LETTER

A new method for conservation planning for the persistence of multiple species

Emily Nicholson,[1]* Michael I. Westphal,[2] Karin Frank,[3] Wayne A. Rochester,[4] Robert L. Pressey,[1] David B. Lindenmayer[5] and Hugh P. Possingham[1]

Abstract

Although the aim of conservation planning is the persistence of biodiversity, current methods trade-off ecological realism at a species level in favour of including multiple species and landscape features. For conservation planning to be relevant, the impact of landscape configuration on population processes and the viability of species needs to be considered. We present a novel method for selecting reserve systems that maximize persistence across multiple species, subject to a conservation budget. We use a spatially explicit metapopulation model to estimate extinction risk, a function of the ecology of the species and the amount, quality and configuration of habitat. We compare our new method with more traditional, area-based reserve selection methods, using a ten-species case study, and find that the expected loss of species is reduced 20-fold. Unlike previous methods, we avoid designating arbitrary weightings between reserve size and configuration; rather, our method is based on population processes and is grounded in ecological theory.

Keywords

Conservation planning, metapopulation, multiple species conservation, optimization, reserve design, simulated annealing, site selection.

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INTRODUCTION

The 'holy grail' of conservation planning is the persistence of biodiversity (Margules & Pressey 2000; Williams & Araújo 2000), yet standard planning methods struggle to deal with species-specific needs for the amount and spatial configuration of conservation areas, particularly when considering many species (Cabeza & Moilanen 2003). Reserve selection methods can deal with multiple species concurrently, but traditionally do not account directly for the persistence of species. Instead they aim simply to represent species within a system of reserves† (Possingham *et al.* 2000; Williams & Araújo 2000; Cabeza & Moilanen 2003). While able to maximize the expected number of species represented within a reserve system, reserve selection methods do not maximize the expected number of species extant at the end of a given time frame (Bevers *et al.* 1995; Cabeza & Moilanen 2003). In contrast, population models can deal with population processes that affect persistence, but tend to be restricted to single-species planning problems (Moilanen & Cabeza 2002; Westphal *et al.* 2003). The inability to deal with reserve adequacy, a key principle of conservation planning theory, on a multi-species level presents a serious problem for advocates of systematic conservation planning.

[1]*The Ecology Centre, School of Integrative Biology, The University of Queensland, St Lucia, Qld 4072, Australia*
[2]*AAAS Science & Technology Policy Follow, US Environmental Protection Agency, Office of International Affairs, Washington, DC 20460, USA*
[3]*Centre for Environmental Research Leipzig-Halle GmbH, Department of Ecological Modelling, Permoserstr. 15, D-04318 Leipzig, Germany*
[4]*CSIRO Marine and Atmospheric Research, Cleveland, Qld 4163, Australia*

[5]*Centre for Resource and Environmental Studies, Building 43, The Australian National University, Canberra, ACT 0200, Australia*
Correspondence: E-mail: e.nicholson@uq.edu.au
†*Conservation areas have a multitude of forms, from private lands managed for conservation to strict national parks, here referred to as 'reserves' for the sake of simplicity (Margules & Pressey 2000).*

Some reserve selection methods use proxies for population viability, such as the number of occurrences or populations of a species, total amount of habitat or number of individuals per species (Burgman *et al.* 2001; Cabeza & Moilanen 2003; Pressey *et al.* 2003). A variety of nonlinear benefit functions have been used to mimic the added value of habitat, based on simple models of population viability as a function of population size or habitat area (Hof & Raphael 1993; Bevers *et al.* 1995; Arponen *et al.* 2005). Spatial design criteria tend to be generic, using rules or indices, such as minimizing the fragmentation of the reserve system (McDonnell *et al.* 2002), or designating minimum patch sizes for species (Ball & Possingham 2000; Burgman *et al.* 2001). Species-specific rules relating to distance between patches are feasible for a single-species problem (Hastings & Botsford 2003; Schulz & Crone 2005), but become hard to implement across multiple species, resulting in a tendency towards landscape indices as a surrogate for multi-species viability (Opdam *et al.* 2003). Moilanen *et al.* (2005) included a dispersal kernel to give a species-specific measure of connectivity for multi-species reserve selection, but did not integrate it into an estimate of persistence. When integrating a measure of landscape connectivity into a reserve design formulation, a balance must be struck between the emphasis placed on species representation and connectivity, which tends to result in arbitrary rules or weighting factors (Briers 2002; McDonnell *et al.* 2002; Siitonen *et al.* 2002).

Several authors have extended the reserve design framework in attempts to include the viability of multiple species by developing more sophisticated data layers and algorithms. Williams & Araújo (2000) used probabilities of occurrence as a first approximation surrogate for probability of persistence, estimated as a function of habitat suitability and occupancy patterns in surrounding cells, a non-specific proxy for dispersal. An important step forward came from using a stochastic population model to estimate of the intrinsic growth rate, λ, per planning unit, and selecting for protection areas with higher population growth rates (Calkin *et al.* 2002; Noss *et al.* 2002; Carroll *et al.* 2003). Root *et al.* (2003) used stochastic metapopulation models to generate a multi-species index of the conservation value of a planning unit, combining species-specific habitat suitability, extinction risk, and contribution to population viability. Stochastic simulation models can be used to develop statistical relationships between the amount and configuration of habitat, in turn used in optimization (Calkin *et al.* 2002; Haight *et al.* 2002; Nalle *et al.* 2004), with configuration incorporated through the contribution of neighbouring cells (Calkin *et al.* 2002; Nalle *et al.* 2004). However, these methods are based on the outputs of Monte Carlo simulation models, rather than using the population model directly within the reserve selection algorithm. As a consequence, the effects of reserve configuration on extinction risk are not measured or optimized explicitly.

The ideal method for developing conservation plans for the persistence of biodiversity would include species-specific processes and use of a single currency of persistence probability (Williams & Araújo 2000; Cabeza & Moilanen 2003; McCarthy *et al.* 2006; Nicholson & Possingham 2006). Most process-based models used thus far in multiple-species planning either exclude dispersal through the use of stochastic approximation models (Lande 1993; McCarthy *et al.* 2006), or are deterministic, such as Rothley's (2002) method for designing reserves for two species within a predator–prey system. Including stochasticity is crucial to understanding and predicting population viability and can have significant qualitative and quantitative effects on the assessment of viability (Lande 1993; Moilanen & Cabeza 2002; Frank 2005). Stochastic population models require extensive Monte Carlo simulation, which generally precludes direct optimization across multiple species, in addition to problems such as substantial data needs. As a consequence, the few cases where process-based stochastic models were optimized directly dealt with single-species problems (Moilanen & Cabeza 2002; Westphal *et al.* 2003). Thus methods for planning for multiple species based on ecological theory and that include processes such as dispersal remain elusive (Cabeza & Moilanen 2001; Burgman *et al.* 2005; McCarthy *et al.* 2006).

In this paper, we present a novel method for finding optimal reserve solutions that maximize the persistence of metapopulations of multiple species. We compare our method for maximizing persistence with more traditional, area-based reserve selection methods (Arponen *et al.* 2005), where the goal is to maximize the area of reserved habitat for multiple species. We estimate the extinction risk of each species using a formula that approximates the mean lifetime of a metapopulation (Frank & Wissel 2002), based on a spatially realistic, stochastic metapopulation model (Frank & Wissel 1998), that allows us to optimize reserve configuration expediently. The extinction risk of the metapopulation is a function of the ecology of the species and the amount, quality and configuration of habitat, and allows direct optimization of persistence. We use simulated annealing, a relatively efficient algorithm that finds optimal or near-optimal solutions, to minimize the expected number of extinctions. We demonstrate our method in a forestry region in New South Wales, Australia, where an extensive database has been established for 10 species across 39 patches of remnant forest. We conclude with a discussion of the limitations and benefits of our method.

MATERIALS AND METHODS

First, we present our new method for optimizing metapopulations, referred to as *maximizing persistence*. This includes the formulation of the problem, and a description of the model used to estimate metapopulation extinction risk. The goal of our reserve selection method is to minimize the expected number of extinctions over a given time frame. Then we present two area-based reserve selection methods for comparison with the maximizing persistence approach, which consider only the amount of habitat available to the species, rather than addressing species persistence. The first reserve selection method, which we refer to as *maximizing area of habitat*, aims to maximize the area of available habitat across all species, but does not include any measure of habitat quality. The second, *maximizing effective area of habitat*, takes into account the suitability of the habitat for each of the species. Finally, we present a case study to illustrate the methods.

Maximizing persistence

Problem formulation

We consider the problem where the objective is to maximize the persistence of a set of species in a reserve system within the constraint of a fixed budget. This is often referred to as the maximal coverage approach to conservation planning (Williams & Araújo 2000; Cabeza & Moilanen 2001; Nicholson & Possingham 2006). In this study, we assume a fragmented system, where only whole patches of habitat can be selected for inclusion in the reserve system, and we assume that areas outside the reserve system do not contribute to viability.

The information that drives the selection of patches for protection is the distribution of species. The distribution of n species across m patches can be described in an $(m \times n)$-matrix $\mathbf{A}$ whose elements a_{ik} are

$$a_{ik} = \begin{cases} 1, & \text{if species } k \text{ is found in patch } i \\ 0, & \text{otherwise} \end{cases}$$

for $i = 1, \ldots, m$ and $k = 1, \ldots, n$,

where n is the number of species and m is the number of patches. Each of the m patches can be included or excluded from the reserve system. The state of the system can be described as a vector, $\mathbf{r}$, of ones and zeros where

$$r_i = \begin{cases} 1, & \text{if patch } i \text{ is reserved} \\ 0, & \text{otherwise} \end{cases} \quad \text{for } i = 1, \ldots, m.$$

For every reserve system, $\mathbf{r}$, each species has a probability of extinction. The probability of extinction of species k over a fixed time period t given reserve system $\mathbf{r}$,

$p_k(\mathbf{r}, t)$, is a function of both the distribution of the species a_{ik} and the reserve system $\mathbf{r}$. We estimate the risk of extinction using Frank & Wissel's (2002) metapopulation model, where extinction risk is a function of the local extinction rate of each patch and the colonization rates between them; i.e. the amount and spatial configuration of habitat.

The probability of extinction or persistence gives a common currency across species when making conservation decisions for multiple species, and can be used in many ways to formulate the conservation objective (Williams & Araújo 2000; Nicholson & Possingham 2006). To illustrate our method, we use a straightforward objective: find the reserve system that minimizes the expected number of extinctions across the set of n species, given by the sum of extinction risks, while ensuring that the cost of the reserve remains within the budget, B:

$$\text{Minimize} \sum_{k=1}^{n} p_k(\mathbf{r}, t) \text{ subject to } \sum_{i=1}^{M} r_i c_i \leq B, \tag{1}$$

where c_i is the cost, in this case area, of patch i. This is equivalent to maximizing the expected number of species persisting at the end of the management time frame (Hof & Raphael 1993; Bevers *et al.* 1995; Williams & Araújo 2000). Here, we assume that the cost of each patch is its area, with a total budget of 220 ha. We could incorporate other costs, related to purchase price, ongoing management costs, forgone timber in a forestry region or other socio-economic factors.

Model for metapopulation extinction risk

The probability of extinction of a metapopulation is a function of the size, spatial configuration and quality of available habitat and the ecology of the species. Let the probability of extinction of an established metapopulation, given reserve system $\mathbf{r}$, at time t, be:

$$p_k(r, t) = 1 - \mathrm{e}^{-t/T_k(\mathbf{r})}, \tag{2}$$

where $T_k(\mathbf{r})$ is the meantime to extinction of the metapopulation (Mangel & Tier 1993; McCarthy *et al.* 2005). In this study, we use a management time frame of 100 years, therefore $t = 100$.

We estimate the mean time to extinction $T_k(\mathbf{r})$ of the metapopulation of species k, given the reserve system $\mathbf{r}$, using a time-continuous Markov chain model (Frank & Wissel 1998). This model is very useful within an optimization framework, because Frank & Wissel (2002) developed an approximation formula:

$$T_k(\mathbf{r}) \approx T_k^a = \frac{1}{v_{\text{agg}}} \frac{(M-1)!}{M(M-1)^{M-1}} \mathrm{e}^{M/z} z^{M-1}, \tag{3}$$

where z is an aggregation of the effective colonization abilities of the subpopulations, and v_{agg} is the effective local extinction rate:

$$z = \prod_{i=1}^{M} \max \left(\sqrt{2}, \sqrt{\left\{ \frac{1}{2} \left[\left(\frac{\sum_{j(\neq i)} c_{ij}}{v_i} \right)^{-2} + \left(\frac{\sum_{j(\neq i)} c_{ji}}{v_i} \right)^{-2} \right] \right\}^{-1}} \right)^{1/M}$$

and

$$v_{\text{agg}} = \left(\prod_{i=1}^{M} v_i \right)^{1/M},$$

where v_i is the local extinction rate of patch i, and c_{ij} is the rate of colonization from patch i to patch j. M is the number of patches in the metapopulation, in this case the number of patches in the reserve system $\mathbf{r}$ where the species may occur. The original metapopulation model can also include correlation in extinction rate across patches (Frank & Wissel 1998), which for simplicity we have not included, instead assuming that local extinctions occur independently.

The local extinction rate v_i of a patch is a function of the number of home ranges for the species in the patch. We include variation in patch quality, assuming that habitat quality affects the density of individuals (Moilanen & Hanski 1998). A patch of lower quality habitat therefore has a reduced effective area, and holds fewer home ranges. Let H_k be the home range size of a breeding female of species k in optimal habitat, and h_{ik} a measure of the proportional decrease in the density of species k in patch i given the sub-optimal habitat type. Therefore, the effective number of home ranges of species k in patch i with an area of A_i is $A_i h_{ik}/H_k$. The sub-model for the local extinction rate of species k in patch i is

$$v_i = \frac{-\ln(0.01)}{100} \left(\frac{A_i h_{ik}}{H_k} \right)^{-x_k}, \tag{4}$$

where A_i is the area of patch i, and x_k, the extinction-area exponent, is a species-specific measure of environmental noise in the population (Hanski 1994; Moilanen & Hanski 1998; Frank 2005). The coefficient $-\ln(0.01)/100$ ensures patch i has a 99% probability of local extinction in 100 years when it is the size of one home range of the species.

We use the pie-slice model to estimate the rate of colonization from patch i to patch j, c_{ij} (Possingham & Davies 1995), where the chance of an individual dispersing to a patch is proportional to the size and distance of the recipient patch,

$$c_{ij} = \gamma_k \frac{A_i h_{ik}}{H_k} b \, e^{-d_{ij}/d_k}, \tag{5}$$

where $b = (1/\pi)\arctan(\sqrt{A_j/\pi}/d_{ij})$ for $d_{ij} \geq \sqrt{A_j/\pi}$ and $b = 0.5$ when $d_{ij} < \sqrt{A_j/\pi}$. A_i is the area of patch i, A_j is the area of target patch j, and d_{ij} is the centre-to-centre distance between the two patches, γ_k is the species-specific emigration rate of juvenile females per home range, H_k, including the habitat quality of patch i for species k, h_{ik}, and d_k is the mean dispersal distance of species k.

Maximizing area of habitat

Having formulated the problem of maximizing the expected persistence of the metapopulations, we now consider two traditional reserve design approaches. First, we maximize the area of habitat available to a set of species within a reserve system, with the constraint of a fixed budget, using the objective function in Arponen *et al.* (2005). The problem formulation when maximizing area of habitat is very similar to maximizing persistence. Once again, the primary driver of the area selection is the distribution of species, using the same $(m \times n)$-matrix $\mathbf{A}$ whose elements a_{ik} are:

$$a_{ik} = \begin{cases} 1, & \text{if species } k \text{ is found in patch } i \\ 0, & \text{otherwise} \end{cases}$$

for $i = 1, \ldots, m$ and $k = 1, \ldots, n$,

Each of the m patches can be included or excluded from the reserve system. The state of the system can be described as a vector, $\mathbf{r}$, of ones and zeros where

$$r_i = \begin{cases} 1, & \text{if patch } i \text{ is reserved} \\ 0, & \text{otherwise} \end{cases} \quad \text{for } i = 1, \ldots, m.$$

The objective of the reserve system is to maximize the area of habitat available to a set of species. The total area of habitat available to species k, $A_k(\mathbf{r})$, is a function of the distribution of the species a_{ik}, the size of the patches and the reserve system $\mathbf{r}$,

$$A_k(\mathbf{r}) = \sum_{i=1}^{m} r_i a_{ik} A_i. \tag{6}$$

When maximizing the area of habitat, every hectare of habitat for the species is treated the same, regardless of the size of the patch it is in or its proximity to other patches; by contrast, when maximizing persistence both patch size and spatial configuration are considered.

We use a nonlinear function that returns an objective value per species of between 0 and 1 (Arponen *et al.* 2005). In this diminishing returns approach, habitat in excess of a target area per species provides less value to the objective (Fig. 1). The objective when maximizing the area of habitat is:

$$\text{Maximize} \sum_{k=1}^{n} 1 - \exp \frac{\ln(0.1) A_k(\mathbf{r})}{G_k}, \tag{7}$$

where $A_k(\mathbf{r})$ is the total area of habitat available to species k within the reserve system $\mathbf{r}$, and G_k is the target area of habitat for species k. In this case, we wish to have an objective value of 0.9 for a species once its target area has been achieved, with only a small contribution to the objective value for any additional area; this is ensured by the coefficient of the natural logarithm of 0.1 (Fig. 1). The
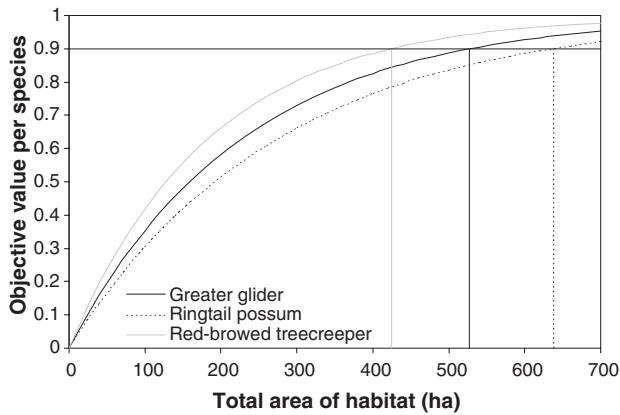
Figure 1 The diminishing returns to the objective value per species with increasing amount of total habitat after reaching the species-specific target area, G_k, shown here for the greater glider (target area of 527 ha), the ringtail possum (638 ha) and the red-browed treecreeper (424 ha).

target is the area of habitat required for a 5% risk of extinction over 100 years, assuming that all habitat is in one block (Hof & Raphael 1993; Burgman *et al.* 2001). Using the sub-model for local extinction (eqn 4) and the functional form relating extinction probability to the mean time to extinction, the inverse of extinction rate (eqn 2), the extinction risk over 100 years of species k in a patch the size of the target G_k, is

$$p_k(G_k) = 0.05 = 1 - \exp[\ln(0.01)(G_k/H_k)^{-x_k}],$$

giving the formula for the target area G_k for species k:

$$G_k = H_k \left(\frac{\ln(0.95)}{\ln(0.01)} \right)^{-1/x_k} \quad (8)$$

Maximizing effective area of habitat

A sensible extension to the problem of maximizing area of habitat is to take account of habitat quality, as with the metapopulation model. Therefore, we seek to maximize the effective area of habitat available to the species by including habitat quality as it influences the population densities of the species. The effective area of habitat available to species k, $A_{\text{eff}, k}(\mathbf{r})$, is a function of the distribution of the species a_{ik}, the habitat suitability or relative contribution of the habitat types as it relates to population density, h_{ik}, the size of the patches, A_i and the reserve system $\mathbf{r}$:

$$A_{\text{eff},k}(\mathbf{r}) = \sum_{i=1}^{m} r_i a_{ik} A_i h_{ik}. \quad (9)$$

The same species-specific targets for the effective area are used when maximizing the area of habitat. The objective

then relates to the effective area of habitat, rather than the absolute area of habitat:

$$\text{Maximize} \quad \sum_{k=1}^{n} 1 - \exp\left(\frac{\ln(0.1)A_{\text{eff},k}(\mathbf{r})}{G_k} \right). \quad (10)$$

Simulated annealing

We use simulated annealing (Kirkpatrick *et al.* 1983) to find optimal or near-optimal solutions for the three reserve design problems. The full objective functions are in Appendix 1. Simulated annealing has often been applied to conservation planning problems, as it provides a relatively fast search method for large, nonlinear combinatorial problems (Ball & Possingham 2000; McDonnell *et al.* 2002; Nalle *et al.* 2004). As the intricacies of the algorithm have been described elsewhere (Kirkpatrick *et al.* 1983; Ball & Possingham 2000), we provide only a general description here. Simulated annealing searches for solutions by randomly adding and removing areas from the reserve system, and comparing the objective values. Good changes are always accepted, and bad changes are permitted at the beginning of the search to avoid becoming stuck in local minima. By producing multiple near-optimal solutions, we can present many good conservation options to managers to allow flexibility. The proportion of times that a patch appears in a good reserve solution can also be used to give an indication of its importance for conservation or its irreplaceability (Ball & Possingham 2000).

Case study

For the case study, we focus on 10 species of vertebrates inhabiting 39 patches of eucalypt (*Eucalyptus* spp.) forest embedded in approximately 100 000 ha of Monterey pine (*Pinus radiata*) plantations. The study area is near Tumut, NSW, Australia, where an extensive database has been built up over many years. The patches vary in size between 0.4 and 40 ha, with a total area of 434 ha, and comprise six broad habitat types (Table 1; Fig. 2).

The 10 species modelled represent a wide range of sizes and life history strategies, and include four bird species, five marsupials and one native rodent. The species have been the subject of several of the population modelling studies (summarized in Lindenmayer *et al.* 2003) used to parameterize the metapopulation models here. Values for home range size H_k, fecundity γ_k and mean dispersal distance d_k are estimated from the literature, in particular published population models (see Lindenmayer *et al.* 2003; McCarthy *et al.* 2005; Nicholson & Possingham, in press), while the values for the extinction-area exponent x_k are either previously published estimates,

Table 1 Model parameters for each of the 10 species. H_k is the home range size in hectares, γ_k the output of female dispersers per home range, d_k the mean dispersal distance in kilometres, x_k the extinction-area exponent, and the relative values h_{ik} of the four habitat types (Fig. 2) used to estimate the effective area of a patch; all parameters were derived from published population models (see references in Lindenmayer *et al.* 2003)

| Species | γ_k | d_k | x_k | H_k | Value of habitat type | | | | | |
					Eucalyptus camphora	*Eucalyptus macrorhynca*	*Eucalyptus radiata*	*Eucalyptus viminalis*	Stream	Slope
Greater glider (*Petaurus volans*)	0.25	0.50	0.87	3.00	0.33	0.69	0.4	1		
Mountain brushtail possum (*Trichosurus cunninghamii*)	0.12	5.00	1.00	6.00	1	0.08	0.17	0.33		
Common ringtail possum (*Pseudocheirus peregrinus*)	0.40	0.85	0.78	2.00	1	0.4	0.2	0.2		
Common brushtail possum (*Trichosurus vulpecula*)	0.45	1.00	1.30	5.00	1	0.25	0.5	1		
Red-browed treecreeper (*Climateris erythrops*)	0.55	1.00	1.20	10.00	1	0.25	0.5	1		
White throated treecreeper (*Cormobates leucophaea*)	0.41	5.00	1.40	5.00	0.5	1	1	1		
Laughing kookaburra (*Dacelo novaeguineae*)	0.35	20.00	1.60	5.00	0.7	0.85	1	0.55		
Sacred Kingfisher (*Todiramphus sanctus*)	3.10	15.00	1.15	7.50	0.7	1	1	1		
Bush rat (*Rattus fuscipes*)	1.25	2.50	0.72	0.30					1	0
Agile antechinus (*Antechinus agilis*)	1.20	5.00	0.45	1.00					1	0.5
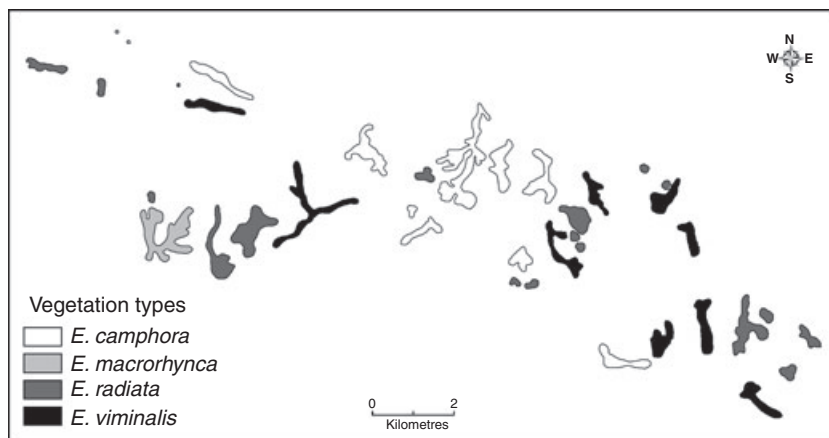
Figure 2 The 39-patch study system, near Tumut, NSW, Australia, showing the four vegetation types that provide the basis for the habitat quality for each of the species (Table 1).

such as for the greater glider (McCarthy *et al.* 2005) or derived from running published models (see references in Lindenmayer *et al.* 2003). Table 1 lists the species-specific parameter values used in the metapopulation model, and the relative value of each habitat type for each of the species, based on density estimates from published survey data and population models (see references in Lindenmayer *et al.* 2003). We assume that the species do not use the pine plantation as primary habitat, but can disperse through it. All species may be found in all habitats, although at varying population densities, with the exception of the Bush rat, *Rattus fuscipes*, which only breeds in gully habitats and is therefore assumed absent from non-gullies. We ran 100 simulations of each of the three

reserve design methods, and recorded the best reserve solution with a budget of 220 ha.

RESULTS

The differences between the best reserve solutions derived using each of the three reserve selection methods can be compared in several ways. First, we contrast their performances in achieving each of the overall objectives, shown in Table 2: the expected number of extinctions (the sum of extinction risks of the species, estimated using the metapopulation models); the total area of habitat (summed across the species); and total effective area of habitat. We find the biggest discrepancy exists in the expected number of

Table 2 The performance of the best reserve solutions derived using each of the reserve selection methods in total area, the number of sites selected, and the three alternative objectives

	Maximizing persistence	Maximizing effective area of habitat	Maximizing area of habitat
Total Area (ha)	218	220	220
Number of sites	10	17	14
Expected number of extinctions	0.046	1.02	1.85
Total effective area of species' habitat (ha)	1610	1767	1679
Total area of species' habitat (ha)	2096	2182	2200

extinctions. Then we look at the individual patches of habitat selected, illustrated in Fig. 3. Finally, we examine the performance of the three reserve solutions using the extinction risk of each of the species, shown in Table 3.

The best reserve solutions derived using the three alternative reserve selection methods perform similarly in the total area, total area of habitat across the species, and total effective area of habitat (Table 2); there are only marginal differences under these criteria. The big difference between the reserve scenarios lies in the expected number of extinctions. When maximizing persistence, the expected number of extinctions is 0.046. When maximizing the effective area of habitat, taking into account habitat quality for each of the species, the expected number of extinctions is an order of magnitude greater. The performance of the reserve solution when maximizing area of habitat without considering habitat quality is worse again, nearly 40 times larger than when maximizing persistence, demonstrating the value of including some measure of habitat quality. The fact that the method that maximizes persistence performs better is not surprising, given that was the objective being optimized. However, the magnitude of the difference is remarkable.

Performance in the expected extinctions under the three reserve scenarios is divergent despite overlaps in the selected areas. The best reserve solutions when maximizing persistence and when maximizing effective area of habitat have seven patches in common; when maximizing persistence and maximizing area of habitat, the reserve solutions overlap by four patches; and 11 patches are selected by both the area-based methods. The difference in performance lies in the omission by the area-based methods of a few larger and more connected patches, and the inclusion of smaller, more distant patches. When maximizing persistence, larger patches and consequently fewer patches are selected (Fig. 3). All 10 sites selected are over 10 ha, as opposed to only nine of 17 when maximizing the effective
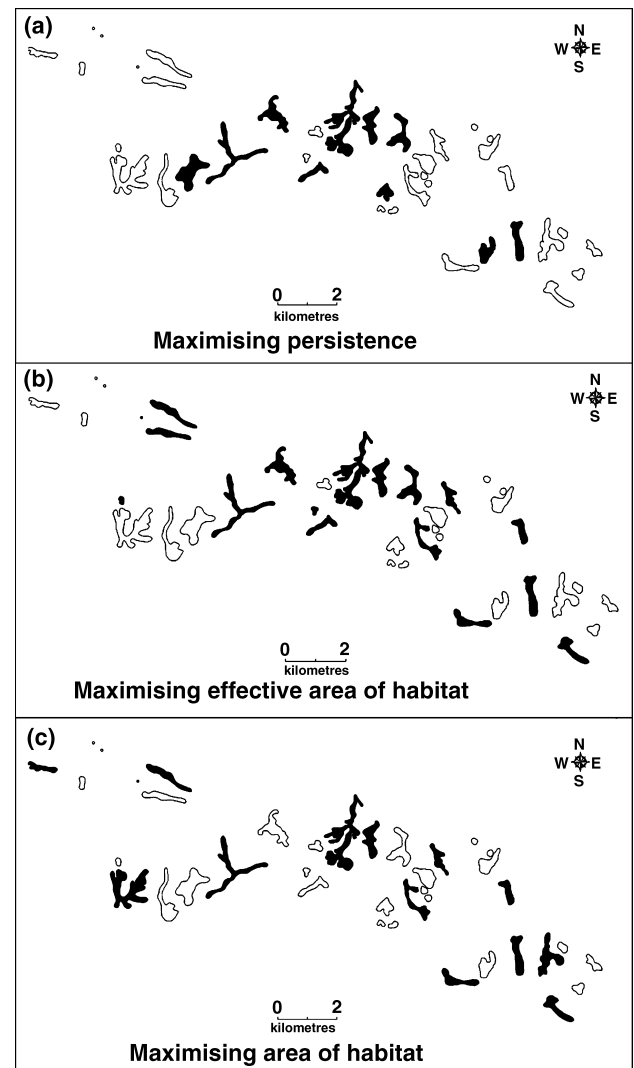
Figure 3 Maps of the best reserve scenarios, with patches selected as reserves in black, generated using each of the conservation planning methods: (a) maximizing persistence (218 ha, 10 patches), (b) maximizing the effective area of habitat (220 ha, 17 patches), and (c) maximizing the area of habitat (220 ha, 14 patches).

area of habitat, and eight of 14 when maximizing area of habitat ignoring habitat quality. The reserved patches are also in the centre of the study area, creating a network of connected larger patches.

When maximizing the persistence of the species, the extinction risks of most of the species is substantially smaller than when maximizing area of habitat (Table 3). The kookaburra, agile antechinus and bush rat perform worse, but the difference is negligible; all reserve scenarios have an extinction risk of close to or effectively zero. The higher risk species, such as the red-browed treecreeper, the short-eared possum and the greater glider, contribute the biggest

Table 3 The extinction risks of each of the species under the best reserve solutions derived using each of the reserve selection methods

Species	Maximizing persistence	Maximizing effective area of habitat	Maximizing area of habitat
Greater glider	0.021	0.64	0.55
Mountain brushtail possum	0.017	0.10	0.64
Common ringtail possum	2.1×10^{-6}	0.00056	0.080
Common brushtail possum	2.9×10^{-7}	0.00027	0.031
Red-browed treecreeper	0.0073	0.27	0.55
White throated treecreeper	5.9×10^{-9}	2.83×10^{-6}	5.83×10^{-7}
Laughing kookaburra	1.9×10^{-10}	6.02×10^{-7}	1.36×10^{-6}
Sacred Kingfisher	9.2×10^{-15}	5.12×10^{-15}	4.77×10^{-14}
Bush rat	2.6×10^{-16}	0.0	0.0
Agile antechinus	5.4×10^{-19}	0.0	0.0

difference between the reserve system that maximizes persistence and the area-based methods. These more extinction-prone species appear to drive the final reserve system when maximizing persistence, as they give the greatest contribution to the objective value, and are the most demanding in terms of the patch and configuration preferences. In the reserve systems derived using the methods based on area of habitat, the species are treated equally and their contributions to the objective values are similar because we do not include any species-specific weightings. When comparing the two area-based reserve selection methods, most species benefit from the consideration of habitat quality. The three possum species in particular exhibit very significant decreases in extinction risk in the reserve system that maximizes the effective area of habitat, compared with the reserve system that maximizes area of habitat ignoring habitat quality (Table 3).

DISCUSSION

We have developed a method that maximizes the persistence of multiple species in a reserve system. Our inclusion of species-specific parameters to account for dispersal ability and patch size requirements presents a significant advance from the more generic spatial design criteria and arbitrary weightings between reserve size and configuration and species representation currently available in conservation planning. This work is more formally rooted in the fundamental theory of population viability than previous efforts to consider reserve adequacy. An objective that

combines the extinction risks of multiple species allows us to find compromise landscapes that are unlikely to be optimal for any one species but provide a good solution for many species. Importantly, many alternative near-optimal solutions can be found to allow managers flexibility.

The method we have presented for maximizing persistence can be extended to include greater landscape complexity and heterogeneity, such as matrix structure and features that may hinder or facilitate dispersal (Moilanen & Hanski 1998). While further adding to the data requirements, such information on landscape structure and use can greatly enhance the predictive ability of models (Lindenmayer *et al.* 2003). We can also widen our management choices from the binary case presented here, where each patch is reserved or not reserved, to varying levels of protection or use (Calkin *et al.* 2002), if we understand the effects of different management systems on the ecology of the species (i.e. local extinction and colonization rates).

Our approach includes limitations and assumptions, relating to the underlying metapopulation theory, the model used, and also to uncertainty inherent in our understanding. Burgman *et al.* (2005) identified many problems associated with the use of population models in landscape management, including choice of the modelling frame through convenience rather than suitability for the problem at hand. In this case, we used the Frank & Wissel (2002) metapopulation model because it provides a closed-form expression for metapopulation extinction risk that can be quickly evaluated and deals with some aspects of landscape complexity and habitat suitability. An alternative function describing the relationship between extinction risk and reserve configuration could be used, provided it is theoretically justifiable, such as other approximation models (e.g. Lande 1993; Mangel & Tier 1993; Ovaskainen 2002), each with their merits and weaknesses. The use of this convenient approximation model leads to questions about both the applicability of the metapopulation framework to the problem at hand, and uncertainties inherent in the specific approximation model of Frank & Wissel (2002).

The debate on the applicability of metapopulation theory to most species and more specifically to conservation has been extensive, and at times heated (e.g. Baguette 2004; Hanski 2004; Manning *et al.* 2004). Are we 'fitting a square peg into a round hole' by using the metapopulation paradigm (Noon & McKelvey 1997)? Although the metapopulation framework potentially suits the discrete patches of remnant forest within a pine matrix of our case study, it is questionable whether the species exist as classic metapopulations, governed by local extinction and colonization dynamics. Some of the species are known to use the pine matrix for foraging; others, such as the kookaburra, may use several small patches within one home range; the common ringtail possum appears to prefer fragmented

remnants over larger tracts of forest, possibly because of positive responses to edge conditions (Lindenmayer *et al.* 2002, 2003). However, the broader term of metapopulation, encompassing spatially structured populations linked by dispersal, is likely to apply, although the dynamics and persistence of the species are difficult to model predictively (Lindenmayer *et al.* 2003). In the method presented here, the metapopulation model can be seen as a process-based means of considering the amount, quality and configuration of habitat – an index rather than necessarily the 'true' risk of extinction. More complex models might be more appropriate, but cannot be optimized in a conservation planning framework because they require Monte Carlo simulations, making the problem too computationally intensive to solve. In a multiple-species approach, the problem becomes increasingly complex and less feasible. The challenge is to incorporate greater complexity, realism and stochasticity in such cases without requiring Monte Carlo simulations.

Model uncertainty extends to the metapopulation model used to approximate species persistence. While the Frank & Wissel (2002) model allows us to estimate extinction risk for multiple species, the cost is a simplification of the landscape and approximation of metapopulation dynamics. Frank has described both quantitative and qualitative limitations of the formula, in particular with small numbers of patches or with patches of highly heterogenous size and distances (Frank & Wissel 2002; Frank 2004, 2005). Although the metapopulation model can include correlation in local extinction rates (Frank & Wissel 2002), we assumed that the local extinction rates of the patches are independent, both for the sake of simplicity and because correlation is difficult to parameterize because of lack of data. This is likely to have two significant consequences on the results. First, we are likely to have an overly optimistic view of the extinction risk, as spatial correlation in environmental stochasticity and catastrophes such as fire can have significant negative effects on persistence (Frank 2005). Second, ignoring correlation in local extinction rates may bias the solution towards highly aggregated reserves, as only the advantages of close proximity (i.e. increased colonization rates) are included. In reality, there is likely to be a trade-off between reserve aggregation to improve colonization rates and reserve dispersion because of the strength of correlation in extinction rates (McCarthy *et al.* 2005).

A shortcoming of most conservation decision-support tools, including our method for maximizing persistence, relates to the robustness of the results. A critical source of uncertainty in the method presented here for maximizing persistence comes from epistemic uncertainty associated with knowledge of the state of a system, such as parameter estimates and species distributions, in addition to model uncertainty (Regan *et al.* 2002; Burgman *et al.* 2005). While single-species studies have shown that rankings are often robust to parameter uncertainty, absolute risks of extinction are not (Drechsler *et al.* 2003). In an analysis of the metapopulation model used to estimate extinction risk here, Frank (2004) found that uncertainty in the extinction-area exponent x_k is most critical when ranking management options in a single-species case, with the other parameters affecting the estimates of extinction risk but not rankings. However, in the multiple-species case presented here, the objective, the expected number of extinctions, depends on the absolute estimates of extinction risk. Therefore, the best reserve solution can be sensitive to uncertainty in all parameter estimates across the species. Nicholson & Possingham (in press) examined the effects of parameter uncertainty on the method presented here for maximizing persistence, focussing on the most uncertain parameters: the mean dispersal distance d_k and the extinction-area exponent x_k. Using a simpler case study with fewer species, patches and ignoring habitat quality, they found that the best reserve system can differ with as little as 10% changes in parameter estimates across multiple species (Nicholson & Possingham, in press). We performed a similar analysis with this case study (E. Nicholson, unpublished data), and found that higher levels of parameter uncertainty (greater than 12% changes in parameter estimates across all parameters for all 10 species) could be tolerated with no change in the best reserve system, although the estimated expected number of extinctions differed. This suggests that adding the further constraints of distribution and habitat quality is likely to reduce the impact of uncertainty in parameter estimates, although uncertainty in distribution data themselves could add further sources of sensitivity (Wilson *et al.* 2005; Moilanen & Wintle 2006).

Although our method for maximizing persistence is subject to greater uncertainty than the area-based methods, the benefits for biodiversity persistence appear to be worthwhile. In the three methods for reserve design used here, increasing the level of complexity included leads to greater benefits in persistence, but also increases the data requirements and associated uncertainties. When maximizing area of habitat, the quality of habitat is ignored, and the only data required are distribution data. When maximizing the effective area of habitat, the additional data on the quality of habitat (in this case the population densities) increases the potential for uncertainty (Moilanen & Wintle 2006), but gives some significant increases in persistence. The method for maximizing persistence gave in this case a 20-fold decrease in the expected number of extinctions. While the Frank & Wissel (2002) approximation formula requires less data than many models for assessing population viability (Akçakaya & Sjögren-Gulve 2000), parameter estimates are likely to be uncertain because of gaps in scientific knowledge. The mean dispersal distance d_k and the extinction-area exponent x_k in particular may be difficult to

parameterize, and robustness to uncertainty of the resultant reserve solutions should be assessed (Moilanen & Wintle 2006; Nicholson & Possingham, in press). The decision maker needs to weigh up the biodiversity gains associated with using the different methods, the costs of gathering additional data, and the potential risks of making a decision that is not robust to uncertainty or sub-optimal because of uncertain data.

The concept that space matters in the conservation of populations has driven conservation planners to seek a more species-specific viewpoint of reserve configuration, to which the metapopulation framework seems readily applicable (Opdam *et al.* 2003). The method presented here explicitly includes the amount and quality of habitat and its spatial configuration from a species-specific perspective, and integrates the value of pattern in a justifiable way, based on ecological theory. The next step is to assess the performance of the resultant reserve systems using independent models, based on different and more complex modelling frameworks, rather than the approximation models used here in both the optimization and assessment. In addition, we need to test the ability of a subset of species modelled, including the methods used to select them (such as the focal species approach, Lambeck 1997), to confer protection to other species presumed to be affected by the same processes. With these further assessments, we can start to answer the question: how much of an improvement is provided by process-based models in multi-species conservation planning? We hope that this work will stimulate further interest and novel approaches to tackling the enormous problem of dealing with adequacy in systematic conservation planning.

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APPENDIX 1

Full objective functions for each reserve design problem

Because the search algorithm is slowed down substantially by constraints, we incorporate the budgetary constraint into the objective function, requiring modification of the objective functions for the three problems. When *maximising persistence*, the objective is to minimise the expected number of extinctions subject to budget B (equation 1). The new objective function, with the constraint included, becomes:

$$\text{Minimize } \sum_{k=1}^{n} Pk(\mathbf{r}) + \delta\left(\max\left[0, \sum_{i=1}^{M} r_i.c_i - B\right]\right), \quad (11)$$

for all k species and i reserved patches, where C_i is the cost of patch i. The weighting parameter δ reflects the cost of a unit area of reserve relative to the value of an incremental decrease in the expected number of extinctions. The larger the value of δ the less able we are to go over budget even temporarily. We use a weight of $\delta = 0.01$ to allow one unit

area, such as one hectare, over budget to secure a reduction in the expected number of extinctions of 1%.

For the area of habitat problem, where the objective function is to *maximise the area of habitat* across all species, subject to budget B (equation 9), becomes:

$$\text{Minimise } \sum_{k=1}^{n} \exp\left(\frac{\ln(0.1).\mathcal{A}_k(\mathbf{r})}{G_k}\right)$$
$$+ \delta\left(\max\left[0, \sum_{i=1}^{M} r_i.c_i - B\right]\right). \quad (12)$$

When *maximising the effective area of habitat* across all species, subject to budget B (equation 10), becomes:

$$\text{Minimise } \sum_{k=1}^{n} \exp\left(\frac{\ln(0.1).\mathcal{A}_{eff,k}(\mathbf{r})}{G_k}\right)$$
$$+ \delta\left(\max\left[0, \sum_{i=1}^{M} r_i.c_i - B\right]\right). \quad (13)$$