

LETTER

Does conservation planning matter in a dynamic and uncertain world?

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Abstract

Loss of biodiversity is one of the world's overriding environmental challenges. Reducing those losses by creating reserve networks is a cornerstone of global conservation and resource management. Historically, assembly of reserve networks has been *ad hoc*, but recently the focus has shifted to identifying optimal reserve networks. We show that while comprehensive reserve network design is best when the entire network can be implemented immediately, when conservation investments must be staged over years, such solutions actually may be sub-optimal in the context of biodiversity loss and uncertainty. Simple decision rules, such as protecting the available site with the highest irreplaceability or with the highest species richness, may be more effective when implementation occurs over many years.

Keywords

Biodiversity, conservation, optimisation, reserve design, uncertainty.

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INTRODUCTION

Creating networks of ecologically representative nature reserves (Balmford *et al.* 2002; Rodrigues *et al.* 2004) is a cornerstone of strategies to safeguard biodiversity. Although, 11.5% of the land and 0.5% of the sea are now protected within reserves (WDPA 2003), these areas do not provide adequate protection for biodiversity, particularly for the species and ecosystems that are most imperilled (Andelman & Willig 2003; Rodrigues *et al.* 2004). Moreover, globally, intact ecosystems are being converted at a rate of over 1% per year (Balmford *et al.* 2002), and global investments in reserve acquisition and management remain inadequate (James *et al.* 2001; Balmford *et al.* 2002). Thus, to improve decisions about which areas of the land and sea to include in reserve networks, most large conservation organisations and natural resource agencies now use systematic conservation planning methods to identify optimal or near optimal reserve networks (e.g. Andelman *et al.* 1999; Malakoff 2002; Noss *et al.* 2002; Airame *et al.* 2003; Cowling *et al.* 2003; Groves 2003).

Current methods for conservation planning treat both biodiversity and human economic systems as static. They rely on a snapshot in time of the distribution and

abundance of biodiversity and assume that once a reserve network is identified it can be implemented immediately. In the real world, the process of identifying and implementing reserve networks violates these assumptions. Conservation investments are constrained by budgets, and opportunities to implement conservation actions tend to be unpredictable, both in space and through time. Thus, implementing reserve networks is a sequential process, requiring decades to achieve conservation objectives (e.g. Balmford *et al.* 2002; James *et al.* 2001; Pimm *et al.* 2001). In the interim, some biodiversity is lost and the geography of both human dominated and natural landscapes changes.

Here we explicitly consider the implications for biodiversity conservation of several key assumptions underlying systematic conservation planning methods. We explore both simple and more complex conservation problems in which (1) entire reserve networks cannot be implemented instantaneously, (2) there is uncertainty about when and where opportunities for conservation investment may arise, (3) budget constraints vary, and (4) there is degradation or loss of biodiversity over time in sites that remain unprotected. Our goal is to begin to understand how the dynamics of ecological and human systems may affect the relative

performance of commonly used strategies for creating conservation networks.

METHODS

Simple dynamic problem and stochastic dynamic programming solution

We first illustrate the dynamic conservation problem using a simple, stylised example involving 12 sites important for populations of 13 bird species in the Columbia Plateau region of the US (Table 1). For the static conservation case with immediate implementation, the most efficient reserve network will protect at least one population of each species (sites 3, 7, and 9). Instead, assume that because of budget constraints, we must build a reserve network over a period of 10 years. Each month there is a small chance (0.5% per month or $\sim 10\%$ per year) that one of the sites becomes available for acquisition, and a small chance (from 0 to 1% per month) that the species at a site are extirpated. Site cost is either 0.1 (cheap) or 1.6 (expensive). During the month a site is available, we must decide whether to add it to the protected area network. Once a site is reserved, we assume that the species at that site will persist. The challenge now is to conserve as many species as possible for the least cost by the end of the decade.

This problem, of optimal decisions for a stochastic discrete-time dynamic system, has an exact solution, which can be found using stochastic dynamic programming (SDP) (Mangel & Clark 1988; Possingham *et al.* 1993; Costello & Polasky 2004). Using Bellman's equation (Bellman 1957), and working backwards from the end of the planning horizon, we can determine the best decision strategy at the

current time, assuming we make the best decision in the future. For this simple problem, we compared the performance of three commonly used decision rules for assembling reserve networks (irreplaceability, richness, and the minimum set) to the dynamically optimal solution obtained using SDP. Below we briefly describe each algorithm:

Stochastic dynamic programming

The SDP algorithm generates a large amount of data for 120 time steps. Therefore, we calculated the complete set of solutions for all time steps, but used only the solutions from time step 1, 72, 108 and 120. For intermediate time steps we used the closest previous SDP solution (e.g. at time step 71 we used SDP(1), while for time step 72 we used SDP(72). While this does not yield the exactly optimal solution, it comes quite close.

Minimum set

The minimum set identifies the complete network of sites that protects each species in at least one site for the least cost (Possingham *et al.* 1999). To implement the minimum set decision strategy for the simple example, we used a simulated annealing algorithm (Possingham *et al.* 1999) to select the static comprehensive reserve network (minimum set). Thereafter, we added a site to the reserve network only if it was identified at the outset as part of the minimum set of sites that would conserve each species in at least one site.

Richness

The richness algorithm prioritises sites based on the number of unprotected species that would be added to the reserve network if the available site were protected. We also calculated the number of unprotected species that would be

Table 1 The distribution of populations of 13 vulnerable bird species among 12 sites in the Columbia Plateau Ecoregion of the U.S. Black circles indicate populations of species represented in the optimal solution to the static conservation problem. Open circles indicate populations not protected by the optimal solution. Note that site 3 is irreplaceable in that it contains the only population of the Columbian Sharp-tailed Grouse. Site 10 has the highest richness, containing 8 species

Species by site	1	2	3	4	5	6	7	8	9	10	11	12
Grasshopper sparrow	○					○	●	○		○		
Sage sparrow					○				●	○		
Ferruginous hawk		○		○				○	●	○	○	○
Western sage grouse		○	●	○						○		
Black tern			●			○						
Bald eagle	○								●	○	○	
Loggerhead shrike	○	○		○	○			○	●	○	○	
Long-billed curlew							●		●			
Sage thrasher		○	●	○	○			○				
American white pelican	○						●			○		
Western burrowing owl			●		○	○	●	○	●	○	○	○
Forester's tern						○	●					○
Columbian sharp-tailed grouse			●									

represented in the reserve network by acquiring each of the other unprotected (but currently unavailable) sites. Although currently unavailable, acquisition of some of these sites (better sites) might result in the protection of more species than would the available site. Conservation of other sites (worse sites) might result in the protection of fewer species. An available site was only acquired if its marginal benefit was greater than some proportion of the other sites, as determined using the following algorithm:

$$\frac{\text{Number of better sites}}{\text{Number of worse sites}} \leq \frac{\text{threshold}}{(1 - \text{threshold})}$$

where threshold is a value between 0 and 1. Thus, with a threshold of 0.5, a site would be acquired if it added at least as many unprotected species to the reserve network as half the other sites would have added. A smaller threshold would result in greater selectivity, and a larger threshold would result in less selectivity.

Irreplaceability

The irreplaceability algorithm (Ferrier *et al.* 2000) prioritises sites based on the proportion of biodiversity within the planning region that would be lost if the site were lost. To estimate irreplaceability, we calculated all possible sets of sites that could conserve each species at least once, and scored each of the sites based on the number of solution sets in which it occurred. We defined this score as the sites' irreplaceability as in Ferrier *et al.* (2000). Using the irreplaceability algorithm, a currently available site was added to the reserve network if it had a higher irreplaceability score than some threshold proportion of the other sites, using the same decision algorithm as above.

Comparing solutions

The value of the final reserve network is a function of the amount of biodiversity conserved by the end of the implementation horizon and of the cost of achieving that level of protection. We ascribed a value to the final reserve network at the end of each simulation, that reflected this trade-off, according to the formula:

$$\text{Value} = \text{number of species conserved} - \text{site cost} \\ * \text{number of sites in reserve network}$$

In this way, if site costs are very low, a simple strategy is to acquire all sites that become available. As site costs increase, then the net benefits of choosing sites that provide protection for only a few species decrease.

Realistically sized dynamic problem

Although the simple example above is illustrative, it is trivially small. Unfortunately, dynamic optimisation methods

such as SDP are computationally intensive. Even in the simple example above, with twelve sites, where each site can be in only one of three potential states, the number of possible system states is 3^{12} . This number of states rises geometrically with the number of sites, and becomes computationally impossible above about 20 sites.

Real world conservation planning must consider hundreds of species or other biodiversity types, and thousands of candidate sites for inclusion in the reserve network. Thus, for realistically sized conservation problems, we were unable to compare the outcomes of alternative decision strategies with the dynamically optimal, SDP-based solution. Instead, we evaluated the relative performance of decision strategies based on the effectiveness (amount of biodiversity represented in the reserve network) and efficiency (number and cost of sites in the reserve network) of the final reserve networks at the end of the 10-year implementation horizon. As with the simple example, we compared the performance of commonly used reserve selection decision rules based on irreplaceability (Ferrier *et al.* 2000), richness, and a near optimal reserve network (minimum set) (Pressey *et al.* 1996). For large data sets, to identify the minimum set solution, we selected an initial set of sites using the PA2 algorithm of Pressey *et al.* (1996), which is known to provide a good approximation to an optimal solution. We used this solution as the initial parent in a genetic algorithm that performed 100 rounds of selection, mutation (replacing, adding and removing sites) and crossing over (exchanging sets of sites between different daughter sets). We then selected the best solution from the genetic algorithm as our minimum set.

For large problems, it is computationally infeasible to exactly calculate irreplaceability. The best estimation approach would be to randomly sample the set of potential reserve networks that could meet the specified conservation goal and, for each site, divide the number of solutions for which the site was essential by the total number of potential solutions. This approach was also computationally infeasible, because it proved difficult to find a large number of randomly selected solutions that were substantially different from one another. Instead, we estimated irreplaceability by selecting random sets of sites that partially met the conservation objective, and removing all sites that were redundant with other sites. We then recorded the effectiveness score for that set of sites. For each site, we summed the effectiveness score (see below) for all random sets in which it was included, and divided this sum by the number of times the site was selected (including instances in which the site was eliminated because it was redundant). We refer to this average score as the site's irreplaceability. Thus, sites included in many high value reserve networks have a high irreplaceability, and sites that are frequently eliminated from solutions because of redundancy will have low irreplaceability scores.

We also considered a fourth decision rule, opportunism. The opportunistic strategy involved acquiring sites in the order they became available, as long as they contained some biodiversity value.

To consider a comprehensive range of biodiversity distributions, representative of different geographic regions, we constructed simulated data sets representing a range of distributions of both rare and common species and different proportions of species rich and species poor sites (Meir & Andelman, in review). The simulated data sets are comparable in size to those used by The Nature Conservancy and other conservation organizations for real world ecoregional conservation planning. In our simulations of complex conservation problems, several sites become available for acquisition each year (probability = 0.01 or 0.10 per site per year). We simulated loss of biodiversity (degradation) as loss of populations of species from individual sites. We varied the rate at which populations were lost from 0.001 to 0.10 per population per year, within the range of habitat conversion and population extinction rates reported globally for several biomes (Balmford *et al.* 2002). We assumed that once a site was part of a protected area network there was no further loss of biodiversity. Although this assumption is almost certainly unrealistic, it underlies most reserve network design methods, and often is implicit rather than explicit. The annual budget was sufficient to add 1, 3, or 10 new sites to the reserve network per year. If fewer sites were acquired than the budget permitted, funds were carried over for use in the next year. The entire simulation process for the realistically sized problem is summarized in Table 2.

Comparing reserve networks

For the realistically sized problems, we calculated the value of the each final reserve network as described above. We

Table 2 Steps in simulation of realistically sized conservation problems

1. Generate biodiversity distribution
2. Set conservation objectives
3. Set annual budget
4. At each time step, some proportion of sites become available
5. Prioritize sites for conservation using different rules
6. If using heuristic rule, set selectively threshold
7. Purchase sites above threshold to incorporate in reserve network, until money runs out
8. If there are insufficient sites above threshold, save money for next time step
9. Some proportion of populations is lost according to the degradation rate
10. Repeat from step 5, for remaining sites
11. Iterate for 120 monthly time steps (10 years total)

also calculated an effectiveness score which measured the number of species conserved within the final reserve network relative to the specified conservation goal:

$$\text{Effectiveness} = \sum_{\text{Species}} \frac{\text{Min}(\text{NumOccurrencesCaptured}_{\text{spec}}, \text{OccGoal})}{\text{Min}(\text{NumOccurrencesExisting}_{\text{spec}}, \text{OccGoal})}$$

where NumOccurrencesCaptured is the number of sites at which each species was conserved within the reserve network, NumOccurrencesExisting is the total number of sites at which that species occurred, and OccGoal was set to 3.

All computer code to generate biodiversity distributions, to implement the basic model, and for reserve sitting algorithms was written in C or Java and is available from <http://www.simbioticssoftware.com>.

RESULTS

Simple dynamic problem

For the simple problem with 12 sites and 13 species, compared with the optimal SDP solution, conserving sites based on either irreplaceability or richness decision rules did reasonably well under both high and low site costs, and across a range of degradation rates, never falling below 80% of the dynamically optimal SDP score (Fig. 1). Irreplaceability was relatively insensitive to degradation rate, while

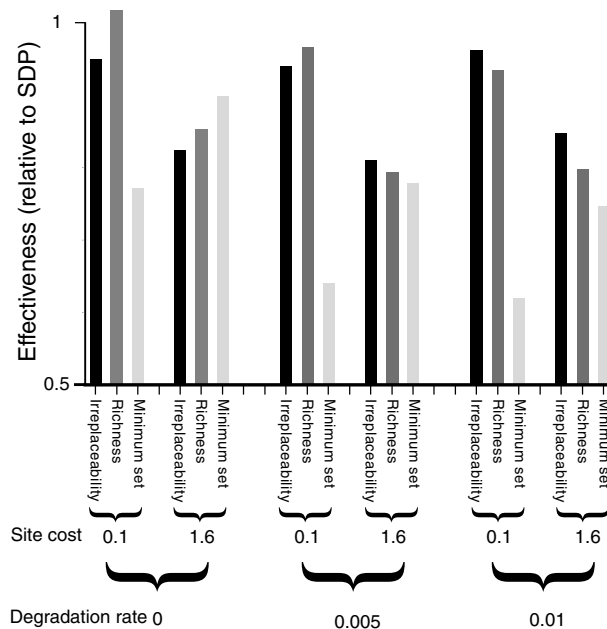


Figure 1 The effectiveness of three different heuristic decision rules compared with the dynamically optimal SDP-based rule applied to the data in Table 1. We ran 100 simulations, each lasting 10 years, for each combination of site degradation and cost.

Figure 2 Comparison of four different decision rules applied to realistically large simulated biodiversity data sets comprising 1000 sites, 100 species and 500 populations of species. The data sets span five different structures, representing different proportions of rare and common species, and different proportions of species rich and species poor sites (Supplementary information, Table 1; also Possingham *et al.* 1999).

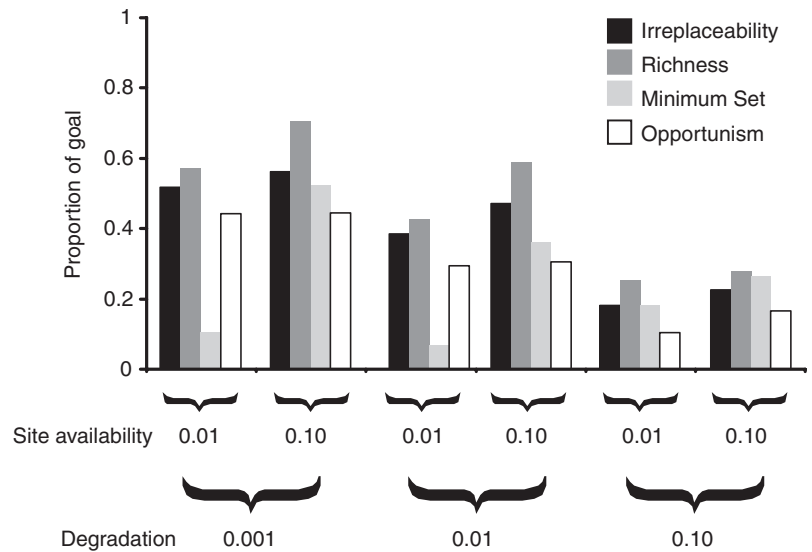
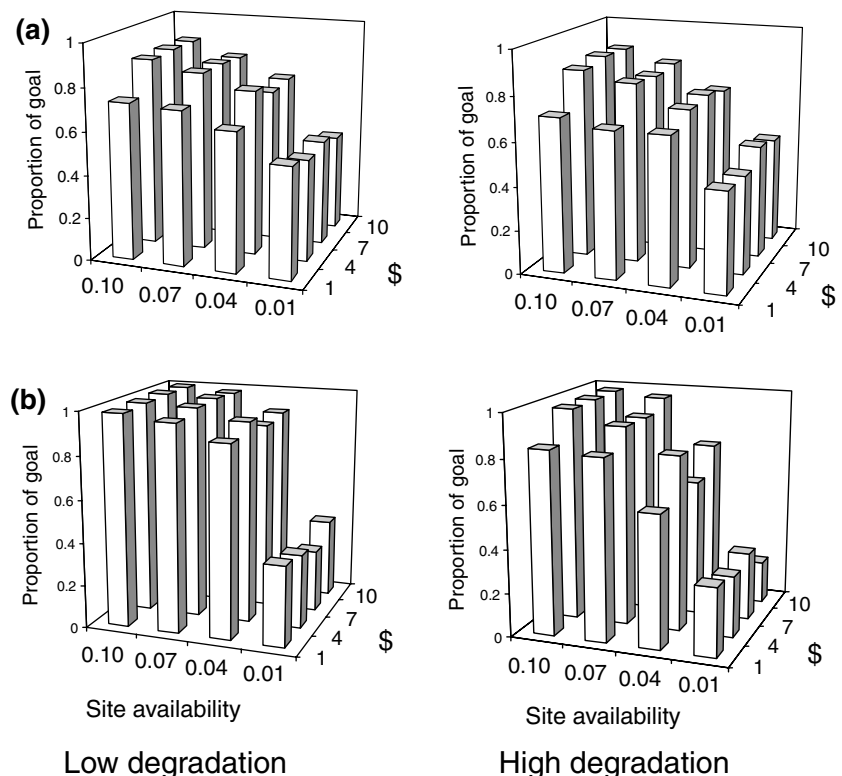


Figure 3 Site availability vs. purchasing power, based on application of the irreplaceability decision rule applied to two simulated data sets, across two levels of degradation rates. Low degradation = probability of 0.001 per year of population loss. High degradation = probability of 0.01 per year of population loss. (a) Results for a simulated data set modelled after a real biodiversity database for the Columbia Plateau region of the US. The real database is described in Davis *et al.* 1999. (b) Results for a simulated data set modelled after a real biodiversity database for Paraguay. The real database is described in Andelman & Willig 2002. At combinations of high degradation rates and low site availability, performance of the decision rule declines considerably for the Paraguay-like example, in which a larger proportion of the species have very local distributions.



richness performed best at lower degradation rates. The performance of both strategies diminished as site cost increased. Ironically, creating a plan for a comprehensive reserve network (minimum set), which was the best approach to the static conservation problem, did the worst in all but one case, particularly when site cost was low (Fig. 1).

Realistically sized dynamic problem

Although the simple example provides important insights, it is trivially small. For realistically sized dynamic problems, the effectiveness of the irreplaceability and richness decision rules varied with the structure of the data (i.e. with the proportion of rare and common species), and

with site availability and degradation rates (Fig. 2). In almost all cases, both of these rules performed better than did the strategy of only acquiring sites within the minimum set or comprehensive reserve network design. As expected, irreplaceability and richness also were more effective than was being opportunistic. Only when site availability and budget were both very high did the comprehensive reserve network design strategy do best. This makes intuitive sense. If it is possible to conserve exactly the sites you want, a conservation blueprint makes sense, but if it is difficult to predict when and where conservation investments will be possible, then the blueprint constrains options.

Potential advantages of paying a premium to increase site availability

Site availability is not necessarily beyond the control of the buyer. An unavailable site may become available at a higher price. This raises the question of when and to what extent one should pay a premium to increase the likelihood that an important site for biodiversity will become available. Given limited resources, is it better to wait for sites to be put up for sale at fair market price, or to pay prices above market value and increase the likelihood a property owner will sell?

To address this question, we ran simulations with four levels of site availability, from 0.01 to 0.1. For each availability level, we implemented budgets with sufficient funds to buy one, four, seven, or 10 sites per year. The low availability, high purchasing power case (i.e. 0.01 availability and seven or 10 sites per year) and the high availability, low purchasing power case (0.10 availability and one or four sites per year) correspond to the trade-off between waiting for sites to become available or paying a premium to increase site availability. We constructed data sets with two distributions of populations across species and sites; one was modelled after species distributions in the Columbia Plateau (Davis *et al.* 1999); the other mimicked species distributions in Paraguay (Andelman & Willig 2002). In both cases the final protected area networks were most effective at conserving biodiversity when both site availability and purchasing power were high (Fig. 3, 0.10 availability and 7–10 sites per year). However, when faced with the trade-off between purchasing power and site availability, it was better to have high-site availability at the expense of lower purchasing power (Fig. 3). Although this example is simplistic in that all sites have the same cost, it implies there may be potential benefits to paying a premium to increase site availability.

DISCUSSION

It is estimated that creating a global, ecologically representative reserve network will require investments of \$3–11

billion per year over the next 30 years (James *et al.* 2001; Pimm *et al.* 2001). NGOs and agencies responsible for biodiversity conservation face a common dilemma: deciding when, where and how to invest their limited funds to maximize conservation benefits. Historically, the question of investing now or in the future has been answered haphazardly, but recently, many organizations have initiated planning processes to identify comprehensive or near optimal networks of reserves in the context of explicit biodiversity conservation objectives. Producing such comprehensive plans involves synthesising existing data and generating large-scale maps of sets of sites that would make ideal reserve networks (e.g. Groves 2003). This process takes time, costs several hundred thousand dollars per region (Malakoff 2002), and requires a variety of subtle analyses.

We have shown that comprehensive conservation plans may be worthwhile when the resulting reserve network can be fully implemented immediately after it is designed (e.g. when the lands or waters involved are entirely in government ownership). However, such comprehensive planning may not be necessary, and may even be counter-productive, when implementation is carried out over years. Our results suggest that relatively simple rules for deciding which areas to protect outperform both *ad hoc* investment strategies and comprehensive conservation plans (Figs 1 and 2). This is especially true when degradation rates and uncertainty are high (Fig. 3). Although the performance of optimal sets and comprehensive conservation plans will undoubtedly improve if the plans are iteratively updated, we found that, given the rates of habitat loss and site availability reported here, comprehensive plans would need to be updated annually in order to perform as well as simple heuristics (Meir *et al.*, unpublished). Since information contained within conservation databases is updated relatively slowly, and considerable work is entailed in developing comprehensive conservation plans, updating these plans annually seems unrealistic. Thus, conservation resources might be better invested in determining the biodiversity value and relative importance of particular sites, rather than in developing comprehensive designs for large-scale networks of sites. Our results also suggest that conservation decisions might be improved through the addition of information that could be used to reduce uncertainty in the site selection process, e.g. comprehensive knowledge of land ownership and land value (e.g. Ando *et al.* 1998), projections of future land conversion patterns (e.g. Theobald & Hobbs 1998; Pontius *et al.* 2001; Waddell *et al.* 2002; Li *et al.* 2003), and projections of future bioclimatic conditions (e.g. Midgley *et al.* 2002, 2003; Pyke 2004).

We have focused on one key assumption underlying current conservation planning methods: that once identified, entire reserve networks can be implemented instantaneously. We explored several dimensions of this assumption,

including budget constraints, uncertainty about when and where opportunities for conservation investment may arise, and the process of degradation or loss of biodiversity over time in sites that remain unprotected. There are other important assumptions underlying systematic conservation planning approaches that we have not yet considered: (1) within protected areas biodiversity will persist, and outside them it will perish; (2) we understand what conditions are needed for biodiversity persistence; (3) environmental conditions are invariant over time; (4) all sites have equivalent costs and (5) cost and economic conditions are invariant over time. These assumptions also are likely to have important implications. For example, assuming that biodiversity is only secure when it exists within reserves means that conservation strategies ignore the contributions to conservation of 88.5% of land (i.e. the proportion of land outside reserves). Yet, land outside reserves often contains important habitat and provides essential ecosystem services. Even after development, some types of biodiversity and some ecosystem services might coexist with human uses (e.g. Franklin 1993; Miller 1996, Daily *et al.* 2001, Rosenzweig 2003). Moreover, biodiversity will not necessarily persist within reserves (e.g. Newmark 1987; Caro 2001; Liu *et al.* 2001; Parks *et al.* 2002). Finally, assumptions about costs also have important implications. For example, explicit consideration of heterogeneity in land costs often leads to distinctly different conservation priorities than when spatial patterns of land cost are ignored (Ando *et al.* 1998; Polasky *et al.* 2001) and the performance of simple decision rules for prioritising conservation investments diminishes when the degree of threat of habitat loss is not explicitly considered, and when the time horizon for implementation and the number of sites increase (Costello & Polasky 2004). The framework we present provides the beginnings of a theory of reserve network design and conservation investments for an uncertain and dynamic world. Our results do not diminish the need for accurate information on the distribution of biodiversity and on the processes that threaten it. Instead, they indicate that creating comprehensive conservation blueprints is not always best. Our results also provide the beginnings of a framework for estimating the marginal benefits of paying a premium to increase the likelihood of protecting important sites for biodiversity. Overall, this is good news for conservationists who face constant pressures to respond to opportunities and to make quick (and wise) decisions about where, when and how to conserve biodiversity with limited budgets.

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REFERENCES

- Airame, S., Dugan, J.E., Lafferty, K., Leslie, H., McArdle, D. & Warner, R. (2003). Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecol. Appl.*, 13, S170–S184.
- Andelman, S. J. & Willig, M. R. (2002). Alternative configurations of conservation reserves for Paraguayan bats: considerations of spatial scale. *Cons. Biol.*, 16, 1352–1363.
- Andelman, S.J. & Willig, M.R. (2003). Present patterns and future prospects for biodiversity in the Western Hemisphere. *Ecol. Lett.*, 6, 818–824.
- Andelman, S. J., Ball, I., Davis, F. & Stoms, D. (1999). *Sites v. 1.0: An Analytical Toolbox for Designing Ecoregional Conservation Portfolios*. The Nature Conservancy, Arlington, VA.
- Ando, A., Camm, J., Polasky, S. & Solow, A. (1998). Species distributions, land values and efficient conservation. *Science*, 279, 2126–2128.
- Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E. *et al.* (2002). Economic reasons for conserving wild nature. *Science*, 297, 950–953.
- Bellman, R. (1957). *Dynamic Programming*. Princeton University Press, Princeton, NJ.
- Caro, T.M. (2001). Species richness and abundance of small mammals inside and outside an African national park. *Biol. Cons.*, 98, 251–257.
- Costello, C. & Polasky, S. (2004). Dynamic reserve site selection. *Res. Energy Econ.*, 26, 157–174.
- Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. 2003. A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biol. Cons.*, 112, 191–216.
- Daily, G.C., Ehrlich, P.R. & Sanchez-Azofeifa, G.A. (2001). Countryside biogeography: use of human-dominated habitats by the avi fauna of southern Costa Rica. *Ecol. Applic.*, 11, 1–13.
- Davis, F.W., Stoms, D.M. & Andelman, S.J. (1999). Systematic reserve selection in the USA: an example from the Columbia Plateau ecoregion. *Parks*, 9, 31–41.
- Ferrier, S., Pressey, R.L. & Barrett, T.W. (2000). A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning and a research agenda for further refinement. *Biol. Cons.*, 93, 303–325.
- Franklin, J. (1993). Preserving biodiversity: species, ecosystems, or landscapes?. *Ecol. Appl.*, 3, 202–205.
- Groves, C. (2003). *Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity*. Island Press, Washington, DC.
- James, A., Gaston, K. & Balmford, A. (2001). Can we afford to conserve biodiversity? *BioScience*, 51, 43–52.
- Li, L., Sato, Y. & Zhu, H.H. (2003). Simulating spatial urban expansion based on a physical process. *Landscape Urban Plan.*, 64, 67–76.

- Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J. & Zhang, H. (2001). Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science*, 292, 98–101.
- Malakoff, D. (2002). Picturing the perfect preserve. *Science*, 296, 245–246.
- Mangel, M. & Clark, C. (1988). *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, New Jersey.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., & Powrie, L.W. (2002). Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecol. Biogeog.*, 11, 445–451.
- Midgley, G.F., Hannah, L., Millar, D., Thuiller, W., & Booth, A. (2003). Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol. Conserv.*, 112, 87–93.
- Miller, K.R. (1996). Conserving biodiversity in managed landscapes. In: *Biodiversity in Managed Landscapes: Theory and Practice* (eds Szaro, R.C. & Johnston, D.W.). Oxford University Press, Oxford, UK, pp. 425–441.
- Newmark, W.D. (1987). Mammalian extinctions in western North American parks: a landbridge perspective. *Nature*, 325, 430–432.
- Noss, R., Carroll, C., Vance-Borland, K. & Wuerther, G. (2002). A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Cons. Biol.*, 16, 895–908.
- Parks, S.A. & Harcourt, A.H. (2002). Reserve size, local human density, and mammalian extinctions in U.S. protected areas. *Cons. Biol.*, 16, 800–808.
- Pimm, S.L., Ayres, M., Balmford, A., Branch, G., Brandon, K., Brooks, T. *et al.* (2001). Can we defy nature's end? *Science*, 293, 2207–2208.
- Polasky, S., Camm, J.D. & Garber-Yonts, B. (2001). Selecting biological reserves cost effectively: an application to terrestrial vertebrate conservation in Oregon. *Land Econ.*, 77, 76–78.
- Pontius, R.G., Cornell, J.D. & Hall, C.A.S. (2001). Modeling the spatial pattern of land-use change with GEOMOD2: application and validation for Costa Rica. *Agric. Ecosys. & Environ.*, 85, 191–203.
- Possingham, H.P., Day, J., Goldfinch, M. & Salzborn, F. (1993). The mathematics of designing a network of protected areas for conservation. In: *The Proceedings of the 12th Australian Operations Research Conference. Decision Sciences, Tools for Today* (eds Sutton, D., Cousins, E. & Pearce, C.). ASOR, Adelaide, pp. 536–545.
- Possingham, H.P., Ball, I. & Andelman, S.J. (1999). Mathematical methods for identifying representative reserve networks. In: *Quantitative Methods for Conservation Biology* (eds Ferson, S. & Burgman, M.). Springer, New York, pp. 291–306.
- Pressey, R.L., Possingham, H.P. & Margules, C.R. (1996). Optimality in reserve selection algorithms: When does it matter and how much? *Biol. Cons.*, 76, 259–267.
- Pyke, C.R. (2004). Habitat loss confounds climate change impacts. *Frontiers in Ecol. Environ.*, 4, 178–182.
- Rodrigues, A.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C. *et al.* (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 640–643.
- Rosenzweig, M.L. (2003). *Win-Win Ecology: How the Earth's Species Can Survive in the Midst of Human Enterprise*. Oxford University Press, Oxford, UK.
- Theobald, D.M. & Hobbs, N.T. (1998). Forecasting rural land-use change: a comparison of regression- and spatial transition-based models. *Geographical Environ. Modelling*, 2, 65–82.
- Waddell, P., Outwater, M., Bhat, C. & Blain, L. (2002). Design of an integrated land use and activity-based travel model system for the Puget Sound Region. *Travel Demand and Land Use 2002. Transport. Res. Record*, 1805, 105–118.
- WDPA (2003). *World Database on Protected Areas (IUCN-WDPA & UNEP-WCMC)*. WDPA, Washington, DC.

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