Systematic conservation planning

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The realization of conservation goals requires strategies for managing whole landscapes including areas allocated to both production and protection. Reserves alone are not adequate for nature conservation but they are the cornerstone on which regional strategies are built. Reserves have two main roles. They should sample or represent the biodiversity of each region and they should separate this biodiversity from processes that threaten its persistence. Existing reserve systems throughout the world contain a biased sample of biodiversity, usually that of remote places and other areas that are unsuitable for commercial activities. A more systematic approach to locating and designing reserves has been evolving and this approach will need to be implemented if a large proportion of today's biodiversity is to exist in a future of increasing numbers of people and their demands on natural resources.

It is an ancient and widespread human practice to set aside areas for the preservation of natural values. The sacred groves of Asia and Africa and royal hunting forests are historical examples[1,2]. Other areas protect ecosystem services such as the delivery of clean water or the supply of timber, or mitigate the expected adverse effects of over-clearing[3]. Others protect recreational and scenic values and some have been planned to foster international cooperation[4]. Many of these areas meet the World Conservation Union's definition of a strictly protected area (IUCN categories I–IV)[5], and hereafter we refer to such protected areas as 'reserves'. These areas are increasingly being complemented by reserves established principally for the protection of biodiversity, including ecosystems, biological assemblages, species and populations[6]. The basic role of reserves is to separate elements of biodiversity from processes that threaten their existence in the wild. They must do this within the constraints imposed by large and rapidly increasing numbers of humans in many parts of the world and their attendant requirements for space, materials and waste disposal[7].

The extent to which reserves fulfil this role depends on how well they meet two objectives. The first is representativeness, a long-established goal referring to the need for reserves to represent, or sample, the full variety of biodiversity[8], ideally at all levels of organization. The second is persistence. Reserves, once established, should promote the long-term survival of the species and other elements of biodiversity they contain by maintaining natural processes and viable populations and by excluding threats[9]. To meet these objectives, conservation planning must deal not only with the location of reserves in relation to natural physical and biological patterns but also with reserve design, which includes variables such as size, connectivity, replication, and alignment of boundaries, for example, with watersheds[10,11]. A structured systematic approach to conservation planning provides the foundation needed to meet these objectives.

Systematic conservation planning has several distinctive characteristics. First, it requires clear choices about the features to be used as surrogates for overall biodiversity in the planning process. Second, it is based on explicit goals, preferably translated into quantitative, operational targets. Third, it recognizes the extent to which conservation goals have been met in existing reserves. Fourth, it uses simple, explicit methods for locating and designing new reserves to complement existing ones in achieving goals. Fifth, it applies explicit criteria for implementing conservation action on the ground, especially with respect to the scheduling of protective management when not all candidate areas can be secured at once (usually). Sixth and finally, it adopts explicit objectives and mechanisms for maintaining the conditions within reserves that are required to foster the persistence of key natural features, together with monitoring of those features and adaptive management[12] as required. The effectiveness of systematic conservation planning comes from its efficiency in using limited resources to achieve conservation goals, its defensibility and flexibility in the face of competing land uses, and its accountability in allowing decisions to be critically reviewed. This is an idealized description of a process that is difficult to achieve in practice. Nevertheless, substantial parts have now been implemented around the world[13–17] and some are used as illustrations below.

The practice of conservation planning has generally not been systematic and new reserves have often been located in places that do not contribute to the representation of biodiversity. The main reason is that reservation usually stops or slows the extraction of natural resources. In some regions, housing and commercial development compete with reserves for land[18]. The economic and political implications can be serious and reserves can be degraded or even lose their protected status when they prove to be economically valuable[19]. As a result, reserves tend to be concentrated on land that, at least at the time of establishment, was too remote or unproductive to be important economically[20]. This means that many species occurring in productive landscapes or landscapes with development potential are not protected, even though disturbance, transformation to intensive uses, and fragmentation continue[21]. Another reason for the inappropriate location of reserves is the very diversity of reasons for which reserves are established. A diversity of goals means that different proponents see different places as important. Because highly valued areas arising from alternative conservation goals often fail to overlap[22], there is competition among proponents for limited funds and the limited attention spans of decision-makers. Moreover, goals such as the protection of grand scenery and wilderness often focus on areas that are remote, rugged and

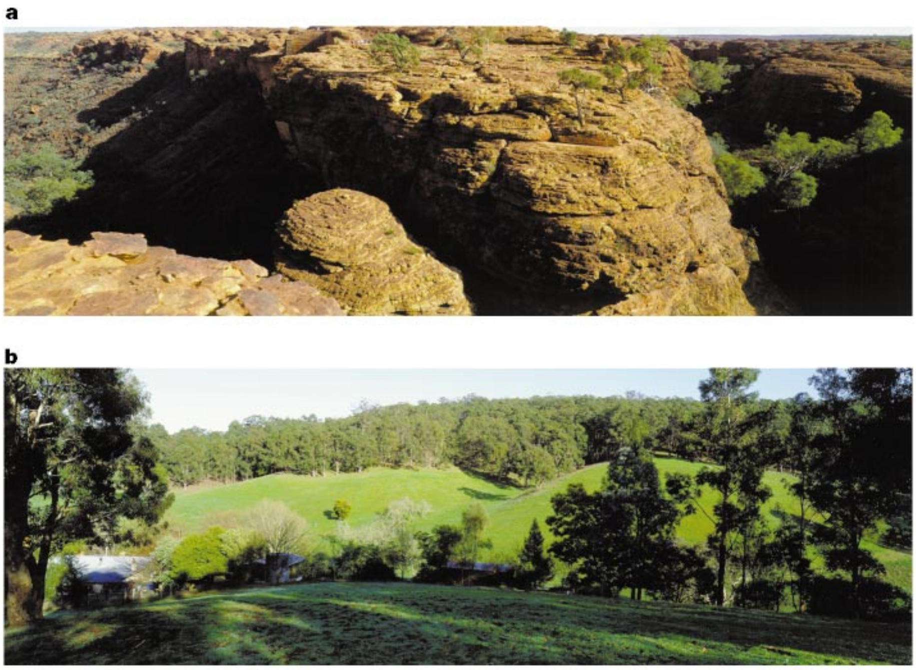

Figure 1 Social, economic and political factors often compete with reserves for land. **a**, Kings Canyon, Watarrka National Park, Northern Territory, Australia. This is a spectacular landscape, worthy of protection both for its outstanding natural beauty and for its biodiversity. But it is a remote and rugged area, valuable for tourism but not for extractive uses so it was easier to protect than more productive and economically valuable landscapes. **b**, An agricultural landscape in the Adelaide Hills, South Australia, with remnant woodland in the background. Remnants such as these contain species that are not represented in more remote and inaccessible areas, so their contribution to the overall goal of maintaining biodiversity is just as great. Despite their natural values it is always a difficult social and political decision to protect them because they have economic value as well as biodiversity value. Photographs by Liz Poon.

residual from intensive uses, giving them a political advantage over goals such as representativeness, which focus also on disturbed, economically productive landscapes (Fig. 1).

Conservation planning is therefore an activity in which social, economic and political imperatives modify, sometimes drastically, scientific prescriptions. This interaction need not be all one way. Science has at least three means of influencing the practice of nature conservation. First, an available body of scientific theory and application can provide some of the raw material for constructing policies[23]. Second, science can offer solutions when called upon to assist in the implementation of policies and conventions, while also clarifying the social and economic implications of alternative methods or scenarios (this role is best filled when science is integral to the process, not simply called in for peer review[24] or when technical or political problems emerge). Third, science can and should be used to review the effectiveness of political processes for achieving stated biodiversity goals. A structured framework for conservation planning will enhance the effectiveness with which science can do these three things.

A framework for systematic conservation planning

Systematic conservation planning can be seen as a process in six stages[25] (Box 1), each of which is discussed below with examples of the tasks and decisions required. The process is not unidirectional — there will be many feedbacks and reasons for revised decisions about priority areas. For example, it will be necessary to re-examine conservation goals as knowledge accumulates, and replacement candidate reserves will have to be identified when unforeseen difficulties arise in implementation. Although our discussion focuses on reserves, the framework applies equally well to many problems in 'off-reserve' conservation, including habitat restoration[25,26]. Decisions about both on- and off-reserve conservation, if they are not to be *ad hoc* and uncoordinated, should be guided by explicit goals, identification of priorities in regional or broader contexts, and clear choices between

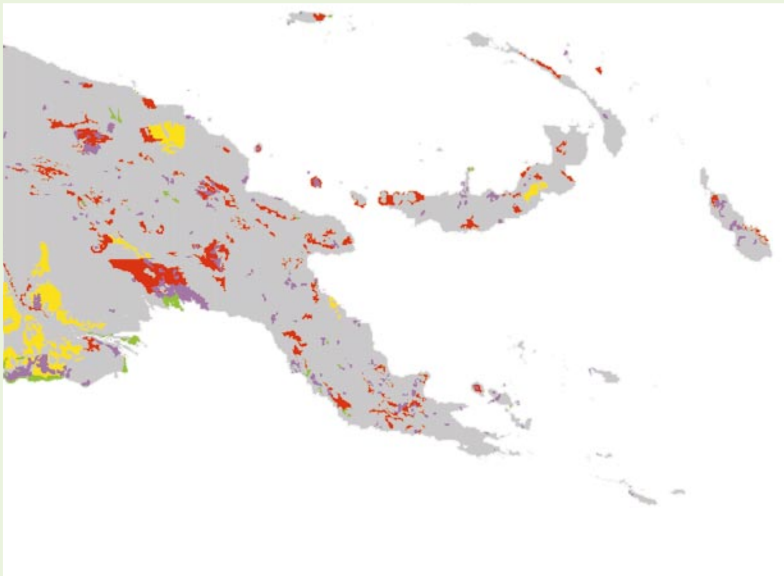

Figure 2 A map of biodiversity priority areas in Papua New Guinea[16]. The targets that are met by this set of areas are the representation of 608 environmental domains[37], 564 vegetation types, 10 species assemblages and 12 rare and threatened species. For the derivation of these targets, see refs 16, 92. In meeting targets, the set of areas also minimizes foregone opportunities for timber extraction, represents all existing reserves, minimizes the number of areas currently used for intensive agriculture, gives preference to areas with low human population density and gives preference to areas identified previously by experts as biodiversity priority areas[92]. The selected areas occupy 16.8% of the country and are inhabited by 210,000 people out of a population of approximately 4 million. A total of 398 areas were selected from 4,470 candidate areas or planning units. These units were aerial photograph patterns that were previously mapped for a database on agricultural and forestry suitability. The trade-off between biodiversity gain and opportunity costs, and the application of the other spatial constraints, was achieved with the TARGET software[94,109]. The colours represent different index classes of timber volume. Yellow is highest, red next highest, purple next and green lowest.

potential conservation areas and alternative forms of management.

Stage 1. Measure and map biodiversity

Because of the complexity of biodiversity, surrogates such as sub-sets of species, species assemblages and habitat types have to be used as measures of biodiversity, and the locations of these surrogates within areas have to be plotted so that similarities or differences among areas can be estimated.

Biological systems are organized hierarchically from the molecular to the ecosystem level. Logical classes such as individuals, populations, species, communities and ecosystems are heterogeneous. Each member of each class can be distinguished from every other member. It is not even possible to enumerate all of the species of any one area, let alone the members of logical classes at lower levels such as populations and individuals. Yet this is biodiversity, and maintaining that complexity is the goal of conservation planning. For the foreseeable future it will be necessary to accept this incomplete knowledge and adopt methods for making the most of what we do know or can discover from new surveys. Thus, surrogate or partial measures of biodiversity must be used to estimate similarity or difference among areas within planning regions.

The choice of surrogate measures is not trivial. The strong temptation is to use a group of species: for example, vascular plants, vertebrates or butterflies. We may know that the presence of a butterfly indicates the presence of its food plant somewhere nearby. The real question, however, is whether the presence of that butterfly, or any other taxon, indicates the presence of other taxa to the extent that it can be considered a suitable surrogate for overall biodiversity. Tests of taxonomic surrogacy in Britain[27] and South Africa[28] are not encouraging, but more promising results have been obtained in Uganda[29]. Divergent results are attributable to differences in analytical methods, geographical scales and biogeographical histories of the study areas. Reliable generalizations and an understanding of how such factors affect taxonomic surrogacy are still developing. Higher levels in the biological hierarchy, such as species assemblages, habitat types and ecosystems lose biological precision, but have other advantages. They can integrate more of the ecological processes that contribute to the maintenance of ecosystem function[30] (although there is active debate on this issue[31]) and the relevant data are more widely and consistently available. In addition, there are sound theoretical reasons why environmental variables should be good estimators of the spatial distribution patterns of species[32–34] and there are now some empirical studies that add support[35–37]. New statistical techniques are also being developed to compare how well different environmental surrogates reflect the distribution patterns of species[38].

Box 1
Stages in systematic conservation planning

Systematic conservation planning can be separated into six stages, and some examples of tasks and decisions in each are presented below[25]. Note that the process is not unidirectional; there will be many feedbacks and reasons for altering decisions (see text for examples).

1. Compile data on the biodiversity of the planning region
- Review existing data and decide on which data sets are sufficiently consistent to serve as surrogates for biodiversity across the planning region.
- If time allows, collect new data to augment or replace some existing data sets.
- Collect information on the localities of species considered to be rare and/or threatened in the region (these are likely to be missed or under-represented in conservation areas selected only on the basis of land classes such as vegetation types).

2. Identify conservation goals for the planning region
- Set quantitative conservation targets for species, vegetation types or other features (for example, at least three occurrences of each species, 1,500 ha of each vegetation type, or specific targets tailored to the conservation needs of individual features). Despite inevitable subjectivity in their formulation, the value of such goals is their explicitness.
- Set quantitative targets for minimum size, connectivity or other design criteria.
- Identify qualitative targets or preferences (for example, as far as possible, new conservation areas should have minimal previous disturbance from grazing or logging).

3. Review existing conservation areas
- Measure the extent to which quantitative targets for representation and design have been achieved by existing conservation areas.
- Identify the imminence of threat to under-represented features such as species or vegetation types, and the threats posed to areas that will be important in securing satisfactory design targets.

4. Select additional conservation areas
- Regard established conservation areas as ‘constraints’ or focal points for the design of an expanded system.
- Identify preliminary sets of new conservation areas for consideration as additions to established areas. Options for doing this include reserve selection algorithms or decision-support software to allow stakeholders to design expanded systems that achieve regional conservation goals subject to constraints such as existing reserves, acquisition budgets, or limits on feasible opportunity costs for other land uses.

5. Implement conservation actions
- Decide on the most appropriate or feasible form of management to be applied to individual areas (some management approaches will be fallbacks from the preferred option).
- If one or more selected areas prove to be unexpectedly degraded or difficult to protect, return to stage 4 and look for alternatives.
- Decide on the relative timing of conservation management when resources are insufficient to implement the whole system in the short term (usually).

6. Maintain the required values of conservation areas
- Set conservation goals at the level of individual conservation areas (for example, maintain seral habitats for one or more species for which the area is important). Ideally, these goals will acknowledge the particular values of the area in the context of the whole system.
- Implement management actions and zonings in and around each area to achieve the goals.
- Monitor key indicators that will reflect the success of management actions or zonings in achieving goals. Modify management as required.

Figure 3 White Rhinos currently persist in relatively small intensively managed populations in game reserves. Off-reserve management in suitable habitat would probably be necessary if populations were to return to self-sustaining levels, although conflict with human populations makes it extremely unlikely that this would ever happen. Photograph by Liz Poon.

Planning is essentially a matter of comparison so it is preferable to compare two or more areas with the same kind of information at the same level of detail. A map of vegetation types (communities or habitat types) and/or environmental classes provides spatial consistency across wide areas. On the other hand, museum and herbarium data on the locations of taxa are notoriously biased, having been collected for a different purpose (systematics), and often in an opportunistic manner, from the places that collectors expected to find what they were looking for or that were conveniently accessible[39,40]. Plots of the field records from many collections therefore map road networks. Various methods — empirical, statistical and computational — are now available for modelling wider spatial distribution patterns from the point records that field samples represent[41–43], but their reliability is also at least partly a function of the degree of spatial bias. New systematic field surveys to fill gaps are the best solution but they can be expensive and time consuming.

There is no best surrogate. The decision on which to use will depend on many factors including what data are available and what resources there are for data analysis (for example, spatial modelling) and the collection of new data. In most parts of the world, the only spatially consistent information available is on higher-order surrogates such as vegetation types and environmental classes. Collections of taxa might form an accurate representation of some biological distributions in some countries where well designed and well resourced surveys have been used to collect the data. Taxa collections may also be used with some reliability at coarse scales (for example, grid cells of 50 km × 50 km), but usually become less reliable at the scale of individual reserves[44]. If taxa sub-sets are used without spatial modelling, it is usually with the understanding that the disadvantage of spatial bias is offset by the advantage of having at least some direct biological information to complement higher-order surrogates. Combinations of surrogates will be most practicable in most situations. In a recent study in Papua New Guinea, environmental domains classified from climate, landform and geology[37], vegetation types mapped from aerial photographs, and the known locations of rare and threatened species were all used as biodiversity surrogates (Fig. 2)[16].

A decision is also needed at this stage on how to define planning units, the building blocks of the reserve system. Planning units can be regular (for example, grids or hexagons) or irregular (for example, tenure parcels, watersheds or habitat remnants). A mix of planning units might be appropriate in regions that contain both fragmented landscapes and extensive tracts of uncleared vegetation. The choice has implications for the efficiency with which representation goals can be achieved as well as for the design and management of reserves[45]. For the reserve selection process described in stage 4, it is necessary to compile data on biodiversity surrogates for each of the planning units in the region. Data on tenure (for stages 3, 4 and 5, below) and other contextual data that might influence selection and implementation (for example, roads, rivers, terrain, timber resources and threats) should also be compiled at this stage.

Stage 2. Identify conservation goals for the planning region

The overall goals of systematic conservation planning — representativeness and persistence — have to be translated into more specific, preferably quantitative, targets for operational use. Targets allow clear identification of the contributions of existing reserves to regional goals and provide the means for measuring the conservation value of different areas during the area selection process in stage 4 below. Targets such as 10 or 12% of the areas of countries or vegetation types have been criticized because they are too small to prevent the extinction of many species, can be subverted by reserving the least productive and least threatened landscapes, and can mislead the public into believing that limited conservation action is adequate[46]. A focus on targets for reserves may also remove incentives to implement other conservation actions such as off-reserve management[1]. These criticisms are valid, but are aimed at how targets are set rather than exposing reasons for not setting targets at all. Planners need to know what they are aiming for. ‘More equals better’ is good in principle, but does little to resolve choices between areas with different biotas when other demands narrow the geographical scope for reservation. Accordingly, planners need targets that do several things: focus on scales that are much finer than whole countries or regions; deal with natural processes as well as biodiversity pattern; reflect the relative needs of species and landscapes for protection; recognize that reserves must be complemented by off-reserve management, preferably also with targets; and leave options open for revision as social and economic conditions change. Ideally, reservation targets will be an integral part of policies and government processes[47]. Failure to achieve targets for economically valuable landscapes is likely, so periodic reviews (stage 3, below) are necessary.

Most exercises in systematic conservation planning have chosen areas on the basis of the occurrences of species. Some have used predicted probabilities of occurrence[48]. Recent applications have set targets for the spatial extent of communities, habitat types or environmental classes, sometimes with explicit formulae for adjusting targets according to factors such as natural rarity and vulnerability to threats[13]. These are all targets for representing a biodiversity pattern. Targets for ecological processes can be more problematic. Because conservation planning is a spatial exercise, protection of natural processes must be based on their spatial surrogates rather than the processes themselves (for example, size, lack of roads, watershed boundaries, and migration routes). Setting process targets can be difficult in practice because the environment is heterogeneous in space and time and different species function at different spatial and temporal scales[49]. Nevertheless, seven aspects of theory on ecological and evolutionary processes, now supported by some empirical evidence, can provide guidelines.

Biogeographical theory

Traditionally, the equilibrium theory of island biogeography[50] and associated biogeographical theory has been used to help set targets for size, shape and distance between reserves (although usually such targets were not quantitative). This body of theory tells us that bigger reserves are better, the closer they are the better, the more circular the better, and that reserves should be linked by habitat corridors[51,52]. In the real world of conservation planning, the opportunity to apply such guidelines is constrained by costs and patterns of land-use history. These design principles also introduced an important trade-off into planning that is seldom acknowledged. If the area available for reservation is limited, a choice might have to be made between a few large reserves that favour the persistence of some species or more smaller reserves that together are more representative of the region's biodiversity but individually are less effective for the persistence of some species, for example, large, wide-ranging species[17,53]. An early and widely ignored criticism of the equilibrium theory was that it treated islands as featureless plains with no internal habitat diversity and species as characterless features with no genetic or geographical variation[54]. There is now some experimental support for the prediction that increased isolation reduces the likelihood of persistence of certain species[55], supporting targets for connectivity. However, attention has rightly shifted to the roles of environmental heterogeneity, species interactions, local- and regional-scale population dynamics, and the effects of habitat modification in reserve planning.

Metapopulation dynamics

In general, a metapopulation[56] is a network of local populations linked by dispersal. More narrowly, the term is used to describe systems in which local populations periodically go extinct with recolonization occurring by migration from other local populations[57]. Metapopulations go extinct when the rate of extinction of local populations exceeds the rate of migration and recolonization. Confining a species to a reserve may disrupt metapopulation dynamics, increasing the risk of local extinction due, for example, to a catastrophic event such as wildfire, and decreasing the chances of recolonization. Metapopulation theory calls for targets that consider reservation across species' natural ranges so that some populations might escape the impact of unpredictable events, thereby spreading the risk of extinction[58]. It also calls for the retention of landscape linkages to promote dispersal and the exchange of individuals between geographically separate sub-populations[59] and for the retention of patches of suitable, but currently unoccupied, habitat[60].

Source-pool effects and successional pathways

The species composition of an area changes over time in a process usually called ecological succession. Some of these changes will be due to dispersal but others will be the products of initial conditions. There is a mix of starting propagules available in an area and subsequent changes reflect a sorting of this mix according to life-history traits and interspecific interactions[61]. Because of periodic, patchy disturbances, most regions contain areas at various stages along these pathways and many species exploit the temporal and spatial variation of natural disturbance regimes[62]. The implications for target setting are that all successional stages might need to be represented, replication of reserves to sample different successional stages might be desirable, and large reserves are better because they can better accommodate natural patch dynamics without succession being reset throughout by a single event such as a wildfire[63].

Spatial autecological requirements

Different species require different amounts of space to complete their life cycles[57] (Fig. 3). Most reserves contain one or more species that would not persist as residents even for one generation if they became isolated. Many other reserves, without supplementation by unreserved habitat, would be likely to lose species in the long term through a variety of chance events. Thus, the long-term persistence of some taxa requires sustainable populations across entire landscapes or regions as predicted, for example, for the northern spotted owl (*Strix occidentalis caurina*) in the Pacific northwest United States[64]. There is a vast literature on population viability analysis[65,66]. Reservation targets should include viable population sizes and structures (for example, age classes and sex ratios) when these are known. Many species exploit temporal variation by moving between different habitats, requiring targets to recognize key habitat combinations where these can be identified. The focal species approach[67] attempts to integrate patterns and processes by identifying those species in a landscape that are most demanding of resources and then targeting them for management. The kinds of resources needed by focal species may be, for example, large areas, connectivity between habitat patches and complex heterogeneous habitats[17]. The argument is that if management can maintain these species in a landscape, then most other species will be maintained as well.

Source–sink population structures

If, in some high-quality habitats (sources) a species' reproduction rate exceeds mortality, but in low-quality habitats (sinks) its reproduction rate is lower than mortality, then a net dispersal away from sources may sustain populations in sinks[57,68]. In southeastern Australia, 63% of the arboreal marsupial population is found in only 9% of the forest with high foliar nutrients[69]. Dispersal throughout the remainder of the forest occurs from these areas of high population

Figure 4 Isolated habitat remnants in the wheat belt of Western Australia. Isolation causes physical changes to habitat remnants, which in turn can lead to changes in species composition and population sizes. Photograph courtesy of CSIRO, Wildlife & Ecology.

density. If population sources for some species are outside reserves or are not targeted for reservation, then the presence of those species within reserves is at risk.

Effects of habitat modification

If reserves become remnants of natural habitat surrounded by alien habitat such as cropland or pasture, changes brought about by isolation and exposure have implications for the persistence of species within them (Fig. 4). Changes in fluxes of wind, water and solar radiation[70] can lead, in turn, to changes in vegetation structure, microclimate, ground cover and nutrient status[71]. These changes may favour some species, but they also lead to reduced population sizes and local extinction of others[72,73]. Once isolated and exposed, habitat remnants may be placed on a trajectory of continued change. Deleterious effects can feed back on themselves to increase their magnitude[74], they can simply accumulate with time[75], or they can cascade, with a change in a species' abundance or productivity leading to unforeseen changes in the populations of other species. In fragmented landscapes, where reserves are likely to be small and isolated, targets for off-reserve conservation are particularly important and they should include buffers around remnants, sympathetic management of poorly protected vegetation types or environments, and habitat restoration

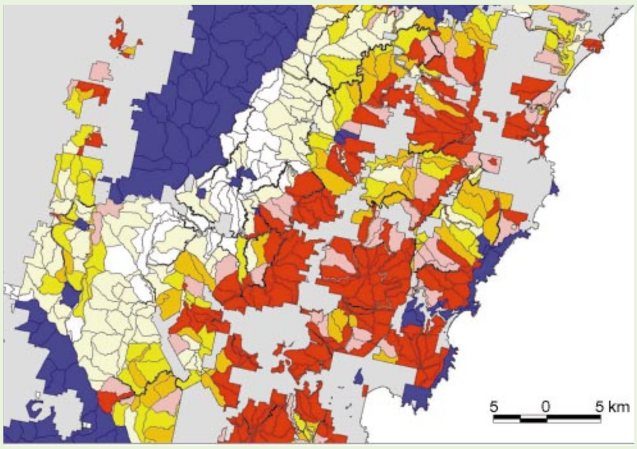

Figure 5 Pattern of complementarity on part of the south coast of New South Wales. The map is based on the same data used in the C-Plan decision-support system[13] in late 1999 to guide negotiations between interest groups over new forest reserves in the region. The eastern boundary is the coastline. Blue areas are reserves established before the negotiations. Grey areas are tenures not considered in the planning process. Other polygons are logging compartments (average area about 200 ha or 2×10^6 m^2) used as the building blocks of the expanded reserve system. Colours of these indicate five intervals of 'percentage contribution', the measure used in this exercise to indicate complementarity with existing reserves. Highest values are red (81–100%) and grade through pink, orange, dark yellow, pale yellow (>0–20%) and white (0%). Values of percentage contribution are based on reservation targets (in hectares) for each of 107 forest ecosystems in the region. Percentage contribution is calculated in two stages. In the first stage, a contribution value (in hectares) for each forest ecosystem in each compartment is calculated using two rules — if $A_i \leq T_i$ then $C_i = A_i$; if $A_i > T_i$ then $C_i = T_i$, where A_i is the extent of forest ecosystem i in the compartment, T_i is the remaining regional reservation target for the forest ecosystem, taking into account the contributions of existing reserves and any compartments previously given notional reserve status, and C_i is the current contribution of the compartment's sample of the forest ecosystem to the target. In the second stage, percentage contribution of the compartment is calculated as the sum of C values across all the forest ecosystems it contains, expressed as a percentage of the compartment's area. Compartments with highest values are largely or fully occupied by forest ecosystems well below target. Compartments with zero values contain only forest ecosystems with targets already achieved. Complementarity values show a marked association with distance eastwards from the large reserves in the westerly escarpment and more rugged foothills. In contrast, the small coastal reserves have no apparent influence on the complementarity of the adjacent compartments because they contain little forest. In the far northwest, higher values reflect the occurrence of forest ecosystems of the tableland, which are poorly reserved in the nearby escarpment reserves. Because complementarity is dynamic, percentage contribution was recalculated and redisplayed during the negotiations whenever one or more compartments were notionally reserved.

Species as evolutionary units

It has long been argued that species should be treated as dynamic evolutionary units rather than as types[76,77]. There are at least two related planning implications. First, areas occupied by taxa that appear from phylogenies to be actively radiating, or are most phylogenetically distinct, might be targeted for protection[78,79]. Second, with an understanding of the physical and biological processes leading to active diversification of taxa, it is possible to identify and set targets for evolutionary templates. The most distinctive evolutionary feature of the Cape Floristic Region of South Africa has been the recent and massive diversification of many plant lineages. This process has been related to landscape features, such as interfaces between different soil types, which are now targeted for conservation action[14].

These seven aspects of ecological and evolutionary processes have been explored largely as independent lines of research, separate also from the extensive work on the derivation and application of targets for biological patterns. An integration of all these research areas is needed for planning applications if the goals of representation and persistence are to be achieved[49]. The best way forward is not yet clear but some attempts in different regions by different planning groups will allow comparisons to be made and, hopefully, some promising directions to be identified.

Stage 3. Review existing reserves

The extent to which targets for representation and persistence have already been achieved in existing reserves has to be determined. This defines the scope of the task in stage 4. Systematic reviews of existing reserve systems have a long history and are the conceptual basis for the Gap Analysis Program in the United States, now incorporating research and development projects and their applications in the 48 contiguous states[44]. This programme was designed originally to identify gaps in the coverage of reserve networks but its increasing activity in identifying candidate conservation areas[80] (stage 4, below) is grounded in the systematic planning methods described here, which from the earliest applications have recognized the contribution of existing reserves to explicit targets[81].

Analyses of gaps in networks of reserves have concentrated on which features are represented or not represented and to what extent. Two other aspects of gap analysis have received little attention. The first is the relative imminence or likelihood of species or habitats becoming extinct without conservation action. Because features that are under-reserved according to representation targets vary in their exposure and vulnerability to threatening processes, some gaps are more important than others[82]. Decisions about the scheduling of conservation action relative to threat are crucial for effective implementation (stage 5, below). Gap analyses that incorporate threats can reveal spatial biases in action by agencies and governments that inhibit effective implementation.

The second neglected aspect of gap analysis relates to natural dynamics and the persistence of biodiversity in the long term. Measures of gaps in process and persistence are few[11,83] and a comprehensive, generic set of criteria for measuring gaps in the coverage of processes is lacking. Although most planners would agree that large size, connectivity and integrity are generally desirable, many species and vegetation types now exist only in remnants of habitat that are altered and surrounded by intensive land uses. The criteria for assessing gaps in coverage will be different in fragmented landscapes than in landscapes in which large contiguous tracts of habitat remain. The relative priority of reserve design criteria when they produce contrasting results (for example, compactness versus replication) has not been adequately addressed, nor has the role of partial contributions to biodiversity protection from areas under different

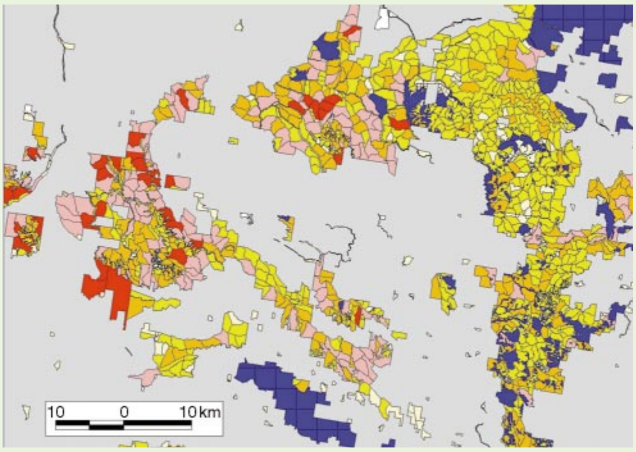

Figure 6 Pattern of irreplaceability in part of the northeast forests of New South Wales. The map is based on the same data and calculations of irreplaceability used in the C-Plan decision-support system[13] in 1998 to guide negotiations between interest groups over new reserves in the region. Blue areas, grey areas and other polygons as in Fig. 5. The gradient from red to white indicates irreplaceability values of logging compartments based on the mix of forest ecosystems within each compartment, the distributions of 198 forest ecosystems across the region, their individual reservation targets in hectares, and the extent to which each target is already met in the existing reserves. Red areas are totally irreplaceable; if they are not reserved, one or more targets will not be met. Progressively lower values (pink, orange, dark yellow, pale yellow and white) indicate logging compartments with progressively more replacements. With lower values, the options for achieving targets are less constrained if compartments are unavailable or prove unsuitable for reservation. Like complementarity, irreplaceability is a dynamic measure. In the 1998 negotiations, values were recalculated each time one or more compartments were notionally reserved.

management regimes outside strict reserves.

In most planning exercises, implementation (stage 5, below) is likely to be gradual or, if rapid, will often fail to achieve all targets, particularly those for landscapes with economic potential. In these cases, the planning process should loop back periodically from stage 5 to stage 3 so that progress can be updated, new areas selected as appropriate (stage 4), and implementation reconsidered.

Stage 4. Select additional reserves

After the review of existing reserves, the need for additional areas to achieve the outstanding targets will become clear. At least some of the area selections at this stage are only preliminary because implementation (stage 5) invariably reveals practical impediments that require a degree of revision of the initial choices. The existing reserves are recognized not only for their contributions to targets but also because they can become the focal points or spatial constraints around which enlarged reserves or new, separate ones are located. The most convenient tools for the task of selection are algorithms, which apply explicit rules to identify notional sets of areas[84]. These algorithms can be used to investigate various policy options, for example, to include or exclude wilderness areas, old-growth forest or regenerating areas, and to compare outcomes in terms of the number or total extent of new reserves needed. They can also indicate to planners whether the full set of targets is achievable within the expected limits of land area, acquisition cost or opportunity costs for other uses and, if not all are possible, the extent to which trade-offs are necessary (for example, between efficiency and design, or between representation of all forest types and the requirements of industry for timber). They provide a basis for negotiation or refinement of the conservation plan by regional or local experts. A recent development is the incorporation of algorithms into decision-support systems to guide structured negotiations between interest groups[13]. Used in this way, algorithms are able to guide decisions not only about how reserves sample biodiversity, but also about the design of reserve systems.

Complementarity

All selection algorithms use complementarity, a measure of the extent to which an area, or set of areas, contributes unrepresented features to an existing area or set of areas[78,85]. The precise measure depends on the targets that have been identified and on the type of data. Most simply, it can be thought of as the number of unrepresented species (or other biodiversity features) that a new area adds. It has also been interpreted as a similarity index based on the number of species shared and not shared between two areas[29,86], as the contribution a new area makes to sampling a complete multivariate pattern generated by a classification or ordination of all areas[87], and as the distance in multivariate space that a new area is from existing areas[88,89]. For targets set in terms of the extent of features such as forest types, complementarity can be measured as the contribution an area makes to outstanding targets according to the proportions of different types within that area (Fig. 5). An area with high complementarity will not necessarily be the richest[90]. If, for example, an area contributes few species or habitat types and those features are not widely represented in the landscape, then its complementarity value could be extremely high. Another important property of complementarity is that it is recalculated for all unselected areas each time a new area is added to the notional reserved set. This recognizes that the potential contribution of an area to a set of targets is dynamic — some or all of the features in an unselected area might have had their targets partly or fully met by the selection of other areas. In contrast, more traditional measures of conservation value such as species richness or the number of rare species are unresponsive to changing targets and decisions to reserve other areas.

Spatial constraints on the selection of reserves

Constraints on the area selection process can be grouped into five kinds. The first, irreplaceability[91], is inherent in any data set. When selection algorithms or regional experts decide on areas for reservation they choose between alternative areas for meeting conservation targets. For some planning exercises, it can be useful to display these alternatives explicitly as a map of irreplaceability (Fig. 6), indicating for each of the areas in a region the options for replacing it while still achieving conservation targets. Some areas have no replacements, whereas others have many. This information can be used to indicate the scope for altering selections by algorithms or experts (for example in trade-offs between targets and extractive land uses), to guide negotiations over new conservation areas, or to set priorities for implementation (stage 5, below). Four other spatial constraints are described below with examples from a recent application in Papua New Guinea (PNG) (Fig. 2)[16,92].

Costs. The use of an area for the protection of biodiversity generally means that it should not be available for commercial uses. Thus, biodiversity protection incurs opportunity costs. Trade-offs between opportunity costs and biodiversity gain can be achieved during the area selection process[93] or as a separate exercise after an initial selection[13]. It is important for the credibility of conservation planning that conservation goals are seen to be achieved in a way that minimizes, as far as possible, forgone opportunities for production. It is now possible to measure the opportunity costs of achieving a biodiversity goal and, conversely, the biodiversity costs of meeting a production goal, where that goal requires land allocation[94,95]. Examples of opportunity costs are timber volume and agricultural production. Figure 2 shows the relative timber volumes on selected biodiversity priority areas in PNG. Other kinds of costs such as acquisition costs and the ongoing costs associated with management and maintenance could also be incorporated as constraints in the area selection process.

Commitments. Commitments are areas that must be selected regardless of their contribution to targets. The most common examples are existing reserves (Fig. 5). Other examples might be areas containing rare and threatened species and areas of endemism. Both existing reserves and areas containing rare and threatened species were used in the PNG study. Existing reserves can also require additional commitments of areas, for example when they need to be linked or have their boundaries rationalized.

Masks. These are areas to be excluded from selection. For the PNG plan, areas smaller than 10 km^2 and areas used intensively for agriculture were masked initially. It was found, however, that some areas heavily used for agriculture were required if the biodiversity goal was to be achieved because they represented environments that were unavailable for selection elsewhere[16].

Preferences. Sometimes certain characteristics of areas for conservation are to be preferred, if possible, over others. For the PNG plan, areas with low human population density and areas previously identified by expert taxonomists and ecologists as biodiversity priorities were given preference for selection, where there was a choice. Combining expert assessments with explicit analyses of spatially consistent data has advantages. Experts are inevitably biased geographically and taxonomically. On the other hand, data matrices inevitably lack the full store of knowledge in experts' heads.

Stage 5. Implement conservation actions on the ground

There is a world of difference between the selection process described above, and making things happen on the ground. Implementation is usually complicated by the variety of people, agencies and commercial interests with a stake in the region and by the time needed to apply conservation management to particular areas. The eventual system of reserves can be very different from the one designed in stage 4.

An example of a relatively straightforward case of implementation is the 1996 expansion of forest conservation areas in eastern New South Wales, Australia[13] (Fig. 7). Planning was restricted to public land and the application of conservation action was rapid once the new areas had been negotiated to meet (most) targets and boundaries had been fine-tuned on the ground. Only a few forms of protection were at issue with little uncertainty about where they should most appropriately be applied. The implemented configuration was little different from that produced in the selection stage. A more complex and probably more widespread situation involves a mix of land tenures, ongoing loss and alteration of indigenous vegetation during a protracted process of applying conservation action on the ground, and the need to decide on an appropriate mix of protection measures. Three types of decisions are particularly important[96]. First, the most appropriate or feasible form of management should be identified for each area. This might be complicated by the need to apply particular forms of management in particular designated places, for example in biosphere reserves, which have core and buffer zones. In some cases, the preferred form of management might be infeasible and will need to be changed. Second, if one or more selected areas prove to be unexpectedly degraded or difficult to protect, it will be necessary to return to stage 4 and identify replacements, where they exist (Fig. 6). Third, decisions are needed on the relative timing of conservation action when resources are insufficient to implement the whole network quickly. With ongoing loss and alteration of habitat, a strategy is needed to minimize the extent to which conservation targets are compromised before being achieved.

One strategy for scheduling conservation action within regions is to plot selected areas on two axes[96]. The first is irreplaceability or the extent to which the loss of the area will compromise regional conservation targets[91]. The second is vulnerability or the risk of the area being transformed by extractive uses. Areas with high values for both should receive priority for conservation action (Fig. 8). They are most likely to be lost and, because of the absence or small numbers of replacements, their loss will have the most serious impact on the achievement of targets. This approach is similar conceptually to the original definition of global hotspots[97–99] and to other assessments of priorities at global or continental scales[100–103]. Plotting selected areas on two axes also has an advantage over combining values for both to produce a single priority score. Different areas of the graph can indicate the need for alternative management prescriptions, subject to regular review (Fig. 8). Three important qualifications are necessary. One is that an exercise in triage[104] might be necessary to decide if strict reservation is infeasible for some very high priority areas, necessitating other forms of protection such as management agreements with landholders, or outright abandonment. A second is the unresolved question of whether and how vulnerability to different threatening processes (for example, clearing, logging and grazing) should be combined for prioritization. A third is that the idea has been used mainly to prioritize areas for achieving biodiversity pattern targets and has yet to be developed fully for process targets. For some process targets it will be necessary to combine individual candidate areas into larger units before identifying priorities. Conservation planners are then likely to confront some difficult choices. They will often have to decide whether a limited annual budget should be used, for example, to keep intact a movement corridor for ungulates, a block of habitat considered minimal for the viability of a carnivore species, or the only known location of an endemic plant[14]. Planning for both the representation of patterns and persistence of species and natural processes requires planners to compare apples and oranges. There are no guidelines for optimizing the outcome and no guarantees that the anticipated outcome will be realized.

Figure 7 Spotted gum, *Eucalyptus maculata*, with an understorey of the cycad, *Macrozamia communis* in southeastern New South Wales, Australia. These forests are now the subject of a regional forest agreement, which allocates some areas to protection based on the contribution they make to agreed biodiversity targets, and allocates other areas to production based on agreed timber harvesting targets[13]. Most public forests in eastern New South Wales and in other Australian states now have regional forest agreements in place. Photograph by Liz Poon.

Stage 6. Management and monitoring of reserves

Establishing a reserve heralds the beginning of another process that is at least as demanding as the preceding planning process and spans a much longer period of time. Management of reserves should ensure that their natural values are retained in the face of internal natural dynamics, disturbances from outside, and a variety of valid human uses. In practice, the management of many reserves is inadequately resourced, unplanned and often threatened by illegal use for basic human subsistence or commercial activities[105,106]. Some exist only on paper, never having been implemented[7].

Sound management effectively involves another cycle of the previous five stages applied to individual reserves. It requires information on the biodiversity of each reserve, knowledge of the processes that underpin ecological functions, and an understanding of the responses of key elements of biodiversity to natural processes and anthropogenic disturbances (stage 1). Management should be based on explicit goals or targets[107] (as in stage 2), preferably acknowledging the contribution of each reserve's particular natural values to the regional system. Based on the extent to which management goals are already being achieved (stage 3), it might be necessary to review prescriptions or zonings and to prepare a new management plan indicating which parts of reserves are appropriate for different uses, require regulation of natural processes or need to be rehabilitated (stage 4). Problems with implementation of the management plan (stage 5) will usually be minimized or avoided if key interest groups are consulted during its development. As with the selection and implementation of new reserves, this process is not fixed and unidirectional. New data on patterns and processes within a reserve might call for revised goals. More generally, ongoing management should be complemented by periodic monitoring (back to stage 3) to assess the effectiveness of management actions in achieving nominated goals, with subsequent adjustment of goals and activities as appropriate. Adaptive management[12], coupled with a genuine commitment to monitoring, is increasingly recognized as crucial, not only to follow the status of selected elements of biodiversity, but also to assess the adequacy of resources for management, the capability of the responsible institutions, and the accountability with which funds are being used[108].

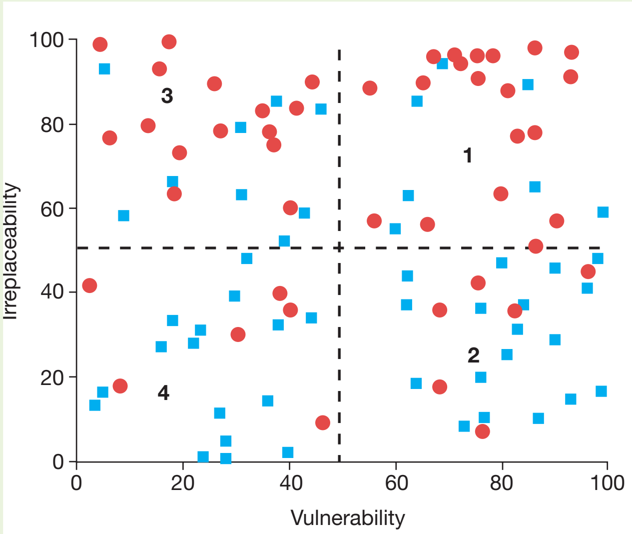

Figure 8 A framework for identifying priority conservation areas in time and space, applicable within regions to environments or other land types[20] or to potential conservation areas[14,96]. The graph shows hypothetical data for 100 potential conservation areas, each with values for irreplaceability and vulnerability (for example, agricultural potential). Red points are a subset of areas that are notionally selected to achieve targets but not yet given reservation status. Blue points are possible replacements. Selected areas occur in all parts of the graph, although the selected proportion increases with higher irreplaceability. If not all selected areas can be protected immediately (a common situation), the positions of areas in the graph will change over time. Some of the more vulnerable areas are likely to be converted to agriculture. As this happens, the irreplaceability of some of the remaining areas will increase as they become more important for achieving targets for features that are now less extensive and/or less frequent elsewhere. Conversely, as areas are progressively reserved, the irreplaceability of others will decrease as the features they contain approach or reach their conservation targets. The vulnerability of areas will also change, most likely upwards as land-use pressures intensify. Appropriate responses by conservation planners can be related to the different quadrants, as in previous studies at broader scales[100–102]. Quadrant 1: areas most likely to be lost and with fewest replacements. Protection is urgent if targets are not to be compromised. Some will probably be fragments of previously extensive vegetation types where strict reservation is difficult to apply (private tenure) or impractical (management liabilities) and must be supplemented with off-reserve management. Quadrant 2: areas vulnerable to loss but with more replacements, either because features are relatively common and extensive relative to targets or because targets have been partly met in existing reserves. Holding measures are necessary to avoid loss of some areas causing others to move upwards into quadrant 1. Options for protection include reservation where appropriate (and without pre-empting reserves in quadrant 1) complemented with off-reserve management. Quadrant 3: areas with lower present risk of agricultural conversion but high irreplaceability (for example, rocky ranges in a matrix of agricultural land or rare land types outside the climatic limits of agriculture). Protection is less urgent and acquisition for reservation more feasible than for quadrants 1 and 2 because of slower rates of transformation and (likely) lower land prices. Quadrant 4: the positions of areas here are likely to be stable and require least intervention, although monitoring of land use is advisable.

Interaction between reserve management and the location and design of reserves is inevitable. Decisions in the earlier stages of the planning process should, if possible, anticipate management issues. Key considerations include size and shape, alignment of boundaries with watersheds, avoidance of intrusive adjacent land uses, negotiations with neighbours, and the maintenance of migration routes. In turn, as the management needs of established reserves become apparent or as new needs emerge, it might be necessary to return to the selection stage (stage 4) to modify the design of individual reserves or the overall conservation network.

The outlook

There are many views about how best to identify priority conservation areas. To some extent this diversity is welcome as it arises from attempts by people with varying backgrounds to solve different problems in different parts of the world. This variety contributes usefully to an ongoing debate about appropriate planning approaches. But some of the divergence is less useful and seems to reflect different, poorly defined conservation goals and different, often implicit assumptions about the constraints under which conservation action will be applied. If these goals and assumptions were defined more explicitly, the relative roles and limitations of alternative approaches might be better understood and more attention could focus on addressing particular knowledge gaps and problems of implementation and management. Both clarity of purpose and productive debate would be achieved more readily if there was more direct interchange between groups working on conservation planning and between these groups and managers who face the daily challenges of staving off threats to biodiversity. Better communication depends inevitably on the interactions between individual researchers and managers, but more regular organized meetings specifically for conservation planning could also achieve much.

Conservation planning is also riddled with uncertainty. In the six stages of planning described here, uncertainty pervades the use of biodiversity surrogates, the setting of conservation targets, decisions about which kinds of land tenure can be expected to contribute to targets and for which features, and decisions about how best to locate, design, implement and manage new conservation areas in the face of limited resources, competition for other uses, and incursions from surrounding areas. New developments in all the planning stages will progressively reduce, but never eliminate, these uncertainties. One implication is that planners, rather then proceeding as if certain, must learn to deal explicitly with uncertainty in ways that minimize the chances of serious mistakes.

An urgent need is for more precision in the measurement of biodiversity and more consistency in mapping it across regions and biomes. In part this can be addressed by the allocation of more resources — funds, personnel and infrastructure — to the collection of field records of species and other biodiversity features. However, because all collections are samples, and as complete inventories of regions are not a realistic option for the foreseeable future, the design of data-collecting activities should be based soundly in ecological theory and should enable the application of proven statistical techniques to the modelling of wider spatial distribution patterns from the point locations that these field records were taken from[39].

Another need is for more effort to be applied to mapping patterns and monitoring rates of spread of threats to biodiversity, as it is such threats to which conservation planning should respond. A better understanding of the present and future distribution patterns of various threats will help focus limited conservation resources on areas and features most at risk. It will also clarify the extent to which conservation priorities overlap with priority areas for extractive and destructive uses. Some threats arise for reasons that can be understood only with the benefit of hindsight, but this is no reason not to improve foresight with refined predictions about the effects of extractive uses, urbanization and the spread of alien species.

More precise management prescriptions for the persistence of biodiversity are also needed. So far, enough is known only about a select few species, mostly large vertebrates and vascular plants, for effective management prescriptions. Finally, and just as importantly, biologists and ecologists must participate more in real planning processes. This is the only sure way to understand fully where the need for new ecological and biological knowledge is and what the social and political constraints on effective planning really are. □

1. Kanowski, P. J., Gilmour, D. A., Margules, C. R. & Potter, C. S. *International Forest Conservation: Protected Areas and Beyond* (Commonwealth of Australia, Canberra, 1999).
2. Chandrashekara, U. M. & Sankar, S. Ecology and management of sacred groves in Kerala, India. *For. Ecol. Mgmt* **112,** 165–177 (1998).
3. Grove, R. H. Origins of western environmentalism. *Sci. Am.* **267,** 22–27 (1992).
4. Hanks, J. Protected areas during and after conflict: the objectives and activities of the Peace Parks Foundation. *Parks* **7,** 11–24 (1997).
5. World Conservation Union. *Guidelines for Protected Area Management Categories* (IUCN, Gland, Switzerland, and Cambridge, 1994).
6. Anon. *Global Biodiversity Strategy* (World Resources Institute, World Conservation Union, and United Nations Development Program, Washington DC, 1992).
7. Terborgh, J. *Requiem for Nature* (Island, Washington DC, 1999).
8. Austin, M. P. & Margules, C. R. in *Wildlife Conservation Evaluation* (ed. Usher, M. B.) 45–67 (Chapman & Hall, London, 1986).
9. Soulé, M. E. (ed.) *Viable Populations for Conservation* (Cambridge Univ. Press, Cambridge, 1987).
10. Shafer, C. L. National park and reserve planning to protect biological diversity: some basic elements. *Landscape Urban Plan.* **44,** 123–153 (1999).
11. Peres, C. A. & Terborgh, J. W. Amazonian nature reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. *Conserv. Biol.* **9,** 34–46 (1995).
12. Holling, C. S. (ed.) *Adaptive Environmental Assessment and Management* (International Institute for Applied Systems Analysis, and Wiley, Toronto, 1978).
13. Pressey, R. L. in *Ecology for Everyone: Communicating Ecology to Scientists, the Public and the Politicians* (eds Wills, R. & Hobbs, R.) 73–87 (Surrey Beatty, Sydney, 1998)
14. Cowling, R. M., Pressey, R. L., Lombard, A. T., Desmet, P. G. & Ellis, A. G. From representation to persistence: requirements for a sustainable reserve system in the species-rich Mediterranean-climate deserts of southern Africa. *Div. Distrib.* **5,** 51–71 (1999).
15. Davis, F. W., Stoms, D. M. & Andelman, S. Systematic reserve selection in the USA: an example from the Columbia Plateau ecoregion. *Parks* **9,** 31–41 (1999).
16. Nix, H. A. *et al. The BioRap Toolbox: A National Study of Biodiversity Assessment and Planning for Papua New Guinea. Consultancy Report to World Bank* (CSIRO Publishing, Melbourne, 2000).
17. Noss, R. F., Strittholt, J. R., Vance-Borland, K., Carroll, C. & Frost, P. A conservation plan for the Klamath-Siskiyou ecoregion. *Nat. Areas J.* **19,** 392–411 (1999).
18. Dobson, A. P., Rodriguez, J. P., Roberts, W. M. & Wilcove, D. S. Geographic distribution of endangered species in the United States. *Science* **275,** 550–553 (1997).
19. Aiken, S. R. Peninsular Malaysia's protected areas' coverage, 1903-92: creation, rescission, excision, and intrusion. *Environ. Conserv.* **21,** 49–56 (1994).
20. Pressey, R. L. *et al.* How well protected are the forests of north-eastern New South Wales?—Analyses of forest environments in relation to tenure, formal protection measures and vulnerability to clearing. *For. Ecol. Mgmt* **85,** 311–333 (1996).
21. Ranta, P., Blom, T., Niemela, J., Joensuu, E. & Siitonen, M. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiv. Conserv.* **7,** 385–403 (1998).
22. Sarkar, S. Wilderness preservation and biodiversity conservation—keeping divergent goals distinct. *BioScience* **49,** 405–412 (1999).
23. Anon. *National Forest Policy Statement: a New Focus for Australia's Forests* (Australian Government Publishing Service, Canberra, 1992).
24. Noss, R. F., O'Connell, M. A. & Murphy, D. D. *The Science of Conservation Planning: Habitat Conservation under the Endangered Species Act* (Island, Washington, 1997).
25. Pressey, R. L. & Logan, V. S. in *Conservation Outside Nature Reserves* (eds Hale, P. & Lamb, D.) 407–418 (Univ. Queensland Press, Brisbane, 1997).
26. Hansen, A. J., Garman, S. L., Marks, B. & Urban, D. L. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecol. Applic.* **3,** 481–496 (1993).
27. Prendergast, J. R. *et al.* Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365,** 335–337 (1993).
28. van Jaarsveld, A. S. *et al.* Biodiversity assessment and conservation strategies. *Science* **279,** 2106 (1998).
29. Howard, P. C. *et al.* Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394,** 472–475 (1998).
30. McKenzie, N. L., Belbin, L., Margules, C. R. & Keighery, J. G. Selecting representative reserve systems in remote areas: a case study in the Nullarbor region, Australia. *Biol. Conserv.* **50,** 239 (1989).
31. Goldstein, P. Z. Functional ecosystems and biodiversity buzzwords. *Conserv. Biol.* **13,** 247–255 (1999).
32. Nix, H. A. in *Evolution of the Flora and Fauna of Australia* (eds Baker, W. R. & Greenslade, P. J. M.) 47–66 (Peacock, Adelaide, 1982).
33. Nix, H. A. in *Atlas of Elapid Snakes of Australia* (ed. Longmore, R.) 4–14 (Australian Government Publishing Service, Canberra, 1986).
34. Austin, M. P. Continuum concept, ordination methods and niche theory. *Annu. Rev. Ecol. Syst.* **16,** 39–61 (1985).
35. Austin, M. P., Nicholls, A. O. & Margules, C. R. Measurement of the qualitative realised niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.* **60,** 161–177 (1990).
36. Wessels, K. J., Freitag, S. & van Jaarsveld, A. S. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biol. Conserv.* **89,** 21–38 (1999).
37. Richards, B. N. *et al. Biological Conservation of the South-East Forests* (Australian Government Publishing Service, Canberra, 1990).
38. Ferrier, S. & Watson, G. *An Evaluation of the Effectiveness of Environmental Surrogates and Modelling Techniques in Predicting the Distribution of Biological Diversity* (Environment Australia, Canberra, 1997).
39. Margules, C. R. & Austin, M. P. Biological models for monitoring species decline: the construction and use of data bases. *Phil. Trans. R. Soc. Lond. B* **344,** 69–75 (1994).
40. Nelson, B. W., Ferreira, C. A. C., da Silva, M. F. & Kawasaki, M. L. Endemism centres, refugia and botanical collection intensity in Brazilian Amazonia. *Nature* **345,** 714–716 (1990).
41. Hutchinson, M. F. *et al. BioRap Volume 2. Spatial Modelling Tools* (http://cres.anu.edu/biorap/tools.html) (The Australian BioRap Consortium, Canberra, 1996).
42. Austin, M. P. & Meyers, J. A. Current approaches to modelling the environmental niche of Eucalypts: implications for management of forest biodiversity. *For. Ecol. Mgmt* **85,** 95–106 (1996).
43. Deadman, P. J. & Gimblett, H. R. Applying neural networks to vegetation management plan development. *AI Applic.* **11,** 107 (1997).
44. Jennings, M. D. Gap analysis: concepts, methods, and recent results. *Landscape Ecol.* **15,** 5–20 (2000).
45. Pressey, R. L. & Logan, V. S. Size of selection units for future reserves and its influence on actual vs. targeted representation of features: a case study in western New South Wales. *Biol. Conserv.* **85,** 305–319 (1998).
46. Soulé, M. E. & Sanjayan, M. A. Conservation targets: do they help? *Science* **279,** 2060 (1998).
47. Commonwealth of Australia. *Nationally Agreed Criteria for the Establishment of a Comprehensive, Adequate and Representative Reserve System for Forests in Australia* (Australian Government Publishing Service, Canberra, 1997).
48. Margules, C. R. & Nicholls, A. O. in *Nature Conservation: The Role of Remnants of Native Vegetation* (eds Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M.) 89–102 (Surrey Beatty, Sydney, 1987).
49. Balmford, A., Mace, G. M. & Ginsberg, J. A. in *Conservation in a Changing World* (eds Mace, G. M., Balmford, A. & Ginsberg, J. A.) 1–28 (Cambridge Univ. Press, Cambridge, 1998).
50. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography* (Princeton, New Jersey, 1967).
51. Diamond, J. M. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* **7,** 129 (1975).
52. Wilson, E. O. & Willis, E. O. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 522–534 (Belknap, Cambridge, MA, 1975).
53. Higgs, A. J. Island biogeography and nature reserve design. *J. Biogeogr.* **8,** 117–124 (1981).
54. Sauer J. D. Oceanic islands and biogeographical theory. *Geogr. Rev.* **59,** 585 (1969).
55. Davies, K. F., Margules, C. R. & Lawrence, J. F. Which traits of species predict population declines in experimental forest fragments? *Ecology* **81** (in the press).
56. Levins, R. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15,** 237–240 (1969).
57. Holt, R. D. & Gaines, M. S. in *Patch Dynamics* (eds Levin, S. A., Powell, T. M. & Steele, J. H.) 260–276 (Springer, Berlin, 1993).
58. Gilpin, M. E. in *Viable Populations for Conservation* (ed. Soulé, M. E.) 126–139 (Cambridge Univ. Press, New York, 1987).
59. Bennett, A. F. *Linkages in the Landscape: the Role of Corridors and Connectivity in Wildlife Conservation* (IUCN, Gland, Switzerland, and Cambridge, 1998).
60. Thomas, C. D. *et al.* in *Conservation in a Changing World* (eds Mace, G. M., Balmford, A. & Ginsberg, J. R.) 107–138 (Cambridge Univ. Press, Cambridge, 1998).
61. Holt, R. D. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schluter, D.) 77–96 (Univ. Chicago Press, Chicago, 1993).
62. Lindenmayer, D. B. & Possingham, H. P. *The Risk of Extinction: Ranking Management Options for Leadbeater's Possum* (Centre for Resource and Environmental Studies, Australian National University, Canberra, 1995).
63. Pickett, S. T. A., & Thompson, J. N. Patch dynamics and the design of nature reserves. *Biol. Conserv.* **13,** 27–37 (1978).
64. Lamberson, R. H., Noon, B. R., Voss, C. & McKelvey, R. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conserv. Biol.* **8,** 185–195 (1994).
65. Burgman, M., Ferson, S. & Akçakaya, H. R. *Risk Assessment in Conservation Biology* (Chapman & Hall, New York, 1993)
66. Lindenmayer, D. B., Burgman, M. A., Akçakaya, H. R., Lacy, R. C. & Possingham, H. P. A review of three models for metapopulation viability analysis—ALEX, RAMAS/Space and VORTEX. *Ecol. Model.* **82,** 161–174 (1995).
67. Lambeck, R. J. Focal species: a multi-species umbrella for nature conservation. *Conserv. Biol.* **11,** 849–856 (1997).
68. Dias, P. C. Sources and sinks in population biology. *Trends Ecol. Evol.* **11,** 326–330 (1999).
69. Braithwaite, L. W., Binns, D. L. & Nowlan, R. D. The distribution of arboreal marsupials in relation to eucalypt forest types in the Eden (NSW) Woodchip Concession Area. *Aust. Wildl. Res.* **10,** 231–247 (1988).
70. Saunders, D. A., Hobbs, R. J. & Margules, C. R. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5,** 18 (1991).
71. Kapos, V. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* **5,** 173 (1989).
72. Didham, R. K., Hammond, P. M., Lawton, J. H., Eggleton, P. & Stork, N. E. Beetle species responses to tropical forest fragmentation. *Ecol. Monogr.* **68,** 295–323 (1998).
73. Margules, C. R., Milkovits, G. A. & Smith, G. T. Contrasting effects of habitat fragmentation on the scorpion, *Cercophonius squama* and an amphipod. *Ecology* **75,** 2033–2042 (1994).
74. Cochrane, M. A *et al.* Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* **284,** 1832–1835 (1999).
75. Yates C. J. & Hobbs, R. J. Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. *Aust. J. Bot.* **45,** 949–973 (1997).
76. Frankel, O. H. & Soulé, M. E. *Conservation and Evolution* (Cambridge Univ. Press, Cambridge, 1981).
77. Rojas, M. The species problem and conservation: what are we protecting? *Conserv. Biol.* **6,** 170–178 (1992).
78. Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. What to protect?—Systematics and the agony of choice. *Biol. Conserv.* **55,** 235–254 (1991).
79. Fjeldsa, J. Geographic patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiv. Conserv.* **3,** 207–226 (1994).
80. Kiester, A. R. *et al.* Conservation prioritization using GAP data. *Conserv. Biol.* **10,** 1332–1342 (1996).
81. Kirkpatrick, J. B. An iterative method for establishing priorities for the selection of nature reserves: an example from Tasmania. *Biol. Conserv.* **25,** 127–134 (1983).
82. Stoms, D. M. GAP management status and regional indicators of threats to biodiversity. *Landscape Ecol.* **15,** 21–33 (2000).
83. Noss, R. F. Assessing and monitoring forest biodiversity: a suggested framework and indicators. *For.*

Ecol. Mgmt **115,** 135–146 (1999).
84. Williams, P. H. in *Conservation in a Changing World* (eds Mace, G. M., Balmford, A. & Ginsberg, J. R.) 211–249 (Cambridge Univ. Press, Cambridge, 1998).
85. Faith, D. P. Phylogenetic pattern and the quantification of organismal biodiversity. *Phil. Trans. R. Soc. Lond. B* **345,** 45–48 (1994).
86. Colwell, R. K. & Coddington, J. A. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B* **345,** 101–108 (1994).
87. Faith, D. P. & Walker, P. A. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* **5,** 399–415 (1996).
88. Belbin, L. Environmental representativeness: regional partitioning and reserve selection. *Biol. Conserv.* **66,** 223–230 (1993).
89. Faith, D. P. & Norris, R. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biol. Conserv.* **50,** 77–89 (1989).
90. Williams, P. H. *et al.* Comparison of richness hotspots, rarity hotspots and complementary areas for conserving biodiversity, using British birds. *Conserv. Biol.* **10,** 155–174 (1996).
91. Ferrier, S., Pressey, R. L. & Barrett, T. W. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. *Biol. Conserv.* (in the press).
92. Faith, D. P., Margules, C. R., Walker, P. A., Hutchinson, M. & Nix, H. A. in *Science for Pacific Posterity: Environments, Resources and Welfare of the Pacific People* (ed. Anon) 153 (Univ. of New South Wales Press, Sydney, 1999).
93. Faith, D. P., Walker, P. A., Ive, J. R. & Belbin, L. in *Conserving Biological Diversity in Temperate Forest Ecosystems—Towards Sustainable Management* (ed. Anon) 74–75 (Centre for Resource and Environmental Studies, Australian National University, Canberra, 1994).
94. Faith, D. P. & Walker, P. A. in *BioRap Volume 3. Tools for Assessing Biodiversity Priority Areas* (eds Faith, D. P. & Nicholls, A. O.) 63–74 (The Australian BioRap Consortium, Canberra, 1996).
95. Faith, D. P. & Walker, P. A. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. *Biodiv. Conserv.* **5,** 417–429 (1996).
96. Pressey, R. L. in *National Parks and Protected Areas: Selection, Delimitation and Management* (eds Pigram, J. J. & Sundell, R. C.) 337–357 (Univ. of New England, Centre for Water Policy Research, Armidale, 1997).
97. Myers, N. Threatened biotas: hotspots in tropical forests. *The Environmentalist* **8,** 178–208 (1988).
98. Mittermeier, R. A., Myers, N., Thomsen, J. B., da Fonseca, G. A. B. & Olivieri, S. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conserv. Biol.* **12,** 516–520 (1998).
99. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403,** 853–858 (2000).
100. Dinerstein, E. & Wikramanayake, E. D. Beyond "hotspots": how to prioritize investments to conserve biodiversity in the Indo-Pacific region. *Conserv. Biol.* **7,** 53–65 (1993).
101. Balmford, A. & Long, A. Avian endemism and forest loss. *Nature* **372,** 623–624 (1994).
102. Sisk, T. D., Launer, A. E., Switky, K. R. & Erlich, P. R. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human enterprise. *BioScience* **44,** 592–604 (1994).
103. Ricketts, T. H. *et al. Terrestrial Ecoregions of North America: A Conservation Assessment* (Island, Washington DC, 1999)
104. Myers, N. *The Sinking Ark: A New Look at the Problem of Disappearing Species* (Pergamon, Oxford, 1979).
105. James, A. N. Institutional constraints to protected area funding. *Parks* **9,** 15–26 (1999).
106. Stolton, S. & Dudley, N. A preliminary survey of management status and threats in forest protected areas. *Parks* **9,** 27–33 (1999).
107. Caughley, G. & Sinclair, A. R. E. *Wildlife Management and Ecology* (Blackwell Science, Cambridge, MA, 1994).
108. Hockings, M. & Phillips, A. How well are we doing?—Some thoughts on the effectiveness of protected areas. *Parks* **9,** 5–14 (1999).
109. Faith, D. P. & Walker, P. A. in *National Parks and Protected Areas: Selection, Delimitation and Management* (eds Pigram, J. J. & Sundell, R. C.) 297–314 (Univ. New England Press, Armidale, 1997).

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