on the best data sets will always be more publishable than those using sketchy data.

However, it is not true that reserve selection algorithms, more than other planning methods, can only be applied to high-quality data sets with accurate information on each species' distributions (see below). What they do require is that the relevant information (even if only expert judgement) is spatially referenced before the planning process begins – conservation planning is a spatial exercise, and therefore needs to be based on spatial surrogates of biodiversity (Margules and Pressey 2000). Also, prioritising areas means comparing candidate areas, so the data used to make such comparisons should be comparable in quality and quantity (Williams et al. 2002). This means a preparatory stage that in other less explicit planning methods (say, putting a number of experts in a room to agree on a map of priority areas) is perhaps too often avoided. Going through the process of reviewing and spatially referencing all the information, as well as data treatment to minimise biases, is time consuming, and makes acutely obvious many of the gaps and biases in the existing data, perhaps discouraging planners from using these methods (Stoms et al. 1997; Davis et al. 1999). However, conservation planning must nevertheless proceed despite these gaps and biases, and it is better that they are acknowledged explicitly, rather than hidden under a subjective planning process.

Making the best use of existing data

Even for the best-studied parts of the world, data sets are imperfect, containing collection biases and inaccuracies in mapping and reporting. Additionally, for no part of the world is there a complete inventory of all of the biodiversity patterns and processes of conservation concern. As a result, conservation planning needs to make the best possible use of the available information, and must inevitably be based on surrogates for biodiversity (see below) that are only partially effective. Perfect information is neither a choice for managers nor a prerequisite of complementarity-based algorithms (Pressey and Cowling 2001; Ferrier 2002). The main challenge is not on the limits of our lack of knowledge, but our failure to synthesise and distribute what we do know (Pimm et al. 2001).

Species are usually considered the most basic, recognisable units in biodiversity and therefore species distributional data is ultimately the most appropriate in conservation planning (Mittermeier et al. 1999). Some authors have, however, called for the need to conserve ecosystems either as biodiversity features in their own right (Noss 1996), or because an ecosystem-based approach is the only way to conserve organisms and processes in poorly known or unknown habitats and ecological subsystems (Franklin 1993). A unifying approach is that both ecosystems and species need to be protected; ecosystems because species need them in the short term, and species because they make ecosystems in the long term (Lawton 1997).

Although most published analyses use species distributional (presence/absence) data, complementarity-based reserve selection algorithms have the flexibility to accommodate virtually any type of data that can be spatially referenced. This is particularly desirable given the increasing availability of extensive layers of biotic and/or abiotic data. Particularly relevant to poorly studied areas is the possibility of using data that can be obtained rapidly and cheaply for wide areas (e.g., through remote sensing) to complement finer (however incomplete) data on the location of particular features, such as species (Ferrier 2002).

Types of data that have been used in published studies include:

- Species distribution data, either mapped as point data (e.g., Lombard et al. 1997), in grid cells (e.g., Williams et al. 1996*a*; Csuti et al. 1997; Fjeldså and Rahbek 1998; Brooks et al. 2001*a*), or associated with polygons (e.g., forest tracts, Howard et al. 1998; islands, Chown et al. 2001; wetlands, Turpie 1995, Rodrigues et al. 1999, data on the distribution of wetland species in fens used in Section 3.2);

- Species distribution data having some information on the structure of ranges, given by measures such as reporting rates (e.g., Gaston et al. 2001; the SABAP data set used in several of this thesis' chapters), census data (e.g., Turpie 1995; Rodrigues et al. 2000*a,b*, the Common Bird Census data used in Sections 4.1 and 4.2), or probability of persistence (calculated from presence/absence data, e.g., Williams and Araújo 2000);

- Species distribution data in which environmental information is used to extrapolate from known records (see Ferrier 2002 for a review) either through expert opinion based on species' habitat requirements (e.g., Fjeldså and Rahbek 1998; Polasky et al. 2000), or by modelling species' distribution (see da Fonseca et al. 2000; Faith et al. 2001*a,b,c*; Williams et al. 2002);

- Maps of vegetation or land cover types, which can be obtained using satellite imagery (e.g., Stoms et al. 1997; Clark and Slusher 2000);

- Environmental data, either used directly (e.g., Faith et al. 1996; Faith and Walker 1996; Araújo et al. 2001; Faith et al. 2001*a,b,c,d*) or to derive and map environmental units (e.g., Pressey et al. 1996*a*).

One important source of flexibility in complementary-based algorithms is that different layers of information can be used simultaneously, with different conservation goals set accordingly. For example, Pressey (1998) used both maps of forest type and maps of plant and vertebrate species distribution; Cowling and Pressey (1999) used distribution maps for Red Data plant species and maps of land classes; and Stoms et al. (1997) combined coarse-filter data on land cover type (based on vegetation alliances mapped from Landsat satellite imagery) and fine-filter point data on occurrences of rare elements (vertebrates, invertebrates, plant species and some rare plant associations); Faith et al. (2001*a,b,c,d*) combined modelled species distributions, "domains" summarising bioclimatic and other data, and vegetation types. Each data layer brings new information and helps compensate for the weaknesses of others.

An additional source of flexibility, albeit one that has not been much explored in the published literature, is that not only different targets but also different levels of information can be used for different biodiversity features (see Section 2.1; Rodrigues et al. 2000*c*). For example, it is usually the case that species data (on distribution, ecology, conservation status) are particularly good for some species (such as flagship species attracting higher conservation investments) and generally poorer for most of the others. Reserve selection algorithms can make good use of this unbalanced data. Consider a hypothetical example in which for a given species there is good census data and a population viability analysis has been made, resulting in the recommendation that a population of 1,000 individuals be conserved; for another species there is only general distributional data and the knowledge that it is threatened. It would be possible to obtain a reserve network representing at least 1,000 individuals of the first species and, say, 80% of the range of the second one.

As with any other analytical procedure, reserve selection or otherwise, the quality of the results depends directly on the quality of the input data, and there is no algorithm, however sophisticated, that can extract good results from bad data (the GIGO rule of computational science: "Garbage In Garbage Out"; Rosing et al. 2002). In particular, it is important to be aware that biased data will inevitably produce biased results. Better data about one particular species means that the reserve network selected will address particularly well the conservation needs of that species, while better data for particular sites (e.g., more complete species lists) means that it is likely that those sites show up as priority. This is by no means exclusive to complementary-based algorithms: many reserves are selected targeting the protection of particular species (several examples in Caughley and Gunn 1996), and in poorly known regions many reserves are created around existing biological stations (examples in Brandon et al. 1998).

These problems can and should be minimised by proper data treatment to correct for biases and gaps in information (see Williams et al. 2002 for a review). Doing so requires a good understanding of the effects of data quality on the results of reserve selection algorithms, and some research has already been done in this regard. For example, Freitag et al. (1996) compare the effects of using primary point data and derived distribution maps; Freitag and van Jaarsveld (1998) evaluated the sensitivity of selection procedures to survey extent, survey intensity and taxonomic knowledge; Freitag et al. (1998*a*) tested the effect of survey bias towards roads and nature reserves; Gaston and Rodrigues (in press) compared the results obtained with data obtained by variable sampling effort (see Chapter 7). Additionally, all the published studies that tested the use of surrogates (see below) are also testing for the effects of data quality (e.g., using data on more or less species). More analyses are needed, which will improve the methods for data pre-treatment, and understanding and judgement of results obtained from poor and biased data.

Accessibility of existing data

There are countless valuable data not readily accessible to conservation planners. They may exist only in the heads or field notes of experts, in inaccessible grey literature such as project reports, or scattered throughout the world in museum records. The bottom line is: while they remain inaccessible, they are useless to conservation practice. Even more so because when conservation planning does takes place, it is usually within a specific political or social context, and more often than not it is expected that the results are obtained within a short period, precluding long preparative stages of data compilation.

To ensure that existing biological data are accessible to conservation planners, proactive measures of systematic compilation and geo-referencing of these data are urgently needed. Examples of such measures include the joint project by Conservation International's Center for Applied Biodiversity Science (CABS-CI) and the National Center for Ecological Analysis and Synthesis at the University of California, Santa Barbara (NCEAS) to map the world's terrestrial vertebrate species and to make the information freely, publicly and electronically available (http://www.nceas.ucsb.edu/). An example at the governmental level for a megadiverse country is CONABIO's (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) continuing efforts to assemble distributional information on Mexican species (National Information System on Mexico's Biodiversity; Sistema Nacional de Información sobre Biodiversidad de México; http://www.conabio.gob.mx).

On the other hand, there are circumstances where existing data have been compiled and are ready to use, but are not made accessible to the public, for example due to tensions between data providers (e.g., museums; governmental organisations) and data users (such as non-governmental organisations; da Fonseca et al. 2000; Brooks and Thompson 2001; Rodrigues 2002). This is particularly unacceptable in circumstances where such data have been collected using public funds, grants for conservation projects, or the generous work of volunteers hoping to make a difference. In some countries, public institutions are legally bounded to ensure freedom of access to, and dissemination of, information they hold on the environment (e.g., EU Directive 90/313/EC; UNECE Aarhus Convention). But scientists share part of the responsibility. Indeed, while much field research is justified, and funded, on the promise that it will provide important information for biodiversity conservation, the pressure for publishing may reduce researchers' willingness to provide the raw data to what they may perceive as "competition". With due respect for copyright and authorship, governmental and non-governmental funding agencies need to make sure that funding of "conservation projects" is subject to agreeing to actively disseminate the results obtained and provide access to the data collected. For example, the Brazilian state agency FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, http://www.fapesp.br/) funds projects for the inventory and characterisation of biodiversity in the State of São Paulo under the condition that the all the biological data obtained will be presented in a standard format and immediately incorporated into the State's Environmental Information System. Measures such as these are needed to maximise the return from the scarce conservation resources allocated to data collection.

New data collection

Because the quality of the results of reserve planning is so unavoidably linked to the quality of the underlying data, investment in data collection – especially in biodiversity rich tropical countries – is badly needed; unfortunately, it is also chronically under-funded (da Fonseca et al. 2000). Although the investment is economically worthwhile, given the improved efficiency in planning it brings (Balmford and Gaston 1999), in practice data collection can be prohibitively expensive and resource-demanding, and therefore often impossible to make before conservation opportunities are lost (Whitten et al. 2001). Some published data on costs of biological surveys include:

- US$1,716/ha to US$8,466/ha for fauna and flora surveys in Australia (Burbidge 1991 in Belbin 1993);
- US$1 million and 100 person-years for a survey of five taxa across 15,000 km2 of forest in Uganda (Howard et al. 1997, 1998; Balmford and Gaston 1999);
- Four years and about 100,000 hours of field work to map bird presence/absence in each of the 3672 10×10 km grid-squares in Britain and Ireland (Gibbons et al. 1993).
- Fifty scientist-hours required for birds (78 species), 150 for butterflies (132), 160 for canopy ants (96), 160 for leaf-litter ants (111), 600 for flying beetles (358), 1,000 for canopy beetles (242), 2,000 for termites (114) and 6,000 for soil nematodes (347) in a sampling effort for an inventory of a number of taxa across a gradient of habitat modification in a Cameroon (Lawton et al. 1998). The inventory was only partial (i.e., not all species present were inventoried) for most groups. The cost increased dramatically for the richest, most specious groups.

An important line of research is therefore on the development of rapid and cheap methods to characterise entire ecosystems (Ehrlich 1992), maximising the amount of information that can be collected under limited economic and human resources (e.g., Oliver and Beattie 1993, 1996; Margules et al. 1994*a*; see also Williams et al. 2002 and references herein) and making the best use of the already available information to decide on the location of new survey sites (Ferrier 2002). Gaston and Rodrigues (in press) found that complementary reserve networks for birds based on data collected by presence-absence low sampling effort were quite effective in representing overall bird species richness, including in the representation of peaks of abundance (see Chapter 7). These results give support to projected low-sampling surveys in tropical countries (Rodríguez and Sharpe 2002).

Surrogates

As the recent collapse of the planned world's first All-Taxa Biological Inventory (ATBI) in Costa Rica demonstrates (Kaiser 1997), the complete inventory – even more the mapping – of biodiversity would be an overwhelming task for any country, developed or not (Franklin

1993). This means that in every part of the world systematic conservation planning has no other alternative than to be based on surrogates (Prendergast et al. 1999). However, not all surrogates are likely to have the same power to represent overall biodiversity, but little is known about which surrogates are expected to do better. Accordingly, selection of surrogates usually remains a matter of using whichever data are available and/or can realistically be collected (e.g., Ehrlich 1992). Nevertheless, guidance on which surrogates can be more cost-effective for conservation planning would be precious to guide future efforts in data acquisition, as well as how to combine existing available information.

Ideally, tests of surrogacy value would measure how well areas selected using a particular surrogate (e.g., subsets of taxa, species assemblages, environmental diversity) perform in terms of representing overall biodiversity. But without a complete knowledge of biodiversity, this is an impossible task in itself, and therefore real tests of surrogacy are actually cross-surrogate congruence analyses – tests of how well a given surrogate performs in representing another one. Given the emphasis on species as conservation units (Mittermeier et al. 1999), most surrogacy analyses focus on evaluating how particular surrogates perform in representing species diversity of known taxa.

Except at a global scale (where most taxonomic diversity tends to increase towards the tropics; see Gaston 2000 for a review) most studies have found little correlation between species richness and/or spatial overlap between diversity hotspots for different taxa (e.g., Prendergast et al. 1993, Gaston 1996*b*; Lawton et al. 1998). However, hotpots of species richness do not generally correspond to complementary areas (e.g., Williams et al. 1996*a*), and therefore these results are not necessarily informative of how well networks of complementary areas representing species diversity in one taxon perform in representing species diversity in others.

There is a growing number of studies analysing cross taxon complementary surrogacy. Results are mixed, but not straightforward to interpret because of the use of different measures of surrogacy (see Reyers and van Jaardsveld 2000). Overall, studies that compared spatial coincidence between complementary sets found little to moderate overlap (e.g., Dobson et al. 1997; van Jaarsveld et al. 1998, Reyers et al. 2000; Lund and Rahbek 2002), little similarity was found in the complementary sequences of areas for different groups (see Gaston 1996*a* and references herein), while studies comparing how much of a taxon's diversity is represented in complementary areas selected for another group give a somewhat more optimistic picture (e.g., Howard et al. 1998; Reyers et al. 2000; Moritz et al. 2001). The most informative measure of surrogacy is this last one (Balmford 1998), which is not dependent on the particular complementary solution found (usually only one of many; e.g., Arthur et al. 1997; Hopkinson et al. 2001; Rodrigues and Gaston 2002*a*; see Figure 5.3 in Chapter 5).

Besides cross-taxon surrogacy, other forms of complementary surrogates tested include: selected sets of species (e.g., flagship, threatened, endemic) in representing overall species for the same taxon (e.g., Andelman and Fagan 2000; Williams et al. 2000*a,b*; Bonn et al. in press); higher taxa (such as genera, families) in representing species (e.g., van Jaarsveld et al. 1998; Balmford et al. 2000*b*; Fjeldså 2000); taxonomic (generic) diversity in representing phylogenetic diversity (Polasky et al. 2001*b*; Rodrigues et al. 2002*a*; see Chapter 5); species diversity in representing intraspecific genetic diversity (Moritz and Faith 1998); and complementarity in environmental space in representing species richness (Faith and Walker 1996; Araújo et al. 2001). Again, these analyses have used a diversity of measures to evaluate surrogacy, complicating the interpretation of the results.

Because each of these analyses is simply a test of a particular surrogate against others, none will provide "proof" or "disproof" of the true value of each surrogate in representing overall biodiversity. In this sense, the results obtained in each case can only be interpreted as anecdotal evidence. Nevertheless, a number of such analyses taken together may eventually start giving a clearer picture of which (if any) surrogates perform consistently better (and perhaps to understand why) which can provide guidance to conservation planning desperately in need of shortcuts. Further analyses, based on appropriate surrogacy measures, should therefore be a high research priority.

Meanwhile, Faith et al. (2001*b*) suggest adopting as many surrogates as possible (e.g., species, communities assemblages, environmental variation) to maximise the likelihood of representing more biodiversity in selected priority areas. Ferrier (2002) suggests incorporating into conservation planning knowledge of heterogeneity within, and distinctiveness between, surrogates obtained from remote environmental mapping such as land classes.

Are decisions obvious?

One line of argumentation as to why reserve selection algorithms are not useful for the conservation of tropical countries, is that in many places where reserve selection is really urgent, the decisions are obvious and do not require elaborate analysis to be identified (Western 1992; Prendergast et al. 1999; Pimm et al. 2001).

There seems to be little disagreement that for highly threatened places, such as the Sumatran lowland rainforests, the Phillipines moist forests and the dry forests of New Calledonia, all efforts should focus on immediate conservation action to protect *all* the last remaining tracts. As Olson et al. (2002) put it, "in these places, recommending new biological surveys or more refined reserve-selection algorithms is akin to fiddling while Rome burns". The controversy arises in relation to those places where substantial natural habitat still remains.

Pimm et al. (2001) countered that "*all* remaining habitats across the species-rich tropics must be priorities, ones that do not depend on our knowing the scientific names for 1 of 10, or the geographical distributions of 1 of 100 species, or not having resolved complex issues of reserve selection". The problem with this argument is that expecting that it will be possible to protect all of those areas is unrealistic. They are still huge areas, sometimes spanning entire countries (Whitten et al. 2001), and they are full of people (Cincotta et al. 2000; Musters et al. 2000).

In a recent analysis, Bruner et al. (2001*b*) estimated that protecting one third of the remaining Wilderness Areas and of the Biodiversity Hotspots (Myers et al. 2000) would cost around $19 billion (see also James et al. 1999; Balmford 2001; Bustamante 2001), a bargain in the global economy. They further estimate that such an investment would protect perhaps 70% of the total global biodiversity on roughly 2% of earth's land, an estimate based on the assumption that 70% of the Wilderness Areas' diversity and 90% of the total Hotspots' diversity would be covered in this way. These analyses demonstrate how a well-targeted strategic investment could protect a high fraction of the global biodiversity. However, within each Hotspot there is certainly a number of possible ways of combining sites to obtain one third of the total area, and it is unlikely that any of these would retain 90% of the Hotspot's diversity. Selecting the best one-third would be a matter of careful conservation planning that would require making use of the best available information.

Hence, even for the highly threatened global Biodiversity Hotspots, the best course of action for protecting biodiversity is not necessarily obvious, and conservation biology has a critical role in identifying what needs to be accomplished and in what order of priority (Olson et al. 2002). As Lawton (1997) puts it "conservation action without good science to underpin it is like alchemy, or faith healing. Both sometimes produce desirable results, but you have no idea why, and mostly they do not".

9.1.3 Explanation 2 - Reserve selection algorithms are useless in those countries where they could be most applicable (developed countries with good biological data)

The flip side of the argument that reserve selection algorithms are excessively data-hungry, is that the developed countries with extensive biological data are the ones where its application makes more immediate sense. However, it has been argued that for these countries the answer does not matter any more (Pimm 2000), as here reserve networks have already been implemented, and there is no longer an option for the selection of key biodiversity areas on the basis of optimality informed by exhaustive biological inventories and the best conservation science (Peres 2002).

The following sections review four ways in which complementarity-based reserve selection can be useful for conservation planning, even in countries with extensive national reserve systems, and how some of those exercises can bring useful information for the conservation of data-poor-biodiversity-rich regions.

Not quite finished yet - gap analysis and the designation of new protected areas

While it is undoubtedly true that conservation effort is much more urgent in developing countries than in developed ones, there is no single country in the world where conservation planning is no longer needed. On one hand, biodiversity is in trouble everywhere, even in those countries where conservation is high in the political agenda and in the public's heart (e.g., bird conservation in the U.K.; RSPB et al. 2001). On the other hand, virtually all studies that evaluated the effectiveness of existing reserves in developed countries found gaps in the representation of species or other biodiversity features (e.g., Castro Parga et al. 1996; Ferrier et al. 1996; Williams et al. 1996*a*; Nantel et al. 1998; Scott et al. 2001). Indeed, the mere existence of the Gap Analysis Program in the US (a cooperative state-federal program established in all the 49 of the continental States; Scott et al. 1993; Caicco et al. 1995; Kiester et al. 1996; Jennings 2000; Scott et al. 2001) proves that even in the richest country in the world reserve planning is not yet a completed task.

While from a global conservation perspective it would be better that such investment was diverted to the tropics (Pimm 2000), in practice that is not going to happen. And since no country in the world is devoid of biodiversity, it is better that the planning in these countries is done as effectively as possible, and this is where complementarity-based reserve planning is proving to be useful (e.g., Davis et al. 1999). Equally important, conservation action in these countries is a fundamental way of raising awareness and funding that can make a great difference for conservation elsewhere (for example, 45% of Conservation International's $83.8 million total revenue in 1999 was obtained through individual contributions; Conservation International 1999).

While most reserve planning in developed countries consists of the expansion of existing networks, it is not entirely impossible that new reserve networks are created from scratch. That is indeed the case with the ongoing implementation of the Natura 2000 network in the European Union (http://europa.eu.int/comm/environment/nature/home.htm), whose purpose is to protect the diversity of species and habitats (with an emphasis on priority ones) in the EU's territory. This is a real planning exercise with characteristics that many would consider possible only in the heads of reserve planning scientists out of touch with real life:

- First, although many of the Natura 2000 sites coincide with previously existing reserves, it was an explicit rule that designation of new areas would have to be independent of prior classification systems (such as National Parks).

- Second, it was explicitly forbidden to take social or economic considerations into account in the designation process, only biological criteria could be considered. Failure to comply with this rule took a few countries to the European Court of Law.

- Third, the Natura 2000 sites are not paper parks. Indeed, in some countries they may very well be among the most strictly protected reserves, thanks to the ruling of the Habitats Directive. Hence, Member States cannot allow the deterioration of sites for the species/habitats for which they were designated. In particular, any project likely to have a negative effect on a given site needs to go through an environmental impact assessment. If negative impacts are predicted, the project can only be carried out if there are no alternatives and only for "imperative reasons of overriding public interest". Even then, the Member State shall take all necessary compensatory measures. Again a number of countries has already been taken to the European Court of Law for breaching these rules. The inclusion of sites designated under the Birds Directive in the most recent United Nations List of Protected Areas recognises the competence which the EU has in the field of conservation (UNEP-WCMC 1997).

While the implementation of the Natura 2000 Network is far from being smooth, it is nevertheless the most ambitious supranational initiative for nature conservation worldwide (Weber and Christophersen 2002). Potentially, it would have been one of the best conceivable applications for reserve planning using complementarity-based algorithms. The designation procedure is mainly finished now, and without information on the methods each Member State applied it is impossible to evaluate whether they employed anything remotely similar to these planning tools. Nevertheless, the future integration of Eastern European countries into the EU will provide another opportunity – if scientists and managers find a common language to do so.

Evaluation of existing reserve systems

The fact that reserve networks have usually been established earlier in the developed countries provides the opportunity for some lessons to be learnt on how they should be selected for maximum effectiveness, reducing the likelihood of repetition of certain mistakes in those countries with incipient networks. For example, well-recorded population extinctions in reserves of developed countries can provide valuable insights on minimum area requirements for individual reserves (e.g., Gurd et al. 2001) and the influence of the matrix for species retention (e.g., Parks and Hartcourt 2002). Also, the evaluation of entire reserve networks can provide insights into the typical biases made in reserve selection and how to avoid them (e.g., Pressey 1994).

While some initial evaluations of existing reserve systems were simplistic, made by strict comparison with minimum complementary sets representing each species once (see Section 3.2 and Rodrigues et al. 1999, for a review and critique), recent methods present much more balanced and integrated approaches (Pressey and Taffs 2001; Pressey et al. 2002), including measures of representativeness, bias and vulnerability.

Regional land use planning

Only a small conceptual jump is needed to see the potential for application of complementarity-based tools to land use planning activities such as the design of management zones within reserves (Pressey 1999; Pressey and Cowling 2001) or the comparison of alternative development scenarios (a legal requisite for Environmental Impact Assessments in the European Union). Little work has been done in this regard, but the studies of Faith et al. (1996) and Faith and Walker (2001*a*) on the trade-offs between biodiversity and forestry production are good examples of how these methods can be applied to regional land-use planning. See also Williams and ReVelle (1997) for a discussion on the use of mathematical programming to forest planning and land use allocation.

Development and test of general guidelines

Probably one of the best contributions that case-studies in data-rich-biodiversity-poor countries can give to global biodiversity conservation is the use of their extensive data sets for the development and assessment of reserve selection guidelines that can be applied to data-poor-biodiversity-rich countries. With due caution when extrapolating results obtained in temperate regions to tropical ones, these data sets can be used to analyse, for example: the performance of various types of surrogates; the influence of data sampling effort and bias in the results (see section 9.1.2 above); and methods and rules of thumb for including viability concerns in the selection of reserve networks based on presence-absence data only (see section 9.1.4 below).

9.1.4 Explanation 3 - Reserve selection algorithms focus on representation of pattern, ignoring the processes that create and sustain biodiversity

One of the major criticisms to complementary reserve selection algorithms is that, being pattern-based (Moritz 2002), they may generate only short-term solutions to long-term conservation goals (Balmford et al. 1998). Because they tend to be based on simple snapshots of where different organisms are found at a particular time, while they may ensure the representation of species (or other biodiversity features) in the reserve networks at the time of their selection, they give no guarantees of their continued persistence, which is the reserves' purpose in the first place (Balmford et al. 1998; Pimm and Lawton 1998; Prendergast et al. 1999; Mace et al. 2000; Curio 2002).

Indeed, it has been demonstrated that minimum complementary sets selected to represent each species once may lose an important fraction of their species as a result of species temporal turnover (see Chapter 4; Margules et al. 1994*b*; Virolainen et al. 1999; Rodrigues et al. 2000*b*,*c*). One of the most valued traits of complementary sets – their efficiency in representation – may actually be responsible for a low effectiveness in species retention over time, as there is a trade-off between these two properties (see Chapter 4; Rodrigues et al. 2000*a*,*b*). The size of the selection units considered plays an important role in this trade-off: small selection units greatly reduce the minimum percentage of area needed to represent all species, therefore increasing network efficiency; however, the size of selection units must be one at which populations are able to persist, which improves long-term effectiveness but at a cost of lower efficiency (Rodrigues and Gaston 2001; see Chapter 8). Additionally, species representation in complementary sets is typically maximised by the selection of highly scattered sites (e.g., Figure 6.2; Williams et al. 1996*a*; Csuti et al. 1997; Fjeldså and Rahbek 1998; Brooks et al. 2001*a*; Gaston et al. 2001), and unless each of the individual sites holds viable populations of the species represented there, this configuration is likely to compromise species persistence, especially as matrix alteration means that reserves become more and more isolated. Furthermore, the efficiency of complementary sets is at least partially obtained by representing species in areas of transition, with species assemblages resultant from a mixture of floras or faunas belonging to different ecological regions (Balmford et al. 1998; Gaston et al. 2001). This explains the finding by several authors that minimum complementary sets tend to represent species at the edges of their ranges (see Sections 4.3 and 6.1; Branch et al. 1995; Nicholls 1998; Araújo and Williams 2001; Rodrigues and Gaston 2002*c*), and brings even greater concern that these areas may be unsuitable to ensure species persistence over time.

To maximise both current representation and long-term persistence, reserve selection algorithms need to address the key ecological and evolutionary processes which generate and maintain biodiversity (Western 1992; Mace et al. 2000). These operate at a diversity of spatial and temporal scales. Hence, while the local and short-term persistence of a given species may be mainly dependent on trophic interactions, its persistence on an ecological time scale of years may depend on the maintenance of metapopulation dynamics, while on an evolutionary time scale of thousands to millions of years species' persistence depends on evolutionary processes such as adaptation to changing environmental conditions. Because reserve planning is a spatial exercise, addressing those processes needs to be based on their spatial surrogates (e.g., size of reserves, watershed boundaries, migration routes) rather than the processes themselves (Margules and Pressey 2000; Balmford 2002). But recommending that consideration for processes be incorporated into reserve design is easier said than done (Flather et al. 1997; Balmford et al. 1998). The difficulty – again, not only for reserve selection algorithms but for any reserve planning method – is the current lack of robust measures for quantifying the extent to which different areas contribute to core processes, or for evaluating the overall performance of priority sets in terms of process maintenance (Mace et al. 2000). As a result, the integration of process maintenance in systematic reserve planning is made via some more or less established guidelines, more or less solidly rooted in ecological and evolutionary theory (Margules and Pressey 2000).

Although minimum complementary sets representing each species once are popular in the literature (e.g., Sætersdal et al. 1993; Kershaw et al. 1994; Margules et al. 1994*b*; Lombard et al. 1995; Castro Parga et al. 1996; Williams et al. 1996*b*; Csuti et al. 1997; Pressey et al. 1997; Hacker et al. 1998; Nantel et al. 1998) they are probably the least interesting of the outputs that can be obtained using complementarity-based reserve selection algorithms. The algorithms' flexibility (see Section 2.1; Rodrigues et al. 2000*c*) means that they can integrate a diversity of concerns related to the maintenance of biological processes – as long as their spatial surrogates are well understood (Balmford 2002). This section presents an overview of how concern for a diversity of processes has been, or can be, integrated in complementarity-based reserve planning. The list of processes mentioned is not exhaustive, and the classification used is a simplification, as they merge into each other at multiple temporal and spatial scales. Except for anthropogenic climate change, only natural (ecological and evolutionary) processes have been considered here. Other anthropogenic processes are considered in the following section 9.1.5.

Processes at narrower temporal and spatial scales

Not all areas within the range of a species are the same (Lawton 1993; Brown et al. 1995*b*): there are textures of abundance within geographic ranges (Lawton 1993), and these are created and maintained by ecological processes which can be broadly classified into intraspecific population dynamics and interspecific interactions.

Intraspecific population dynamics

There are several reasons based on intraspecific population dynamics that can explain why a species may be recorded at a given place but fail to persist there even at relatively short temporal scales (as in Margules et al. 1994*b*; Virolainen et al. 1999; Rodrigues et al. 2000*a*,*b*: see Sections 4.1, 4.2). First, species' ranges are naturally dynamic, especially at their edges (Hengeveld 1990). As a result, a species may occur only intermittently at a given place, which is not unusual in species with high dispersal abilities such as birds or butterflies (e.g., Thomas et al. 1998). In extreme situations, the species may simply be a vagrant (see Chapter 6; Rodrigues and Gaston 2002*c*), but it may also occur more or less regularly in response to variable ecological conditions (e.g., changes in the edges of bird ranges following harsh winters; Mehlman 1997).

Second, the selected area may be a sink habitat, which is not self-sustaining (local reproduction is insufficient to balance local mortality) but may be locally maintained by continued immigration from nearby source populations (Pulliam 1988). A reserve encompassing only the sink habitat will not retain the species if the neighbour source habitat is lost (e.g., Powell and Bjork 1995; Safford 1997; Stotz 1998; Hansen and Rotella 2002; see also Gaston et al. 2002).

Third, for some species, especially those depending on ephemeral habitats, population extinction and recolonisation within the time scale of just a few years are natural phenomena in their population/metapopulation dynamics, as individuals track the most favourable habitat patches (e.g., checkerspot butterfly, Ehrlich 1992).

Finally, a reserve may contain a population which is below a minimum viable number and which is therefore at imminent risk of extinction due to demographic stochasticity, environmental stochasticity, genetic drift and/or inbreeding depression (Caughley 1994).

In an ideal world, population viability analyses would be made for each species in each of the candidate sites, and reserves would be placed only on sites encompassing viable populations/metapopulations. This approach is currently prohibitive due to the huge amount of data it would require (Cabeza and Moilanen 2001).

Despite these difficulties, population dynamics processes are better understood and easier to address than other processes (see below), as they tend to occur at narrow temporal and spatial scales. Accordingly, the main emphasis on incorporating processes in reserve selection algorithms has been on these, and a number of shortcuts have been proposed to address them in the selection of reserve networks, including:

- Selecting large areas (e.g., Balmford et al. 1998; Cowling and Pressey 2001; Gaston et al. 2002), clustered sites (e.g., core areas and buffer zones, Williams and ReVelle 1996, 1998), and/or connected networks (e.g., Williams 1998*a*; Briers 2002). This strategy is firmly rooted in the theory of island biogeography (MacArthur and Wilson 1967) and its purpose is to ensure that (individually of together) reserve networks will be sufficient to maintain viable populations/metapopulations of each species. Ensuring the viability of top predators is often a main concern motivating the selection of large/connected areas (e.g., Noss et al. 1996; Cowling and Pressey 2001). Depending on species' ranges and dispersal abilities, metapopulation dynamics may occur at the scale of only a few square kilometres (e.g., Glainville fritilary, Hanski 1998) – easily accommodated inside a small reserve – to thousands or even or millions of square kilometres (e.g., polar bears; Ferguson et al. 1998) – requiring a continental approach. Moilanen and Cabeza (2002) is perhaps the only published study that explicitly integrated metapopulation dynamics in the selection of reserve networks aiming at optimising persistence, but it is applied to the conservation of a single butterfly species. Hanski (1998) defended the need for further work to extend the single-species metapopulation models to multispecies communities, to merge the spatially explicit and dynamic metapopulation models with non-dynamic site-selection algorithms used in conservation, and with models of habitat connectivity used in landscape ecology.

- Ensuring multiple representation of each species or other biodiversity feature in the reserve networks (e.g., Margules et al. 1988; Pressey and Nicholls 1989*a,b*; Rebelo and Siegfried 1992; Williams et al. 1996*a*; Willis et al. 1996; Freitag et al. 1998*a*; Rodrigues et al. 2000*c*; Gaston et al. 2002; see also Section 4.2). Nicholls (1998) went further in suggesting spreading the selected sites as uniformly as possible across the region of interest or across the range of the individual species. This strategy – which in economics is known as bet-hedging and in common sense translates into "not putting all the eggs into the same basket" – reduces the probability that each species will go extinct from the reserve network, as asynchrony in population fluctuations in different sites reduces overall variance in the aggregate of populations (Boyce et al. 2002). In contrast, the previous strategy of ensuring connectivity in the reserve network increases the environmental correlation between sites and the risk that all populations go simultaneously extinct. Multiple representation reduces – but does not eliminate – the risk that areas selected are unsuitable for ensuring the long-term persistence of each species (see Section 4.2). The following strategies tried to address this concern more directly by incorporate some information on relative value of different parts of each species' range.

- Selecting areas in the geographical core of species' ranges (e.g., Balmford et al. 1998; Nicholls 1998; Araújo et al. 2002). This strategy avoids peripheral areas, where species tend to have lower abundance and therefore lower probability of persistence (e.g., Lawton 1993; Brown et al. 1995*b*; although anthropogenic forces can render these patterns irrelevant; see Channell and Lomolino 2000*a,b*) and it may be particularly relevant given the apparent bias of complementary sets to select areas at the edges of species' ranges (see references above).

- Selecting areas within each species' range where they have higher abundance (e.g., Turpie 1995; Nicholls 1998; Rodrigues et al. 2000*b*; see also Section 4.1). Only a few sites within each species' range are "hotspots of abundance" (see Chapter 7; Brown et al. 1995*b*; Gaston and Rodrigues in press), and this strategy aims as selecting those. It is supported by analyses indicating that populations have a higher probability of persistence in areas where they are more abundant (Rodrigues et al. 2000*b*; see Section 4.1), and that the location of peaks of abundance remains fairly constant through time (Brown et al. 1995*b*), even as species decline (Rodríguez 2002).

- Instead of using abundance or spatial position in the range (e.g., core areas) as surrogates for persistence, a few studies incorporating species probability of persistence more directly. Based on monitoring data, Rodrigues and Gaston (2000*a*) calculated a permanence rate for each species in each site (demonstrated to be directly proportional to species' local persistence) and targeted sites where species had higher permanence rates (see Section 4.2). Araújo and Williams (2000) convert species probability of occurrence (obtained from occurrence data and habitat suitability and/or dispersal) into probabilities of persistence, and then select areas such that for each species the overall probability of persistence is above a certain threshold.

- Setting higher targets for species or land class which are rarer and/or more vulnerable. Not all species are equally vulnerable to extinction (e.g., Mace and Lande 1991; Keith 1998; BirdLife International 2000), nor all habitats are equally threatened (e.g., European Union Habitats Directive). Given scarce conservation resources, it is a common strategy to give higher priority to those biodiversity features that need a more immediate investment (e.g., BirdLife International's Endemic Bird Areas, Stattersfield et al. 1998; WWF's Global 200, Olson and Dinerstein 1998*a,b*; Conservation International's Hotspots, Mittermeier et al. 1999; Myers et al. 2000), and this can easily be implemented using reserve selection algorithms (e.g., Davis et al. 1999; Rodrigues et al. 2000*c*; see Section 2.1).

Interspecific ecological interactions

Species' ranges – their structure, shape, size and delimitation – are highly influenced by biotic factors which affect one or more key demographic rates (birth, death, immigration and emigration) and therefore local abundance and viability (Hengeveld 1990; Lawton 1993). These biotic factors are trophic and non-trophic interspecific interactions. For animal species, the most relevant interactions are those determining the availability of food, such as herbivory, predation, and competition, or those inducing mortality, such as predation and parasitism. Plant populations are highly regulated by herbivory, competition, and interactions such as animal-mediated pollination and seed dispersal that determine reproduction success. Some interactions are particularly important not only for the species involved but for entire ecosystems (keystone interactions; Thompson 1996).

Ensuring species' viability within a reserve network may therefore be heavily dependent on keeping the relevant interspecific interactions functioning. If we could identify all of them, it would be trivial to incorporate them in reserve selection algorithms. For example if all the relevant links in a food web (e.g., rabbit - lynx) were determined, reserve networks could be found in order to represent all of them, simply by considering each link as a targeted feature itself (that is, making sure at least *n* sites in the selected reserve network would have simultaneously rabbit and lynx). Or, if negative interactions were identified (e.g., introduced rat – nesting seabird), reserves could be selected such that the species of concern (seabird) would only be considered represented in areas where the interaction (predation by rats) does not occur.

The approach of specifically targeting particular interactions is feasible only when considering reserve networks for the protection of one or a few species (e.g., prey availability for the Iberian lynx; Palomares 2001), or when some very specific interactions are being addressed. In the literature on reserve selection algorithms, these processes have been taken into account only sporadically, and considering very particular interactions. For example, Cowling and colleagues (Cowling 1999; Cowling et al. 1999; Cowling and Pressey 2001) select areas with exposed walls of drainage lines because these provide nesting sites for important hymenopteran pollinators; additionally they target mega wilderness areas as ways of maintaining the predator-prey processes involving top predators, and the interactions between plants and larger herbivores (which here requires maintaining the migratory movements of springbok). Rothley (2002) used multiobjective integer programming and simulated data to identify optimal reserve configurations for the conservation of hawks feeding on voles. Chown et al. (2001) selected areas in which negative interactions (between alien and native species) were avoided by selecting sets of islands which minimise numbers of alien species (see Appendix II).

Although possible in theory, it is obvious that it would require far too much biological data to identify and map all the relevant interspecific interactions to explicitly include or exclude each one of them in reserve planning. A possible shortcut is to go back to targeting individual species. The rationale is that if a particular species occurs in a particular place, all of the relevant narrow-scale processes needed to ensure the species' persistence must be present in that place as well. For example, if lynxes cannot survive without rabbits, then selecting sites for lynxes will certainly retain both rabbits and the rabbit-lynx trophic link. Naturally, this is a gross simplification (see above for an overview of situations where a species may be present, but not viable in a given area), except perhaps for the situations of mutualistc interactions. Even in these circumstances, a species may sometimes persist long after extinction of its mutualist partner (e.g., plants whose recruitment fails which can be still be found for hundreds of years after its seed disperser has gone extinct; Bond 1994). No doubt many interactions are kept by targeting species, especially if representing them in areas adequate for their persistence. Nevertheless, targeting the interaction itself whenever possible is a safer bet for preventing its extinction (Bond 1994).

Processes at spatially wider and temporally longer scales

If a site selected to represent a species today may not be able to retain it even in the short-term of just a few years (see above) this problem is greatly amplified over the much longer time scales that characterise most ecological and evolutionary processes (Balmford et al. 1998). However, the difficulty of addressing these in an explicit way means that very few studies on reserve planning actually do it. A honourable exception is the work by Cowling and colleagues (Cowling 1999; Cowling et al. 1999; Cowling and Pressey 2001), whose planning proposal for the Succulent Karoo in South Africa explicitly aims at preserving a diversity of ecological (migration, disturbance, species interactions) and evolutionary (species diversification) processes.

Migration

Many species undergo regular movements during their life cycle, termed here migrations. Although most frequent in birds, important migratory movements occur also for a diversity of other taxa such as mammals (e.g., ungulates in Africa), reptiles (e.g., marine turtles), insects (e.g., butterflies) and fish (e.g., salmon, tuna). Migrations are processes that usually occur at broader spatial scales than metapopulation dynamics, but they can range from regional (e.g., springbok in South Africa, Cowling et al. 1999), to continental (e.g., monarch butterfly in North America, Brower et al. 2002; neotropical and Afrotropical migrants, Ricklefs 2002) or even global magnitude movements (e.g., arctic tern, Harrison 1983). To complicate matters further, in some species different populations follow different migratory routes (e.g., yellow-rumped warbler, Curson et al. 1994; and see Ricklefs 2002; Webster et al. 2002), or some populations are migratory and others sedentary (e.g., yellow warbler, Curson et al. 1994). Naturally, the persistence of migratory species depends not only on what happens in the regions at the end of their migratory routes (such as breeding and wintering habitat) but is often critically affected by the quality of habitat in intermediate locations (Ricklefs 2002). For some species, those can be more or less discrete "stepping stones", such as the Caribbean Islands for a number of neotropical migrant birds (Raffaele et al. 1998). But others species require continuous corridors, for example: neotropical birds intolerant to non-forest habitats, which undergo extensive annual migration across elevational gradients (e.g., resplendent quetzal in Costa Rica; Powell and Bjork 1995; Stotz 1998); catadromous and anadromous migratory fish, whose migratory routes are frequently disrupted by river damming (e.g., Powles et al. 2000).

Reserve planning which accounts for migration patterns is a conceptually simpler task when migration happens at the regional scale, so that the entire migratory route can be included inside one reserve or within a few reserves connected by corridors (e.g., Williams 1998*a*; Cowling and Pressey 1999). But conservation of species whose migratory pathways cross international boundaries tends to be planed independently for the different regions where the species spend different periods of their life-cycle, because reserve planning usually takes place at a national scale (e.g., reserve planning for wintering and migratory waterfowl in Denmark, Madsen et al. 1998). Irrespective of how well-designed and protected these reserve networks are, this strategy is not sufficient if the species is not protected throughout its entire life cycle (e.g., decline of the lesser kestrel on both its European and African range mainly because of habitat loss in its breeding grounds in western Europe; BirdLife International 2000).

That the conservation of migratory species is often an international matter has long been recognised, as testified by a number of international agreements oriented for their protection (e.g., Bonn Convention on Migratory Species, http://www.wcmc.org.uk/cms/; Ramsar Convention on Wetlands, http://www.ramsar.org/; North American Wetlands Conservation Act, http://laws.fws.gov/lawsdigest/nawcact.html; European Union Birds Directive, http://europa.eu.int/comm/environment/nature/; Convention on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean, http://www.ocean-affairs.com/convention.html). There are also a number of international prioritisation schemes whose purpose includes the conservation of migratory species (e.g., BirdLife International's Important Bird Areas, http://www.birdlife.org.uk/sites; Ramsar Wetlands of International Importance, http://www.ramsar.org/ index_list.htm; EU's Special Protection Areas under the Birds Directive, http://europa.eu.int/comm/environment/nature/natura.htm). These provide opportunities for much needed international coordination in the conservation of migratory species, and there are several examples of their success in improving the conservation status of migratory species (e.g., RSPB et al. 2001). However, selection of sites under these schemes usually follows criteria applied on a site-by-site basis, such as species composition and numbers (e.g., criteria for Ramsar Wetlands, http://www.ramsar.org/about_infopack_5e.htm), and therefore suffers from the general type of problems associates with scoring procedures, such as failing to recognise that the value attached to adding a given reserve depends on the attributes of others in the network (see Chapter 1). This is even more problematic when considering sites connected by migratory movements, as these are truly inter-linked and inter-dependent networks whose conservation planning needs to be made in an integrated way.

Because reserve selection algorithms explicitly aim at selecting networks, they are obvious tools for addressing the conservation of migratory patters. And yet, this is a much-neglected subject in the published literature (Brooks and Thompson 2001). A few studies have used complementarity in evaluating reserve networks for the conservation of migratory birds, but have done so at a national scale and therefore only considering part of each specie's life cycle (e.g., Turpie [1995] in South Africa; Pérez-Arteaga et al. [2002] in Mexico; Jackson et al. [in press] in the UK). The above-mentioned ways of integrating spatial considerations in reserve selection algorithms (selection of large areas, clustered sites and/or connected networks; e.g., Williams and ReVelle 1997; Williams 1998; Rothley 1999) are all conceptually applicable to conservation planning aiming at including entire migratory routes. The work by Cowling and colleagues (Cowling 1999; Cowling et al. 1999; Cowling and Pressey 2001) is perhaps the only example of a practical application, by selecting large areas (50,000-1,000,000 ha) spanning the gradient from uplands to coastal lowlands and interior basins in western South Africa in order to maintain the seasonal migration of springbok and other ungulates. The recently published study by Malcom and ReVelle (2002) is perhaps the only so far addressing the selection of reserves along migratory flyways for birds, using directed conditional covering as an optimisation tool.

More developments in reserve selection algorithms are needed to address migratory processes. Meanwhile, advances in the knowledge of migratory routes for individual species and populations (Webster et al. 2002) will provide valuable information for their application to practical reserve planning.

Disturbance regimes

All species on Earth have evolved under ecological conditions that are unstable, having continuously been exposed to more or less regular disturbance events of variable magnitude and frequency. These disturbance regimes are powerful selection forces, drivers of major evolutionary and ecological processes that have shaped all natural ecosystems (Whittaker 1995). Hence, they are fundamental processes that need to be taken into account in the selection of reserves aiming at the persistence of biodiversity (Balmford et al. 1998).

The spatial scale at which disturbance events take place ranges from local (e.g., a termite mound), to regional (e.g., a forest fire), continental (e.g., El Niño), and global (e.g., a glaciation event). The temporal scale is equally variable, including events whose average frequency can be measured in hours (e.g., wind), years (e.g., hurricanes), centuries (e.g., earthquakes), or thousands of years (e.g., climate oscillations). There is an inverse relationship between the frequency and magnitude at which disturbance occurs: little perturbations happen often, major catastrophic events are rare (Lawton 1997; Brooks and Smith 2001).

The effects of disturbance regimes on species are highly variable. Disturbance may, for example, determine survival rates (e.g., lizard mortality caused by hurricanes; Schoener et al. 2001), reproduction rates (e.g., plant recruitment in forest gaps; Coates 2002), habitat quality (e.g., early successional habitat for the large blue butterfly, maintained by burning and grazing; Elmes and Thomas 1992), and genotype (e.g., frequency of polyploids influenced by Milankovitch climate oscillations; Dynesius and Jansson 2000). Anthropogenic action has created new disturbance regimes (e.g., forest logging), replaced natural ones (e.g., grazing by livestock replacing grazing by native ungulates), changed the frequency and/or magnitude of natural disturbance events (e.g., fire in mediterranean ecosystems) and changed the way ecosystems respond to natural disturbance (e.g., capacity to recover after a hurricane).

Conservation of natural disturbance regimes, and the processes determined by them, can happen in two ways: by managing the disturbance processes themselves, which is possible only for certain types of disturbance, typically high-frequency/low-magnitude ones (e.g., management of fire regime by fire-suppression or prescribed burns; Keeley and Fotheringham 2001); or, by keeping the ecological conditions in which those processes take place. It is on the latter that reserve planning has a role to play. Without active management, the perpetuation of disturbance regimes implies keeping a minimum land area which incorporates the temporal and spatial scale of the disturbance, maintaining a shifting mosaic of landscape patches which, overall, remains temporally stable (Baker 1992). That is, keeping Nature's options open (Lawton 1997), which can only happen if the reserved area is sufficiently large in relation to the scale of the disturbance process. Small-scale disturbances (e.g., grazing), can easily be accommodated in small reserves. However, if reserves are too small in relation to the scale of disturbance, a single disturbance event may threaten or destroy the entire reserve at once (Baker 1992). For example, although hurricanes are natural disturbance events in the Caribbean, to which natural forest communities are highly adapted, the extensive deforestation that took place in this region (only 10% natural forest remains; Mittermeier et al. 1999) has resulted in the confinement of several endemic birds to tiny current range sizes (e.g., Puerto Rican parrot, currently restricted to a 16 km^2 area, 0.2% of its former range; BirdLife International 2000), making them highly vulnerable to extinction if a hurricane sweeps across their remaining ranges. Selecting for large reserves is therefore the best strategy for conserving disturbance regimes (Balmford et al. 1998), although in many cases there is not an option to do so, especially for disturbance events at large spatial scales. Selecting for multiple reserves is also recommended to reduce species' extinction risk, as this approach reduces the probability that all the reserves will be affected by the same disturbance event simultaneously (Boyce et al. 2002). However, reserves need to be interconnected for species being able to colonise empty patches following local extinction events.

Besides influencing the area and number of reserves, consideration of disturbance regimes may influence reserve location as well. Certain types of disturbance regimes should be protected by ensuring that both the disturbance initiation zones and the disturbance export zones are contained in the reserve. Without the initiation zones (e.g., an avalanche source area) it will be difficult to manage disturbance in the reserve, while without the export zone (e.g., an avalanche run-out zone) it will be politically difficult to maintain a natural disturbance regime within a protected area (Baker 1992).

The concern for keeping the processes associated with disturbance regimes has been mainly absent from the literature on reserve selection algorithms. An exception is the study by Cowling and colleagues (Cowling 1999, Cowling et al. 1999; Cowling and Pressey 2001) which targeted at areas sufficiently large for the maintenance of the grazing and trampling impacts of migratory herds of springbok in South Africa. However, these authors recognise that a practical limitation to this approach is that for many disturbance regimes – such as rare, catastrophic, large-scale droughts in South Africa's Succulent Karoo - it is not known what are the areal requirements for effective conservation (Cowling et al. 1999).

Climate change

Consensus is building that global climate is changing rapidly as a result of anthropogenic activities, that these changes are already affecting biodiversity (e.g., Pounds et al. 1999; Hughes 2000; McCarty 2001; MacLaughlin et al. 2002; Walther et al. 2002), and that projected changes are likely to cause extensive disruption to most ecological communities (Hannah et al. 2002; IPCC 2002) and major changes in the biological composition of many protected areas (e.g., Villers-Ruíz and Trejo-Vázquez 1998; Hannah et al. 2002).

Climate oscillations are a particular type of natural disturbance, and although in the past the most rapid oscillations and/or those of higher magnitude have been associated with extinction events (Huntley 1998), most species that exist today have experienced many such episodes, showing that they have the potential to survive human-induced climate changes (Dynesius and Jansson 2000). In the past, species have compensated for climate change through two main mechanisms (Balmford et al. 1998; Huntley 1998): by shifting their ranges in order to track their habitats through space; and by local adaptation, with small-scale, apparently adaptive changes in morphology (and presumably related aspects of physiology and ecology). The predicted anthropogenic climate change creates challenges to both mechanisms, and it is therefore expected to result in higher levels of species extinction than a comparable natural change. Indeed, a main difference between this and previous climate oscillations is that humans have come to dominate and transform most of the ecosystems on Earth (see Chapter 1). As a result, many species' ranges are reduced to a small number of isolated populations, seriously limiting their ability to track their habitats through space (Balmford et al. 1998; Dynesius and Jansson 2000; McLaughlin et al. 2002). The widespread loss of populations (Hughes et al. 1997), and corresponding erosion on intraspecific genetic diversity, also implies than many species now have a reduced capacity of local adaptation to climate change (Balmford et al. 1998; Lande 1998). Additionally, the direction and magnitude of the predicted climate change will lead to global conditions warmer than at any time during the recent geological past, as during the Quaternary most departures of global conditions from those of today have been global cooling during glacial stages (Huntley 1998). The resulting combinations of climate and latitude will have no parallel during the period that has seen the evolution of species of most of the world's present biota, and as a result they may lack the ability to adapt genetically to the new combination of conditions (Huntley 1998).

The uncertainty that remains with respect to the magnitude and rate of the predicted anthropogenic climate change, and our ignorance of the biological characteristics of the vast majority of the world's biota, difficult the prediction of the effects on biodiversity (Huntley 1998). Nevertheless, the growing evidence that these effects will be highly significant and are already taking place (e.g., Pounds et al. 1999; McCarty 2001; Walther et al. 2002), the improvements in climate prediction models (e.g., Zwiers 2002), and the development of models predicting species' range adjustments (e.g., Peterson et al. 2000) provide the opportunity, and the responsibility, for having climate change into account in reserve planning (Hannah et al. 2002). A number of ways of doing so have been suggested in the literature, and these aim at maintaining the potential for species' dynamic responses by range shifts and adaptive evolution (Balmford et al. 1998):

- Reserve large areas (Balmford et al. 1998; Cowling et al. 1999) and provide buffer zones around reserves (IPCC 2002). However, only extremely large reserves can possibly accommodate the predicted magnitude of species' latitudinal range shifts (e.g., Parmesan et al. 1999 found that range boundaries of European butterflies have already shifted to the north by 35-240 km since 1900), unless perhaps by targeting areas with sufficiently complex topography to embrace a series of climatically discrete habitat types (see below).

- Create networks of reserves connected by corridors which provide dispersal and migratory routes for plants and animals, facilitating range shifts through today's highly fragmented landscapes (Balmford et al. 1998; IPCC 2002).

- Maintain intact natural vegetation along environmental gradients (e.g., latitude and altitude gradients, soil moisture gradients; IPCC 2002). Related to this is the recommendation to select preferentially areas at ecotones and areas of steep environmental gradients which reduce the need for large scale migration (Balmford et al. 1998; Huntley 1998; Cowling et al. 1999; Pounds et al. 1999; Dynesius and Jansson 2000; Smith et al. 2001; Balmford 2002; Reyers et al. 2002). Altitudinal gradients are particularly relevant because they provide opportunities for species to adjust to climate change by relatively small range shifts. For example, a 3°C change in mean annual temperature corresponds to a latitudinal shift in isotherms of 300-400 km (in the temperate zone) but to a 500 m shift in elevation (Hughes 2000).

- Target those areas of high climatic stability where global climate change is buffered against (Dynesius and Jansson 2000), which again seem to be located in topographically complex regions (Fjeldså and Lovett 1997*a*,*b*; Fjeldså et al. 1997, 1999).

- Conserve adaptive evolution by maintaining genetic diversity within and among populations of native species, including by targeting ecotones as repositories for genetic diversity (IPCC 2002). See below for a discussion of how to integrate the conservation of evolutionary processes in reserve selection.

All of these recommendations can be incorporated into reserve selection algorithms, although few published studies have done it explicitly so far. Cowling and colleagues (Cowling 1999; Cowling et al. 1999; Cowling and Pressey 2001) targeted large areas (5,000 – 3,000,000 ha) with steep climatic gradients. Additionally, they also suggested planning ahead and considering locating conservation areas for selected species in areas that are now climatically marginal but which are likely to become suitable (Cowling et al. 1999). Reyers et al. (2002) have also selected preferentially heterogeneous areas, with high species turnover, transition zones and environmental gradients. Additionally, see references above for studies that incorporate spatial considerations into reserve selection (large areas, clustered sites and/or connected networks) which, at the appropriate scale, can provide valuable guidelines for the development of reserve selection methods addressing climate change.

Evolutionary processes

What determines the number of species alive in a biological province (such as the Neotropics) is the cumulative difference between the creative process of speciation and the destructive process of extinction (Rosenzweig 2001). This means that future biotas on earth will be impoverished not only by the predicted extinctions, but also by a likely depletion and/or disruption of certain basic processes of evolution that will reduce speciation rates (Myers and Knoll 2001; Rosenzweig 2001). Both processes are area-dependent, extinction rates decreasing with area and speciation rates increasing. There is evidence that, as a result, the species richness at the steady state (when extinction and speciation balance) follows a linear relationship with area – a loss of x% of area will produce a loss of x% species (Rosenzweig 2001). If so, then the effects of habitat destruction on species diversity on an evolutionary time scale will be even more severe than predicted at the ecological scale by the classical species-area relationship (e.g., Diamond 1975; Pimm et al. 1995).

Besides biological impoverishment, the disruption of evolutionary processes will also result in distinctive features of future evolution, which may include: homogenisation of biotas, proliferation of opportunistic species, a pest-and-weed ecology, an outburst of speciation among taxa that prosper in human-dominated ecosystems, a decline of biodisparity, an end to the speciation of large vertebrates, the depletion of "evolutionary powerhouses" in the tropics, and unpredicted emergent novelties (Myers and Knoll 2001). The consequences are likely to persist for a longer time than the disruption of any other ecological process: in previous mass-extinction events documented in the geological record, 5 million years was a representative recovery time for the subsequent episodes of rediversification and ecological reorganisation (Myers and Knoll 2001).

The species, populations and individuals that exist today – and their genetic diversity – are the raw material on which future evolutionary processes will operate. Keeping these pieces (Moritz 2002) means maximising the protection of that genetic diversity, leaving the options open for future evolution. Above the species level, this concern can and has be integrated in reserve selection algorithms if instead of species richness another currency of biological difference is maximised which takes into account the phylogenetic relationship between species, such as: taxonomic distinctness (e.g., May 1990; Humphries et al. 1991; Vane-Wright et al. 1991); character diversity (e.g., Williams and Humphries 1994; Hacker et al. 1998); and phylogenetic diversity (PD; Faith 1992, 1994; Polasky et al. 2001*b*; Rodrigues et al. 2002*a*; see Chapter 5). The same measures can easily be applied to the representation of genetic diversity below the species level, as long as the intraspecific phylogeographies for each species are known, which requires knowing which are the relevant Evolutionary Significant Units (ESUs) for each species and their geographic distribution. The definition of ESU remains contentious, with some authors (e.g., Moritz 2002) defending that it should be based on genetic traits only and others (e.g., Crandall et al. 2000) defending that both ecological and genetic characteristics be considered. Moritz and Faith (1998) and Moritz (2002) have used multiple intraspecific phylogeographies and explored the extension of the concept of PD to the selection of complementary sets of areas. While conceptually simple, data availability will prevent the application of this approach to a significant number of species in the near future (Moritz et al. 1997; Patton et al. 1997). Unfortunately, Moritz and Faith (1998) and Moritz (2002) found that complementarity analysis using species data as a surrogate produces different results from those obtained using genetic data, and concluded that "no single prescription best predicts how to protect the evolutionary and ecological viability of the biota; rather, the underlying evolutionary and ecological process should be considered for each species/system and a strategy devised accordingly". Nevertheless, perhaps future analysis will find rules of thumb for reliably targeting areas that best represent the (vicariant) intraspecific genetic diversity, that can be applicable to many species at once and identifiable from surrogate data such as, perhaps, environmental information (e.g., topography, climate) or based on the vicariance patterns for a few surrogate species (Moritz et al. 1997). As a simple measure to protect some intraspecific genetic diversity, Nicholls (1998) suggested dividing each species' range in parts and placing reserves in each of those parts (see also Chapter 6; Rodrigues and Gaston 2002*c*).

Consensus has not yet been reached regarding which areas should be targeted in order to keep evolutionary processes, as there is ample discussion about which processes are dominant and how and where they operate. The following overview is not on the diversity of speciation theories that have been proposed in the literature but on the corresponding suggestions on how to retain evolutionary processes; it is not exhaustive, and refers mainly to speciation in tropical ecosystems.

Moritz and colleagues (Moritz et al. 2000; Moritz 2002) suggest that the diversity of hypotheses concerning factors that promote genetic diversity and speciation in tropical fauna generally falls into two main evolutionary processes:

- Neutral divergence due to vicariant evolution, in populations genetically isolated or partially isolated, in which founder effect, genetic drift, inbreeding, and selection interact to cause evolutionary change that is free from the homogenising effects of gene flow (Smith et al. 1997). This includes the refuge theory (see review by Haffer 1997), which assumes that climate variation caused fragmentation of originally continuous habitat, leading to allopatric speciation in each of the remnants (refugia).

- Adaptive variation that arises through natural selection and can cause divergence even in the presence of high gene flow (in excess of a few migrants per generation). This includes the gradient model (e.g., Smith et al. 1997; Moritz et al. 2000) in which no isolating barrier is needed but in which speciation occurs through linkage between reproductive traits and those traits under selection (Smith et al. 1997).

Moritz et al. (2002) defend that while speciation may occur by either process alone or, more commonly, the two together, they relate to different conservation issues and management strategies:

- Conservation of vicariance is related to the protection of the major evolutionary lineages as these, once lost, cannot be recovered other than by repetition of long-term isolation, which is beyond the scale of realistic time frames for management. Consequently, Moritz et al. (2002) suggest that their conservation can be better addressed by the above-mentioned approaches for retaining inter- and intraspecific phylogenetic diversity ("keeping the pieces").

- On the other hand, maintenance of adaptive speciation is needed for the retention of individual fitness and population viability (capacity for evolutionary response) in current and future environments. Adaptive phenotypes, if lost, can potentially be recovered through recurrent selection subject to the viability of the populations under selection and to maintenance of appropriate environmental context. Therefore, Moritz (2002) defends a conservation strategy directed towards protection of the process (the context for natural selection) rather than the products themselves.

Because species current ranges do not necessarily coincide with the original speciation locations (Hengeveld 1990), it can be argued that "protecting the pieces" may not be sufficient for maintaining the process of speciation by isolation into the future. Instead, a possible approach may be to target the particular sites where such speciation has occurred in the past, such as known past refugia.

In order to protect adaptive evolution, a number of recent studies advocate the protection of ecotones (e.g., Smith et al. 1997; Schenider et al. 1999; Schilthuizen 2000; Moritz 2002) and areas of secondary contact (admixture of lineages formerly isolated, where current hybridisation may be happening; Moritz 2002). These studies defend an emphasis on the protection of connectivity across transitional and topographically complex areas, i.e., across mosaics of habitats and environmental gradients, which maximise the range of genetically based phenotypic variation available for future speciation, and provide the differing selective regimes that may ultimately generate biodiversity. Note that an emphasis on the protection of ecotones is in contradiction with the strategy of avoiding these transitional areas for being places where species have lower probability of local persistence (see above); if so there may be a conflict between short-term conservation strategies and long term ones.

Another line of research, by Fjeldså and colleagues (e.g., Fjeldså and Lovett 1997*a,b*; Fjeldså et al. 1997, 1999), compared the distribution patterns of species of different ages (neoendemics vs. paleoendemics). They found that clusters of both neoendemics and relict paleoendemic species (both narrowly distributed, but for different reasons) tend to concentrate in particular areas of high ecological stability, in ecotonal or topographically complex regions, such as the Andean slopes, the central African ecotones and the East African rift mountains. On the other hand, the richness of extensive lowland forests postulated to include Pleistocene forest refuges (in the

Congo and Amazon basins) seems to be mainly due to the presence of widely distributed paleoendemic species, suggesting that these areas were not speciation centres but acted instead as "museums" where species of potentially multiple origins survived because of diversity-maintaining processes. Accordingly, they suggest two different strategies for the protection of each one of these regions (e.g., Fjeldså and Lovett 1997*a*):

- In speciation centres, high levels of local endemism mean that there is a risk of rapid and irreversible loss of biodiversity; additionally, these tend to be 'insular' areas and with high human population pressures. They should therefore be protected by very targeted conservation efforts.

- Extensive areas where high biological diversity has accumulated over long periods of geological time are important for the sheer magnitude of life forms, but since most species are widespread and maintained by landscape dynamics acting over large geographical areas, it is difficult to target priorities for site-oriented conservation. For the protection of these areas, political-macroeconomic decisions will probably have a much greater impact that any local actions.

A potential conflict has been suggested between the protection of "biodiversity hotspots" and transitional areas (ecotones). Smith et al. (2001) criticises the current emphasis on placing conservation investment on the former, arguing that the hotspots of today may not be the same of tomorrow and defending the protection of environmental gradients as regions important to the generation and maintenance of biodiversity, regardless of where they are species rich. In reply, Brooks et al. (2001*c*) quote research suggesting that climate change has driven dramatic speciation along intra-hotspots gradients, rather than along inter-regional gradients, and that the long-term accumulation of exceptional hotspot biodiversity might in fact require relative stability in the face of environmental change, which provides a reason to believe that the hotspots of today might well be the hotspots of tomorrow. This conflict may partially derive from a confusion between the widespread use of the term "hotspot" as areas of highs species richness (Reid 1998), and Conservation International's global Biodiversity Hotspots (Meyers et al. 2000), and may be only apparent. The work by Fjeldså and colleagues (see references above) suggests that areas with high concentration of endemic species – valued by a number of conservation priority initiatives including Conservation International's Biodiversity Hotspots, BirdLife International's Endemic Bird Areas and WWF-IUCN Centres of Plant Diversity (see Chapter 1; Table 1.I) – may correspond to centres of speciation. Additionally, these tend to concentrate in ecotonal or topographically complex regions, the same that would be recommended to protect adaptive evolution (e.g., Moritz et al. 2000; Smith et al. 2001; Moritz 2002), although for somewhat different reasons.

The above considerations refer mainly to species-centred concerns for the maintenance of evolutionary processes. However, much of the life histories, physiologies and morphologies of organisms are shaped by interspecific interactions, which are themselves simultaneously targets and drivers of evolutionary processes. Thompson (1996) noticed that: many species are composed of populations specialised to different interactions and these may be on the way to become distinct species (indeed, there are examples of cases where what was considered a single generalist species turned out to be, upon closer analysis, a complex of more specialised sibling species); some interactions can evolve rapidly under changed ecological conditions; there is no inherent directionality in how interactions evolve, which means that the evolutionary links between one species and other taxa within a community may often differ geographically and continue to change over time as ecological conditions change and interactions evolve; some interactions evolve, and coevolve, over large geographic areas; maintenance of resistance genes against some parasites may require a metapopulation structure; hybrid zones between species may be important for the maintenance, and possibly the evolution, of some interactions. These points argue for a broad geographic perspective on the conservation of interaction biodiversity, and agree with the need for preserving biodiversity at a level that goes beyond species' representation and target for the intra-specific genetic diversity found across each species' range.

In summary, while the debate on the nature of evolutionary processes is far from finished, a few general guidelines are emerging which, at least in theory, may be directly applicable to conservation planning aiming at maintaining these processes:

- It is important to "keep the pieces" beyond simple species representation, by maintaining the currently existing phylogenetic and intraspecific genetic diversity, including the protection of populations across species' ranges for the preservation of adaptive evolution, including intraspecific interactions. See above for references of how the concern for maintaining phylogenetic diversity been integrated into reserve selection algorithms and how it can be extended to the protection of intraspecific diversity.

- It is important to keep large areas (Balmford et al. 1998; Rosenzweig 2001; Woodruff 2001). However, the required areas may have to be so large that the maintenance of evolutionary processes may only be realistic by a "reconciliation ecology" that maximises species persistence in anthropogenic habitats (Rosenzweig 2001). Cowling and Pressey (2001) selected mega wilderness areas (> 500,000 ha) in order to maintain evolutionary processes.

- Transitional and topographically complex areas should be targeted for conservation, either because these are believed to be places where divergent selection pressures generate novel adaptation (Smith et al. 1997; Schneider et al. 1999; Balmford 2002) and/or because local ecoclimatic stability allows for both the generation of neoendemics and the retention of relict species (Fjeldså and Lovett 1997*a*,*b*; Fjeldså et al. 1997, 1999). In order to preserve the ecological diversification of plant and animal lineages in the Cape Floristic Region in South Africa, Cowling and Pressey (2001) targeted: juxtaposed edaphically different habitats, entire sand movement corridors, gradients from uplands to coastal lowlands and interior basins, and macro-scale climatic gradients.

9.1.5 Explanation 4 - Reserve selection algorithms are too simplistic and do not account for all the social, economic, and political aspects of real-life planning

Ecological and evolutionary processes are fundamental for the generation and maintenance of biodiversity (see above), but currently the most important driving force in biodiversity loss is by far the effect of threatening processes of anthropogenic nature (Caughley 1994): habitat clearance and degradation, overexploitation, introduced species, and chains of extinctions (the "evil quartet"; Diamond 1984). The purpose of reserves is, naturally, to protect pieces of land against these processes, but this is seldom straightforward. On one hand, humans and biodiversity seem to have preference for the same parts of the planet (e.g., Fjeldså and Lovett 1997*b*; Fjeldså et al. 1999; Cincotta et. al. 2000; Balmford et al. 2001; Moore et al. 2002), which often means that areas which are conservation priorities are subject to intense conflict by other forms of land use. On the other hand, many of those threatening processes do not cease after reserves are designated, continuing to originate both inside and outside the reserves' boundaries (see Section 3.1).

Addressing human-related constraints in the selection of reserve networks is complex (Prendergast et al. 1999) but unavoidable, and as a result conservation planning often becomes an activity in which social, economic and political imperatives modify, sometimes drastically, scientific prescriptions (Margules and Pressey 2000). These constraints affect, for example, decisions on location (e.g., which sites are available for conservation) and design (e.g., if there is an option for large reserves, corridors), as well as the definition of priorities (e.g., more urgency for those areas with higher levels of threat). But, additionally, the effectiveness of reserve networks as conservation tools is largely dependent on how they minimise the effect of current and future anthropogenic threatening processes, which depends not only on subsequent management procedures but also on decisions on location and design.

Reserve selection algorithms have been criticised for being far too simplistic to deal with the complexities of socio-political, institutional and economic realities of site planning and acquisition (e.g., Stoms et al. 1997; Davis et al. 1999; Prendergast et al. 1999). Indeed, the vast majority of published studies addresses unrealistic simplifications of real conservation problems, in which reserve selection algorithms are separated from a broader conservation planning process. The concern for the minimisation of the total area (cost) of the network (inherent to complementary reserve selection), and the consideration for existent reserve networks are the only human-related constraints addressed routinely by studies applying reserve selection algorithms. This extreme simplification may happen because scientists are so dissociated from conservation reality that they fail to see how naïve their approach is (Pimm 2000). Another explanation is that scientists are evaluated by their publishing achievements (Bazzaz et al. 1998) and the nature of scientific publishing (both in terms of space constraints and demands of scientific objectivity) means that papers that focus on partial and simplified views of the reserve selection problem are by far more publishable than those giving accounts of the complexity and subjectivity of real case studies. Accordingly, the few published analyses of real-life applications are found in relatively obscure sources (e.g., Pressey 1998; Davis et al. 1999). Other applications may have not even been published, as this is often not a priority for governmental and non-governmental conservation planners.

There is therefore an urgent need for the dissemination of studies which address the complexities of real conservation planning processes, both in order to provide opportunities of learning by example to managers and to guide scientists into which are the relevant questions that should be addressed in their analyses. However, the fact that most published studies on reserve selection algorithms are simplified approaches does not render them worthless. A number of them have illustrated ways in which social, economic and political concerns can be taken into account which can be useful in real applications, and the inherent flexibility of these tools makes them suitable for addressing far more complex situations. Flexibility arises from the non-unique occurrences of many biodiversity features, meaning that most reserves are fluid to some extent: while some component sites are fixed (irreplaceable) others can be replaced more or less easily (Pressey et al. 1993).

Flexibility has early on been established as a key principle of systematic reserve selection (Pressey et al. 1993), and it can be explored to address human-related concerns in two ways (See Chapter 1): by exploring the diversity of solutions (e.g., Arthur et al. 1997) that can be obtained for problems based on biological considerations only; and/or by integrating constraints accounting for political, social and economical aspects simultaneously to the consideration of biological values (as trade-offs). However, Faith and Walker (2002, and references herein) found that following the latter approach makes a substantial difference to the identity of sites selected in relation to analyses based on biological value only, suggesting that human-related concerns cannot simply be an add-on consideration to refine land allocations. Interactive reserve selection tools, such as CODA (Bedward et al. 1992), C-Plan (Pressey 1998), and WORLDMAP (Williams 1996), include the possibility for exploring alternative configuration networks, and this has been important in facilitating negotiation processes where these tools were applied (e.g., Stoms et al. 1997; Pressey 1998; Davis et al. 1999; Clark and Slusher 2000). The software TARGET (Faith and Walker 2002) was specifically developed for exploring the trade-offs between achieving biodiversity representation targets and opportunity costs determined by human-related concerns.

The following sections overview how human-related concerns (threat, land cost and ownership, scheduling of reserve implementation and political considerations) can and have been addressed by reserve selection algorithms. As expected, those studies that addressed real conservation planning (e.g., Pressey 1998, Davis et al. 1999) incorporated these concerns in a much more integrated way than simplified case-study analyses.

Threat

Threat (often used interchangeably with vulnerability) can be measured directly by the number of threatened species in a region (e.g., Dobson et al. 1997; Maddock and Benn 2000; Memtsas et al. 2002), or by a combination of the levels of threat of different species (Lombard et al. 1999). However, different regions and different taxonomic groups have been subject to variable levels of assessment, introducing biases in this measure that make some comparative assessments difficult (e.g., Brooks et al. 2002). Given the well-known relationship between human presence and species extinction risk (e.g., Brooks et al. 1997; Rivard et al. 2000; McKinney 2001; Parks and Hartcourt 2002), other commonly used measures of threat are human density (e.g., Abbitt et al. 2000; Cincotta et al. 2000; Balmford et al. 2001; Araújo et al. 2002) or levels of human activity, measured by variables such as land development/degradation (e.g., Abbitt et al. 2000; Wessels et al. 2000), presence of roads (e.g., Abbitt et al. 2000; Reyers et al. 2001), presence of alien species (e.g., Lombard et al. 1997; Chown et al. 2001), and potential for agriculture/forestry (Pressey et al. 1996*a*; Nantel et al. 1998; Faith et al. 2001*a*; Pressey and Taffs 2001).

If data on threat is available, it can be easily integrated into reserve selection algorithms, and a number of studies have done so. However, threat has been addressed in two, apparently opposite, ways:

- Some studies give priority to areas of higher threat. For example: Pressey et al. (1996*a*) and Pressey and Taffs (2001) gave priority to areas with high suitability for clearing or cropping (see bellow for an application to conservation scheduling); Cowling (1999) and Lombard et al. (1999) targeted areas with more threatened species.

- Other analyses explicitly avoid areas of higher threat. For example: Wessels et al. (2000) and Reyers et al. (2002) excluded degraded areas; Lombard et al. (1997), Heydenrych et al. (1999) and Chown et al. (2001) avoided the presence of introduced species (see Appendix II); Balmford et al. (2001), Faith et al. (2001*a*) and Araújo et al. (2002) avoided areas of high human density; Nantel et al. (1998) avoided areas with high potential for conflicting land use (measured by an index combining agriculture, forest and recreational potential, presence of infrastructure and proximity to human communities); Faith et al. (2001*a*) minimised opportunity costs (measured as value for forestry and for agriculture potential), while giving preference to areas of low human population density; Stoms et al. (1997) and Davis et al. (1999) assessed land suitability for conservation by an index which included the presence of roads, human population and percentage of land converted to human uses.

This contrast is not exclusive of studies using reserve selection algorithms; for example, valuing threat is intrinsic to Conservation International's Biodiversity Hotspots (which by definition have lost at least 70% of their natural habitat; Mittermeier et al. 1999; Meyers et al. 2000), while the opposite approach is followed by Conservation International's Wilderness Areas (which have kept at least 70% of their original habitat; Mittermeier et al. 1998; see Chapter 1, Table 1.I).

Both of these approaches have merits. The rationale for the first one is that areas of high threat are those where conservation resources are most needed, as without conservation investment their natural values are predicted to be lost. The second approach assumes that areas of low threat have higher opportunity value for conservation, as they can be implemented avoiding current conflict, and that they can also improve reserves' effectiveness over time, by avoiding future conflict (Brooks and Thompson 2001). However, given scarce resources, these two approaches are potentially in contradiction and therefore in competition for those resources. No obvious best option exists, but decisions in any case are likely to be determined by the biological values under threat (such as their endemism/irreplaceability, i.e., how flexible are the options for protecting them elsewhere; Pressey et al. 1994) and the anticipated return from conservation investments. Ideally, no biological features should get to the point of being threatened, and an investment on "prevention rather than cure" would be the best approach (Gaston et al. 2002). Given an option (i.e., if irreplaceability is low in the sense that the same features can be protected by a number of alternative networks) the best compromise can be achieved by representing the biological features in areas with lower threat. Unfortunately, the coincidence between human and biological distribution patterns (e.g., Cincotta et. al. 2000; Balmford et al. 2001) means that highly irreplaceable biological values are often in direct conflict with human activity, limiting the possibility for a compromise (e.g., Balmford et al. 2001). Considering *a priori* that areas of high threat are lost causes may prove to be an error (e.g., Collar 1998). A possible compromise may perhaps be to identify areas of high irreplaceability and high threat as priorities for conservation investment at a larger scale (e.g., CI's Biodiversity Hotspots) but then look for implementation solutions at the local scale (e.g., within each Hotspot) which target the best conservation opportunities by minimising conflict.

Land cost

In recognition that resources available for conservation are limited, the concern for efficiency in minimising overall cost of reserve networks is intrinsic to complementarity-based reserve selection algorithms (e.g., Pressey and Nicholls 1989*a*; Pressey et al. 1993). Accordingly, all applications of these algorithms aim at minimising cost, and a number of studies have focused on the development of these methods in order to improve their efficiency in doing so (e.g., Underhill 1994; Csuti et al. 1997; Rodrigues et al. 2000*c*; Rodrigues and Gaston 2002*b*; see Chapter 2).

Most published studies use area as a surrogate for land cost, and in many the data are provided in equal size selection units (such as cells or hexagons; e.g., Castro Parga et al. 1996; Williams et al. 1996*a*,*b*; Csuti et al. 1997; Nantel et al. 1998; Gaston et al. 2001; Rodrigues and Gaston 2002*c*; the SABAP data used in several chapters in this thesis) so that minimising cost actually corresponds to minimising the number of sites selected. However, land values change considerably across a region, affecting considerably the results of complementary reserve selection (e.g., Ando et al. 1998). Whenever available, direct measures of land value can be readily incorporated, and this has been the case in a few studies (e.g., Ando et al. 1998; Polasky et al. 2001*a*). Other studies used indirect measures such as timber value (Pressey 1998), value for forestry (in Faith et. al 1996, measured by an index that reflected factors such as distance to saw mill, regeneration potential and site productivity) and an index of timber volume (Faith et al. 2001*a*). The software TARGET (Faith and Walker 2002) explores trade-offs between achieving biodiversity representation targets and opportunity costs measured by variables such as foregone forestry production opportunities.

Land tenure

Besides land value, a fundamental aspect influencing opportunity costs in reserve acquisition is land ownership, status and control, which can be of great complexity in some countries. For the U.K., for example, Prendergast et al. 1999 noticed that "reserves may be procured by a diversity of organisations (statutory government agencies, non-government organisations, private landowners), be under a diversity of control systems (fully owned, leased, rented, managed under agreement with owners), and subject to a diversity of planning regulations (local, national, national, international)" and concluded that "it would take a remarkable feat of cooperation for the various owners or managers to coordinate a common policy of reserve acquisition, based on scientific objective criteria such as size, shape, proximity to other reserves, representativeness or complementarity".

The only way land tenure has been routinely considered in studies applying reserve selection algorithms is by taking into account existing reserves (see above section 9.1.3). Additionally: Trinder-Smith et al. (1996) considered a reserve scenario in which all publicly owned areas where included; in their application to reserve planning in the Columbia Plateau for The Nature Conservancy, Stoms et al. (1997) and Davis et al. (1999) integrated land tenure by mapping the suitability of sites not already reserved following an index which included the percentage of land in private ownership as a measure of "site manageability". There is potential for integrating land tenure in a more explicit way. For example, Rodrigues et al. 2000*c* suggested a formulation for a restriction which imposes that at least a predefined fraction of the total area selected be, for example, owned by the State (see Section 2.1).

Scheduling reserve implementation

A common criticism to reserve selection algorithms is that they assume that all selected areas are immediately available for conservation and the reserve implementation happens with the stroke of a pen (Pimm and Lawton 1998; Cowling 1999; Cowling et al. 1999; Curio 2002). In practice, these are processes that usually take years or decades, during which the agents of biodiversity loss continue to operate. For example, Clark and Slusher (2000) predict a 30-40 year acquisition time-line by the US Fish & Wildlife Service in the implementation of the Grand Kankakee Marsh National Wildlife Refuge. It follows that the most important areas need to be selected first (Pressey and Taffs 2001).

To address this issue, Pressey and Taffs (2001) developed a procedure for scheduling conservation action based on two characteristics of potential conservation areas: vulnerability and irreplaceability. Vulnerability refers to the likelihood or imminence of areas being destroyed of disturbed (may be considered equivalent to threat, see above). Irreplaceability is calculated considering complementarity, and it refers to the likelihood that an area will be needed to contribute to a set of pre-defined conservation targets (see also Pressey et al. 1994; Pressey 1999; Ferrier et al. 2000). High priority for conservation action is given to areas of both high vulnerability and high irreplaceability (but see above the section on threat). If the implementation of a conservation network occurs in several phases, the irreplaceability value of the areas not yet designated is recalculated in each phase, having into account the contributions made by already selected reserves to the pre-defined conservation targets. The objective is to minimise the loss of biological value for a given conservation investment, by minimising the extent to which conservation targets are compromised before they can be met in new conservation areas.

Political considerations

Given the ongoing biodiversity crisis, which reaches desperate levels in parts of the world (e.g., Whitten et al. 2001), many calls have been made for scientists to have a more active advocacy role in conservation biology (e.g., Meffe 1998*b*; Prendergast et al. 1999; Brown 2000). Whitten et al. (2001) goes further and defends that "if there is to be any hope from the growing body of conservation biologists, [...] they will have to move away from priority-setting exercises, scientific studies, and theoretical modelling to on-the-ground management and policy decisions". Without denying the need for a deeper involvement of scientists in conservation practice and politics, moving away from research is unlikely to be the best strategy. As highlighted by the above overview, research is still badly needed in order to improve the effectiveness of conservation planning methods in their applications to real-life planning.

One way conservation scientists can make a difference is by injecting good science into policy (Mann and Plummer 1997; Meffe 1998*b*). Methods based on robust and explicit criteria for making decisions about conservation planning have the potential to be powerful tools in political negotiation. A world-class example of such a negotiation took place in Australia in 1996 and 1998 for the assessment of two forest areas in New South Wales (for details see Finkel 1998*a*,*b*; Pressey 1998). This was a joint initiative by the federal and state governments to negotiate long-term agreements for forest reserves that allow continued logging while maximising biodiversity retention in New South Wales. It was based on a 3-year, $23 million biota survey, and it engaged a diversity of stakeholders including governmental agencies (responsible for conservation and for forest production), and lobby groups (forestry industry, forestry workers, conservation movement). The negotiations were preceded by detailed preparation which included agreement on priority species and conservation targets (set by a group of experts chosen by the various stakeholders) and demonstration of the software for familiarisation and improvement. At the core of the negotiations, the software C-Plan was used to assess a multiplicity of different scenarios for conservation and trade-offs with timber exploitation in the region, aiming at having a negotiation process as scientific and transparent as possible involving all the stakeholders. This process was praised as "setting the gold standard in the field" and a "world-class" example (Finkel 1998*a*,*b*). Yet, the final decisions where taken behind doors, in a political and bureaucratic process, and the final plans covered an area wholly insufficient for achieving the required conservation targets and that doubled, from 10 to 20 years, the length of time industry could continue logging at its current quota. The process did lead to the creation of new nature reserves and national parks, but these were located in mainly unloggable escarpment forests, while other more biologically valuable areas were left out (Finkel 1998*b*). As this example sadly demonstrates, not even the best science, put to the best use, is immune to political weight. Nevertheless, robust and explicit processes such as this are badly needed to provide the kind of information required to empower conservationists to engage in on-the-ground management and policy decisions (Olson et al. 2002).

9.1.6 Explanation 5 - Reserve selection algorithms are not easily accessible to conservation practitioners

The ultimate goal of conservation biology is to inform and affect conservation decisions. Decisions are made by managers, not by scientists. There is a wide communication gulf between the two communities (Prendergast et al. 1999; Brown 2000), and, unless greater dialogue is achieved, the scientific developments in reserve selection methods are likely to remain largely useless and may perhaps be addressing the wrong questions. Managers need to know what scientists can deliver and scientists need to deliver what managers want (Prendergast et al. 1999).

In order to reach the managers, ideas must be comprehensible to the user, and in order to be applicable they need to be simple workable solutions, not the hypotheses, controversies and contradictions which scientists thrive on. As Western (1992) puts it "conservationists and managers need simple prescriptions – criteria and guidelines for when and how to manage nature – no less than a technician needs a service manual rather than a doctorate in physics to repair a refrigerator".

Making ideas comprehensible

Currently, the information on the use of reserve-selection algorithms is highly scattered and fragmented (Prendergast et al. 1999). Most papers focus on partial and simplified views of the reserve selection problem, and taken individually they are not useful to managers, who therefore tend to view reserve selection models as purely academic exercises (Davis et al. 1999). Individual authors need to make an effort to spell out what are the implications of their results for conservation practice. But beyond this, there an urgent need for synthesis papers that look at the big picture and draw recommendations and rules of thumb from the many results already published, and as new developments are being made. Managers have no time to digest the proliferation of papers produced by academia (Pressey [2002] found 245 references on reserve selection algorithms up to the year 2000).

Additionally, there is an urgent need for the publication of the details of real-case studies (as in Pressey 1998; Davis et al. 1999), which provide opportunities for managers to learn by example and insights for scientists about what are the relevant concerns in real problems. Prendergast et al. (1999) suggests workshops for information exchange between scientists and managers.

Another problem is that scientists and managers consult different information sources, such as different journals, therefore scientists need to make an effort to publish in journals more accessible to managers (Prendergast et al. 1999). To address this same concern, *Conservation Biology* created a new manuscript category "Conservation in Practice" (Meffe 1998*a*). The new journal *Conservation Biology in Practice* was created with the purpose of bringing together those managing the resources, those making policy, and those working to understand the nature of ecological systems and species (Kohm et al. 2000).

Workable solutions

Stoms et al. (1997) and Davis et al. (1999) reported that reserve selection algorithms are initially not well-received by conservation practitioners, as even the basic step of setting explicit conservation goals can be unfamiliar and contentious; additionally, the mathematical procedures can be intimidating. Widely available, user-friendly software is fundamental to overcome these difficulties. C-Plan was at the core of the negotiation process on the forests of New South Wales (Pressey 1998, see above) and was used directly by the stakeholders after these had time to become familiarised with it. On the other hand, the planning exercise for the Columbia Plateau ecoregion for The Nature Conservancy (TNC) was based on the Biodiversity Management Area Selection (BMAS) model, implemented using GIS at the University of California, Santa Barbara (Stoms et al. 1997; Davis et al. 1999). Davis et al. (1999) reported that the need to operate the BMAS model in the research lab in Santa Barbara was a drawback which eliminated the possibility of TNC's planning team using the model as an interactive tool for decision support. As these examples demonstrate, an interactive use of these packages is fundamental for engaging the managers in the decision process, for the integration of their own personal experience and expertise, and to make it clear that they are simply analitical tools to guide and inform rather than to prescribe planning decisions (enhancing, but not replacing, the expertise and judgement of managers; Pressey and Cowling 2001).

However, for many organisations, especially in countries where conservation is grossly underfunded, the cost of hardware, an expert operator, and the experimentation required may inhibit the use of reserve selection algorithms, even if the software itself is free (Prendergast et al. 1999). It is necessary to transfer technology and human resources from the countries and institutions where these methods have been developed to the ones where conservation planning is needed. The unprecedented growth of the internet has the potential to transform the way scientists and managers communicate, both between and among themselves (Prendergast et al. 1999). Prendergast et al. (1999) suggest that a logical extension to making the reserve planning software available through the internet, is the provisioning of an internet-mediated conservation planning capability to assist countries where conservation is critically under-funded. Given imagination, resolve, and appropriate funding, there seems little reason why expertise for reserve selection and other types of highly technical analyses could not be made universally available (Prendergast et al. 1999).

9.1.7 Where next?

Conservation planning for biodiversity persistence is far from being a simple task. Given the complexity of ecological and evolutionary processes that need to be considered (see section 9.1.4 above) and the gaps in basic biological data (section 9.1.2), reserve planning would be very complicated even if only biological considerations had to be taken into account. The fact that the social, political and economical context (see section 9.1.5 above) needs to be brought into the equation makes the whole task tremendous. To make matters worse, these two types of concerns – biological and human-related – are generally in direct conflict in their recommendations. For example, while protecting large (*very* large) areas of wilderness is the single most quoted guideline for the long-term persistence of biodiversity, the options for doing so become more and more reduced on a planet more and more crowded and demanding more and more of its natural resources.

Given this complexity, it is no surprise that published analyses using reserve selection algorithms are generally simplifications of the problem. However, most of the criticisms made to these methods apply to any reserve planning procedure, and are part of the broader recognition that the science of conservation biology is failing to make a substantial difference to halt the ongoing biodiversity crisis (e.g., Western 1992; Whitten et al. 2001).

Mathematical algorithms do not equal to the entire process of systematic reserve planning (Pressey and Cowling 2001), and they are simply good science applied to value judgements, with all their human foibles (Lawton 1997). They can identify sets of potential conservation areas which integrate many data sources and multiple concerns, be used to explore a diversity of other potential solutions and scenarios, and operate as part of decision-support systems that promote negotiations and integrate data on the constrains on and opportunities for conservation (Pressey 1998; Pressey and Cowling 2001). Algorithms are part of an explicit, defensible planning process, not the process itself (Pressey and Cowling 2001). And they do not replace the decision-making, which, ultimately, is not a scientific process but a political, ethical, aesthetic, even religious one (Lawton 1997).

The currently published literature on complementarity-based reserve planning has addressed a remarkable diversity of concerns and suggested a diversity of tactics to incorporate them into explicit decision-making procedures. Complementary-based reserve selection methods are starting to be effectively applied to real-life planning processes (e.g., Stoms et al. 1997; Pressey 1998; Davis et al. 1999; Clark and Slusher 2000) and their basic concepts are permeating into the conservation strategies of key players in conservation practice (e.g., TNC's strategic approach "Conservation by Design"; Valutis and Mullen 2000). It is encouraging that the results reported by Kirkpatrick (1983; the first published reserve selection algorithm) were highly influential for the designation of seven reserves in Tasmania, even though the implementation process took seven years (Pressey 2002).

This does not mean that reserve selection algorithms are all set for practical conservation planning, and as the above review demonstrates much improvement is needed in several aspects. My final recommendations on the main developments needed to improve the effectiveness of these methods in real-life conservation planning are the following:

- Advances in how to make the best use of the existing (necessarily limited) data, including the test and development of surrogates.

- Advances in the definition of the conservation goals: what biological requirements reserve networks should fulfil (even if only ideally) in order to ensure the long-term persistence of biodiversity? This includes testing and developing rules of thumb for the incorporation of the multiple ecological and evolutionary processes responsible for generating and maintaining biodiversity.

- Developments in the integration of social/economic/political constraints, looking for creative solutions to avoid conflict and target the most cost/effective conservation opportunities.

- Interpretation, synthesis and translation of the results obtained by isolated publications into practical recommendations for managers.

- Dissemination of the details of, and lessons learnt from, practical case studies where both scientists and managers participate and the procedures are put to the test, for the benefit of both managers (who can learn by example) and scientists (who can learn about the complexities of real conservation problems).

- Improvements in the communication between scientists and managers, preferably by joint work on practical conservation planning. Includes the development of accessible and flexible decision-support tools integrating the best available data, the most robust scientific recommendations and the possibility of integrating the diversity of concerns that typically impinge on real conservation problems.

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Appendix I - Balmford, A., Gaston, K.J., Rodrigues, A.S.L., James, A. 2000. Integrating costs of conservation into international priority setting. *Conservation Biology* **14**, 597-605.

Issues in International Conservation

Integrating Costs of Conservation into International Priority Setting

Rationale

Although political and legal constraints force countries and agencies to use some of their conservation funds locally, substantial sums could be spent by national and international bodies virtually anywhere on the planet. Given the gross underfunding of conservation efforts as a whole (James et al. 1999*a*), the identification of robust priorities for allocating such money is important, but the most widely used approaches do not take into account the relative costs of conserving different areas (Myers 1988, 1990; McNeely et al. 1990; Mittermeier & Werner 1990; Sisk et al. 1994; WWF & IUCN 1994–1997; Caldecott et al. 1996; Bryant et al. 1997; Mittermeier et al. 1997, 1998; Olson & Dinerstein 1998; Stattersfield et al. 1998). Techniques for integrating cost measures into priority assessment have recently been developed (e.g., Williams 1996; Ando et al. 1998). Until now, however, the paucity of global data on conservation costs has precluded the application of such methods at an international level.

We used newly compiled data to examine the merits of explicitly including information on costs in global priority setting. The biological data used to inform priority selection come from a summary of the distribution of all mammal species across all countries (Mace & Balmford 2000). The cost data consist of estimates of the likely costs of effectively conserving each country's reserve network up to around 15% of land area (James et al. 1999*a*, 1999*b*, 2000). Based on a series of different methods, we used these data to order countries according to conservation priority and then assessed how incorporating cost information affects cost effectiveness, measured in terms of the number of mammal species represented in the priority set, per dollar spent.

This approach has many important limitations. First, lack of global data at other scales means that we used countries as our units for priority setting. There is, of course, considerable merit in identifying global conservation priorities in terms of other sorts of land units, such as finer-scale geopolitical units, ecosystems, or equal-sized grid squares (Williams 1993; Mittermeier et al. 1998; Olson & Dinerstein 1998; Stattersfield et al. 1998). Nevertheless, country-based priority setting is useful because conservation investments are frequently directed toward countries, and because conservation policies and treaties are generally implemented by national institutions. Further, the country-level analysis demonstrates how cost data might be used to improve priority setting at other levels.

Second, data constraints force us to consider only mammals. Previous efforts to establish key countries for biodiversity conservation have used data on a broader range of groups but have been obliged to set priorities based on national totals for species or for single-country endemics (McNeely et al. 1990; Mittermeier & Werner 1990; Sisk et al. 1994; Caldecott et al. 1996; Mittermeier et al. 1997). The efficiency of priority sets is considerably improved, however, if those areas are chosen so as to account not just for their absolute biological richness but also for how well they complement one another biotically (Pressey et al. 1993, 1997; Csuti et al. 1997; Williams 1998). To address complementarity fully, we need data on which species—and not just how many—each area holds. To our knowledge, the mammal database is the first to list species occurrence by country for any taxon of this size.

Last, and critically, we quantified the extent to which different hypothetical priority sets achieve conservation objectives in terms of species representation in reserves. Of course, conservation is about far more than this: species are just one aspect of biodiversity. They differ in their cultural, ecological, and evolutionary signifance, and for species to be maintained (rather than merely represented), we must conserve ecological and evolutionary processes beyond as well as within reserves. Nevertheless, we currently lack ways of quantifying how far these other conservation objectives are met. Hence, despite its being simplistic, we have little choice here but to concentrate on species representation as the most widely used metric of conservation performance, in the hope that insights gained here can shed light on how other, more sophisticated measures of conservation performance can be developed.

These and other concerns mean that our results must be seen as a heuristic exploration of how and why to integrate economic concerns into priority setting, rather than an attempt to generate a definitive blueprint for cost-effective conservation investments.

Databases

Costs of Effective Conservation in Reserves

The starting point for this database was information collected in two questionnaire surveys conducted in 1993 and 1995 by the World Conservation Monitoring Centre (WCMC; James et al. 1999*b*). The surveys asked personnel of national protected-area agencies how much they spent annually on the terrestrial reserves under their jurisdiction. The resulting information, when supplemented by published and unpublished data (James et al., 2000), summarizes current expenditure on roughly 48% of the world's protected-area estate, representing all or some of the reserves of 117 countries (data for reserve area and status and for country area were all taken from World Conservation Union [IUCN] 1998). Within those countries, expenditure on reserves for which there was no response in the survey was estimated by extrapolating from spending on reserves that were reported on, which generated estimates of overall national expenditure. These and all other costs were expressed in 1996 dollars (U.S.). All countries for which no data on current reserve spending were available were excluded from subsequent country-level analyses.

Current expenditure on reserves is generally perceived to be inadequate to meet conservation objectives; moreover, the extent of this inadequacy varies widely both across countries and across years within countries. We therefore decided not to use the WCMC figures on current spending by themselves. Instead we built on them to derive rough estimates of the total cost of effective protected-area networks in each country. This involved three further steps: assessment of additional resources required to manage current reserves effectively; estimates of costs of gazetting new reserves; and estimates of compensation levels required by residents of developing countries to offset opportunity costs imposed by reserves.

In the 1995 WCMC survey, agencies in 52 countries reported how much extra money they needed to meet their stated conservation objectives, and we again used these reported figures to estimate shortfalls in countries that did not respond. Second, to account for widespread concerns that existing protected-area networks are often too small to sustain a country's biodiversity (e.g., IUCN 1993; Soulé & Sanjayan 1998), we estimated the costs of expanding each country's reserve system so that 10% of its land area is covered by strict reserves (IUCN categories I-III) while retaining all existing reserves in categories IV-VI (which cover an average 5% of land area). The approximate cost of this expansion was calculated by summing estimates for survey, purchase, and maintenance of the new reserves. We estimated the cost of biodiversity surveys (20% of country area) and land purchase based on a separate data set. As one-time costs, we annualized these expenses over a 30-year implementation period. Third, we included an estimate of the expenditure required to meet the opportunity costs of lost resource use due to existing reserves in the developing countries. We estimated these annual opportunity costs from the product of the local land price and the discount rate (because land values reflect the discounted, long-term opportunity costs of alternative land uses), applying this formula to all existing reserves in IUCN categories II-IV (omitting category I reserves because they are generally uninhabited, category V and VI reserves because they permit substantial resource use, and new reserves because our figures for these already include land purchase at market rates; for details on calculations, see James et al. 1999*a*, 2000).

Added up, our figures for expenditure and shortfall for existing reserves, reserve expansion, and compensation to local residents represent a first attempt to calculate the likely costs of effective and extensive protected-area networks for a large number of countries. Many individual country figures—particularly for reserve expansion and compensation—may be in error by as much as 50%, and our subsequent results should be interpreted with this in mind. Moreover, our estimates deal only with the approximate costs of conservation in reserves and not with the even less readily quantified (and probably far higher) costs of conservation in the human-dominated landscapes surrounding reserves (James et al. 1999*a*, 2000). Nevertheless, our reserve costs represent a starting point from which we can explore what will happen if we incorporate economic concerns into conservation decision making.

Distribution of Mammals

In building the database on mammal distributions, we adopted the classification of Wilson and Reeder (1993), with minor additions and amendments of the IUCN (1996). We included all extant and recently extinct mammals (4761 species) and then, using a variety of sources (referenced in full by Mace & Balmford 2000), we attempted to record all countries in which each species has been documented. Because we did not have access to detailed distributional information for recently independent countries of the former Soviet Union and former Yugoslavia, these countries were excluded.

The mammal distributional database, like the literature it is derived from, doubtless contains many mistakes. Some idea of the combined effect of errors of omission and commission can be gained by comparing each country's total number of species according to the database with other estimates of national richness for mammals. When we regressed our figures against those given by WCMC (1994), we found that they agreed well (if run through the origin, $r^2 = 0.98$, $\beta \pm SE = 0.94 \pm 0.01$, and $p < 0.001$ for those 106 countries jointly covered by our mammal database, the WCMC database, and the costs database). Hence, although the mammal data are imperfect they are far more accurate than our costs data.

Countries Covered

Altogether, we had both mammal lists and estimates of overall reserve costs for 111 countries (from which we had records of 4228 mammal species). Notably biodiverse countries missing from this set (largely because they did not respond to the WCMC surveys) include Belize, Bolivia, Costa Rica, Cuba, El Salvador, French Guiana, Guinea, Guyana, Haiti, Japan, Nicaragua, Panama, Philippines, Russia, Spain, Surinam, Venezuela, Vietnam, and Zambia.

Priority-Setting Analyses

Absolute Species Richness

We ranked our set of countries in order of decreasing species richness for mammals (according to the distributional database) to provide a baseline against which other, more sophisticated approaches could be assessed. The resulting priority sequence was unsurprising, with the first 8 countries matching Caldecott et al.'s (1996) top eight countries for mammal species richness (although not in exactly the same order), and included seven of the 12 so-called megadiversity countries (McNeely et al. 1990; Mittermeier & Werner 1990; see Table 1).

Prioritizing conservation investment by species richness alone would be expensive. Comparing our overall budget estimates with the mammal richness scores, we found that countries with more mammal species would have to spend more to conserve their species richness properly ($r_s = 0.53$, $n = 111$ countries, $p < 0.001$). This result is probably driven at least partly by both variables being positively correlated with country area (mammal species richness vs. area: $r_s = 0.78$, $n = 111$, $p < 0.001$; estimated conservation cost vs. area: $r_s = 0.72$, $n = 111$, $p < 0.001$).

As a consequence of the high cost of conservation in mammal-rich countries, priority sets based on absolute country richness generally included far fewer countries than priority sets costing the same total amount but derived in other ways (Table 1 lists alternative priority sets, each of them cut off at roughly the same arbitrarily determined total cost). Moreover, because of the positive link between country species richness and national reserve cost, the cumulative number of species represented when a set of countries is picked in order of decreasing species richness rises slowly when plotted against the countries' cumulative budget (Fig. 1).

Absolute Richness in National Endemics

Does focusing on nationally endemic species improve the cost-effectiveness of priority sets? To test this idea, we classified a species as an endemic if it was recorded from just one of the 111 countries in the database. (A species may occur in other countries, but for illustrative purposes we treated our subset of countries as though they represented the entire world.) We then ranked countries in order of decreasing richness for single-country endemics. There were again few surprises in the resulting priority set (Table 1), with the two biggest island "megadiversity" nations, Australia and Indonesia, heading the list and the top five countries corresponding to five of Caldecott et al.'s (1996) first six nations for endemic mammals (their other top priority, the Philippines, was not included in our analyses).

Countries rich in endemic mammals (like countries rich in mammals as a whole) are generally large and have high costs for conservation (endemic species richness vs. area: $r_s = 0.67$, $n = 111$, $p < 0.001$; endemic species richness vs. estimated conservation cost: $r_s = 0.61$, $n = 111$, $p < 0.001$). Consequently, and because Australia in particular has higher cost structures than other countries with fewer endemic species but more mammals overall, the accumulation of species with increasing overall budget was generally even slower when countries were picked in order of decreasing richness for endemics than when decreasing richness for all mammals was the criterion (Fig. 1). It appears that increasing the cost-effectiveness of across-country priority setting may require explicitly taking conservation costs into account.

Richness to Cost Ratios

One simple but potentially effective way to build cost considerations into cross-country priority setting is to divide a country's richness score (for all mammal species or for endemics) by its estimated conservation costs. The resulting ratio of total species richness to cost is independent of country size ($r_s = 0.11$, $n = 111$, not significant), and the ratio of endemic species richness to cost was less closely correlated with area than was absolute endemic richness (for all countries: $r_s = 0.39$, $n = 111$, $p < 0.001$; excluding 34 countries with zero mammal endemics: $r_s = -0.04$, $n = 77$, not significant). Hence, small countries, unlikely to rank highly for absolute richness or endemism, can nevertheless have high scores for either overall richness or endemic richness relative to cost.

This means that for the same overall cost, priority sets derived by picking countries in order of decreasing ratios of total richness to cost or endemic richness to cost include far more countries, and in particular smaller countries, than sets derived

Table 1. Cumulative costs, species representation, and country membership of priority sets picked by alternative techniques, and all costing roughly $6.25 billion per year.[a]

Technique	*Absolute species richness*	*Absolute richness for endemics*	*Ratio of total species richness to cost*	*Ratio of endemic species richness to cost*	*Linear programming, maximizing species for cost*
Cumulative annual budget (billions of 1996 $ US)	7.55	6.41	6.45	6.61	6.25
Number of countries	8	5	76	39	50
Cumulative number of mammal species represented	2561	1811	3461	3640	3696
Countries selected[b]	Indonesia Brazil China Mexico Democratic Republic of Congo Peru Colombia United States	Australia Indonesia Brazil Mexico United States	Togo Montserrat Gambia Trinidad and Tobago Burundi Luxembourg Guatemala Chad Malawi Kenya Ghana Myanmar Côte D'Ivoire Gabon Honduras Rwanda Peru Senegal Bhutan Sierra Leone Nepal Israel Belgium Uganda Colombia Central African Republic Ethiopia Chile Cameroon Lao P.D.R. Saint Kitts and Nevis Angola Dominica Burkina Faso Zaire Mozambique Niger Seychelles Congo Jamaica Tanzania Ecuador Nigeria Brunei Darussalam Sudan Cambodia Zimbabwe Samoa Madagascar Malaysia Panama Antigua and Barbuda Namibia Mexico Netherland Antilles Indonesia Papua New Guinea Botswana	Seychelles Madagascar Peru Jamaica Indonesia Australia Colombia Ethiopia Kenya Mexico Chile Papua New Guinea Trinidad and Tobago Côte D'Ivoire Bahamas Malaysia Mauritius Israel Panama Zaire Ecuador Honduras Cameroon Sri Lanka Taiwan Brazil Myanmar Guatemala Guadeloupe Tanzania Argentina Morocco Fiji Dominican Republic Sudan Lao P.D.R. Vanuatu Afghanistan China	Indonesia Brazil Mexico Democratic Republic of Congo Peru Colombia Kenya Tanzania Australia Ecuador Malaysia Cameroon Argentina Sudan Angola Ethiopia Myanmar Papua New Guinea Panama Ghana Côte D'Ivoire Mozambique Guatemala Honduras Namibia Pakistan Nepal Senegal Lao P.D.R. Burundi Afghanistan Madagascar Mongolia Chad Chile Trinidad and Tobago Israel Sri Lanka Morocco Greece Taiwan Finland Belgium Dominican Republic Jamaica Bahamas Guadeloupe Fiji Mauritius Seychelles

continued

Table 1. (continued)

Technique	*Absolute species richness*	*Absolute richness for endemics*	*Ratio of total species richness to cost*	*Ratio of endemic species richness to cost*	*Linear programming, maximizing species for cost*
			Afghanistan		
			Bangladesh		
			Pakistan		
			Sri Lanka		
			Kuwait		
			Morocco		
			Czech Republic		
			Taiwan		
			Yemen		
			Finland		
			Hungary		
			Bahrain		
			Thailand		
			Austria		
			Greece		
			Bahamas		
			Australia		
			India		

[a] *The $6.25 billion per year is equivalent to 0.3 C_m, and C_m is the minimum cost of including all 4288 mammal species in the set.*
[b] *Countries are listed in order of decreasing priority, except in the final column (because for a given cost the linear programming solution picks all countries simultaneously), where they are listed in order of decreasing absolute species richness.*

by focusing only on absolute richness measures (Table 1). Given the inaccuracies in the cost data for individual nations, it would be inappropriate to explore in detail how the ranks of specific countries change once the priority-setting scheme incorporates cost. A general pattern that emerges (Table 1) is that, when cost data are included, some species-rich countries—for which protecting entire reserve networks is extremely expensive (e.g., United States) or quite expensive (China in one set, India in another)—decrease in priority. They are replaced by many relatively species-rich but smaller and cheaper countries that collectively span a broader geographical array of areas. Noteworthy additions to priority sets derived from scores for richness or endemic richness relative to cost include several central American countries, the remaining South American countries in the database, many more African nations, Madagascar, and Papua New Guinea (Table 1).

The broader geographical coverage of these new priority sets explains why they are more cost-effective than the previous priority sets (Fig. 1). According to our mammal database, for example, the priority sets based on ratios of total richness to cost and of endemic richness to cost, which are listed in Table 1, collectively contain 35% and 42% more mammal species, respectively, than an absolute total richness set with roughly the same overall budget, and 91% and 101% more species than the same-cost absolute endemic richness set. These comparisons also show that substituting some

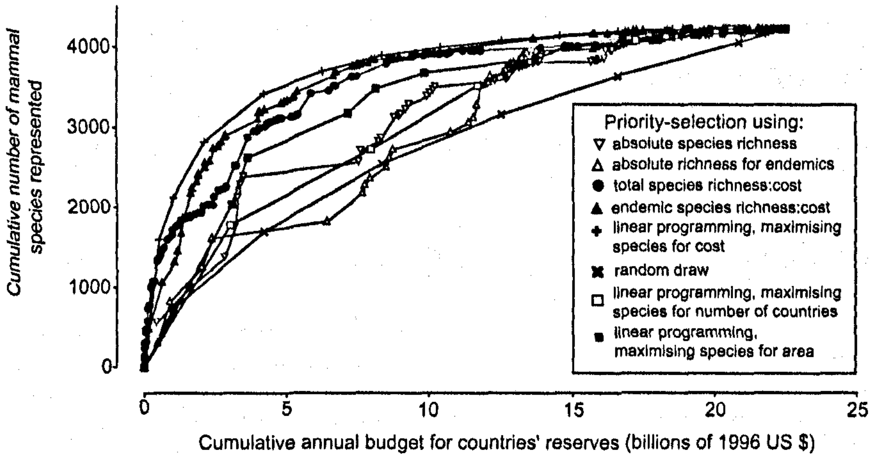

Figure 1. The cumulative representation of all mammal species, plotted as a function of the estimated cumulative annual budget of reserves in all selected countries, picked by alternative priority-setting methods. Confidence limits for the random draw lie so close to the mean that for clarity they are not plotted.

large but costly countries with more, cheaper countries increases the cost-efficiency of the priority set even more when attention is focused on endemics rather than on all species (i.e., when at least some consideration is given to complementarity).

Maximizing Species Representation for a Given Cost

To find out how much more cost-efficiency could be improved if priority setting took into account patterns of complementarity for all species, including nonendemics, we used lienar programming in the penultimate set of analyses (implemented through CPLEX [ILOG 1999]) and established the maximum number of mammal species that could be represented in priority sets costing particular amounts. This required that we solve a series of separate problems.

First, we identified the cheapest set of countries that collectively represented all 4228 mammal species, and the minimum overall cost of so doing (C_m). To do this, we sought to minimize the total cost of conservation (summed across all countries selected),

$$\sum_{j=1}^{n} c_j x_j , \qquad (1)$$

and ensured that each mammal species was represented at least once,

$$\sum_{j=1}^{n} a_{ij} x_j \geq 1 \;\; (i = 1, 2, \ldots, m.) \qquad (2)$$

Because our analysis was at the country level, countries were either selected or not, in their entirety:

$$x_j \in \{0,1\} \;\; (j = 1, 2, \ldots, n.) \qquad (3)$$

In these expressions, m is the total number of species, n is the total number of countries, c_j is the cost of country j, a_{ij} is 1 if species i is present in j and 0 otherwise, and x_j is 1 only if country j is selected.

In the real world, finding even the minimal funding needed to conserve all mammal species (C_m) may not be possible. Hence, we wanted to examine how changes in funding affect the number of species protected. To do this, we calculated the maximum number of species that can be protected at a given fraction (f) of the minimum overall cost of protecting all 4228 mammal species (C_m). We examined this for 11 levels ranging from 90% of funding to 2.5% of minimal funding ($f \in \{0.9, 0.8, 0.7, 0.6, 0.5, 0.4, 0.3, 0.2, 0.1, 0.05, 0.025\}$). We determined the maximum number of species that can be represented at a cost not exceeding a given fraction of C_m ($f \times C_m$) by solving the maximal covering location problem

$$\text{maximize} \sum_{i=1}^{m} y_i , \qquad (4)$$

subject to species i being counted as represented only when at least one of the countries where it occurs is selected,

$$\sum_{j=1}^{n} a_{ij} x_j \geq y_i \;\; (i = 1, 2, \ldots, m;) \qquad (5)$$

the total cost of the countries selected not exceeding $f \times C_m$,

$$\sum_{j=1}^{n} c_j x_j \leq f \times C_m ; \qquad (6)$$

and countries being either selected or not and species represented or not, in their entirety,

$$y_i \in \{0,1\} \;\; (i = 1, 2, \ldots, m.) \qquad (7)$$

In these expressions y_i is 1 if species i is covered and 0 otherwise (and the other variables are as before).

This problem may have different optimal solutions (with several sets of countries all containing the same number of species, but at slightly different costs, all $\leq (f \times C_m)$). In those cases we identified the one with the minimum cost.

The output from these analyses were lists of those countries which collectively represent the maximum number of mammal species for a given fractional cost of C_m, and the species they contain. These optimal solutions are plotted in Fig. 1, from which it can be seen that this approach—paying attention to all patterns of complementarity, including those of nonendemics—does identify priority sets that are more cost-efficient than those derived by simple ranking of ratios of total richness to cost or of endemic richness to cost. The differences are not great, however. The three cost-linked techniques pick many of the same priority countries, and the optimal priority sets identified by linear programming contain a geographically broad scattering of small and large countries (Table 1).

Evaluating Other Approaches

To put all our results in context, we conducted three additional analyses. First, we quantified the cost-effectiveness of priority sets picked entirely at random. We calculated the mean number (±95% confidence limits) of species represented in 10,000 sets of countries with approximately the same total cost, for each of six different figures of total cost. We plotted the curves of the mean values derived from this random simulation (Fig. 1). This reveals that nearly all systematically selected priority sets performed better than randomly selected sets, although sometimes not markedly so for those derived using species numbers alone.

Second, to find out whether the gains in cost-effectiveness achieved by the linear programming approach are due primarily to addressing cost or to improved accounting for patterns of complementarity, we ran a second series of linear programming analyses (essentially paralleling those detailed above) using just the species × country data matrix. These analyses identified the smallest number of countries that represented all 4228 mammal species at least once (N_m) and the maximum number of species that could be represented in sets of countries ranging from 5% to

90% of N_m. These priority sets were consistently less cost-efficient than any of the sets derived from cost data (Fig. 1). The gains in efficiency achieved by our first linear programming analyses are therefore largely due to inclusion of cost information and secondarily because they fully address patterns of complementarity.

Finally, given that cost data are scarce and hard to acquire, we asked whether similar increases in the cost-efficiency of priority sets might be achieved by means of a more readily acquired proxy for the overall cost of a country's protected areas. Because of the reasonably close correlation between total conservation cost and country area, we decided to focus on country area and examine the cost-efficiency of priority setting based solely on species distribution patterns and country size (assuming no knowledge of costs). We again used linear programming to identify the set of countries that between them represented all 4228 mammal species in the smallest combined area (A_m). We then identified the maximum number of mammal species that could be represented in each of a series of total areas, ranging from 5% to 90% of A_m, and the countries comprising each of these optimal sets. Determining the cost of each of these solutions revealed that in practice they are generally more cost-efficient than priority sets derived from species numbers alone (Fig. 1). They are also consistently less cost-efficient than any of the prioritization schemes that coupled biological and cost data. Hence, in the total absence of direct data, area may be worth using as a proxy for cost, but attempting to collect and collate whatever cost information is available seems highly desirable.

Implications for Priority Setting

Our heuristic analyses of the relative performance of different priority-setting techniques suggest that integrating cost data with biological information substantially increases the cost-efficiency of resulting priority sets. Moreover, direct information on costs appears far more useful than data on potential proxies for cost, such as country size, although more thorough statistical models of international variation in conservation costs may suggest additional, readily measured variables that, in combination with country area, predict overall costs with reasonable accuracy. Last, the linear programming results indicate that using information on which species (rather than simply how many) occur where should yield additional conservation gains. These conclusions are subject to several important caveats, however.

First, there are evident limitations to what we can infer given the scope and accuracy of our data on distributions and, more important, conservation costs. The lists in Table 1 must be interpreted as merely indicative of the composition of different types of priority sets rather than in any way definitive. Many key nations were omitted from our analyses because of a complete lack of information on costs and the ranking of certain others for which rather few cost data were available (e.g., India and China) may be misleading. Because of an even greater paucity of data, we ignored the costs of conservation in land that is not reserved, yet the fate of much biodiversity depends on activities in the human-dominated matrix surrounding reserves. And we focused entirely on mammal species, whose value as indicators of priority areas for other taxonomic groups is open to question. These and other issues of data coverage mean that the priority attached to individual countries can be assessed properly only when more accurate cost data are assembled, for nearly all countries, and when information on mammals is supplemented by data on at least one or two other groups.

A second shortcoming in our approach is that, for simplicity, we treated conservation investments in countries as if they occurred in an integral manner: under this scenario, the protected-area network of priority country A is conserved in its entirety before any funds are spent on the next priority, country B. In reality this simplification is inappropriate because optimal investment strategies involve investing in country A only as long as the marginal benefits of further investment, measured at the global level, exceed those of starting to invest in country B (C, D, etc.). Solving this more sophisticated investment problem is theoretically tractable (by applying the marginal value theorem; Charnov 1976) but requires far more detailed information than is currently available on how conservation returns diminish with increasing conservation investment within individual countries.

Third, as we have seen, addressing concerns about both costs and complementarity results in a geographical broadening of international conservation priorities, but scattering efforts widely may have several serious drawbacks. In particular, some of the smaller countries highlighted by cost-linked priority setting may be able to accommodate only relatively small reserves, compared with the protected areas of larger countries, raising a raft of concerns about the long-term viability of conserved communities. As yet, we lack robust techniques for quantifying the ability of areas to retain their ecological and evolutionary viability in the face of ongoing anthropogenic challenges (see papers in Mace et al. 1998). There is a pressing need to develop such measures and to devise methods for integrating them, alongside data on species distribution and conservation cost, into more holistic procedures for systematic site selection (Nicholls 1998; Williams 1998; Rodrigues et al. 1999). Only then will we be able to properly evaluate how the potential costs of scattering conservation effort (in terms of reserve viability) compare with the benefits (in terms of increasing the efficiency of species representation).

Despite these concerns about the limitations of our findings, we suggest that they do argue strongly for the direct incorporation of information on costs into international priority setting. According to a recent, if rough, estimate, global spending on conservation in reserves currently runs at just 20% of that needed to establish and maintain extensive and effective reserve networks in all countries (James et al. 1999*a*). As long as this situation persists (and we remain on the left-hand side of Fig. 1), then paying direct attention to between-country differences in the costs (and benefits) of conservation may greatly increase the overall proportion of biodiversity that we conserve.

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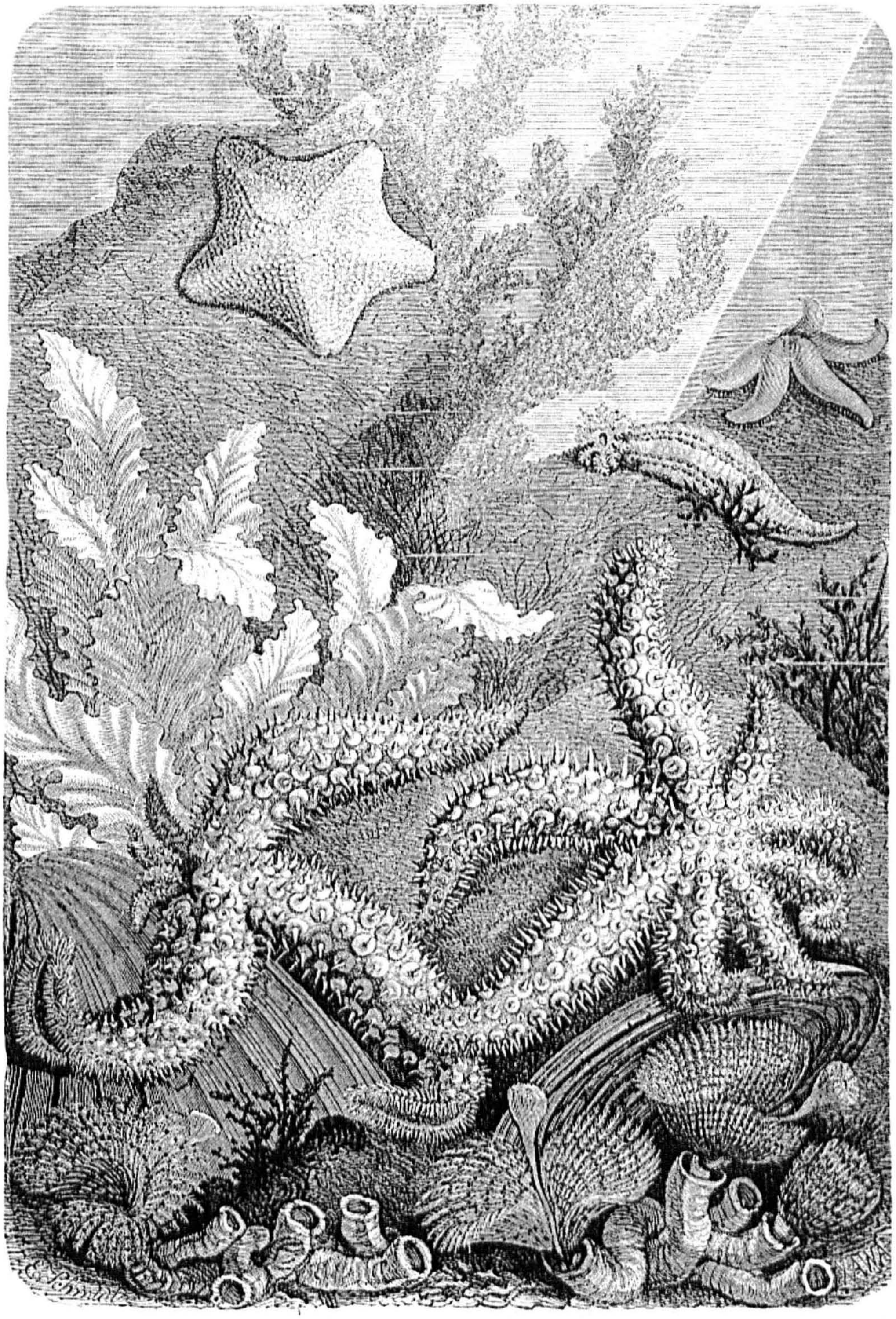

Appendix II - Chown, S.L., Rodrigues, A.S.L., Gremmen, N.J.M., Gaston, K.J. 2001. World Heritage Status and conservation of Southern Ocean Islands. *Conservation Biology* 15, 550-557.

Issues in International Conservation

World Heritage Status and Conservation of Southern Ocean Islands

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Background

The islands of the southern ocean are of considerable conservation importance. They provide the nesting grounds of a significant portion of the world's procellariiform seabirds (Chown et al. 1998*a*), house a variety of endemic species (Holdgate 1965; Gressitt 1970; Gremmen 1981; Woods 1988; Evenhuis 1989; Greenslade 1990; Turbott 1990; Patrick 1994; Morrone 1998), and, because of the paucity of land in this region, provide the only examples of mid- to high-latitude southern terrestrial ecosystems (Bergstrom & Chown 1999). Principally for these reasons, and based on two major workshops held by the Scientific Committee for Antarctic Research (SCAR) and the World Conservation Union (IUCN), international agreement was reached that a joint review of the World Heritage potential of all of these islands, which are managed by several different nations, should be undertaken to provide a basis for their coordinated conservation (Walton 1986; Dingwall 1987; IUCN 1991; Dingwall 1995). An IUCN working group was subsequently established to make a comparative assessment, in accordance with World Heritage criteria, of the natural values of these islands (IUCN 1992).

Using the objectives of the World Heritage Convention with respect to natural properties—i.e., sites that are outstanding examples of major stages in the Earth's history, sites representing significant on-going ecological and biological processes, sites containing superlative natural phenomena or areas of exceptional natural beauty, or sites containing the most important and significant natural habitats for in situ conservation of biological diversity—this working group identified seven criteria in assessment of the conservation and World Heritage value of the sites (IUCN 1992). Most notable among these criteria were that emphasis should be given to assessments of the comprehensive value of a particular island to science and global heritage conservation and that a comparative approach using objective and uniformly applicable guidelines among the islands should be adopted for site selection (IUCN 1992). The working group also noted that assessing the relative merits of the islands in terms of the four natural-properties criteria might prove problematic, chiefly because of the difficulties in comparing evolutionary processes and natural beauty across islands and of assessing the relationship between endemism and threat (Synge 1991). After noting several caveats, the working group nonetheless concluded that the most useful approach would be to undertake a comparative assessment of the indigenous biodiversity of the islands and the extent of alien introductions and their effects (IUCN 1992).

Such an assessment, based on a delphi analysis examining geological character, landscape features, biodiversity, and human effects, was subsequently done for the majority of the Southern Ocean islands, excluding those within the Antarctic Treaty Area covered by international legislation (Table 1; IUCN 1995). It was concluded that, so long as some caution is exercised, the delphi analysis provides a reasonably objective ranking of various World Heritage attributes for the Southern Ocean islands and of the islands themselves (IUCN 1995).

Since this analysis, several nations have successfully nominated Southern Ocean islands under their control for World Heritage status (Table 1). In the case of the New Zealand subantarctic islands, both the IUCN report (IUCN 1992) and the outcome of the delphi analysis (IUCN 1995) were used in support of the nomination (Anonymous 1997). Indeed, this nomination concluded that the delphi analysis "is a useful guide to the relative standing of the islands as potential World Heritage sites." Similarly, the 1990 nomination of

Table 1. Comparison between the islands nominated as World Heritage sites and the sets of islands selected based on the delphi and complementarity analyses.

Island	No. indigenous species	No. unique species[a]	No. alien species	World Heritage (WH) sites[b]	*Delphi analysis*[c]						*Complementarity analysis*[d]				
					total		*biodiversity*		*lowest human effect*		*max. no. indigenous species on 12 islands*	*max. no. indigenous species on 18 islands*	*min. no. alien spp. (≥90% indigenous spp.)*	*min. no. alien mammal spp. (≥90% indigenous spp.)*	*min. no. alien mammal spp. (≥90% indigenous bird spp.)*
					top 5	*top 5 + WH*	*top 5*	*top 5 + WH*	*top 5*	*top 5 + WH*					
East Falkland	338	65	109		nr	nr	nr	nr	nr	nr	✓	✓	✓	✓	
West Falkland	289	33	103		nr	nr	nr	nr	nr	nr	✓	✓		✓	✓
Beauchene	63	16	1		nr	nr	nr	nr	nr	nr		✓	✓	✓	✓
South Georgia	69	17	69		✓	✓	✓	✓	✓	✓		✓			
Tristan da Cunha	136	20	164				✓	✓			✓	✓			
Gough	111	17	36	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓
Inaccessible	128	16	39				✓	✓			✓	✓	✓	✓	✓
Nightingale	90	13	12				✓	✓				✓	✓	✓	✓
Marion	67	0	38				✓	✓				✓		✓	
Prince Edward	67	0	5		✓	✓	✓	✓	✓	✓			✓	✓	✓
Cochon	68	4	14				✓	✓					✓	✓	
Possession	97	18	111				✓	✓			✓	✓			
Kerguelen	92	12	59		✓	✓	✓	✓			✓	✓			
New Amsterdam	60	19	106								✓	✓		✓	✓
St. Paul	31	6	25									✓			
Heard	40	1	2	✓	✓	✓		✓	✓	✓			✓	✓	✓
McDonald	21	0	0	✓		✓		✓	✓	✓			✓	✓	✓
Macquarie	89	20	20	✓	✓	✓	✓	✓		✓	✓	✓	✓		
Auckland	470	175	59	✓		✓	✓	✓		✓	✓	✓	✓	✓	✓
Campbel	339	84	123	✓		✓		✓		✓	✓	✓	✓	✓	✓
Snares	180	91	25	✓		✓		✓	✓	✓	✓	✓	✓	✓	✓
Antipodes	158	30	26	✓		✓		✓		✓	✓	✓	✓	✓	✓
Bounty	21	5	0	✓		✓		✓	✓	✓			✓	✓	✓
No. islands				9	6	12	12	18	7	11	12	18	15	17	14
Indigenous species (%)				61	21	66	59	75	28	65	94	99	90	93	92
Alien species (%)				34	28	47	70	79	24	42	92	99	49	73	73

[a] *Species occurring on just one island.*

[b] *Marked sites nominated based on biodiversity.*

[c] *We considered the total delphi score and, separately, the delphi scores based on the assessment of biodiversity and of human effect. For each score, the first column (top 5) refers to the set of islands that ranked ≤5 (in case of ties, more than five islands were selected); the second column (top 5 + WH) refers to the union of the top 5 islands and those designated as World Heritage sites; and nr means not ranked.*

[d] *Five sets of islands are represented under the complementarity analysis: (1) and (2) maximize number of indigenous species that can be represented on 12 and on 18 islands, respectively (see Fig. 1 for details); (3) minimizes the number of alien species that need to be included, subject to having more than 90% of all indigenous species represented (see Fig. 2 for details); (4) minimizes the number of alien mammal species that need to be included, subject to having more than 90% of all indigenous species represented; and (5) minimizes the number of alien mammal species that need to be included, subject to having more than 90% of indigenous bird species represented. The archipelago of Crozet (Possession, Coachon, Est, Pingouins, and Apotres) was treated as a unit in the delphi analysis; only Possession and Cochon were included in the complementarity analysis because it was not possible to obtain complete species lists for the remaining islands.*

Heard and McDonald islands for inclusion on the World Heritage list was deferred by the World Heritage Committee until the islands' unique values had been compared to those of other subantarctic islands (Anonymous 1994). Heard Island was subsequently ranked highly by the IUCN working group (IUCN 1995) and was included on the World Heritage list in 1997. Clearly, the outcome of the delphi analysis is now being widely used in assessing the relative merits of the Southern Ocean islands for inclusion on the World Heritage list.

Several other nations are currently preparing to nominate islands under their control for inclusion on the list (e.g., Anonymous 2000*a*). There is some concern, however, that the conclusions of the IUCN islands working group and the successful inclusion of several Southern Ocean islands on the World Heritage list might make subsequent nominations considerably more difficult, especially if they do not rank highly in the delphi analysis (Anonymous 2000*b*; J. Cooper, personal communication). In other words, Southern Ocean islands might now be considered well represented, thus lessening opportunities for improving the conservation status of single islands or island groups, and consequently the region as a whole.

At the same time, concern for the conservation of the biotas of the Southern Ocean islands has been increasing. Several recent studies have shown not only that there is a clear relationship between the number of humans visiting an island and the number of alien species present (Chown et al. 1998*b*), but also that climate change is enhancing the likelihood of establishment of alien species and increasing the effect of those species already there (Kennedy 1995; Bergstrom & Chown 1999; Chown et al. 2000). In addition, there has been a dramatic increase in the effect of fisheries on populations of seabirds breeding on the islands (Cherel et al. 1996; Gales et al. 1997; Weimerskirch & Wilson 2000). As tourism to these islands increases (South Georgia received 473 tourists in 1995–1996 and 1357 in 1998–1999; IAATO 2000), more islands attract the attention of tourist ships (Heydenrych & Jackson 2000), climates change (Frenot et al. 1997), the effects of invasive species increase (Huyser et al. 2000), and fishery activity grows, the long-term conservation future of the Southern Ocean island biotas is increasingly being questioned (Chevrier et al. 1997; Gremmen & Smith 1999; Chown & Gaston 2000). Consequently, there are substantial grounds for consolidating conservation actions, including World Heritage listings, in the region.

To do so will require several important policy decisions, including whether islands with relatively high human effects (e.g., Falklands, Tristan da Cunha) should be ignored in favor of those that are more pristine, whether islands identified as most significant by the IUCN islands working group (Table 1) should be given priority, and whether tourism to certain islands should be prohibited, all based on the IUCN working group's analysis. Such decisions are likely to be effective only if they are based on appropriate regional information. At the moment, however, the only comparative information available is that contained in the delphi analysis undertaken by the IUCN (1995), the descriptive treatments of the majority of the archipelagos provided in the report on the 1992 IUCN workshop (Dingwall 1995), and earlier, although similar, such treatments (Clark & Dingwall 1985). Given the IUCN working group's caveats regarding the outcomes of their delphi analysis (IUCN 1992, 1995) and its increasing use in the World Heritage site nomination and selection process, there is a clear need for a more rigorous comparative assessment of the islands to consolidate conservation action in the region.

Analyses

To provide such a comparative assessment, we used a comprehensive data set on the species richness of indigenous and introduced mammals, birds, insects, and vascular plants of these islands (Chown et al. 1998*b*) and explored the flexibility of modern analytical techniques for the selection of priority areas for conservation (Rodrigues et al. 2000). These analytical techniques have been receiving increasing support as tools for practical conservation planning (e.g., Pressey et al. 1993; Dobson et al. 1997; Howard et al. 1998; Margules & Pressey 2000). Because resources available for conservation purposes are limited, these tools are used to attain high efficiency (sensu Pressey & Nicholls 1989) in the representation of biodiversity at minimum cost (here, in the minimum number of islands) by identifying sets of sites that are complementary in terms of their biological composition.

We also used this approach to assess the utility of the prioritization scheme developed by the IUCN Southern Ocean islands working group for regional conservation decisions. There are several reasons we consider such a species-based approach to be useful.

- Both Synge (1991) and the IUCN working group (IUCN 1992) argue that the most useful approach to developing regional conservation plans within a World Heritage site framework, for islands in general and the Southern Ocean islands specifically, is to make use of a comparative biodiversity-based assessment.
- The majority of Southern Ocean islands that have already been declared World Heritage sites were nominated on grounds of biodiversity (Table 1).
- Among the most important characteristics of these islands are pronounced endemicity and high seabird diversity.
- The data set compiled by Chown et al. (1998*b*) includes both indigenous and introduced species, so it provides a means to assess the conservation value of the islands

from the perspective of both biodiversity and human effects.

- Species form a useful measure of biodiversity at both higher and lower hierarchical levels (Gaston 1996), thus providing some measure of the more nebulous and difficult concepts, such as ecosystem functioning, included in the World Heritage criteria.

In the delphi analysis done by the IUCN working group (IUCN 1995), the Southern Ocean islands were divided into cool temperate and sub-Antarctic islands. They were then scored separately on landscape and geological features, biodiversity, and human effects, and finally on all four factors in a composite assessment. In this analysis (and by Dingwall [1995]), the Falkland Islands were inexplicably excluded, some archipelagos were by necessity treated as single units (e.g., Crozet Islands), and the South Sandwich Islands and Bouvetøya were included. In our analysis we excluded the latter islands because they do not house higher plants or insects (Dingwall 1995), and we included the Falkland Islands because they house many species and are biogeographically linked to other Southern Ocean islands (Chown et al. 1998*b*; Morrone 1998). In addition, we treated all islands as single biogeographical units (Chown et al. 1998*b*; Morrone 1998).

Thus, in examining the utility of the delphi analysis we re-ranked the islands assessed by the IUCN working group (IUCN 1995) based on a comparison of the scores of all of the islands as a group (where there were ties, islands were accorded the same rank). We then identified the five top-ranking islands (with ties, more than five islands were sometimes selected) based on their composite, biodiversity, and human-effect scores (IUCN 1995). We also included in a second set of islands those that had already been accorded World Heritage status and the five top-ranking islands after the World Heritage sites were excluded from the ranking (Table 1). For each set we then summed the number of indigenous vascular plant, insect, landbird, and seabird species represented on these islands. For each set we compared the total species richness with that obtained from a random selection of the same number of islands and with the maximum number of species that can possibly be represented within that number of islands.

Outcomes

Irrespective of the way the islands are scored, islands selected by the delphi analysis and the analysis including currently designated World Heritage sites represented no more species than a random selection of the islands (Fig. 1). This is true also of the current set of World Heritage sites. When the biodiversity assessment is considered alone, the top sites (rank ≤5) perform substantially worse than random. These 12 sites represent just 59% of the indigenous vascular plants, insects, and birds, whereas 12 appropriately selected sites would represent 94% of the species (Table 1). The set obtained by including the currently designated World Heritage sites (18 sites)—building on the existing network—also performs significantly worse than random and significantly worse than the set of 18 islands that maximizes the total number of indigenous species

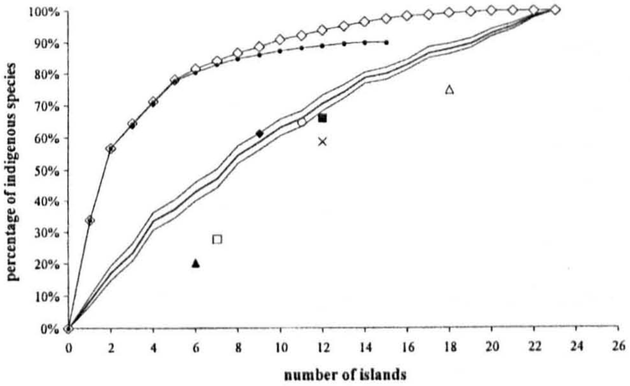

Figure 1. Relationship between the percentage of indigenous species represented and the number of islands selected by different strategies: set of top-ranking islands (rank ≤5) in terms of the total delphi analysis score (black triangle); set of islands designated as World Heritage (WH) sites (black diamond); set of top-ranking islands (rank ≤5) in terms of the total score plus WH sites (black square); set of top-ranking islands (rank ≤5) in terms of the biodiversity score (cross); set of top-ranking islands (rank ≤5) in terms of the biodiversity score plus WH sites (open triangle); set of top-ranking islands (rank ≤5) in terms of the low human-impact score (open square); set of top-ranking islands (rank ≤5) in terms of the low human-impact score plus WH sites (open circle); maximum percentage of species that can be represented by a given number of islands (open diamonds), found by solving consecutive maximal-covering-location problems (Church et al. 1996) with CPLEX (ILOG 1999); most efficient sorting of the set of 15 islands that represents 90% of all indigenous species and minimizes the number of aliens (black dots; see Fig. 2), obtained by selecting the island with more species first and proceeding stepwise by selecting at each step the island that contributes the higher number of unrepresented species; percentage of species represented by sets of islands selected randomly (mean values represented by the thick continuous line; limits of the 95% confidence interval represented by the thin continuous lines; n = *100).*

(which represents 99% of all species; Table 1; Fig. 1).

However, a high number of alien species is included in these two sets, which maximizes species representation (Table 1). Although the number of alien species on an island might be no certain guide to the effect of such species (IUCN 1992), it seems reasonable to assume that the lower the number of alien species the less the total effect is likely to be (Chapuis et al. 1994; Williamson & Fitter 1996; Chown et al. 1998*b*; Bergstrom & Chown 1999), if only on the basis that the probability declines that particularly problematic species will be represented. It is possible to perform a complementarity analysis that efficiently represents indigenous species and takes into account the effect of introduced species by minimizing the number of alien species that need to be included and ensuring the representation of a given number of indigenous species (Fig. 2).

When compared with the minimum number of alien species that need to be included while representing the same number of indigenous species, the delphi analysis and the analysis including currently designated World Heritage sites perform poorly (Fig. 2). The sets based on the biodiversity assessment perform even worse than a random selection of islands with the same number of indigenous species. Not surprisingly, the sets of islands that maximize species representation on a given number of islands perform poorly as well, especially those representing high percentages of natives (Fig. 2). This is because some of the islands with the largest human presence (e.g., Falklands, Tristan da Cunha), and often with the largest complement of alien species, are also among those that contribute most to the representation of large numbers of species in the region. This illustrates the need to select sites based on both alien and indigenous species.

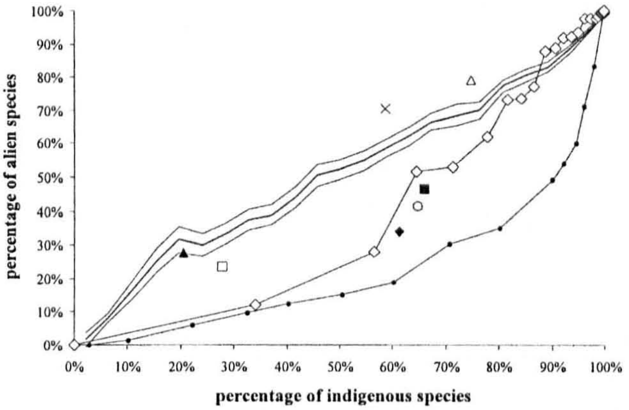

Figure 2. Relationship between the percentages of alien and indigenous species represented in sets of islands selected by different strategies: set of top-ranking islands (rank ≤5) in terms of the total delphi analysis score (black triangle); set of islands designated as World Heritage (WH) sites (black diamond); set of top-ranking islands (rank ≤5) in terms of the total score plus WH sites (black square); set of top-ranking islands (rank ≤5) in terms of the biodiversity score (cross); set of top-ranking islands (rank ≤5) in terms of the biodiversity score plus WH sites (open triangle); set of top-ranking islands (rank ≤5) in terms of the low human-impact score (open square); set of top-ranking islands (rank ≤5) in terms of the low human-impact score plus WH sites (open circle); maximum percentage of species that can be represented by a given number of islands (open diamonds; see Fig. 1); minimum percentage of alien species that need to be retained while representing at least a given percentage of indigenous species (black dots); percentage of alien species represented by randomly selected sets of islands with a given percentage of indigenous species (mean values represented by the thick continuous line; limits of the 95% confidence interval represented by the thin continuous lines). Each data point for the curve of the minimum percentage of alien species that need to be retained while representing at least a given percentage of indigenous species was obtained by solving two coupled optimization problems. The first obtains a set of islands that minimizes the number of aliens captured, subject to representing more than a given number of indigenous species; if more than one solution exists, a second problem is solved that finds the set of islands maximizing the number of indigenous species that can be represented while keeping the number of aliens equal to the minimum value found in the first problem. All problems were solved with CPLEX (ILOG, 1999). The curve representing a random selection was obtained by randomly selecting 5000 sets of islands (each set with a random number of islands) that were then grouped in 23 equal-interval classes in terms of overall species richness. For each class, the average percentage of alien species and the corresponding 95% confidence intervals were obtained (the number of sets in each class varied between 22 and 351).

Although there is a significant relationship between the number of indigenous and alien species on each island ($r_s = 0.66$; $p < 0.001$), there is still enough flexibility for the selection of sets of islands that represent a large fraction of the indigenous species yet keep the fraction of alien species relatively low (Fig. 3). This explains the shape of the curve of the minimum number of alien species that needs to be included to represent a given number of indigenous species (flat at first, with a steep rise at the end; Fig. 2). If sites are selected carefully, more than 90% of all indigenous species can be represented and the number of alien species can be kept below 50% (Table 1). If it is presumed that the alien species with the most marked effect on terrestrial fauna and flora are mammals (Chapuis et al. 1994; Huyser et al. 2000), the curve obtained is steeper from the beginning, but it is still possible to obtain a set of islands with a high proportion of all indigenous species relative to the total number of aliens (93% indigenous, 73% aliens; Table 1). A similar result is obtained when only indigenous birds are considered (92% indigenous, 73% aliens; Table 1). Although illustrative and perhaps significant from the perspectives of mammal management and avian conservation, these latter results will not be considered further because there is considerable evidence that introduced invertebrate and plant species also have marked effects on Southern Ocean island communities (Ernsting et al. 1995; Gremmen et al. 1998; Hänel & Chown 1998).

The complementarity analysis that minimizes the incidence of alien species also indicates that for a 90% representation of species, only one island with significant numbers of human occupants (East Falkland) continues to be included on the list of sites (Table 1; Fig. 3). Islands such as Tristan da Cunha, which has high human occupancy (Chown et al. 1998*b*), and South Georgia, which has high numbers of annual visits by tourists (International Association of Antarctica Tour Operators), are no longer included. Nonetheless, many islands, such as the Auckland Islands and Macquarie Island, which are regularly and increasingly visited by tourists (Dingwall 1995), remain listed. Given the significant relationship between number of human occupants and number of alien species (Chown et al. 1998*b*) and recent realizations that even low-intensity human use can have substantial effects on natural systems (Redford 1992; Terborgh 1999), this provides grounds for concern.

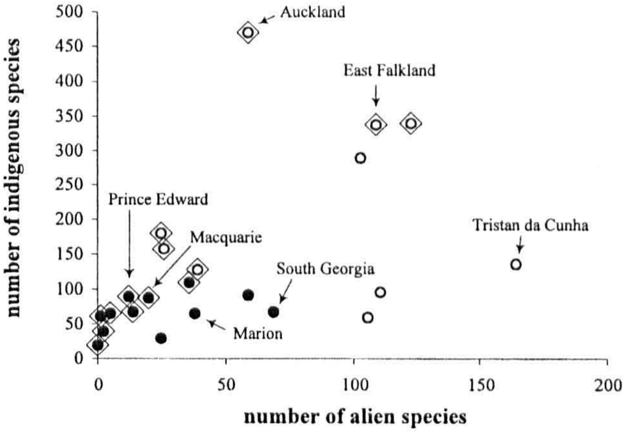

Figure 3. Relationship between the number of alien and indigenous species on each of the 23 islands analyzed ($r^2 = 0.24$; $p < 0.02$). Open circles refer to the set of islands that maximizes the number of indigenous species in 10 islands; circles enclosed by diamonds refer to the set of islands that minimizes the number of alien species, subject to having more than 90% of all indigenous species represented (see Table 1). Despite both sets having nearly the same number of indigenous species represented (91% and 90% of all natives, respectively), they have a different number of alien species (89% and 49%, respectively). This is because two different strategies have been applied to select the islands in each case. In maximizing the number of indigenous species, the primary tendency is to select islands with relatively high numbers of these species, irrespective of the number of aliens present. When minimizing the number of aliens, the tendency is to select islands with few of these species plus those that have high numbers of indigenous species in relation to the number of aliens.

Even in the case of islands that are not likely to be visited at all, visits to adjacent islands are likely to represent conservation problems over the long term. For example, although Prince Edward Island is included in the set that would represent 90% of indigenous species with minimum incidence of alien species (Table 1; Fig. 3), nearby Marion Island (20 km distant) is not and has been proposed as a tourist destination (Heydenrych & Jackson 2000). There is now clear evidence that alien species introduced to Marion Island have dispersed naturally to Prince Edward Island (Gremmen & Smith 1999). Thus, selection of sites to minimize the number of alien species while representing a high proportion of indigenous species is no guarantee of long-term conservation success in the region. Rather, the selected sites will have to be carefully managed, largely by restricting human activities and carefully controlling human activities in surrounding areas. This must include controlling on-going research activities, especially because it appears that research activities are a major cause of among-island species transfers as scientists move between islands. For example, the establishment of *Sagina procumbens* (Caryophyllaceae) on Gough Island (Gremmen 2000) appears to have taken place via the South African research enterprises that routinely move between Marion Island, where the species has been recorded for many years (Gremmen 1981) and Tristan da Cunha and Gough Island.

Conclusions

Our analyses indicate that an optimally selected set of 15 islands would result in representation of 90% of the higher plant, insect, and bird taxa found on Southern Ocean islands and would reduce alien species presence to a minimum (Table 1). Somewhat fortuitously, but most likely due to the small numbers of sites involved, these 15 islands include all of the currently declared World Heritage sites (Table 1). In addition to these islands, East Falkland, Beauchene, Inaccessible, Nightingale, Prince Edward, and Cochon also merit special conservation attention. We are not suggesting that the islands excluded from our list should not be conserved. Indeed, smaller, rarely visited islands, such as some of those in the Crozet and Kerguelen archipelagos, can easily be protected with minimum effort. Rather, to retain 90% of the species with minimal disturbance by aliens, the islands we list here should not be subject to additional visits by large numbers of island-hopping visitors and should have active programs to reduce the number and effects of the alien species on them or on the islands in their vicinity (e.g., Chapuis & Frenot 1997).

Our analyses also raise several more general issues. First, they show that the outcome of the delphi analysis (IUCN 1995), while perhaps useful at the time it was undertaken, should no longer guide conservation policy. It performs no better than a random selection of islands in terms of the number of species represented (Fig. 1) and it is not effective in minimizing the occurrence of alien species (Fig. 2). More broadly, this result indicates that at least three, if not all, of the natural-properties criteria for selecting World Heritage sites could be assessed more objectively, at least in an island-based regional framework, through the kind of approach we have adopted. Thus, many of the problems associated with the selection of island sites for World Heritage status would be resolved (Synge 1991).

Second, 90% representation is an arbitrary benchmark that might be unacceptable to many conservation organizations. In the context of the Southern Ocean islands, this is perhaps a reasonable level (Chown et al. 1998*a*), but in many continental areas such a benchmark may already be unrealistic. Nonetheless, there is no objective way to set benchmarks; "What kind of world do you want to live in?" (Morowitz 1991) perhaps expresses the conundrum most succinctly.

Finally, if Southern Ocean islands are declared World Heritage sites, then exclusion of most human activity should accompany this declaration. Although such a decision would seem unpalatable, the available evidence suggests that it is the only way to ensure the persistence of many remarkable species and ecosystems.

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