

Persistence and vulnerability: retaining biodiversity in the landscape and in protected areas

K J GASTON, R L PRESSEY* and C R MARGULES**†

Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

**New South Wales National Parks and Wildlife Service, PO Box 402, Armidale, NSW 2350 Australia*

***CSIRO Sustainable Ecosystems, Tropical Forest Research Centre and the Rainforest Co-operative Research Centre, PO Box 780, Atherton, Queensland 4883, Australia*

†Corresponding author (Fax, + 61-7-4091-8888; Email, chris.margules@csiro.au)

An objective of biodiversity conservation activities is to minimize the exposure of biodiversity features to threatening processes and to ensure, as far as possible, that biodiversity persists in the landscape. We discuss how issues of vulnerability and persistence can and should be addressed at all stages of the conservation planning and implementation process. Procedures for estimating the likelihood of persistence and for measuring degrees of vulnerability at different spatial and temporal scales using subjective assessments, rules of thumb and analytical and simulation models are reviewed. The application of information on vulnerability and persistence to conservation planning and management is discussed under the headings of natural dynamics, replication of protection, levels of representation, source and sink population structures, refuges and critical resources, reserve design, habitat fragmentation and levels of management.

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1. Introduction

The natural features that occur in protected areas and in the wider landscape – populations, species, assemblages, environmental domains – obviously differ in spatial and temporal patterns and their risk of loss. It is therefore necessary for biodiversity conservation planning and management to address issues of vulnerability and persistence. This should occur during the six distinct phases of the conservation planning process (figure 1; see also Williams 1998; Margules and Pressey 2000; R L Pressey and R M Cowling, unpublished results). In the first phase, it might be desirable to compile data on species or other biodiversity features believed to be at highest risk in the region. In the second phase the goals in establishing a network might be defined with regard to the vulnerability of species or other features to disappearance. In the third

phase, the identification of gaps in the existing protected area system should be based, at least partly, on vulnerability. In the fourth phase, the selection of new protected areas can depend, at least partly, on criteria that will determine the persistence of biodiversity features in those areas. In the fifth phase, the implementation phase, the timing of the inclusion of areas in the emerging conservation network can be modified to minimize the risk of species or other biodiversity surrogates disappearing or declining before being given adequate protection. Finally, in the sixth phase, a range of maintenance activities can increase the ‘viability’ or persistence times of features within individual protected areas and the whole network. Vulnerability therefore contributes to determining where, when and how the other principles of conservation planning (e.g. complementarity, flexibility and irreplaceability, Margules *et al* 2002) should be applied.

Keywords. Design of protected areas; persistence of biodiversity features; species vulnerability; threatening processes

1. COMPILE DATA ON THE BIODIVERSITY OF THE PLANNING REGION

- Review existing data and decide 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 based only on 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 (e.g. at least three occurrences of each species, 1500 ha of each vegetation type, or specific targets tailored to the apparent 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 (e.g. 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 have been achieved in existing conservation areas.
- Assess the extent to which qualitative targets or preferences have been achieved.

4. SELECT ADDITIONAL CONSERVATION AREAS

- Regard established conservation areas as “constraints” or focal points for the design of an expanded system of conservation areas.
- 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 systems 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 phase 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 (e.g. 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 1. Six phases of the conservation planning process, with some examples of tasks and decisions in each phase (modified from Pressey and Cowling 2001). Vulnerability and persistence are important considerations in all phases. Note that the process is not unidirectional. There will be many feedbacks and reasons for altered decisions. For example, unforeseen difficulties in implementation (phase 5) will often call for new choices to be made in phase 4.

The first part of this paper presents an overview of the conservation planning process. The second is concerned with estimating the likelihood of persistence and measuring degrees of vulnerability. It begins with a discussion of the dependence of persistence and vulnerability on spatial and temporal scales, moves on to consider ways of determining the degree of vulnerability and the likelihood of the persistence of taxa, sets of taxa, and habitats or environments, and concludes with a consideration of the potential importance of determining the causes of threats. The third part addresses the application of information on vulnerability and persistence in the conservation planning process.

2. The conservation planning process

An initial step in conservation planning (figure 1, phase 1) is to measure and map biodiversity: that is, compile the data that will form the picture of biodiversity across the planning region and which, in conjunction with goals, will guide the location and design of new conservation areas. Since it is impossible to measure all of biodiversity, it is necessary to use partial measures, or surrogates, which should stand for biodiversity in all subsequent uses (Sarkar and Margules 2002). We use the term 'biodiversity features' for these surrogates in the remainder of this paper. The choice of which data to assemble from museums and herbariums, for example, or how much additional data to collect will depend on the quality of current information and the time and resources available for the planning exercise. In any event, it will often be desirable to compile data on those species or other biodiversity features believed to be most at risk from threatening processes for realistic conservation priorities to be set.

The chances of features persisting within a network of areas will be increased if targets for representation (figure 1, phase 2) include a measure of quantity and not just presence. Quantity might be expressed, for example, as the areal extent of a vegetation or habitat type, the total population size of a species, or the number of different areas in the network in which it should be present (replication). Targets may well vary between features, reflecting differences in what is needed to ensure that probabilities of persistence exceed a given threshold. This phase of conservation planning also involves goals relating to design, such as the size, dispersion, shape and connectivity of areas, all with the intention of reducing the vulnerability of features and increasing the likelihood of their persistence. The form such design constraints take depends greatly on the nature of the landscape matrix in which the network resides, with present and likely future patterns of land use needing careful con-

sideration. While biodiversity features play a key role in identifying the locations of new protected areas, additional features can also be important in minimizing vulnerability and maximizing persistence. These other features might include areas in which taxa have sink or source populations (with sources being targeted for inclusion in a network), refuge areas in which taxa can survive extreme environmental conditions such as drought or wildfire, and areas which are central or peripheral to the spatial distribution of taxa (with central areas usually being targeted). The persistence of features in protected areas will also depend strongly on the type of protection given to them. This could range from strict protection, with management only for biodiversity conservation, or it might include various levels of extractive use combined with conservation, such as agreements with landholders to limit numbers of stock, or the volume of timber removed from an area. Deciding on the types of protection to be afforded is a critical part of the goal-setting exercise and requires a knowledge of the threatening processes operating in particular parts of the region.

Issues of vulnerability and persistence also affect the assessment of gaps in existing networks and the process of selecting new areas (figure 1, phases 3 and 4). In phase 3, it will often be desirable not just to identify those vegetation types or other features without adequate representation in protected areas, but also their relative risk of loss or decline if protection is not increased. This can set the scene for scheduling conservation action on the ground (phase 5, below) and can also reveal any biases in the locations of existing reserves toward unproductive, unthreatened landscapes. This could, in turn, be used to argue for a change of emphasis in protected area planning. In phase 4, where there are optional areas for achieving representation targets, the choice may depend on factors such as past land use and condition, activities that impinge from adjacent areas, support from local residents, and opportunities to achieve design goals. The selection of areas may also be influenced by any risks to the features they contain. If it is determined, for example, that an area is seriously threatened or that a population of a species has a small probability of persisting there unaided, then that area might be favoured for inclusion in a network. On the other hand, if such areas were replaceable; that is, there were one or more other areas that could be substituted for them, another option would be to exclude them from the selection process and seek alternatives. Even if they are irreplaceable, it is conceivable that a greater contribution to the overall conservation goal might be obtained by abandoning them and diverting scarce management resources to other areas. There is ongoing debate over the extent to which limited resources should be devoted to imminently and, perhaps irretrievably, threatened species (e.g. Myers 1979;

Bowman and Whitehead 1993; Woinarski 1993; Vane-Wright 1996).

During the process of implementing a network of protected areas (figure 1, phase 5), which could stretch over years or decades, expected persistence times could play a major role in deciding on the urgency with which appropriate forms of protection are introduced to different areas. If there are funds to establish only few additional protected areas each year, which areas should be given protection first? The answer requires an assessment of the rate at which various threatening processes are impinging on areas as well as the irreplaceability of those areas. This broad approach might require some modification if it is determined, for example, that a greater long-term benefit could be gained by diverting management resources away from highly threatened areas to other parts of the proposed network with a higher probability of persistence. Implementation will probably involve several or many successive feedback loops to the previous phase in the planning process, if some selected areas prove unavailable for the appropriate conservation action and need to be replaced. Feedbacks might extend back to the goal-setting phase of the process as some levels of representation prove to be unachievable, some protection measures are not feasible or some costs of protection are unacceptably high. Other feedbacks relate to the success or otherwise of new conservation areas established by the process. For example, if new protected areas increase the abundance and distribution of highly threatened species or other features, or change their patterns of occupancy within the network, both the goals and the further selection of areas might need to be adjusted.

In the final phase of the conservation planning process (figure 1, phase 6), the maintenance of biodiversity in established protected areas will depend on a range of actions necessary to maximize the persistence of features. These activities include ensuring adequate resources for conservation management, adjusting boundaries and connections to other areas, and managing areas to lessen, for example, the impact of recreational use or to maintain fire or flooding regimes important to some species and communities. The extent of habitats and their composition are naturally dynamic in both space and time. Management to ensure persistence should see that successional processes (in the broadest sense) are maintained. Conservation has perhaps had an undue preoccupation with communities characteristic of the end of successional sequences (Usher 1993). The conservation of other stages is equally important, as is the recognition that some areas are typified by disturbance regimes which prevent attainment of 'climax' associations over short to moderate periods (Sprules 1991). Further, feedbacks will extend from this phase of the planning process. For example, the success or otherwise of maintenance activities in esta-

blished protected areas could change future approaches to area selection in order to pre-empt problems for on-the-ground management.

3. Assessment of vulnerability and persistence

3.1 Persistence and scale

3.1a Spatial scale: The concept of persistence is dependent on both spatial and temporal scales. In the spatial domain, we are concerned primarily with the persistence of features within entire regions or across whole landscapes. This means taking account of persistence and vulnerability outside protected areas as well as within them. For most features, it is desirable that they persist at the scale of the individual protected areas within networks. However, for many this may not be an attainable objective. Taxa with population dynamics that are characterized by frequent local extinctions and subsequent recolonizations may, or may not persist continuously in individual areas, depending on the size and suitability of the habitat. Taxa associated with disturbance events may, likewise, have a transitory presence in some areas. The maintenance of successional processes (or, more broadly, vegetation dynamics) within the network as a whole may necessitate the loss of habitat types from individual areas for potentially long periods. Broadly speaking, and although not necessarily a sufficient condition (see below), the greater the size of individual areas within the network the greater the likelihood that individual features will persist within them. In the case of taxa, this is simply because they will tend on average to have larger populations, and larger populations tend to have smaller risks of extinction (e.g. Berger 1990; Pimm 1991; Schoener and Spiller 1992; Burgman *et al* 1993; Gaston 1994). In the case of habitats, larger areas are more likely both to contain greater amounts of single habitat types, and to cover a matrix of different successional stages and alternative stable states (Pickett and Thompson 1978; White and Bratton 1980; Forman 1995). For neither taxa nor habitats does this mean that small areas have no role to play in networks (Schwartz 1999).

Networks established within given regions may contain features which, at the regional scale, have a low probability of persistence but which, across several regions, or within larger regions, may be expected to persist for much longer periods. Common examples are taxa close to the limits of their geographic ranges. Here they may have low probabilities of persistence over short time frames, whilst being under little immediate threat at a broader scale. For example, many species occurring in Britain are on the edge of their European range, and a number maintain a somewhat tenuous existence as breeding popula-

tions (e.g. Gaston and Nicholls 1995). These include birds such as the honey buzzard *Pernis apivorus*, marsh warbler *Acrocephalus palustris*, and golden oriole *Oriolus oriolus*. Although the contribution of these British populations to the persistence of the taxon as a whole may be small, they can, nonetheless, be used to establish regional protected area networks, and may be important to the people living in the region (see Hunter and Hutchinson 1994 for a discussion of the virtues and shortcomings of parochialism, and Avery *et al* 1994 for a discussion of combining national and international status in determining national conservation priorities).

3.1b Temporal scale: Factors that threaten the persistence of natural features in a region change through time in extent, rate, intensity and type. The likelihood of features persisting within a network of protected areas, also changes with time, depending on events outside the network as well as the way in which the network is designed and managed. Some of the events that occur outside protected areas may enhance extinction risk within those areas. The destruction of native habitat in surrounding lands, for example, may reduce the overall population size or extent of a feature, reducing its probability of persistence in the network. Likewise, such changes can focus increasing exploitative pressure (legal or illegal) on features within the network, because they are no longer represented outside it or only in small areas and in small numbers (Terborgh 1999). Thus, two management or planning responses should be distinguished: one, to patterns of threat that existed prior to, and the other to patterns of threat likely to occur following, the establishment of the protected area network. Some integration of the two seems desirable. For example, conservation goals (figure 1, phase 2) could be set and specific areas selected (figure 1, phase 4) in anticipation of changes in land use in a region. Even so, goals will often need to be revised as threats to features and their apparent conservation requirements change through time.

Options for reducing the effects of threats in the longer term need to be exercised as early as possible. It could be appropriate, for example, to promote connectivity between areas in a network by maintaining or creating a series of 'stepping stones', or linking corridors. This might facilitate the movement of taxa in response to long-term climate change, and it might reduce the impact of isolation within habitat fragments on the mobility of some taxa (such as butterflies, Dempster 1991). Inevitably, however, most efforts will be consumed in simply ensuring the persistence of features over the more immediate future.

3.2 Risk assessment

The probability of persistence should ideally be assessed separately for each biodiversity feature because it may be

subjected to different patterns and levels of threat, although this might be possible only for a limited number of species or for higher order surrogates such as species assemblages or environmental domains. If it is not possible to estimate the likelihood of persistence of each feature, decisions will have to be made as to which features are likely to be most informative or which are currently most at risk. Risk assessments based on habitat types may be more useful in designing networks to achieve the goal of representing biodiversity more broadly but the bulk of the literature on risk assessment deals with taxa and in particular those with small population sizes, so we begin there.

3.2a Taxa: Risk assessments for taxa range from simple discrimination between different broad classes of likelihood of extinction or decline (local, regional or global), to estimates of the probability that, within a specified time frame, (i) the taxon will become extinct, (ii) the overall population of the taxon will have declined by a given amount or proportion, (iii) particular populations will become extinct, (iv) particular populations will have declined by a given amount or proportion, or (v) combinations of these four.

Many kinds of information could be relevant to making such assessments. Following Burgman *et al* (1993), these might include (i) demographic data, (ii) behavioural data, (iii) habitat data, (iv) functional and physiological data, (v) spatial data, (vi) genetic data, and (vii) stochastic data. Invariably, only some, and usually, only a very few of these data are available, normally only for short time frames. This places a major constraint on risk assessment, and, typically, has resulted in various simplifying assumptions being made.

A variety of methods exist for risk assessment. Following Durant and Mace (1994), these can be divided broadly into subjective assessments, rules of thumb, and analytical and simulation models. These are all in some sense methods of population viability analysis (PVA), although this term is frequently applied solely to simulation models. In moving from subjective assessments and rules of thumb to analytical and simulation models, the number of taxa which can potentially be included declines, because the data requirements increase steeply.

(i) *Subjective assessments:* The majority of risk assessments are essentially subjective judgements. These provide the basis for many listings of taxa believed to face a high risk of extinction [many Red data books and associated publications (see Burton 1984; Munton 1987 for numerous examples)]. They represent judgements made by individuals or groups of researchers as to the likelihood or relative likelihood that the taxa will become extinct. This likelihood is not expressed in terms of a defined

level of risk in an associated time frame, or of a likely time to extinction. The bases for decisions are not usually provided, although they often have some foundation in experience about the types of characteristics that predispose taxa to extinction and the conditions those taxa are currently found in. Consistency in the application of assessments, particularly by different individuals, is difficult to achieve. Subjective assessments tend to be of value in identifying broad groups of taxa potentially at high risk, as well as in suggesting broad spatial and temporal generalities about patterns of risk.

(ii) *Rules of thumb*: Various rules of thumb have been proposed whereby greater levels of objectivity, and transparency, and greater ease of replication, can be incorporated. These include numerous attempts to distinguish taxa of differing risk using a few named life history and/or population parameters (e.g. East 1988a; 1989a; 1990a; Perring and Farrell 1983; Millsap *et al* 1990; Molloy and Davis 1992; Reed 1992; Dickman *et al* 1993; Given and Norton 1993). In the main, though not exclusively, such assessments tend to be based primarily on the population and/or range sizes of taxa, and the premise that taxa with small populations and small ranges have a disproportionately high risk of extinction. They often pay less explicit attention to temporal trends in either population levels or distribution patterns, and focus on where individuals occur, not where local reproduction exceeds local mortality. They usually ignore genetic factors, and the potential role of catastrophes. There are concerns that as a result of these constraints, and particularly because substantial variance is often associated with individual correlates of risks of extinction, such assessments may fail to identify some groups of taxa at high risk. These may include, for example, some taxa with large geographic range sizes but low densities (McIntyre 1992; Gaston 1994), and some with large proportions of individuals in sink rather than source populations (*sensu* Pulliam 1988; Dias 1996). Finally, these assessments are typically relative in that, whilst attempting to distinguish different categories of risk they are not associated with probabilities or time scales.

There are on-going attempts to derive and apply rules of thumb which resolve some of these limitations and still provide an advance over subjective assessments (Mace and Lande 1991; Mace *et al* 1992; Collar *et al* 1994; IUCN 1994a; Mace 1994a,b,c; Mace and Collar 1994; Mace and Stuart 1994; Keith 1998). This is being done using criteria that take explicit account of genetic factors, trends in population sizes and distribution patterns, and of the spatial subdivision of populations. In some cases there is an attempt to classify taxa in terms of their probability of extinction within a specified time frame. Durant and Mace (1994) have also explored the potential of demographic factors such as sex ratios, age structures,

and the frequency of years of zero recruitment as indicators of extinction risk. Other avenues, which may prove worthwhile, concern rules incorporating the dynamics of habitats, and the positions of populations within the geographic ranges of taxa. Boyce (1992) raised some further possibilities, and continued the debate over the usefulness of what is now probably the most (in)famous and widely quoted rule of thumb, Franklin's (1980) 50/500 rule for minimum effective population size (see also Simberloff 1988; Caughley 1994). Recent contributions also include the explicit recognition of uncertainty in allocating taxa to threat categories (e.g. Burgman *et al* 1999; Colyvan *et al* 1999).

As with subjective assessments, rules of thumb should identify those taxa of greatest concern. They should tend to be precautionary within appropriate bounds in that, if taxa are misclassified, this is in the direction of over- rather than under-estimation of the risks they face. Rules of thumb are an important basis for setting conservation priorities for taxa and areas world-wide. They are also the basis of much activity in the development and application of species recovery plans.

(iii) *Analytical and simulation models*: The widespread application of models to estimate the likely persistence times of taxa and populations is a recent phenomenon. Analytical models (reduction of population processes to analytical formulae) have been used and have some significant merit, not least the substantial literature concerning their construction (Belovsky 1987; Burgman *et al* 1992, 1993; Dennis *et al* 1991; Foley 1994; Mangel and Tier 1994). However, simulation models (direct population modelling by simulation) seem to have become the tool of choice (for overviews see Simberloff 1988; Boyce 1992; Caughley 1994; Settele *et al* 1996; for examples see Menge 1990; Clark *et al* 1991; Lindenmayer *et al* 1993; Lindenmayer and Lacy 1995). Most are tailored to particular species, although generic models exist that can be applied more widely (e.g. Possingham *et al* 1992; Lacy 1993).

The major disadvantages of these models are that they tend to demand a lot of data that are not readily available and may be difficult to collect, they are sensitive to small changes in parameter values, and generate predictions which demand careful interpretation based on a detailed knowledge of model structure (which is difficult because those model details seldom are published) and are difficult to validate. The major advantage is that they have the potential to provide important insights into levels and patterns of risk, which take explicit account of the biological characteristics and circumstances of individual taxa. They may also have the potential to suggest appropriate management strategies to reduce predicted levels of risk (Lindenmayer and Possingham 1996). The extent to which model-based risk assessments have begun

to fulfil either of these potentials remains open to debate (e.g. Boyce 1992; Caughley 1994).

(iv) *Integrating different methods*: These different methods of assessing risks to taxa do not exist in isolation from one another. Analytical and simulation models can be, and have been, used to determine potential rules of thumb (e.g. Mace and Lande 1991; Mace *et al* 1992; Durant and Mace 1994). Ideally, the application of the different methods might be seen as something of a filtering process. Taxa identified as threatened or vulnerable using subjective assessments and rules of thumb would be subjected to more detailed analyses, using analytical and simulation models to estimate the likelihood of persistence over designated time frames. Taxa not regarded as at risk using subjective assessments and rules of thumb would be eliminated from detailed consideration, freeing resources to those of more concern (a form of 'elimination planning' *sensu* Kirkpatrick and Brown 1991a). This is already happening at some levels, in that simulation models are seldom, if ever, applied to taxa that are not already assumed to be of concern (Caughley 1994). However, implementation of this strategy at even a moderate scale would be limited severely by a lack of appropriate data and by the numbers of taxa involved.

In a related vein, there are a growing number of plans providing explicit recommendations for action to increase the persistence times of individual taxa. These are so-called 'action plans' (e.g. East 1988b, 1989b, 1990b; Chapman and Flux 1990; Foster-Turley *et al* 1990; Ginsberg and Macdonald 1990; Nicoll and Rathbun 1990; New and Collins 1991). Many are published in the 'grey literature' making access difficult, and there is wide variation in content and the practicality of proposed actions. Nonetheless, wherever available, these recommendations should be considered for incorporation into the goals for, and implementation of, a network of protected areas.

3.2b Sets of taxa: The numbers of threatened taxa present, or some combination of the levels of threat to different taxa, can provide threat scores for different areas (e.g. Hall and Veldhuis 1985; Jarman 1986; Lahti *et al* 1991; Rebelo 1992; Frissell 1993; Rebelo and Tansley 1993; Väisänen and Heliövaara 1994; Kershaw *et al* 1995; Lombard 1995; Freitag and van Jaarsveld 1997). Such an approach has value for identifying areas that contain concentrations of taxa with high probabilities of extinction. Nonetheless, these assessments must be interpreted cautiously. First, likelihoods of extinction of individual taxa frequently reflect processes occurring in the region as a whole (or perhaps a yet larger area). Threat scores calculated for individual areas on the basis of such information may map patterns of occurrence of

taxa at threat within the entire region and not measure the threat taxa face in each of the areas that make up that region. Some taxa, which are not at high risk of extinction at the scale of the region, may be at risk at the scale of individual areas. Conversely, the occurrence of one or more regionally threatened taxa in an area does not necessarily indicate that the area is at risk from vegetation clearance or other processes. Second, threat scores are usually calculated from the number of taxa in an area which are estimated to be highly threatened, possibly with those at greater threat being given differential weighting. In consequence, equivalent scores can mean rather different things. For example, an area with a large number of moderately threatened taxa may have an overall score similar to that of an area containing a few taxa under imminent threat of extinction.

Several alternative approaches to assessing the viability of sets of taxa have been proposed. These include those of Witting and Loeschke (1995) and Ward (1989). The former is a multi-species risk evaluation based on the expected loss of genetic information from a set of species, and incorporating the influence of between-species interactions. It is very demanding of data and likely to be applicable only in a very few cases.

Ward's (1989) community attrition index takes the form $c = (n + e - s)/2n$, where n = number of taxa, e = number of extinct taxa, and s = number of taxa with stable populations. In this context a stable population is regarded as one which is not declining. The index has a value of zero if no taxa have become extinct and none are declining, a value of one if all taxa have become extinct, and a value of 0.5 if all taxa are in decline but none have become extinct. It may provide a useful method for comparing rates of the decline of different assemblages. It is, nonetheless, very coarse, and care must be taken not to confound stability in an assemblage with low risk of extinction. Burbidge and McKenzie (1989) have made use of the index in exploring patterns in the decline of the vertebrate fauna of western Australia.

3.2c Habitats: Amongst conservation biologists and also in legislation, increasing attention is being paid to the notion of threatened habitats and communities. For example, under the Australian Commonwealth Endangered Species Protection Act 1992, there is a provision for listing 'endangered ecological communities'. A similar provision exists for formal listing of threatened communities in New South Wales. One of the first listings is Cumberland Plain Woodland, a vegetation formation on the plains west of the Sydney Metropolitan Area that was once widespread but is now reduced to small remnants at risk from further urban encroachment (Benson and Howell 1990). There are many parallels between the assessment of areas on the basis of threats to taxa and

threats to whole habitats or environments. This is unsurprising given that habitat alteration, past, present and future has a profound effect on the persistence of taxa. Studies of habitat persistence have, however, attempted to estimate the likelihood of persistence more directly than has been the case for most taxa, by estimating rates of change in the amount of habitat (usually expressed in terms of changes in areal extent), and projecting those rates into the future. In taking this approach, there are three principal difficulties to confront. First, habitat types need to be defined clearly and identified in a spatially and temporally consistent manner. Failures to do this have made it very difficult to judge, for example, absolute and relative global and regional losses of tropical moist forest (Fearnside 1990; WCMC 1992; Menon and Bawa 1998). The second, and related issue, is the need for careful definition of what is meant by 'habitat loss'. At what stage does the degradation or alteration of a habitat type (e.g. due to logging, drainage) equate to its loss? The use of remote-sensing technology is increasingly improving the assessment of habitat changes in the recent past, and the monitoring of on-going changes (e.g. Chatelein *et al* 1996), but differences in interpretation of imagery have led to large discrepancies in estimated rates of deforestation (Downton 1995) and ground surveys are often necessary to quantify changes to the structure and composition of remaining vegetation (e.g. Nepstad *et al* 1999). The third difficulty is the inevitable uncertainty about future rates of habitat loss, driven as they are by dynamic factors such as human population growth, immigration to regions, and international markets. Simulations of alternative future landscapes (e.g. Veldkamp and Fresco 1996; Mouat and Steinitz 1997) have the potential to take these factors into account and, just as importantly, to investigate the robustness of particular conservation strategies to variations in the rates of loss of particular habitats.

Probably the best known approach to assessing the vulnerability of geographical areas in relation to observed habitat loss is Myers' (1988, 1990) identification of 'hotspots', applied at a global scale. He defined hotspots as localities with two characteristics: (i) exceptional concentrations of species with exceptional levels of endemism, and (ii) exceptional degrees of threat. Myers' assessments were based on his own experience and on the available literature. It is possible that the list of priorities would have been different if information had been available from systematic assessments of both endemism of species and rates of habitat loss. Nevertheless, the basic rationale is sound and the papers are important pioneering contributions to global biodiversity conservation. They identify areas for which there is limited time for action and few or no alternatives to protect the biodiversity features they contain.

In a later assessment, Myers (1993) applied a somewhat more systematic approach to defining global-scale vulnerability with data from remote sensing. Recently, Myers *et al* (2000) have updated the list of hotspots using the most recent data on endemism and threats, calling for a 'silver bullet' response focusing on hotspots according to their share of species at risk.

This same rationale drove the quantitative approach to identifying protected areas for conservation efforts by Dinerstein and Wikramanayake (1993). They compiled a conservation index for 23 Indo-Pacific countries based on the size of protected areas, the extent of remaining forest habitat, deforestation rates, and biological richness. More recent studies comparing regions or countries have employed similar methods (e.g. Sisk *et al* 1994; Mittermeier *et al* 1998; Olson and Dinerstein 1998). National and global-scale studies have also shown that patterns of habitat loss can be explained, and therefore potentially predicted at broad scales, by factors such as rates of increase in human populations and global economics (Hannah *et al* 1994; Houghton 1994; Rudel and Roper 1996; Laurance 1998).

Within regions and jurisdictions, the vulnerability of habitats has been estimated at scales that are relevant to the location and design of individual protected areas. Assessments of risk have been used to adjust representation targets of vegetation types in Tasmania by Kirkpatrick and Brown (1991b), with targets of up to 90% of pre-European extent nominated for some rare or vulnerable types. Planning for new conservation areas in the eastern forests of New South Wales in 1996 was based on conservation targets for individual forest types set in relation to their natural rarity and vulnerability to clearing (RACAC 1996; Pressey 1998). Benson (1991) has given codes of risk and conservation status to major vegetation groups in New South Wales. The groups have not been mapped but the assessment comes from much field experience and a review of the literature. The results are a basis for setting representation goals for protected areas as well as identifying the relative urgency with which different vegetation types should be placed under protection. Other regional approaches include GIS analyses of trends in land cover (e.g. Kienast 1993) and classification schemes that are specifically designed to reflect vulnerability to prevailing threatening processes (Lloyd *et al* 1993). In north-eastern New South Wales, the vulnerability to clearing of 81 environmental classes has been rated according to the extent of past clearing (Pressey 1996). Across the whole State, values for vulnerability to clearing have been allocated to 1500 landscapes as a basis for setting conservation priorities (Pressey *et al* 2000).

Some risk assessments within regions are *de facto* predictions, based on the assumption that past patterns in

destructive land use foreshadow future patterns. For example, if a vegetation type has been largely cleared, this is because it is predisposed to clearing by the topography and soils that underlie it. Vegetation remnants in the flat arable wheatbelt of New South Wales have therefore been, and continue to be, much more vulnerable to clearing (Sivertsen 1994, 1997; Sivertsen and Metcalfe 1995) than unreserved land on dissected, infertile sandstone around Sydney (Benson and Howell 1990). An explicitly predictive approach to habitat vulnerability at a regional scale is that of Braithwaite *et al* (1993). They derived a productivity index for land in southern New South Wales and combined this with an index of accessibility to identify tree associations at most risk of loss through clearing or disturbance.

Predictions of the vulnerability of habitats or environments, whether extrapolated from recent trends or based on an understanding of likely future trends, have much unrealized potential in conservation planning. They are a way of determining the need for protection and the type of protection that might be effective in preventing a loss of biodiversity. At regional scales, differences in land use and the status and likely fate of natural habitats can be largely accounted for by a few physical and climatic variables. These include temperature, rainfall, slope and geological substratum [as it reflects soil characteristics and finer-scale aspects of terrain (Braithwaite *et al* 1993; Pressey 1996)], variables that are also important in determining the distributions of species (e.g. Nix 1982; Austin *et al* 1984; Margules and Stein 1989; Nicholls 1989; Lindenmayer *et al* 1991, 1995; Iversen and Prasad 1998; Jarvis and Robertson 1999). By mapping combinations of these variables, or by using statistical modelling to weight the variables according to their importance, a landscape of the potential for destructive land uses can be constructed. Any extant habitats in areas particularly suitable for activities such as clearing for agriculture can then be identified as highly vulnerable.

This predictive approach has several advantages: (i) the necessary data are usually available or can be derived quickly; (ii) the data can provide insights into the possible trends in land use and the future prospects for habitat destruction in areas not currently disturbed, perhaps because of current lack of markets or population pressure; and (iii) the approach can identify inliers of likely 'safe' habitats within vulnerable regions or broad vegetation types or, conversely, particularly vulnerable parts of generally unthreatened regions.

There are at least three qualifiers to this recommendation. First, vulnerability to processes such as clearing is not only a function of climatic and physical characteristics of the landscape. The location of vegetation relative to towns, transport routes and other infrastructure will also be a major factor determining risk of clearing.

Government policies including subsidies, tax incentives and tariff protection can make clearing land of marginal productivity economically viable and open up new primary industries requiring new types of land. In some cases, vulnerability depends very much on the attitudes of individual landholders. Maintaining the constituency for nature conservation in general and protected areas in particular is therefore critically important throughout the conservation planning process. A second qualification is that the reliability of predicted trends in land use decreases as the trends are projected further into the future. Vegetation types in the wheatbelt of New South Wales recently considered to be relatively secure, because of poor soils and steeper slopes, were under pressure for conversion to agriculture four years later (Sivertsen 1997). Predictions of vulnerability are nonetheless useful tools in conservation planning. In all but the worst cases, conservation actions can probably be prioritized more effectively with such predictions than without any information on patterns and imminence of land use pressures. Models of land use trends also have two other advantages: they make explicit, and help to refine the assumptions of planners that would otherwise remain unstructured; they allow uncertainties over rates and patterns of habitat loss to be openly explored so that the sensitivity of conservation strategies to errors in predictions can be assessed. A third qualification is that, even with the difficulties just discussed, clearing of vegetation is the easiest threatening process to monitor and predict. Accurate assessment of vulnerability to processes such as grazing or logging is generally precluded over extensive areas by lack of data on variations in the intensity of the processes and limited information on the different responses of particular species, landscapes or vegetation types.

3.2d The dynamics of risk assessment: Risk assessments are dynamic in two closely related senses. First, they are dependent on available information. Improved data may substantially alter projections of risk. Thus, the white-breasted guineafowl *Agelastes meleagrides* was judged in the 1980s, on the basis of available sources, to be one of the most threatened birds in Africa (Collar and Stuart 1985), but was subsequently estimated to have a population of 30,000 to 40,000 birds in Taï National Park (Côte d'Ivoire) alone (Francis *et al* 1992). Many of the recent changes in the numbers of bird species of the Americas listed in different Red Data book categories have resulted from improved information (Bibby 1994). Second, in general, risk assessments become poorer the further into the future they are projected. The dynamics of underlying processes are not temporally stable and neither are parameter values. Errors in predictions tend to become progressively magnified as time frames lengthen. Furthermore, the act of establishing networks of pro-

tected areas in itself should change risk assessments for features falling within those networks.

These observations again point to the need for a dynamic and flexible approach to identifying protected areas for conservation. Knowledge and understanding of the problems of persistence will improve, and this will require changes in all the phases of the planning process in figure 1.

3.3 Causation

Having identified those features in a region which have a low probability of persistence without conservation intervention, or those features that appear at risk within one or more protected areas, consideration moves to the causes of this circumstance. The process of assessing risks may itself serve to highlight these, particularly for habitats in which the causes of decline are usually clear. However, especially for taxa, these causes may not necessarily be obvious. Information on the dynamics of the abundances of taxa may, for example, be sufficient to indicate that they have a low likelihood of persistence without indicating the cause.

Gross causes of high extinction risk are easily identified. Clear felling, land drainage, and hunting, for example, are seldom difficult to detect. However, many causes of decline or risk are subtler. Problems may become particularly acute because threats to persistence can be diverse, spatially and temporally dynamic, and may act via a multitude of mechanisms and synergisms. Caughley (1994) provides a prescription for the process of identifying the causes of decline.

- (i) Study the species (or other feature) to gain a knowledge of, and feel for, its ecology, context and status.
- (ii) When confident that this is adequate to avoid silly mistakes, list all conceivable agents of decline.
- (iii) Measure their levels where the species is now located and where the species used to be; test one set against the other; any contrast in the right direction identifies a putative agent of decline.
- (iv) Test the hypotheses so produced by experimentation to confirm that the putative agent is causally linked to the decline and not simply associated with it.

Only application of the final step can enable escape from the problem of confusing correlation with causation. This step, requiring field experimentation, is difficult and often time consuming. The opportunities to test hypotheses are not always available given often-serious constraints on time and other resources. Nevertheless, any reasonable opportunity to establish such experiments (e.g. Margules *et al* 1994a; Robinson *et al* 1992) should be grasped because conservation biology sorely needs the body of knowledge such experiments would build up.

The conservation of butterfly species in Europe provides salutary examples of some of the problems associated with determining the reasons why taxa are in decline. Ignorance of subtle habitat requirements meant that the loss of many local populations was not prevented. In seventeen out of twenty species analysed by Thomas (1991), 'the young stages were found to require considerably more specialized conditions than had been suspected, which restricted them to narrow niches within their biotopes, usually corresponding to a short-lived seral stage and often to a warm microclimate'.

4. Applying information on vulnerability and persistence

Having identified features at risk, and perhaps the causes of this circumstance, attention turns to using this information to set goals for the protected area network. At the outset, a distinction must be drawn between threat and priority for conservation action: priority setting embraces factors in addition to threat. There is, for example, a need for some balance to be struck between strategies for rescuing those features which are imminently threatened, and strategies for preventing those features which are apparently more secure at present from becoming less so. These two strategies can allocate conservation resources to very different places, as shown by the contrast between the biodiversity hotspots of Mittermeier *et al* (1998) and their major tropical wilderness areas. Given the frequently high costs associated with reclaiming features from the brink of extinction (epitomized by captive breeding programs for some large vertebrates), an increased emphasis on a 'prevention is better than cure' approach is attractive. This is an important rationale for the Gap Analysis Program in the USA (Scott *et al* 1993) and is evident in approaches to setting conservation priorities that favour relatively intact areas, where choices exist, to minimize constraints on implementation (e.g. Olson and Dinerstein 1998). Equally, however, it may be repulsive to abandon those features requiring cures – those for which the time for prevention is effectively past. Some middle way is required, and is likely to prove a contentious path to tread.

The relation between patterns of risk and the best distribution of conservation action is not clear, both at the scale of areas and of entire regions, because actions to reduce the risk of extinction of individual features may seldom be neutral with regard to the likelihood of persistence of other features. For example, prevention of the extinction of some individual taxa can prevent cascade effects (perhaps mediated by predators or competitors) which result in the extinction or drastic decline of other taxa (e.g. see Terborgh 1988; Owen-Smith 1989; Sieving

and Karr 1997; Crooks and Soulé 1999). Equally, some actions that are directed toward saving some taxa might be detrimental to other taxa (e.g. Scott *et al* 1987; Scholtz and Chown 1993). The potential for such clashes may be increased when the taxa concerned operate on different spatial scales.

Information about vulnerability and persistence can, nonetheless, help set the goals of a protected areas network. These might include issues such as how large areas should be, possible targets for the sizes of populations of certain taxa they should contain, and the degree of replication of features in different areas. Likewise, information on vulnerability and persistence can help determine the design of areas in the network (e.g. shape, connectivity), and the level of protection that areas receive.

The kinds of responses to identified threats will depend largely on: (i) the options for increasing estimated persistence times of features – e.g. addition of further areas to a network, increasing size of areas in a network, strict reservation of areas as opposed to management agreements with landholders; (ii) the longevity of options – e.g. unless an area is brought under strict reservation immediately it may be turned over to agriculture; (iii) the relative and absolute costs of options in terms of the overall availability of resources for conservation action; (iv) the extent to which carrying through each option forecloses other options, whether this be in physical, resource or other terms – e.g. the costs of acquiring rights over an area in which features are predicted to have short persistence times under current management practices may prevent enforcing stricter protection of other areas over which rights are already held.

4.1 Natural dynamics and static networks

The persistence of features in a network will be enhanced most when it is designed around the spatial and temporal dynamics of those features. There is an innate contradiction in attempting to conserve features which exhibit spatial and temporal dynamics in a static network. There must be feedback between the design of a network and those dynamics. Presently vacant areas may be vital to the longer-term persistence of a taxon in a region, and should not automatically be excluded from the selection process because they are unoccupied. Similarly, the areas that are important for a species might all be outside the protected area system in a region from time to time.

Margules *et al* (1994b) provide one example of what the potential impact of temporal variability might be. Using iterative heuristic algorithms they identified sets of limestone pavements in part of Yorkshire, UK which sampled all 50 nationally rare plant species on the pavements in 1974, and then again in 1985. Table 1 summarises the results. Over a period of only 11 years, plant species disappeared from some pavements and colonized others. Eighteen pavements were identified which sampled all 50 species in 1974, but by 1985 only 32 of those 50 species remained on those pavements. If a further 6 designated pavements had been set aside in 1974 with the benefit of foresight, bringing the total to 24, then all 50 species would still have been sampled in 1985.

Virolainen *et al* (1999) and Rodrigues *et al* (2000) have documented similar effects of temporal turnover in species identities in sets of areas. The latter, using data

Table 1. Sets of limestone pavements beginning with existing reserves, needed to sample one, two, three, four and five populations of the 50 nationally rare species in 1974, the number of species these pavements still sampled in 1985 and the extra pavements that would have needed to have been set aside in 1974, with the benefit of foresight, to ensure the desired number of populations in 1985 (from Margules *et al* 1994b).

Conservation goal in 1974	No. of pavements	No. of spp meeting conservation goal*	No. of spp in 1985 sampled at least once	No. of spp in 1985 meeting the 1974 conservation goal	No. of extra pavements needed in 1974 to achieve goal in 1985	Total No. of pavements in 1974 to achieve conservation goal
At least 1 population	18	50	32	32	6	24
At least 2 populations	22	39	33	27	8	30
At least 3 populations	27	33	34	23	9	36
At least 4 populations	35	31	35	22	9	44
At least 5 populations	39	26	35	24	9	48

*This refers to the number of species with the number of populations required to meet the conservation goal. Thus, only 39 of the 50 species had 2 or more populations, i.e. 11 species occurred on only 1 pavement.

for birds in Britain, also found that networks which were more robust could over time, be obtained, simply by ensuring the inclusion of those areas in which species were judged to be more likely to persist on the basis of their abundance (see also Nicholls 1998).

Some species depend on food resources and breeding sites that occur in different parts of the landscape in different years, as well as varying in extent and quality from time to time (Noss and Harris 1986; Woinarski *et al* 1992; Morton *et al* 1995b; Dean 1997). Management of such resources to ensure the persistence of the dependent species might constrain the level of protection that can be provided. Strict protection may not be the most appropriate form of management simply because it is more difficult to turn on and off as the patterns of resource availability change. The planning approaches needed to deal with these short-term dynamics remain poorly developed.

It is also likely that protected areas will have to deal with dynamics on a longer time scale and over larger areas. Under several global environmental change scenarios a large proportion of major conservation areas will in the future no longer comprise the vegetation types which they do at present (WCMC 1992; Leemans 1996). Currently, facilitating the movement of features in response to changing environmental conditions seems to be the principal approach to this problem (Peters and Darling 1985; Peters and Lovejoy 1992), although some attempts are also being made to examine the relative vulnerabilities of different taxa to climatic change (see Dennis and Shreeve 1991; Dennis 1993 for examples of studies on butterflies).

4.2 Replication of features in protected areas

It is impossible to replicate areas incorporated in a conservation network with precision. No two moderately sized areas will be identical in their environmental conditions. Nonetheless, attempting to replicate areas, or at least the occurrence of features, provides one of the major methods of insurance against the loss of those features from the network. The long-term persistence of features in individual areas cannot be guaranteed, even in the best circumstances. Indeed, extinctions are likely events (e.g. Mangel and Tier 1994). Replication serves three functions in relation to these problems. First, it tends to reduce the likelihood that a feature will be lost by chance from a network through the action of stochastic processes. Although the feature may become extinct in one area, its presence in other areas will mean that it persists in the network. Second, replication increases options when risks to the persistence of features in individual areas become high. For example, the pre-

sence of a feature in more than one area may reduce the need for costly management action to maintain it in an area where its expected persistence time has become short, or may equally encourage bold and innovative approaches to reducing the risk in this area. Third, replication increases the likelihood of incorporating areas in which features have a particularly high probability of persistence. This is because frequency distributions of persistence times tend to be strongly right-skewed, such that most populations have a relatively low expected persistence time.

Another role of replication is to increase the likelihood that unknown or poorly known biodiversity will be protected. When the features being targeted are landscape subdivisions such as vegetation types, species assemblages or environmental domains, replication of examples of these features is likely to increase the number of unmapped smaller-scale features (such as cryptic species) that are effectively protected (Pressey 1996). This type of replication has been made explicit in setting goals for conservation planning in the forests of New South Wales. For a major planning exercise in 1996, many forest types were subdivided by experts familiar with variation in their species composition, effectively creating subtypes, each with their own targets for representation in reserves (RACAC 1996; Pressey 1998). The distributions of some taxa were similarly subdivided to maximize the likelihood that intraspecific genetic variation would be contained in new conservation areas. In the absence of expert judgement on where features should be subdivided geographically, a rule of thumb is to replicate the occurrences of species across environmental gradients and geographic barriers.

The costs of replication in terms of the increased land area required can be estimated readily using the systematic selection procedures described in Margules *et al* (2002). Nearly 45% of the area of all wetlands on a floodplain in northern New South Wales was required to sample at least one population of each of 98 indigenous plant species, and this increased to 78.5% to sample at least five populations (Margules *et al* 1988). Similarly, 69% of the area of all remaining vegetation remnants in the South Australian croplands was required to represent each of 45 vegetation alliances at least once, increasing to 84.25% for five representations (Margules 1989; table 2). These figures may seem high, but in the case of the South Australian croplands, very little indigenous vegetation remains, so to ask that 85% of the remaining natural vegetation be set aside does not seem unreasonable. It is notable that area costs are not proportional to the number of replicates required. Five replicates, for example, requires less than five times the area for one replicate (see also Williams *et al* 1996). A target of a particular number of replicates inevitably results in some

features being represented at more than the target frequency because of incidental representation (Pressey and Logan 1998).

Size of geographic range and number of sites occupied both tend, broadly, to be positively correlated with local abundance across taxa (Hanski 1982; Brown 1984; Gaston and Lawton 1990; Gaston 1994, 1996; Gaston *et al* 1997). More widely distributed species tend to have higher local densities. This means first that the options for replication tend to be fewer for those taxa for which replication is most desirable; that is, those which do not have large populations anywhere. Second, it means that a given level of replication of the occurrence of a restricted species will include fewer individuals than for a widespread species. In addition, it suggests that the reduction of a species' spatial distribution may, at least under some circumstances, result in a decline in population density in surviving populations, even if these are under some form of protection (Lawton 1994; Gaston 1999).

4.3 Levels of representation in protected areas

The persistence of features within a protected area network will be greatly enhanced when appropriate explicit targets are set and met for the number (e.g. population size) or extent of each feature in that network. Ideally, such targets for taxa are expressions of the levels of representation required in order for them to persist with a given probability over an associated time frame. They need to be formulated in the context of the landscape matrix of which protected areas will be a part, paying particular attention to the extent to which patterns of land use outside of protected areas are sympathetic or antagonistic to conservation goals. In practice, representation targets tend to be rules of thumb with only limited explicit justification. Two things are clear, though: larger targets will increase the persistence times of most species and populations; and since larger targets will increase the

spatial extent of higher level features such as vegetation types or environmental domains represented in protected areas, they will also increase the degree of heterogeneity of those features that can be represented.

In setting targets for the representation of taxa, attention needs to be paid to their spatial distribution patterns. For example, in general the sizes of populations and the local densities of taxa are right-skewed such that populations are large in only a few areas and small in most, and likewise local densities are low in most areas and high in a small number of areas (e.g. Gaston 1994 and references therein). A similar pattern seems often to hold for the spatial distribution of different sized patches of a given habitat type.

Assessments of the risks which taxa face will provide important guidance in determining desirable minimum levels of representation. Insights from formal population viability analyses using simulation models may be helpful, enabling exploration of the potential consequences of setting different targets (e.g. Lindenmayer 1996). Particular attention needs to be paid to two things. First, because circumstances differ, the required size for populations to persist with a given probability over a specified time frame is variable both in time and space. Second, the possible significance of catastrophes needs to be considered. Population sizes need to be much larger to increase the probability of persistence if catastrophes are likely (Mangel and Tier 1994).

Habitats or environments should also be given representation targets that reflect their perceived need for protection. Targets for the conservation of individual forest types in New South Wales have been set with an explicit formula that includes a base percentage of total extent and weightings for both natural rarity and vulnerability to clearing (RACAC 1996; Pressey 1998). The resulting numbers are not "right" but are at least explicit and in proportion to the risk of a forest type being eliminated or substantially reduced in extent by a change in land use. Notably, the targets for this and subsequent planning exercises have been set in terms of percentages of pre-European areas, as estimated by spatial modelling and analysis of forest remnants. This avoids several related disadvantages of setting targets in terms of extant areas. For example, many people would question the validity of a conservation target being set as a small percentage of the extant area of a forest type that covers only a small proportion of its original area. Similarly, conservation targets set as percentages of extant areas will become smaller as habitat loss proceeds, even if no further areas are protected. One implication of setting targets, which are proportions of the extent of vegetation types in Australia prior to European settlement, is that all of the extant occurrences of some depleted forest types can be required for conservation (RACAC 1996). This

Table 2. The remnant mallee patches in south Australia required to represent each of 45 vegetation alliances once, and if there was more than one occurrence, twice, and if more than two occurrences, three times and so on up to five times (from Margules 1989).

Conservation goal	No. of patches	Area (%)
Each alliance represented:		
Once	18	69.11
Twice	30	79.72
Three times	41	82.04
Four times	49	83.48
Five times	55	84.25

might be difficult to achieve, especially when the remainder exists as remnants on private land, but correctly acknowledges the need for protection of such habitats.

Representation targets are also related to the efficiency (Pressey and Nicholls 1989) with which they can be achieved. Over-representation of features can be greater for smaller targets because of the more frequent incidental occurrences of features in the candidate areas being assessed for possible protected area status (Pressey and Logan 1995, 1998). This means, for example, that the area needed to represent 10% of each vegetation type is less than ten times that needed for 1% of each type. Efficiency, in terms of the area needed to achieve a representation target therefore increases with the size of the target, even though larger targets must clearly require larger areas. Efficiency is also a function of the size of the candidate areas, with smaller areas achieving a given representation target more efficiently, with less incidental representation, than larger areas (Pressey and Logan 1995, 1998).

The relationship between the total size of the protected area network and the likelihood that features will persist within it means that there will have to be a trade-off between the total area given formal protection and the probability of persistence. Increasing the size of individual areas and increasing the extent to which features are represented will result in an increase in the total area needed to achieve a representation goal, but may substantially improve the probability of persistence. The trade-off between efficiency and persistence is most obvious when the size of individual management areas is considered. It is possible to envisage highly efficient networks based on areas that are so small that almost no features can persist in them.

4.4 Sources and sinks

The distinction between sources and sinks provides a good example of the need for considered evaluation of patterns of risk. Within sink populations local reproduction is insufficient to balance local mortality, and persistence results from continued immigration of individuals from source populations (Pulliam 1988; Dias 1996). Sink populations may contain a large fraction of all individuals, and may increase the size of and enhance the persistence of a metapopulation (a set of subpopulations which exchange individuals) (Howe *et al* 1991). Nonetheless, neither they nor the metapopulation will persist in the absence of source populations. Sources must therefore be of primary conservation concern, regardless of whether or not they are estimated to have the greatest risk of extinction, represent the largest or smallest populations, or occupy the habitat in which a

taxon is most or least frequently encountered. Unfortunately, distinguishing sources from sinks may often prove exceedingly difficult (Watkinson and Sutherland 1995).

Conflict between the persistence of source populations and extractive use is probably common. It is well illustrated with an example from the coastal *Eucalyptus* forests of eastern Australia, described in a series of publications by Braithwaite and colleagues (Braithwaite 1983; Braithwaite *et al* 1983, 1984, 1988), although it remains to be demonstrated that this does indeed represent a true sink-source system. They found that densities of arboreal mammals, most commonly the greater glider *Petauroides volans*, feathertail glider *Acrobates pygmaeus* and the sugar glider *Petaurus breviceps*, were highest in certain forest types (tree communities). These types characteristically occur on a particular granitic substratum known locally as Devonian intrusives. Foliage from the trees of these forest types contains higher concentrations of nutrients such as nitrogen, phosphorus and potassium. By establishing the link between high animal densities, foliage nutrient levels and geological substratum, they were able to estimate that 63% of the animals occupied a mere 9% of the forest. Remaining animals were spread, still unevenly but in lower densities, throughout another 41% of the forest. About 50% contained no arboreal mammals at all. The source areas for arboreal mammals, tree communities on Devonian intrusives, happen to contain the best timber trees; species such as *Eucalyptus fastigata*, *E. radiata*, *E. cypellocarpa*, and *E. elata*. Such species were recognized as indicators of higher soil fertility by early European settlers and were cleared for farming from all of the broader valleys on which they occurred. The smaller pockets that now remain are of great value to the timber industry and to the arboreal marsupials.

Human disturbance, especially habitat destruction, has led to changes in species distribution patterns and it would be unwise today to assume that the habitat in which a taxon is presently found, is found in greatest numbers, or occurs most widely, represents its optimum or preferred habitat (Gray and Craig 1991). Taxa may well be driven into marginal habitat if that is all that is available. The takahe *Porphyrio mantelli*, a flightless gallinule from New Zealand, provides an example (Bunin and Jamieson 1995).

4.5 Refuges and critical resources

Focusing conservation action on part of a species' range involves other problems similar to those for sources and sinks. Within the distribution range of a species, certain habitats could provide resources such as shelter from fire or drought; plentiful food at times when food is absent or

scarce elsewhere, or particular requirements for successful reproduction. If such critical resources are not maintained, even populations in protected areas will eventually decline or disappear, a problem referred to by Terborgh (1992) as “truncation of the habitat matrix”. Unfortunately, the areas critical to the survival of species are not always known. Where they are known, however, their vulnerability to present or likely future impacts should be assessed and plans made for their inclusion in the system of protected areas.

Some critical resources are scattered through the landscape, such as figs that provide a reliable food source in tropical forests (Terborgh 1986). Such resources might be effectively conserved by protecting sufficiently large tracts of habitat, coupled with actions to maintain those species in accessible sites outside of protected areas. In other cases, critical habitats can be localized (e.g. Morton *et al* 1995b). Sometimes these localized resources can be predicted and mapped. For example, areas of water run-on in deserts (those areas that water flows to during rare rainfall events) serve as drought refuges for animal species (Morton 1990). Potential refuges can be identified from topographic and soil maps, checked for significance, and then managed to maintain their values (Morton *et al* 1995a). Another example is the prediction by Nix (1976) that the coastal lowlands of north-eastern New South Wales and south-eastern Queensland would be an important overwintering food resource for birds from higher latitudes and altitudes. This prediction was based on the calculation of a growth index, derived from data on rainfall and temperature, and has been supported by field observations, although the impacts of coastal development on this critical area continue (Pressey and Griffith 1992).

4.6 Reserve design – goals for protected areas

The design of conservation areas (their size, dispersion, shape, and connectedness) has been the subject of considerable discussion in the conservation biology literature. To date this has largely been an academic debate in which the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) and other biogeographic concepts have played major roles. The equilibrium theory proposes that there is an equilibrium number of species on islands, which is a function of immigration and extinction rates, which, in turn, are a function of island size and distance to the mainland where source populations occur. There is turnover, in that species come and go, but their number is at equilibrium. Reserve design guidelines have been derived from this theory.

Diamond (1975a) and Wilson and Willis (1975), for example, argued for large reserves over small ones, for single large reserves over groups of small ones, for reserves being close together rather than far apart, for

them to be connected if possible, and for them to be more or less circular rather than long and thin. However, whilst these guidelines are intuitively appealing, and their publication marked the beginning of a major growth period in the field of conservation biology, it is now evident that they provide little practical help in the selection and design of conservation areas (Simberloff and Abele 1976; Margules *et al* 1982; Burgman *et al* 1988; Simberloff 1988; Boecklen 1991; Shrader-Frechette and McCoy 1993; Doak and Mills 1994; Whittaker 1998). The reasons include the following: (i) theory and predictions do not always match, and biogeographic theory is in fact neutral with respect to several design criteria; (ii) the theory and predictions lack general empirical support, although there is now some experimental evidence to support the prediction that isolation leads to population declines (Davies *et al* 2000); (iii) the theory takes no account of environmental heterogeneity and the habitat variations this gives rise to (Sauer 1969); (iv) the theory and predictions concern numbers of species on islands, yet in trying to maintain regional biotas in conservation networks, it is necessary to know which species are, or are not, in different areas, not how many (Margules *et al* 1994b); (v) in real landscapes the options for design are limited by land use history and cost.

Planners are often constrained by existing spatial configurations so the choice between, for example, a large reserve or a group of smaller ones may not be available. Equilibrium theory has advanced the sciences of biogeography and ecology by drawing attention to the dynamic nature of isolated biotas and setting a research agenda, but has not provided a mechanistic explanation for use in conservation planning (Haila 1986; Margules *et al* 1994b). A similar conclusion applies to faunal collapse and relaxation models, for which the species-area model was the progenitor (Boecklen and Simberloff 1986).

Generalized statements about ideal reserve design remain difficult to substantiate. There are pros and cons to most facets of design. For example, for habitat corridors between areas potential benefits include increased immigration rates and the provision of increased or alternative refugia, whilst potential disadvantages include facilitated transmission of fire, disease and predators, and reduction in between-population genetic variation (e.g. Noss 1987; Simberloff and Cox 1987; Saunders and Hobbs 1991; Newmark 1993; Kupfer 1995). Empirical evidence for the value of corridors as facilitators of the exchange of individuals between populations seems on balance to support their utility but well-designed studies, especially experimental ones, remain in short supply (Nicholls and Margules 1991; Beier and Noss 1998; Harrison and Bruna 1999).

Decisions about reserve design essentially have to be made on a case-by-case basis. For individual taxa, impor-

tant issues contributing to decision making on reserve design are likely to include incidence functions (the proportion of habitat patches of different sizes which are occupied by a taxon; Diamond 1975b; Hanski 1991, 1992; Taylor 1991), overall population structure (demographic and genetic; e.g. single population, classical metapopulation, mainland-island metapopulation, patchy population, non-equilibrium metapopulation; Harrison 1991, 1994; see also Gilpin and Hanski 1991; Doak and Mills 1994), levels of temporal population fluctuation (Pimm *et al* 1988; Gaston and McArdle 1993, 1994), spatial concordance in temporal population fluctuation (to what extent do the sizes of populations fluctuate in synchrony?; e.g. Harrison and Quinn 1989; Pollard 1991; Hanski and Woiwood 1993; Pollard and Yates 1993), and dispersal and establishment abilities and rates (how often do individuals move between habitat patches and how easily can they colonise unoccupied patches?). Again, formal population viability analyses may assist in weighing different options (Possingham *et al* 1993; Possingham 1996). Likewise, guidance will be provided by a general knowledge of patterns of risk of extinction, such as which populations have the greatest estimated likelihood of persistence. Lambeck (1997) has proposed the concept of "focal species" for the design of protected areas and the associated restoration of habitats necessary in heavily modified regions. Focal species are those most susceptible to a particular threatening process (e.g. reduction of habitat, loss of connectivity, weed invasion). Managing for these species should, he predicts, maximize the likelihood of less sensitive species persisting.

Design constraints will have associated costs, such as reducing the range of options (e.g. combinations of areas) for constructing a network, and increasing the numbers or sizes of areas required if other goals are also to be met. These costs need not always be excessive and, in any case, can be assessed with area selection algorithms when the goals are being set for conservation planning. Nicholls and Margules (1993), for example, found that 11.7% of a forested region on the east coast of Australia was required to represent at least 10% of the extent of 31 distinct forest tree communities, and that this rose to 12.5% if the selection algorithm included an adjacency constraint. Faith and Walker (1996) have proposed a method for incorporating opportunity cost trade-offs in the selection of biodiversity priority areas and Faith *et al* (2001) have described an application of this method in Papua New Guinea.

4.7 Reserve design – the effects of habitat fragmentation

Considerations of reserve design and the persistence of populations in protected areas are important, not only in

the second phase of conservation planning when goals are being identified (figure 1), but throughout the whole process. Area selection (phase 4) may be based on design criteria, the timing of implementation (phase 5) should take into account the likelihood of areas becoming fragmented or isolated and ongoing maintenance of protected areas (phase 6) will seek to ameliorate the impacts of surrounding land uses. It is probably this last phase in which the problems of fragmentation are most serious. In this phase, land use across the whole region will determine the extent to which protected areas become islands in a sea of transformed land (McIntyre and Barrett 1992; Miller 1996; Sisk *et al* 1997) and management of the protected areas will determine their resilience to these changes.

The sizes of a substantial proportion of (most?) areas in existing conservation networks may be insufficient for the persistence of at least some, and potentially many, features in the short to medium term (Soulé *et al* 1979; Newmark 1985, 1987; Simberloff 1988; Redford and Robinson 1991; Burkey 1995). The majority of protected areas are small, the most common size on a world-wide basis being 10–30 km² and the majority of the overall total protected land is found in a very few large areas (WCMC 1992; Dinerstein and Wikramanayake 1993). The problems with the sizes of areas become more marked as surrounding habitat is destroyed. Newmark (1987) documented the loss of mammal species from 14 western North American national parks since their establishment. He argued that this was a result of their isolation and predicted that all but the very largest national parks in this area were too small to retain an intact mammalian fauna.

Conservation networks are parts of overall landscapes that have been modified to a greater or lesser extent by human activity. Two extreme scenarios can be envisaged. In the first, the proportion of features shared between the network and the surrounding landscape is very high. There is little differentiation between the areas of the network and the surrounding matrix. The areas of the network could, for example, be parts of a much larger continuous region of forest. In the second scenario, the network is embedded in a matrix with which it shares only a minimal number of features, and the differentiation between the network and the rest of the landscape is marked. The areas of the network might comprise patches or remnants of habitat embedded in an agricultural landscape. Numerous ways exist to describe and quantify patch patterns (e.g. Forman and Godron 1986; Turner *et al* 1991; Forman 1995; Hargis *et al* 1998).

The features contained within conservation networks in these two scenarios will probably have quite different patterns of likely persistence, and necessitate different forms of management. Broadly, the greater the differentiation between the network and the matrix in which it is

embedded, the lower will be the probable persistence of features within that network, the fewer options there will be to increase persistence, and the more interventionist, drastic and hence costly the remaining options will need to be if managers are committed to retaining habitats and species. Yet habitat fragmentation is one of the most common and conspicuous consequences of agricultural development and closer settlement throughout the world.

The consequence of fragmentation is isolated remnants of natural habitat, which vary in size and distance from one another. Because habitat on more productive soils and in more accessible locations tends to be cleared by preference, remaining fragments primarily represent one or a few of the available habitat types (Terborgh 1992) and the organisms occupying them form sub-populations of previously more widespread populations. Some may form meta-populations while others become completely isolated, forming new smaller discrete populations. It is the persistence or extinction of such populations that will ultimately determine whether or not biodiversity protection succeeds or fails. Unfortunately, little is known about the responses of populations of different species to habitat fragmentation, but it is necessary to attempt some generalizations because much habitat is already fragmented and being managed in some way. Practice will test, modify and probably discard some of these generalizations (Settele *et al* 1996), while taking on new ones, as the mismatch between ecological theory and empirical studies is reduced (Harrison and Bruna 1999). Monitoring will be necessary if that is to happen (see below).

- (i) Population level responses will be mediated by changes to the physical environment, themselves due to habitat fragmentation, and species will respond differently with some increasing and others decreasing in abundance (Davies and Margules 1998).
- (ii) No two habitat remnants will be exactly the same environmentally, regardless of their proximity or similarity in size, shape and orientation.
- (iii) Species susceptible to changes in fluxes of wind, water and solar radiation (Saunders *et al* 1991) are likely to be more seriously affected by habitat fragmentation. Margules *et al* (1994a) and Davies and Margules (1998) provide some recent experimental support. Forest habitat remnants, for example, are more exposed to the drying agents, wind and solar radiation. They are also more likely to suffer flooding when it rains because clearing has increased run-off in the catchment above them. This can lead, in turn, to changes in vegetation structure, micro-climate, ground cover and nutrient status.
- (iv) Habitat fragments may be placed on a trajectory of continued change once they have been isolated and exposed (Margules and Pressey, 2000). Effects deleterious to some species might accumulate and increase in

magnitude, or they may even cascade, with a change in one species' population size or productivity leading to changes in the populations of other species.

(v) Species which avoid habitat edges have disproportionately less habitat available as fragmentation proceeds and are also, therefore, likely to be more seriously affected (e.g. Sisk and Margules 1993).

(vi) Consequently, two general management guidelines emerge. First, remnants should be managed to ameliorate the increased local climatic fluctuations they experience, which may be a major cause of changes in abundances and therefore increased extinction risk for susceptible species. Two possible strategies might be to maintain the undergrowth in habitat remnants and to ensure that buffer zones, which might consist of new plantings of indigenous species, are maintained. Second, programs should be designed and implemented to monitor the consequences of management practices. Resources for management are always limited and there is a tendency to overlook the importance of monitoring, which can be expensive, time-consuming and labour-intensive. Carefully designed monitoring programs, which properly address the questions of what, where and when to monitor are necessary if mistakes are not to be repeated (Margules *et al* 1995; Lindenmayer *et al* 2000). Too many programs monitor in the wrong places and unnecessarily frequently, and fold through lack of support.

4.8 Levels of conservation management

The future of biodiversity rests on a range of measures for *in situ* protection, not simply on some classification of 'protected' as distinct from 'unprotected' (Soulé 1991). IUCN (1994b) has recognized a spectrum of management regimes under the broad term 'protected areas'. These lie on a gradation of interventionist management from wilderness and strict nature reserves at one end to largely natural areas such as forests or rangelands that are managed sustainably for extractive use. All protected areas listed by IUCN are recognized as being managed primarily for the conservation of biodiversity and other natural resources. Outside this range of protection measures lies another, and sometimes larger, set of natural and semi-natural areas that are too small, too altered, lacking a formal management regime, or being managed in a way that does not give priority to biodiversity.

A major part of the goal-setting phase of conservation planning is to decide on the levels of protective management needed for particular features in a region. The actual mechanisms needed to achieve these levels of management might vary and can be determined later in the process, in phase 5 (figure 1). For example, the prevention of clearing for agriculture might be achieved

with acquisition for a nature reserve, a legal agreement with the landholder, perhaps with compensation for lost production, or legislation to control clearing subject to biodiversity assessments in the region (e.g. the Native Vegetation Conservation Bill, 1997, in New South Wales).

The aim of deciding on levels of protective management is to match these levels with the threatening processes that need to be reduced or excluded. Protected areas vary in how effective they are at excluding threatening processes (Pressey 1996). For example, they can be very effective at preventing clearing, logging, and grazing by domestic stock, depending on enforcement, but can be ineffective at excluding exotic plants and animals and hydrological impacts from nearby developments unless complemented with intensive on-site management and regional-scale adjustments of land use patterns and processes. On the other hand, impacts of logging or stock grazing on biodiversity do not always necessarily warrant strict reservation. In some cases, they could be brought to a satisfactory level by adjusting the level or timing of grazing or the types of logging operations. Thus, there is no necessary correlation between the degree of threat faced by an area in the network and the stringency of the protection measures required. High degrees of threat may sometimes be mitigated through even moderate changes in patterns of land-use, without the requirement for strict reservation, while at other times it may only be possible to reduce levels of threat to other areas through the instigation of tight and wide-ranging controls. These choices depend critically on the resources likely to be available for enforcement, maintenance and monitoring well into the future (Terborgh 1999).

5. Concluding remarks

The central significance of issues of persistence and vulnerability in the processes of identifying, establishing and managing a conservation network is clear. If the network is to prevent the disappearance of natural features from regions it is essential to understand the risks faced by biodiversity features, how those risks change in time and space, and how they can be mitigated. Nonetheless, and it is a sobering lesson, it is impossible at the present time to be strongly prescriptive with regard to how these ends should be attained. General practical principles (akin to those of complementarity and irreplaceability; see Pressey *et al* 1993; Margules *et al* 2002) with which we can be guided are still lacking. This is not, however, a counsel of despair. First, conservation biology has come a long way towards identifying and understanding the key problems, and continues to do so apace. Second, whilst general principles may not yet exist, in any given region and for any given set of features, it

remains possible to assess patterns and levels of risk, and to find constructive ways of addressing them.

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