

Designing nature reserves in the face of uncertainty

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Conservation reserves are one of the most important tools for managing biodiversity¹. Ever since Diamond², based on theory of island biogeography³, proposed that a single large reserve was preferable to several small reserves of the same total area, there has been an enduring debate about the veracity of his assertion⁴⁻¹². The so-called SLOSS debate – should we have a Single Large reserve Or Several Small reserves – features in every conservation text book and is central to conservation theory. Population dynamic models suggest that the design that minimizes the risk of extinction of species is case-specific, with the optimal number of reserves ranging between one and very many¹³⁻¹⁷. Uncertainty is pervasive in ecology, but, the previous analyses of the SLOSS debate have not considered how uncertainty in the model of extinction risk might influence the optimal design. Here we show that when uncertainty is considered, the SLOSS problem is simplified and driven more by the aspirations of the manager than the population dynamics of the species. For a given budget of land area to be reserved in a region, the optimal solution is to have on the order of twenty or fewer reserves for any

species. This result shows counter-intuitively that considering uncertainty actually simplifies rather than complicates decisions about designing nature reserves.

When minimizing the probability of extinction, the optimal number of reserves (n^*) is extremely sensitive to the extinction risk faced by species¹⁷. In the absence of dispersal between individual reserves, and if the risk of extinction is small, the number of reserves that minimizes extinction risk can be very large (several thousand). When there is dispersal, few or many reserves can also be optimal¹⁶. However, aiming to minimize the probability of extinction (or maximize the mean time to extinction) exposes managers to possible errors, with the results potentially relying on the relationship between local extinction and area being very close to the truth. Aspects of metapopulation dynamics such as extinction risk of patches are difficult to estimate with precision; bounds on estimated probabilities of extinction can sometimes encompass almost all possible values between zero and one for even well-studied species^{18, 19}. In circumstances where the risk of extinction is uncertain, managers may instead seek a reserve design that has an acceptably small extinction risk that is robust to uncertainty. Rather than minimizing the expected extinction risk, a better objective may be to maximize the chance that the risk is acceptably small. Conservation biologists often set a maximum acceptable risk of extinction for legislative and planning purposes^{20, 21}. For example, there may be a requirement that the probability of extinction cannot exceed 1% over a specified time period. Here we use models of metapopulation dynamics with and without dispersal to show that, when a given budget of land is available for the reserve system, a large number of reserves is never optimal in the presence of uncertainty.

We extend a model of the extinction of species in a set of reserves to account for uncertainty (see Methods Summary). We initially assume there is no dispersal among reserves, and then include dispersal. The model without dispersal has two parameters,

the probability of extinction of the species within the timeframe of management concern when all the available area for the reserve system is in a single reserve (x_1), and the scaling parameter describing how the mean time to local extinction changes with the size of an individual reserve (b , typically in the range $0.5 - 2.5^{22}$). This leads to the probability of extinction of the species from the total reserve system within the timeframe of management concern

$$x_n = \left[1 - (1 - x_1)^{n^b} \right]^n, \quad (1)$$

if the reserve system is composed of n reserves of equal size¹⁷.

The extinction probability if the budget of available land area is placed in one reserve, x_1 , is usually very uncertain, leading to uncertainty in the risk of metapopulation extinction x_n . The probability that the risk of metapopulation extinction x_n is acceptably small (less than a , see Methods) is maximized when the following implicit equation is solved for the number of reserves n ,

$$\frac{a^{1/n} \ln a^{1/n}}{(1 - a^{1/n}) \ln(1 - a^{1/n})} = b. \quad (2)$$

When $b=1$ the optimal number of reserves is simply $n^* = -\ln a / \ln 2$. For $b < 4$, (2) is approximated by $n^* \approx \ln a / (0.4363 - 1.1295b)$. For $b > 4$, a better approximation is $n^* \approx -\ln a / b$.

If the aim is to maximize the probability that the extinction risk is below a required threshold of between 0.01% and 10%, the optimal number of reserves is small, and typically less than 20 (Fig. 1). With the aim of having an extinction risk of less than 1% and with $b=1$, the optimal number of reserves is seven. Remarkably, the results are independent of the uncertainty in x_1 , or even its expected value. However, for the most endangered species or if there is little area available for establishing the reserve system,

the aspiration may be low (e.g., $a=0.1$) in which case the optimal number of reserves is less than five. Thus, when considering uncertainty in the estimate of extinction risk and maximizing the chance that the risk of extinction is acceptably small, the optimal number of reserves is never large. For example, if we choose a land area budget of 15,000 ha of mountain ash forest to conserve the greater glider (*Petauroides volans*) in the Central Highlands of Victoria, then $b = 0.87$ and the probability of extinction within 100 years for a single 15,000 ha patch is predicted to be $x_1 = 0.00277^{17}$. In this case, x_n is minimized when $n = 735$, with each reserve being approximately 20 ha in size. This is a highly fragmented reserve system, and one that may be risky if the prediction of x_1 is unreliable. In contrast, if we consider uncertainty in x_1 and assume a high aspiration because greater gliders are relatively common ($a = 0.01\%$), a system of $n = 17$ reserves, each of almost 900 ha, is maximally robust to uncertainty in the extinction risk (x_1).

Our multi-reserve extinction model (eqn 1) is based on assuming no dispersal among patches, so there is no recolonization of reserves that experience local extinction. Models that include dispersal can be analyzed in a similar manner to find the number of reserves that lets us be as wrong as possible about the model (see Methods Summary). The results (Fig. 2) are qualitatively similar to those in the absence of dispersal (Fig. 1), especially by noting that $1/a$ will approximate the required mean time to extinction. These results (Figs 1 and 2) indicate that a large number of reserves is never optimal in the face of uncertainty.

In the presence of uncertainty about the extinction risk, the optimal number of reserves is never large because such a strategy is particularly bad if the extinction risk is larger than expected. For example, assume that the predicted extinction risk of a species when all available habitat is in a single patch is $x_1 = 0.01$ over the time frame of management concern, and $b=1$. Ignoring dispersal, seven reserves maximizes the probability that the extinction risk is below 0.01. Seven reserves would still lead to a

small extinction risk ($<10^{-9}$) if $x_1 = 0.01$, although not the smallest possible, which is approximately 10^{-21} with 69 reserves. However, if the extinction risk was estimated incorrectly and the actual risk in a single patch is $x_1 = 0.1$, then a reserve system of 69 reserves would lead to a very large extinction risk (0.95), while seven reserves would still provide a small extinction risk (0.01). Therefore, seven reserves provides a robust solution. In contrast, a system of 69 reserves is a dangerous option if the extinction risk turns out to be greater than expected (if $x_1 > 0.01$).

The reserve designs that maximize the probability of achieving an acceptable outcome (Figs 1 and 2) are independent of the uncertainty in the extinction risk (x_1) or metapopulation growth parameter (r_1), but instead depend on our minimum aspirations (a and A). This is an unexpected result, but extremely useful for managers and conservation planners because aspirations for extinction risks are much easier to determine reliably than actual extinction risks. The population dynamics influence the results through the scaling parameters. In the absence of dispersal, the relationship between patch area and extinction risk, b , is influential. When there is dispersal, the parameter c , which combines the influence of patch size on both extinction and colonization, is most influential. However, these parameters are usually much easier to estimate than the background risk (x_1 or μ_1), and they have a relatively small influence on the results.

Uncertainty in the estimation of extinction risk occurs for several reasons. Risks are forecast over time periods that are often much longer than the time span of the available data, many aspects of population models that are used to predict risk are poorly understood, and forecasting population sizes requires assumptions about how the environment will change in the future, something that is prone to large error^{18, 19}. However, the difficulty of estimating extinction risk actually simplifies the problem of reserve design. Uncertainty removes the many-reserve option from consideration

because it is not robust to uncertainty. Our results have practical implications for guiding the use of reserve design software that typically requires arbitrary decisions about how clumped a reserve system should be²³. In the presence of uncertainty about extinction risk, the optimal number of reserves for single species is on the order of twenty or fewer, and the number is driven primarily by the aspiration of the manager rather than the dynamics of the species.

Methods summary

We assume there is a total budget of available land that may be distributed among one or more individual reserves. We model the extinction of species in a set of reserves¹⁷, assuming that the mean time to extinction of a species within a single reserve is a power function of the area of the reserve²⁴, with scaling exponent b . In addition to b , the other parameter of the model without dispersal is the probability of extinction of the species when all the available area for the reserve system is in a single reserve (x_1). We describe uncertainty in x_1 by representing the value as a random variate with density function $f(x_1)$. For any density function $f(x_1)$, we find the number of patches n that maximizes the probability that the extinction risk of the reserve system over the time frame of management concern (x_n) is less than a value that is deemed to be acceptable (a , see Methods).

Models that predict the mean time to metapopulation extinction in the presence of dispersal^{25,26} can be analyzed in a similar manner. In this case, the key uncertain parameter is r_1 , the metapopulation growth rate, which defines the ratio of the colonization and extinction rates. Dividing up the reserve system into multiple reserves aims for a mean time to metapopulation extinction that is larger than achieved with only a single reserve. We aim to ensure that the mean time to extinction is at least A times what would be achieved with a single reserve. We then find the value of n that

maximizes the probability of achieving this objective given uncertainty in r_1 (see Methods).

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Methods

In the absence of dispersal, the analysis is based on assuming that times to extinction within individual reserves have an exponential distribution, which is reasonable if the populations in the reserve are not declining deterministically. In the presence of deterministic declines, it is easy to show that in the absence of dispersal the optimal

number of reserves is small ($n^* = 1$), so we confine our analysis to the assumption that the time to local extinction is exponential. The number of reserves that minimizes the predicted probability of extinction depends on the probability of extinction if all the available land is placed in a single reserve (x_1) and the scaling parameter (b) that describes how quickly local extinction risk changes with the size of the reserve¹⁷

$$n^* \approx [-1/b \ln(1-x_1)]^{1/b}. \quad (3)$$

The optimal number of reserves (n^*) when aiming to minimize the predicted probability of extinction is extremely sensitive to the extinction risk (x_1). If x_1 is very small the number of reserves that minimizes extinction risk can be very large (up to several thousands). For example, when $b=1$, the optimal number of reserves is 693 if $x_1=0.001$ and 2023 if $x_1=0.00001$.

While the above solution (3) provides the optimal number of reserves if x_1 is known, error in the estimation of this extinction risk means that any solution based on (3) may be very misleading. Using a classical probabilistic approach, uncertainty in x_1 may be represented by treating x_1 as a random variable with probability density function $f(x_1)$. Then, for a given density function $f(x_1)$ and number of reserves n , it is possible to determine the probability that the extinction risk of the reserve system (x_n) is less than a required value that is deemed to be acceptable (a). Let x_1' be the probability of extinction in a single patch such that the probability of extinction in an n -patch system is equal to the acceptable value a . Thus, for the extinction model (1)

$$x_1' = 1 - (1 - a^{1/n})^{n-b}. \quad (4)$$

Then, the probability that the extinction risk of the n patch system is acceptable is equal to the probability that x_1 is less than the critical value x_1' . This probability is simply obtained as the definite integral of $f(x_1)$ between zero and x_1'

$$\Pr(x_n < a) = \int_0^{x_1'} f(x_1) dx_1. \quad (5)$$

The optimal reserve design is obtained by finding the number of reserves n that maximizes (5), i.e., maximizes the probability that the risk of extinction is acceptably small. For any arbitrary probability distribution $f(x_1)$, this is achieved by maximizing the upper bound of the integral x_1' with respect to n . The value of x_1' (4) is maximized when the following implicit equation is solved for n

$$\frac{a^{1/n} \ln a^{1/n}}{(1 - a^{1/n}) \ln(1 - a^{1/n})} = b. \quad (6)$$

This can be solved numerically for n , although when $b=1$ the analytical solution is $n^* = -\ln a / \ln 2 = -1.443 \ln a$. (7)

An approximate solution of (6) can be obtained by expressing b as a function of $\ln(a^{1/n})$, and based on a Taylor series expansion at the point $a^{1/n} = 0.5$, the solution of (6) is approximated by $n^* \approx \ln a / (0.4363 - 1.1295b)$. For $b > 4$, a better approximation is $n^* \approx -\ln a / b$.

The above multi-reserve extinction model is based on assuming no dispersal among patches, so there is no recolonization of reserves that experience local extinction. Models that include dispersal can be analyzed in a similar manner to find the number of reserves that lets us be as wrong as possible about the model. In this case, we represent the reserve as a metapopulation, with the occupancy of the reserve network modeled as a stochastic birth-death process, governed by a birth (colonization) rate λ and death (extinction) rate μ . Exact solutions for the mean time to extinction exist for these models^{25, 26}. As above, we assume that the mean time to local extinction scales with patch area with exponent b . Consequently, for a given amount of habitat being reserved, the extinction rate parameter scales with the number of reserves as $\mu = \mu_1 n^b$. Similarly, we assume that the colonization rate parameter scales with patch area as $\lambda = \lambda_1 n^{-b'}$, such that we define $r = \lambda \mu = r_1 n^{-c}$, where $c = b + b'$, and $b \leq c$ (see ref 16). Thus, the parameter c combines the influence of patch size on both extinctions and colonizations.

With these assumptions, the mean time to extinction of a system of n initially-occupied patches is given by^{24, 25}:

$$\hat{T}_n = \left(\sum_{k=1}^n \frac{1}{k} + \sum_{i=1}^{n-1} \sum_{k=i+1}^n \frac{1}{k} \prod_{m=i}^{k-1} r \left(1 - \frac{m}{n}\right) \right) / \mu. \quad (8)$$

If this is expressed relative to the mean time to extinction that would be achieved when all available habitat is placed in a single patch ($n = 1$, in which case $\hat{T}_1 = 1 / \mu_1$), we have

$$\hat{T}_n / \hat{T}_1 = \left(\sum_{k=1}^n \frac{1}{k} + \sum_{i=1}^{n-1} \sum_{k=i+1}^n \frac{1}{k} \prod_{m=i}^{k-1} r_1 n^{-c} \left(1 - \frac{m}{n}\right) \right) / n^b. \quad (9)$$

In this formulation $r_1 = \lambda_1 / \mu_1$ is the key uncertain parameter. Dividing up the reserve system into multiple reserves aims for a mean time to metapopulation extinction that is larger than achieved with only a single reserve. We assume that the aim is to ensure that the mean time to extinction is at least A times what would be achieved with a single reserve. Then, assuming particular scaling coefficients b and c , we determine the number of reserves that lets r_1 , the metapopulation growth rate, be as small as possible. This provides the reserve design that is most robust to uncertainty in r_1 by maximizing the probability that $\hat{T}_n / \hat{T}_1 > A$ for any probability distribution for r_1 . This is achieved by finding the value of n that minimizes r_1 subject to the constraint that $\hat{T}_n / \hat{T}_1 = A$, which we obtained by iterative numerical evaluation of eqn (9).

Figure legends

Fig. 1. The number of reserves that maximizes the probability that the extinction risk is smaller than required (a) versus the reciprocal of the requirement ($1/a$), for different values for the extinction scaling parameter b . Results are presented relative to the reciprocal of the required extinction probability to facilitate comparison with Fig. 2 because $1/a$ will approximate the required mean time to extinction.

Fig. 2. The number of reserves that maximizes the probability that the mean time to extinction of a metapopulation is at least A times the value obtained if all available habitat were in a single reserve. Results are shown for different values for c , the scaling coefficient for the metapopulation parameter r ($c = 0.75, 1.0, 2.0$) and for b , the scaling coefficient for the extinction rate ($b=0$, solid line; $b=c$, dashed line).

Fig. 1

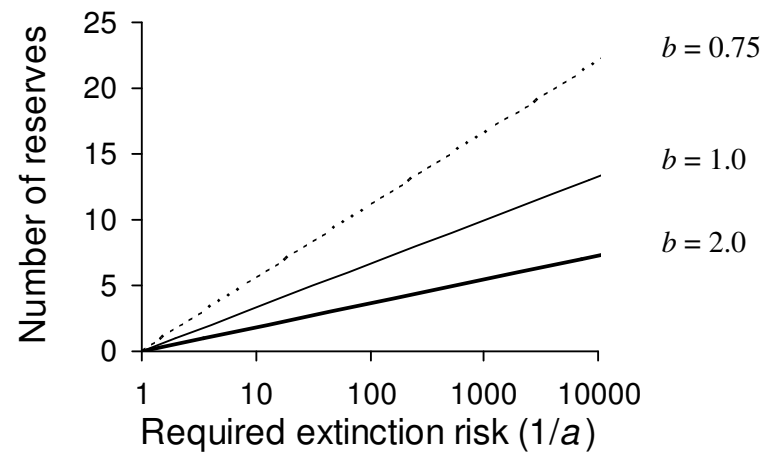


Fig. 2

