

# Logic for Designing Nature Reserves for Multiple Species

Michael A. McCarthy,<sup>1,\*</sup> Colin J. Thompson,<sup>2</sup> and Nicholas S. G. Williams<sup>1,†</sup>

1. Australian Research Centre for Urban Ecology, Royal Botanic Gardens Melbourne and School of Botany, University of Melbourne, Parkville, Victoria 3010, Australia;

2. Department of Mathematics and Statistics, University of Melbourne, Parkville, Victoria 3010, Australia

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**ABSTRACT:** We examine the logic of designing nature reserves to understand better how to integrate the concepts of representativeness and persistence. Simple models of viability are used to evaluate how the expected number of species in the reserve system changes with variation in the risk of extinction among species, their rate of occurrence, and the distribution of species. The optimal size of individual reserves increased with the mean and variance of the probability of extinction among species and with the rate at which the risk of extinction declines with the cost of each reserve. In contrast, the rate of occurrence of species within reserves and their rate of accumulation with increasing reserve area had a relatively minor influence on the optimal size of reserves. Patterns of endemism were most important for the location of reserves. Including differences among species in the analysis reduced the optimal number of individual reserves (and increased the size of each) when operating under a fixed budget compared with reserve designs based on single species. A case study in the city of Melbourne, Australia, demonstrates the conservation value of small (~1 ha) grassland reserves and the underrepresentation of Melbourne's volcanic plains in the region's conservation network.

**Keywords:** conservation planning, extinction risk, fragmentation, metapopulation, single large or several small (SLOSS), urban ecology.

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Conservation reserves are one of the main tools for protecting the world's biodiversity (Margules and Pressey 2000). In the past, conservation reserves have often been confined to parcels of land that are not wanted for other

purposes (Pressey et al. 1993). While some of these areas may be spectacular and are iconic symbols of conservation, they do not necessarily contain representative samples of the world's biodiversity. More recently, there have been attempts to design new reserves that are more representative of the biodiversity that we wish to conserve (Pressey et al. 1993; Possingham et al. 2000). However, disagreement remains about how best to select areas for reservation.

One approach is based on the concept of complementarity, in which areas are selected such that the species they contain are complementary samples of the range of biodiversity found in a wider area (Vane-Wright et al. 1991). In this case, areas with species that are rarely found elsewhere are more likely to be included in the reserve system. However, this is not always the case, depending on how the complement of species can be most efficiently reserved. Methods based on complementarity require information about the distribution of the species that we wish to conserve. For the vast majority of species and geographic regions, reliable information on distribution is not available. Only a small fraction of the world's species are thought to be known to science (Hammond 1992), and accurate information on distribution is available for only some of these (Burgman and Lindenmayer 1998).

In response to this lack of information, simpler schemes have been developed for determining the location of reserves and planning for biodiversity conservation in general. These are often based on selection of surrogate species. For example, the focal species approach (Lambeck 1997) involves developing conservation plans that are designed to protect the species that are most adversely affected by the threatening processes that are being managed. In the case of reserve design, the size of reserves might be based on those species that have the largest area requirements. Other approaches to selecting surrogates might focus on those species that have the narrowest distributions (endemics), particularly important ecological roles (key-stone species), or have low rates of occurrences ("rare" species). These choices seem to make sense when evaluated subjectively, but the logic of their choice has not been evaluated formally. Further, an empirical study by Andelman and Fagan (2000) indicated that reserve designs

\* E-mail: mamcca@unimelb.edu.au.

† E-mail: nsw@unimelb.edu.au.

based on a range of different surrogate schemes were largely inefficient. A formal logical evaluation of the choices would help to determine the most important variables.

The range of methods for determining how to design conservation reserves (and conduct conservation planning in general) is based largely on empirical studies and opinion. With the exception of reserve design based on the concept of representativeness in the presence of complete information (Possingham et al. 2000), none of these methods have been developed with a formal mathematical basis using principles of decision theory. In many cases, the link between the objective (e.g., to minimize the number of species going extinct) and the actions (e.g., reserve this parcel of land) is not explicit. Therefore, many of the arguments about how best to design nature reserves are based on opinion in the presence of incomplete information. Importantly, one region might be regarded as better than another (e.g., it might have more endemic species), but it is not clear how much conservation effort should be expended on the former compared to the latter. A theoretical analysis of the problem based on principles of decision theory can help to resolve these arguments by indicating the important variables to be considered and providing a logical framework for analysis.

Almost all methods for determining the configuration of nature reserves ignore the long-term persistence of the species in those reserves (Pressey et al. 1993; Possingham et al. 2000). The exceptions tend to focus on one or a few species (Quinn and Hasting 1987; McCarthy and Lindenmayer 1999; Etienne and Heesterbeek 2000; Ovaskainen 2002; McCarthy et al. 2005), which may not be useful in reality because reserves are only rarely established for individual species. Numerical methods are being developed that aim to integrate representativeness and persistence of multiple species (Margules et al. 1994; Williams and Araújo 2000; Cabeza and Moilanen 2001). These studies emphasize that conservation reserves cannot guarantee persistence. A reasonable aim of conservation in such circumstances may be to minimize the number of species becoming extinct or perhaps to minimize the loss of phylogenetic diversity (Vane-Wright et al. 1991) with the resources that are available. However, the complexity of these numerical methods can make it difficult to uncover the important variables of the reserve design problem; that is, it can be difficult to analyze the underlying logic of the problem.

In this article, we examine the logic of nature reserves that are designed to minimize the expected number of species going extinct. Our aim is to increase understanding of how to integrate the concepts of representativeness and persistence. We evaluate how the optimal size of reserves changes with variation in the risk of extinction among

species, their rate of occurrence, and distribution of species. This helps to indicate how surrogate species might be selected to best conserve biodiversity. For example, should reserve designs be based on the species with the most restricted distributions, those that are most threatened, or those that occur least frequently? We also evaluate how the geographic distribution of species influences the optimal location of reserves. We intentionally use simple models so we can explore the underlying logic of the reserve design problem. These models allow us to evaluate the variables that are most important in simple reserve design problems. Variables that are important in simple cases are likely to remain important in more complicated scenarios.

### Optimal Reserve Systems within a Region

In this section, we model population viability to explore the issue of reserve design for multiple species within a single region. A region is defined as an area that does not have strong gradients in the occurrence of species; that is, the species have a relatively uniform distribution. Variation in the distribution of species is considered in the next section. The models are based on a single-species model analyzed by McCarthy et al. (2005). In this model, the mean time to local extinction of each reserve is a power function of its size, there is no dispersal between reserves, and extinction events are uncorrelated. The single-species model of persistence is modified to account for the fact that not all species will be initially present in all of the local reserves and that the probability of a species being present will increase with the size of each reserve, depending on a species-area relationship.

#### *Initial Model*

The analyses in this article are based on an economic perspective (Pressey et al. 1993; Possingham et al. 2000; Groeneveld 2005) in which there is a certain budget available for establishing reserves ( $B$ ). The aim is to determine the optimal number of individual reserves ( $n$ ) such that the protection of species within the reserve system is maximized. Initially, we develop a model in which we assume that all species have the same risk of extinction and that all species have the same frequency of occurrence in reserves. These assumptions are then relaxed in subsequent models.

The model is based on a single-species version developed by McCarthy et al. (2005). It is assumed that the mean time to extinction ( $M$ ) of each species within an individual reserve scales as a power function of habitat area ( $M = aA^b$ ; Lande 1993; Cook and Hanski 1995), where  $a$  and  $b$  are constants and  $A$  is the area of a single

reserve. Thus, the probability of persisting for  $T$  years within an area of size  $A$  is approximately equal to  $\exp(-T/aA^b)$ . Given that it is optimal to have all reserves the same size (McCarthy et al. 2005), the probability of persistence of species within each reserve when the system is divided into  $n$  equally sized reserves can be determined. If it is assumed that there is a specified budget  $B$  that is available for establishing reserves and that the cost of a single reserve ( $c$ ) is a power function of its area ( $A$ ) such that  $c = lA^k$ , then we are operating under the constraint that  $B = nc$ . Given this, the probability of persistence of each individual reserve is given by  $p^{n^{b/k}}$ , where  $p$  is the probability of persistence if the entire budget ( $B$ ) were spent on establishing a single reserve ( $p = \exp[-T/a(B/l)^{b/k}]$ ). The ratio of the two scaling exponents ( $b/k$ ) describes the rate at which the mean time to extinction of a reserve increases with the amount of money spent on increasing its size.

The cost of reserves might be simply proportional to their area, in which case  $k = 1$ . However, if costs are mainly driven by management and maintenance of the edge of the reserve (e.g., fencing costs, managing movement of introduced species from adjacent areas, perimeter fire control) and reserve shape is roughly the same regardless of reserve size, then the costs would be proportional to the perimeter of the reserve. In this case, the scaling parameter for costs ( $k$ ) would equal 0.5.

Changing the size of each reserve will affect not only the probability of persistence of species within it but also the number of species that it originally contained. We define  $s$  as the proportion of species in a region that would be contained within the reserve if the entire budget ( $B$ ) was spent on establishing a single reserve ( $n = 1$ ). Using a standard species-area relationship with  $z$  as the power constant, the proportion of species contained within each reserve will equal  $s/n^{z/k}$  if the available budget is used to establish  $n$  equally sized reserves. The value of  $z$  is commonly close to 0.25. Thus, the probability of a randomly chosen species being present within each reserve at the end of  $T$  years is equal to the probability that it is present initially ( $s/n^{z/k}$ ) multiplied by the probability that it persists ( $p^{n^{b/k}}$ ). Finally, the probability that it is absent from all  $n$  reserves is equal to the probability that it is absent from one reserve raised to the power of  $n$ , assuming each individual reserve is independent of the others. Thus, the expected proportion of species in a region not present in the reserve system after  $T$  years ( $L$ ) is given by

$$L = \left(1 - \frac{p^{n^{b/k}} s}{n^{z/k}}\right)^n \quad (1)$$

The assumption of independence requires that there is no dispersal or correlation in extinction events among

reserves and that reserves are distributed independently of any gradient in the occurrence of species within the region. The multiregion model (next section) is appropriate when there are strong gradients in the occurrence of species.

The aim is to find the value of  $n$  that minimizes the loss of species  $L$ . It is relatively easy to find this value of  $n$  numerically. However, a useful analytical solution can be obtained by approximating equation (1) by  $L \approx 1 - np^{n^{b/k}} s/n^{z/k}$ , which is the limit as  $p^{n^{b/k}} s/n^{z/k}$  approaches 0. Taking the derivative of this expression with respect to  $n$ , setting this equal to 0, and solving for  $n$  provides an approximation for the optimal number of reserves ( $n^*$ ), which is given by

$$n^* \approx \left[ \frac{-(1 - z/k)k}{b \ln p} \right]^{k/b} \quad (2)$$

This optimal number of reserves is very similar to the number that maximizes the persistence of single species ( $n^* \approx [-k/b \ln p]^{k/b}$ , see also McCarthy et al. 2005). The difference is that the inclusion of the concept of species accumulation (represented by the variable  $z$ ) reduces the optimal number of reserves slightly. Note that  $s$ , which measures the rate of occurrence of species in individual reserves, has no influence on this approximation. In fact, equation (2) is the limiting solution when  $s$  approaches 0, so the equation is most accurate when only a small proportion of the species in a region occur within individual reserves.

#### Variation in the Occurrence of Species and Their Risk

In the above analysis, it was assumed that all the species had the same rate of occurrence and all faced the same risk of extinction. Of course, species differ in both of these aspects. One issue of interest is how variation in these factors would influence the optimal reserve design. For example, should reserve systems be designed for the rarest or most threatened species, or should they be based on the average species in a region?

These two questions can be addressed by treating the rate of occurrence ( $s$ ) and the probability of persistence ( $p$ ) in equation (1) as random variables that differ between species. Then, the expected loss of species ( $L$ ) can be obtained by integrating over the variation in these parameters. Therefore, the expected loss of species when the probability of persistence of species has a probability density function  $f(p)$  is given by

$$L_p = \int_0^1 \left(1 - p^{n^{b/k} \frac{s}{n^{z/k}}}\right)^n f(p) dp. \tag{3}$$

Similarly, if the occurrence of species has a probability density function  $g(s)$ , the expected loss of species is given by

$$L_s = \int_0^1 \left(1 - p^{n^{b/k} \frac{s}{n^{z/k}}}\right)^n g(s) ds. \tag{4}$$

Because both variables ( $p$  and  $s$ ) are constrained to lie between 0 and 1, a natural probability distribution to describe variation in these parameters ( $f(p)$  and  $g(s)$ ) is a beta distribution (Balakrishnan and Nevzorov 2003), which is defined by two parameters  $\alpha$  and  $\beta$ . For example, a beta distribution for  $f(p)$  would have the probability density function

$$f(p) = \frac{p^{\alpha-1}(1-p)^{\beta-1}}{B(\alpha, \beta)},$$

where  $B(\alpha, \beta)$  is a beta function. The mean of  $f(p)$  is equal to  $\bar{p} = \alpha/(\alpha + \beta)$ , and the variance is equal to  $\alpha\beta/(\alpha + \beta)^2(\alpha + \beta + 1)$ . This variance can be expressed as a function of the mean by  $\sigma^2 = \bar{p}(1 - \bar{p})/(\alpha + \beta + 1)$ . Thus, for a given mean ( $\bar{p}$ ), the variance of a beta distribution decreases as the sum of  $\alpha$  and  $\beta$  increases, with the probability distribution approaching a point estimate as  $\alpha + \beta$  approaches infinity. This feature is used to describe the variance of the beta distributions that are used in this article. To describe variation in the rate of occurrence, we assumed a beta probability density function for  $g(s)$  with parameters  $\alpha'$  and  $\beta'$ .

For equation (3), the approximate value of  $n$  that minimizes the expected loss of species can be obtained by solving the following implicit equation for  $n$  (appendix in the online edition of the *American Naturalist*):

$$n^* = \left[ \frac{b/k}{1 - z/k} \ln \left( 1 + \frac{\beta - 1}{\alpha - 1 - sn^{*b/k+1-z/k} e^{-[(1-z/k)/(b/k)]}} \right) \right]^{-k/b}, \tag{5}$$

when  $\beta \neq 1$ . This approximation is valid when  $\alpha/\beta$  and  $n$  are large. When  $\beta = 1$ , there is an explicit equation for the optimal number of reserves (appendix):

$$n^* = \left[ \frac{(\alpha - 1)e^{(1-z/k)/(b/k)}}{s} \right]^{1/[1+(b-z)/k]}. \tag{6}$$

Because the ratios of the scaling exponents (i.e.,  $b/k$  and  $z/k$ ) rather than their individual values control their influence, general results are only presented for the case  $k = 1$ , which means the cost of each reserve is proportional to its area.

When there is little variation in risk among species, a small number of reserves is optimal when the extinction risk is high (fig. 1; see also McCarthy et al. 2005). Increased variation in the risk of extinction among species also tends to decrease the optimal number of reserves (fig. 1). This implies that if the size of reserves is determined by maximizing the persistence of the more endangered species (leading to few large reserves), the expected loss of all species will also tend to be minimized, especially when there is reasonably large variation in risks among species ( $\alpha + \beta$  is small) or the average risk of extinction is high (e.g.,  $\bar{p} < 0.99$ ). Additionally, when there is large variation in the probability of persistence (e.g.,  $\alpha + \beta = 10$ ), the mean probability of persistence has relatively little influence on the optimal number of reserves (fig. 1).

Because the rate of occurrence of species ( $s$ ) has very little influence on the optimal number of reserves (eq. [2]), variation in this parameter also has little influence on the optimal reserve design (appendix). Thus, the approximation provided by equation (2) remains useful when  $s$  varies among species, with it being best when the mean rate of occurrence is small (fig. 2).

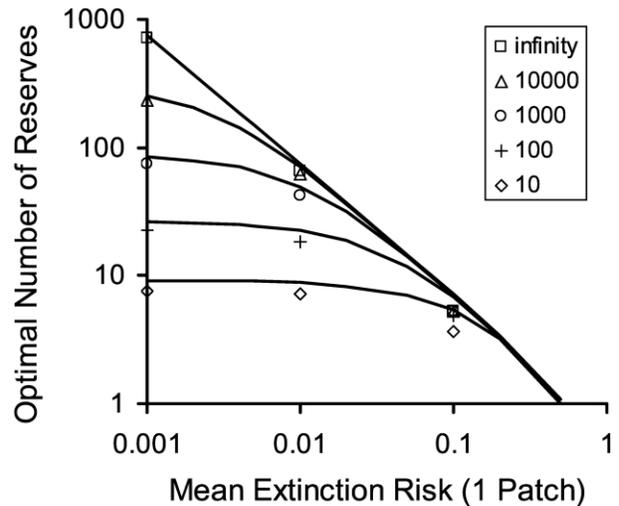


Figure 1: Optimal number of reserves versus the mean extinction risk that would be obtained if all resources were used to establish a single reserve ( $1 - \bar{p}$ ). Results are shown for cases in which the variation in the risk among species is large ( $\alpha + \beta = 10$ ) to insignificant ( $\alpha + \beta = \infty$ ) and for parameter values  $b = 1$ ,  $s = 0.9$ ,  $z = 0.25$ , and  $k = 1$ . The symbols show the exact solutions and the lines show the approximations provided by equations (5) and (6).

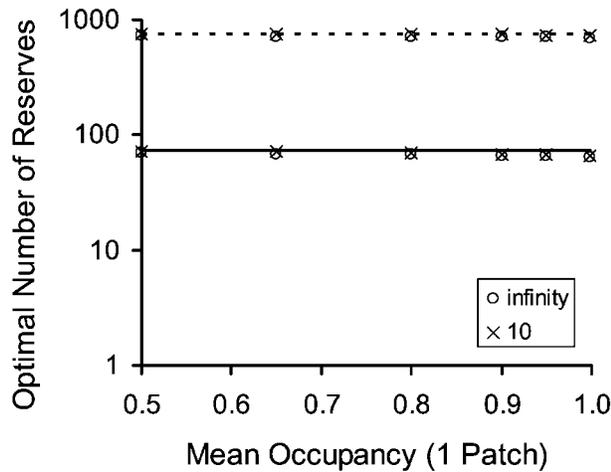


Figure 2: Optimal number of reserves versus the mean occupancy of species within the reserve that would be obtained if all resources were used to establish a single reserve. Results are shown for cases in which variation in occupancy among species is large ( $\alpha + \beta = 10$ ) and when it is insignificant ( $\alpha + \beta = \infty$ ) for two extinction risks ( $p = 0.99$ , solid line; and  $p = 0.999$ , broken line). The symbols show the exact solutions and the lines show the approximations provided by equation (2). The other parameter values were  $b = 1$ ,  $z = 0.25$ , and  $k = 1$ .

The main determinants of the optimal number of reserves are the probability of persistence when all the available habitat is in a single patch (both the mean and variance of  $p$ ) and the scaling exponent for mean time to extinction ( $b/k$ ; fig. 3). The scaling exponent for the species-area relationship ( $z/k$ ) has a relatively minor effect, although interestingly, whether the effect is positive or negative depends on the magnitude of the variance in  $p$  (fig. 4).

#### Interregional Variation in Biodiversity

For the above models, it was assumed that reserves are essentially placed at random within a region without considering possible gradients in the occurrence of species. The assumption of randomness is reasonable if we are concerned about conserving the vast majority of species because the distribution of these is usually unknown. Reserves based on conserving the small proportion of known species are likely to be established somewhat randomly with regard to the location of unknown species. Furthermore, if reserves are distributed along environmental gradients, the power law relationship of the species-area model is still likely to provide a useful approximation of how species accumulate with increasing area, albeit with different parameters. Given the relatively small influence of the parameters of the species-area relationship (figs. 2, 4), locating reserves to optimize species occurrence is pre-

dicted to have a small influence on the optimal size of reserves.

However, it is reasonable to assume that there is spatial variation in the occurrence of species, and such variation is likely to influence the optimal location of reserves. Some areas are known to contain more species than others. In fact, this idea is central to the concept of hotspots, with a relatively small fraction of the world's surface area accounting for a high proportion of terrestrial biodiversity (Pressey et al. 1993; Myers et al. 2000). Spatial variation in the distribution of species can be considered by analyzing how species are distributed across different areas. These areas may be different vegetation types, bioregions, or ecosystems, although in the following we will refer to them as regions.

The question in this analysis is, what proportion of the available conservation resources should be allocated to the different regions? We assume that there is a certain number of reserves to set aside ( $N$ ) and that the area of each reserve is such that a fraction of the species of a region is expected to persist within each reserve at the end of the planning time frame. This fraction of species is a combination of the number of species that were initially within each reserve when it was established and their subsequent persistence. We assume that the fraction of species of a region not present in each reserve at the end of the planning time frame is the same for all reserves and is equal to  $E$ .

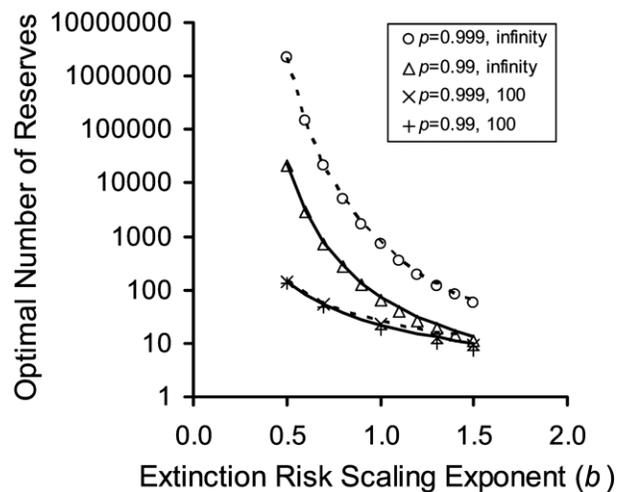


Figure 3: Optimal number of reserves versus the extinction risk scaling exponent ( $b$ ). Results are shown for cases in which variation in the extinction risk among species is large ( $\alpha + \beta = 100$ , crosses) and when it is insignificant ( $\alpha + \beta = \infty$ , open symbols) for two mean extinction risks ( $\bar{p} = 0.99$ , solid line; and  $\bar{p} = 0.999$ , broken line). The symbols show the exact solutions and the lines show the approximations provided by equations (5) and (6). The other parameter values were  $s = 0.9$ ,  $z = 0.25$ , and  $k = 1$ .

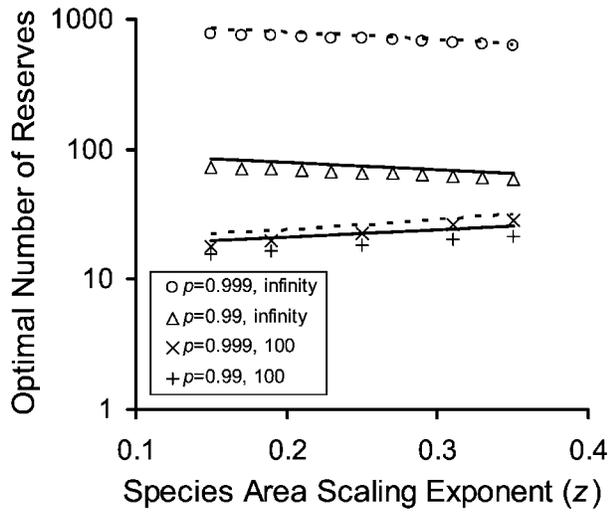


Figure 4: Optimal number of reserves versus the species area scaling exponent ( $z$ ). Results are shown for cases in which variation in the extinction risk among species is large ( $\alpha + \beta = 100$ , crosses) and when it is insignificant ( $\alpha + \beta = \infty$ , open symbols), and for two mean extinction risks ( $\bar{p} = 0.99$ , solid line; and  $\bar{p} = 0.999$ , broken line). The symbols show the exact solutions, and the lines show the approximations provided by equations (5) and (6). The other parameter values were  $s = 0.9$ ,  $b = 1$ , and  $k = 1$ .

We first solve the optimal allocation of reserves for two regions before expanding the solution to three and more regions. We let  $d_A$  be the proportion of species confined to the first region,  $d_B$  the proportion of species confined to the second region, and  $d_{AB}$  the proportion of species found in both. Then, the expected loss of species if  $n_A$  of the  $N$  reserves are allocated to the first region (and  $n_B = [N - n_A]$  to the second region) is given by

$$L_r = d_A E^{n_A} + d_B E^{N-n_A} + d_{AB} E^N. \tag{7}$$

The optimal allocation of reserves to the two regions can be found by determining the value of  $n_A$  ( $n_A^*$ ) that minimizes  $L_r$ . Using a continuous approximation, this can be found by taking the derivative of  $L_r$  with respect to  $n_A$ , setting the resulting expression to 0, and solving for  $n_A$ . This leads to

$$n_B^* - n_A^* = \frac{\ln(d_A/d_B)}{\ln E} \tag{8}$$

after substituting  $n_B^* = N - n_A^*$ . Thus, the difference in the number of reserves to allocate to the two regions ( $n_B^* - n_A^*$ ) depends on their relative endemism ( $d_A/d_B$ ) and the proportion of species within a region that are expected

to be absent from each reserve at the end of the planning time frame ( $E$ ).

There are some important insights from this result. First, the actual proportion of the reserves to allocate to each region depends on the total number of reserves that are to be allocated. When this number is small, most (or even all) of the reserves would be allocated to the region with the most endemic species. As the number of reserves to allocate increases, there will be a more even distribution of reserves among regions. The actual optimal allocation depends on ensuring that the difference in the number of reserves remains constant at the optimal value as more reserves are added.

Another important insight is that if the proportion of species in a region that will be absent from each reserve ( $E$ ) is small, the difference in the optimal number of reserves ( $n_B^* - n_A^*$ ) is small, almost regardless of the level of endemism. Additionally, because the difference in the optimal number of reserves is proportional to the logarithm of the relative endemism, even areas with relatively few endemic species may be important areas for allocating at least some conservation reserves (fig. 5).

The same analysis can be conducted for the situation where there are more than two regions. In this case, it is necessary to describe the distribution of species among regions by counting the proportion of species that are confined to the various possible combinations. For three regions, the expected loss of species is given by

$$L_r = d_A E^{n_A} + d_B E^{n_B} + d_C E^{n_C} + d_{AB} E^{n_A+n_B} + d_{AC} E^{n_A+n_C} + d_{BC} E^{n_B+n_C} + d_{ABC} E^{n_A+n_B+n_C}, \tag{9}$$

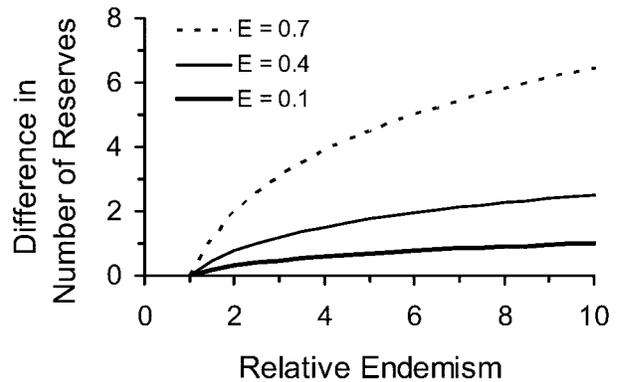


Figure 5: Optimal difference between the number of reserves in two regions ( $n_A^* - n_B^*$ ) depending on the relative endemism of the regions ( $d_A/d_B$ ) and the proportion of species that are expected to be absent from individual reserves over time horizon of management concern ( $E$ ).

subject to the constraint that  $n_A + n_B + n_C = N$ .

We have no closed-form solution for determining the optimal allocation of reserves to three different regions, but it can be obtained numerically (appendix). However, if at least some reserves are allocated to each region, then the terms other than those containing the strict endemics (e.g.,  $d_{AB}E^{n_A+n_B}$  rather than terms such as  $d_A E^{n_A}$ ) will tend to be numerically small. In this case, the function  $L_r$  (eq. [9]) can be approximated by

$$L_r \approx d_A E^{n_A} + d_B E^{n_B} + d_C E^{n_C}, \quad (10)$$

which can be minimized easily (see appendix). As in the two-region case, the difference in the optimal number of reserves between any pair of regions is given by equation (8). This approximation works best when the average number of reserves per region is relatively large and the number of endemic species is not too small.

The above model can be generalized to any number of regions,  $M$  (see appendix). Provided that at least some reserves are allocated to each region, then the terms other than those containing the strict endemics will tend to be numerically small, and

$$L_r \approx \sum_{i=1}^M d_i E^{n_i}, \quad (11)$$

where  $n_i$  is the number of reserves allocated to region  $i$  and  $d_i$  is the proportion of all species that are endemic to region  $i$ . Minimizing this expected loss of species leads to the optimal allocation of reserves among regions such that the difference in the number of reserves among any two regions is again given by equation (8).

### Case Studies: Reservation of Plants in the Melbourne Region

The models will be illustrated with two examples of plant conservation in Melbourne, a city of more than 3.5 million people in southeastern Australia and the capital of the state of Victoria (see appendix for information about the study area).

#### Optimal Reserve Size for Grassland Remnants

Native grasslands in the Melbourne region represent some of the last remaining remnants of a vegetation type that has been almost completely lost from southeastern Australia (Groves 1979; Stuwe 1986; figs. A1–A3 in the online edition of the *American Naturalist*). Much of the area that was formerly covered by grassland has been replaced by exotic pastures or converted to various forms of urban development (Kirkpatrick et al. 1995; Williams et al.

2005a). The remaining grasslands with the highest plant species diversity occur in cemeteries and on road and rail easements, all of which have a history of regular burning but little stock grazing (Stuwe 1986; Kirkpatrick et al. 1995). However, many of these important sites, which often support endangered species, are very small (less than 5 ha) and are subject to weed invasion. Consequently, there is some debate about whether such small patches are worth saving (Department of Natural Resources and Environment 1997). The debate essentially revolves around determining the optimal size of grassland reserves. For example, if we have a certain budget for reserving land and are forced to decide between selecting two reserves or one of the same total size (or more specifically, the same cost), by determining the optimal reserve size, we can determine whether the two small reserves would be better than one larger one.

Data on extinction rates of 130 different native plant species in 17 grassland patches were obtained from Williams et al. (2005b), who resurveyed grassland patches of different size 20 years after initial surveys (Scarlett and Parsons 1981; Scarlett 1985; Stuwe 1986). The parameters ( $b$ ,  $\alpha$ , and  $\beta$ ) of the function  $f(p)$  were estimated using WinBUGS, a program for analyzing Bayesian statistical models (Spiegelhalter et al. 2004). These parameters describe the influence of patch area on extinction rate and the variation in this rate among species, and we used uninformative prior distributions for them to reflect a lack of prior knowledge. We used a species-area curve for grasslands in the Melbourne region in which  $z$  was equal to 0.2 (Chisholm 2004) and for which a 100-ha patch was expected to contain ~52% of the species in the region. We assumed initially that the cost of reserves was proportional to their area ( $k = 1$ ).

The analysis of the plant extinction data suggests that  $p$  is highly variable among species, with  $\alpha \sim 4$  and  $\beta \sim 1$  ( $\bar{p} = 0.8$ ). The scaling exponent for extinction risk is estimated to be small ( $b \sim 0.3$ ). The optimal reserve size when allocating 100 ha to reserves with these parameter values ( $s = 0.52$ ,  $z = 0.2$ ,  $\alpha = 4$ ,  $\beta = 1$ ,  $b = 0.3$ ) is ~1 ha (1.8 ha from the approximation). This implies that the optimal reserve size is small.

Actual costs may scale less than linearly with reserve area. If costs of reserves are proportional to their perimeter ( $k = 0.5$ ), then the relevant scaling parameter for persistence versus cost ( $b/k$ ) is 0.6 and for species area ( $z/k$ ) is 0.4. With  $b/k = 0.6$  and  $z/k = 0.4$ , the optimal number of individual reserves is 14 if there are sufficient resources for acquiring a total of 100 ha of grasslands in a single reserve. This is fewer than in the case  $k = 1$  because of the increased cost of having many small reserves. Nevertheless, the size of each of these reserves remains small

**Table 1:** The number and average size of conservation reserves (national parks and other designated conservation reserves) in the three bioregions of Melbourne

Region	Average (SD) size	
	of reserves	No. reserves
Victorian Volcanic Plain	53 (61) ha	14
South East Coastal Plain	66 (222) ha	39
South Eastern Highlands	40 (186) ha	61

when  $k = 0.5$ , with the optimal size in this case being  $\sim 0.5$  ha.

The assumption of independence of occurrence for the grassland species was assessed by comparing their rate of occurrence in pairs of sites. For example, if  $s_1$  and  $s_2$  are the proportions of species that are present in two different reserves, then  $s_{12}$ , the combined rate of occurrence of species in both reserves, should equal  $1 - (1 - s_1)(1 - s_2)$  if the occurrence of species is independent. For these data,  $s_{12}$  varied between 0.34 and 0.75, and  $s_1$  and  $s_2$  varied between 0.09 and 0.67. There was a strong correlation ( $r = 0.995$ ) between  $s_{12}$  and  $1 - (1 - s_1)(1 - s_2)$ , and the relationship was close to 1 : 1. There was a tendency for  $1 - (1 - s_1)(1 - s_2)$  to be less than  $s_{12}$  (average difference of 0.07), suggesting that the current reserves are not entirely independent of gradients in species occurrence, although the difference between the predicted and actual rates of occurrence was small.

The overall conclusion from this analysis suggests that many small grassland reserves are likely to be efficient for conserving plant species diversity. While managers need to consider other characteristics of sites when selecting reserves, our analysis demonstrates that small grassland remnants should not be excluded from reservation simply because they are small. All else being equal, small reserves actually appear to be optimal when attempting to protect the range of species from extinction, and they can therefore contribute to the long term conservation of grassland species in the Melbourne region.

#### *Optimal Distribution of Reserves among Melbourne's Bioregions*

The greater Melbourne area is located at the junction of three bioregions, which are characterized by their geomorphology and biota: the Victorian Volcanic Plain, the South East Coastal Plain, and the South Eastern Highlands (fig. A4 in the online edition of the *American Naturalist*). The volcanic plains are located on basaltic soils, and the indigenous vegetation is predominantly grassland and grassy woodlands. The indigenous vegetation of the coastal plain is dominated by heathlands and eucalypt woodlands with a heathy understory. The highland region has higher

rainfall and deeper soils and tends to be dominated by open eucalypt forest.

Each of these three bioregions contains a different suite of flora. Some species are found in all three bioregions, while others are found in only one or two. Analysis of the Victorian government's Flora Information System (as at June 2003), a geographically registered, relational database of Victorian plant survey records (<http://www.viridans.com.au/FIS/VICFIS1.HTM>), indicates a relatively uniform distribution of species among the three regions. Of the approximately 1,500 indigenous plant species that have been recorded in the Melbourne region since 1995, 13% have been recorded in only the volcanic plains, another 13% in only the coastal plains, and 17% in the highlands. Only 6% of species have been found in the volcanic and coastal plains (but not the highlands), 15% in the coastal plains and highlands, and 8% in the highlands and volcanic plains. The remaining 28% of species have been recorded in all three regions.

Given these data, the question is how many reserves should be allocated to each of the three regions. In the Melbourne area, the average size of conservation reserves is approximately 50 ha (table 1). Assuming the same species-area relationship as used for grassland plants in the previous section, reserves of 50 ha in area are expected to contain slightly less than half of a region's plant species. Assuming that extinctions from reserves are relatively rare over the time horizon of interest (i.e.,  $E = 0.55$ ), the optimal allocation of reserves among regions requires an approximately equal number of reserves in all three regions. This relatively uniform distribution of reserves among regions is somewhat insensitive to the actual value of  $E$ , with only approximately one extra reserve in the highlands when  $E$  is as large as 0.8 (corresponding to  $\sim 1$ -ha reserves when extinctions are rare) and an even distribution of reserves for smaller values of  $E$ .

The optimal distribution of reserves among regions in the Melbourne area can be compared with the actual distribution (table 1). This comparison shows that the volcanic plains are underrepresented by conservation reserves and the highlands are overrepresented. Therefore, any new conservation reserves should be added to the volcanic plains region. The volcanic plains are particularly impor-

tant for conservation because the vegetation types in this region have been severely depleted. Of particular concern is native grassland that has less than 1% of its pre-European extent remaining (Barlow and Ross 2001). Furthermore, there continue to be losses of native grassland in the Melbourne region (Williams et al. 2005a) despite protection under state legislation and their nomination as being critically endangered under federal legislation.

### Discussion

This is the first attempt to examine the logic of reserve design where the aim is to maximize the long-term representation of species within reserve systems. The results indicate several important points that need to be considered. First, variation in extinction risks among species is an important consideration for reserve design when the average extinction risk is relatively small and/or the variability among species is high. In this case, the optimal number of reserves is smaller than would be obtained from using the average extinction risk of the species (fig. 1). This result has implications for the selection of surrogate species when designing nature reserves. Lambeck's (1997) focal species approach to nature conservation selects the species that are most at risk from particular threats and then designs conservation strategies for those target species, with the hope that they act as a multispecies umbrella. Lindenmayer et al. (2002) criticized the focal species approach on several grounds, one of which was that it could not guarantee the persistence of all species. While we cannot guarantee the persistence of all species within conservation reserves when using surrogates (Andelman and Fagan 2000), our results suggest that if the size of conservation reserves is based on the more-threatened species, they will also tend to minimize the expected loss of all species. Thus, our results provide at least partial support for the logic of using the focal species approach to nature conservation, although endemism rather than the level of threat had the greatest influence on the location of reserves.

A second important point arising from our analysis was that the optimal number and size of reserves was largely insensitive to the rate of occurrence of species ( $s$ ). Thus, reserve designs based on the most rarely encountered species are unlikely to be optimal, except insofar as rarity is correlated with endemism and the risk of extinction. Therefore, the location of reserves might be influenced by rare species where their distribution influences levels of endemism, but the optimal size of reserves appears to be largely insensitive to rarity. Using species with low rates of occurrence per se as surrogates in reserve design is unlikely to be efficient.

The third important point is that endemism is an im-

portant driver of the optimal allocation of conservation reserves among bioregions. While our case study covered a relatively small geographic area (fig. A4), the allocation of conservation effort among global hotspots presents another important application of our analyses. While it has been recognized that certain parts of the world are disproportionately important for conservation (Myers et al. 2000), our analysis helps to indicate the relative effort that should be expended on establishing reserves in different hotspots. Interestingly, when many species within a region are contained in individual reserves ( $E$  is small, implying large reserves), our analysis suggests that the optimal number of reserves is relatively insensitive to differences in the number of endemic species. However, as  $E$  increases (implying smaller reserves), the sensitivity to the relative endemism increases.

A fourth important point is that the rate at which extinction risk changes with the size (or cost) of reserves ( $b/k$ ) has a large influence on the optimal size of reserves. This is a relatively well-known outcome (Quinn and Hastings 1987; McCarthy and Lindenmayer 1999; Etienne and Heesterbeek 2000; Ovaskainen 2002; McCarthy et al. 2005). While we used a power relationship between patch size and mean time to local extinction, other functional forms are likely to provide qualitatively similar results, with the optimal size of reserves depending on how extinction risk changes with reserve size.

In addition to providing relatively general insights into the optimal design of nature reserves, our results are also important for informing the conservation of Melbourne's flora in the face of continuing urban expansion. The optimal allocation of reserves among different bioregions should be relatively uniform, but the highlands have a relatively large portion of the current "conservation pie." Thus, further protection of native vegetation within Melbourne should focus on the other two bioregions, with particular emphasis on the volcanic plains. This is important, given the imperiled conservation status of the native grasslands in this bioregion. Our results suggest that the conservation of even the relatively small remnants of this vegetation type remains a useful and efficient means for protecting the diversity of plant species from extinction. Given the high rates of species loss from remnant grasslands, management practices that reduce extinctions will also be extremely important (Eddy 2002; Lunt 2003).

Natural resource managers may be interested in not just conserving species but also unique combinations of species (e.g., communities). The analysis of the optimal allocation of reserves among regions can still proceed in such cases by determining the distribution of communities across the different bioregions. It is likely that many plant communities will be restricted to one or only a few bioregions. If this is so, the approximation provided by equation (8)

will be particularly suitable because the number of communities found in many bioregions will be relatively small. Thus, the higher-order terms in equation (9), for example, will be small, and the strict endemics (the level of endemism) will dominate the solution. Thus, our approach to multispecies conservation remains applicable at other levels of ecological organization.

There are clear limitations of our model. We assumed that the individual reserves were completely independent, with no dispersal and uncorrelated extinction events. These assumptions might be reasonable if the reserves are sufficiently far apart. We believe that there would be little dispersal of plant propagules between the remnant areas of vegetation in our Melbourne cases studies and that correlation in extinction events would be low. However, it may be important to consider these factors, especially in other cases studies where dispersal and the ability to recolonize empty patches of habitat may be higher (e.g., for some birds). An additional limitation of our study is that we assumed that the probability of species being absent from regions in each reserve ( $E$ ) was the same for all reserves and all regions. In reality, reserves are likely to vary in size, and the proportion of species that they contain is likely to vary among regions. Further, differences in species accumulation curves among regions may alter the optimal allocation of conservation resources among regions. Determining the optimal allocation of resources to establishing reserves in such circumstances is likely to be considerably more complicated.

In addition to the caveats listed above, there are numerous other factors that influence the actual reservation of land for nature conservation. These include political, social, historical, and geographical constraints and the availability of different remnants for reservation. The aim of this article is to highlight the important factors in reserve design in the simplest scenarios. We expect that these factors will remain important in more complicated analyses. Further, the less important factors might remain unimportant as complexity is added. These claims deserve closer examination in particular case studies but are beyond the scope of this article.

While the models have several simplifying assumptions, they permit the logic of reserve design problems to be examined explicitly. By analyzing these simple models, we have identified that the viability of species and the rate at which the risk of extinction varies with the cost of each reserve are the most important factors when considering the size of conservation reserves. In contrast, the rate of occurrence of species within reserves and their rate of accumulation with increasing area had a relatively minor influence on the optimal size. Patterns of endemism appeared to be most important when considering the location of reserves.

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