

Short communication

Uncertainty analysis favours selection of spatially aggregated reserve networks

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ABSTRACT

It has been widely argued that habitat fragmentation is bad for (meta)population persistence and that a high level of fragmentation is a similarly undesirable characteristic for a reserve network. However, modelling the effects of fragmentation for many species is very difficult due to high data demands and uncertainty concerning its effect on particular species. Hence, several reserve selection methods employ qualitative heuristics such as boundary length penalties that aggregate reserve network structures. This aggregation usually comes at a cost because low quality habitats will be included for the sake of increased connectivity. Here a biologically justified method for designing aggregated reserve networks based on a technique called distribution smoothing is investigated. As with the boundary length penalty, its use incurs an apparent biological cost. However, taking a step further, potential negative effects of fragmentation on individual species are evaluated using a decision-theoretic uncertainty analysis approach. This analysis shows that the aggregated reserve network (based on smoothed distributions) is likely to be biologically more valuable than a more fragmented one (based on habitat model predictions). The method is illustrated with a reserve design case study in the Hunter Valley of south-eastern Australia. The uncertainty analysis method, based on information-gap decision theory, provides a systematic framework for making robust decisions under severe uncertainty, making it particularly well adapted to reserve design problems.

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1. Introduction

The primary goal of reserve planning is to increase the probability of the long-term persistence of biodiversity (Vane-Wright, 1996; Pimm and Lawton, 1998; Margules and Pressey, 2000; Cabeza and Moilanen, 2001; Araújo and Williams, 2001; Polasky and Solow, 2001). It is widely recognized that the spatial pattern of reserved habitat may influence the biological value of reserves through its influence on spatial population dynamics. A basic tenet of spatial (meta)population theory is that dispersal of individuals between sites and colonization of empty habitat are influenced by connectivity (distance) and thus aggregated networks are predicted to maintain species better than fragmented ones (Hanski, 1998). This effect has

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been demonstrated but it is difficult to incorporate in reserve designs when several species are involved due to uncertainty about the effects of fragmentation on individual species, the lack of data for quantifying such effects, and the computational demands of incorporating individual fragmentation effects in design algorithms.

Heuristic methods have been devised that increase aggregation in reserve networks, based on the assumption that aggregation is good, especially if it can be achieved with low extra cost. A common way of aggregating reserve networks is the boundary length penalty (Possingham et al., 2000; McDonnell et al., 2002.; Nalle et al., 2002; Önal and Briers, 2002; Fischer and Church, 2003; Cabeza et al., 2004a,b). This method is qualitative in the sense that the biological value of the reserve network is not influenced by the degree of fragmentation. Instead, aggregation is induced via a qualitative penalty given for the boundary length of the reserve.

Aggregation involves trade-offs. There is usually a notional biological cost to increase aggregation because it is usually necessary to include lower quality habitats in order to increase connectivity. However, most studies using the boundary length penalty (cited above) have found that a major decrease in the boundary length of the reserve network can be achieved with a small biological or financial cost. The choice of the most appropriate value for a penalty is heuristic, guided by the trade-off between biological value and reserve aggregation.

Here we investigate aggregated reserve structures obtained by another method – distribution smoothing (Moilanen et al., 2005). In this technique, the distribution of the species is smoothed using a kernel with its width set by an estimate of dispersal distances for the species. The smoothing effectively identifies important semi-continuous regions where the species has overall high levels of occurrence, although not necessarily in every grid cell.

It is shown that if there is uncertainty about the biological value of habitat close to the edge of a reserve then aggregated reserves also provide more robust conservation outcomes in terms of biological value. Biologically, it can be expected that negative edge effects (increased disturbance or predation, invasive species, and changes in abiotic conditions; Debinski and Holt, 2000; Gaston et al., 2002) and metapopulation dynamics (Hanski, 1998) would lead to decreased biological value in cells close to the edge of the reserve network. However, this can be difficult to quantify for many species due to the complexity and high data demands of spatial population modelling. Therefore, an uncertainty analysis approach to assess potential effects of fragmentation on conservation outcomes was used here.

Decision analytical methods (Drechsler, 2000; Harwood, 2000; du Ray et al., 2005; Westphal and Possingham, 2003; Wilson et al., 2005) are well suited for application in conservation planning where resources are limited, tradeoffs between different goals are common, and many uncertain factors may plague biological data and analyses. The aim of this paper is to investigate a method for incorporating uncertainty about species responses to fragmentation into reserve design. Info-gap decision theory (Ben-Haim, 2001) was developed for decisions in the face of severe uncertainty. The objective of info-gap analyses is to identify decisions that achieve a desired outcome or aspiration with the maximum possible level of robustness to uncertainty. In this study, info-gap decision theory is used for quantifying the robustness of reserve design options to uncertainty in species responses to fragmentation. Using a case study in the Hunter Valley region of south-eastern Australia, the potential of uncertainty analysis to assist in the design of aggregated reserve networks is investigated.

2. Methods

2.1. An uncertainty analysis on the effects of fragmentation

Before going to the details of the uncertainty analysis, it is necessary to clarify the meaning of linear and nonlinear reserve selection models (Moilanen, 2005). The analysis that follows below is most relevant for linear reserve selection models. In such models the structure and quality of the landscape may influence the initial conservation value (here probability of occurrence) of sites (grid cells). However, the structure of the selected reserve network does not have an effect on conservation value in reserved sites during the reserve selection optimisation process. For example, effects of future habitat loss around the reserve network would implicitly be ignored in computations. This a typical assumption, for example, in integer programming approaches to reserve planning (see Williams et al., 2004). This kind of an approach is called a linear reserve selection model (Moilanen, 2005).

By contrast, in non-linear reserve selection models, the structure and quality of both the landscape and the reserve network influence the conservation value of selection units, and this is explicitly accounted for in the reserve selection process (Moilanen and Cabeza, 2002; Cabeza, 2003; Westphal and Possingham, 2003; Moilanen, 2005; van Teeffelen et al., 2006). However, most reserve selection is based on linear models, either because fitted nonlinear models (that include effects of connectivity) do not exist for many species or because the planning is in terms of land cover types. Also, substantial computational difficulties associated with the implementation of nonlinear models on large GIS grids may prevent the use of such models in large problems with many landscape units.

Assume first two reserve structures, S_A and S_F . Of these, S_F is fragmented and has been generated by a linear reserve selection model. Spatial aggregation has been induced into S_A heuristically by using some qualitative criteria, such as the boundary length penalty. S_F has apparently higher biological value, because to achieve the aggregation in S_A , some suboptimal habitat has been included to reduce the edge in S_A . It is worth noting that a non-linear reserve selection algorithm (Moilanen, 2005) could identify S_A as having greater biological value than S_F . But, when using standard linear reserve selection methods effects of habitat loss are not seen, and the question is then, what are the true relative values of S_F and S_A , assuming that habitat around the reserve sites will eventually be lost, which in turn would have an effect on the biological value of the reserve network?

This question is approached via an uncertainty analysis, using an application of information-gap decision theory (Ben-Haim, 2001; Regan et al., 2005). The core components of the information-gap uncertainty analysis are (i) an uncertainty model for probabilities of occurrence, (ii) a performance measure, a measure of the conservation value of a reserve network candidate, and (iii) definition of the robustness of the reserve network candidate. Of two reserve network candidates, the best candidate (more robust) is the one which achieves a given conservation target while allowing for higher uncertainty in data.

More formally, the info-gap theory states that the uncertain variable has a nominal estimate \tilde{p}_{ij} , which here is the best estimate of the probability of occurrence (related to habitat quality) for species *j* at cell *i*. The nominal estimate may have been obtained using any standard statistical method (e.g. habitat model). There is also an error rate E_{ij} (also called uncertainty weight) associated with each species in each cell. According to the simplest case, the so-called envelope bound model, the true probability of occurrence in the site belongs to the interval

$$p_{ij} \in [\max(0, \tilde{p}_{ij} - \alpha E_{ij}), \min(\tilde{p}_{ij} + \alpha E_{ij}, 1)], \tag{1}$$

where α is the uncertainty parameter (Ben-Haim, 2001). (The min and max are needed to bound the probabilities to the interval [0, 1].) The error rate E_{ij} could be related, for example, to the standard error of \tilde{p}_{ij} derived from a habitat model. In the present case, since the main interest is uncertainty in biological conservation value due to habitat loss and fragmentation, error rates are explicitly related to the amount of habitat surrounding the reserve network is degraded.

It is assumed that cells deep inside a reserve will not be influenced by habitat loss around the edges of the reserve. Cells close to the edge may lose some of their biological value due to known (via the habitat models) and unknown negative effects of fragmentation. The higher the proportion of habitat lost around a cell, the less certain one would be of the remaining conservation value. To model such effects, Eq. (1) was modified to explicitly include the proportion of cells lost from the neighbourhood of cell i, L_i . We specify that

$$f(\alpha L_i)\tilde{p}_{ij} < p_{ij} < \frac{\tilde{p}_{ij}}{f(\alpha L_i)} \quad p_{ij} \in [0, 1],$$

$$(2)$$

which is a proportional error model in the info-gap terminology (Ben-Haim, 2001). In Eq. (2), $f(\alpha L_i)$ could be any decreasing function of L_i with f(0) = 1, and $f(x) \in (0, 1)$ for all $x \ge 0$. We used a simple relationship $f(\alpha L_i) = \exp(-\alpha L_i)$, but any other decreasing function would give similar results. With this relationship, if $\alpha = 0$ (no uncertainty) or if there is no habitat loss ($L_i = 0$), then f(0) = 1, which means that $p_{ij} = \tilde{p}_{ij}$. Increasing the uncertainty parameter or the fraction of habitat lost will result in a widening bound for p_{ij} . Increasing α results in a rapid potential loss of value from target cells as neighbours are lost. For example, with α = 1, complete loss of neighbouring cells (L_i = 1) indicates a ~70% loss in conservation value. The biological interpretation of $f(\alpha L_i)$ is the proportional loss of conservation value resulting from the loss of structural connectivity incurred as neighbouring cells are removed. Importantly, this quantity can be estimated or measured for many species (see Section 2.3). Note that it is not claimed that any correct value for α is known. Rather, the uncertainty analysis will proceed to analyse how robust different solutions (reserve network candidates) are to increasing uncertainty (α). Of course the best possible reserve network will be absolutely certain to have high conservation value for all species, but unfortunately such candidates are unlikely to be available in reality. Thus, uncertainty analysis will be relevant.

So far it has been specified that nominal probability estimates are not to be fully trusted and that there is a simple model for the bounds between true probabilities could be. The second component that is needed for the uncertainty analysis is a measure of the performance (conservation value) of a candidate reserve network.

In concrete terms, each cell in the grid-based landscape has a probability of occurrence for each species, defined according to a habitat model for that species (Wintle et al., 2005). Here, the value, V_j (**X**, **p**) of the reserve network **X** for species *j* is defined as the proportion of the original full distribution of the species remaining in the given reserve structure **X** with probabilities of occurrence **p** = p_{ij} :

$$V_{j}(\mathbf{X}, \mathbf{p}) = \frac{\sum_{i} \mathbf{x}_{i} \mathbf{p}_{ij}}{\sum_{i} \tilde{p}_{ij}},$$
(3)

where the selection vector $\mathbf{X} = x_i$ has elements $x_i = 1$ for cells in the reserve network and $x_i = 0$ otherwise. Different reserve structures will be differentially resistant to negative effects of fragmentation, which will be analysed via the following robustness analysis.

The question is, given the most adverse choice of p_{ij} possible within the uncertainty bounds (in the present case located at the lower end of the interval given by Eq. (2)), how robust is the conservation decision (reserve structure) to increasing uncertainty (α) concerning negative effects of fragmentation? Formally, in the info-gap theory, the robustness of a solution is defined as

$$\hat{\alpha} = \max\left\{\alpha : \min_{j} \left[\min_{\mathbf{p} \in U(\alpha, \tilde{p}_{ij})} V_j(X, \mathbf{p}) - T\right] \ge 0\right\},\tag{4}$$

where T is a proportional coverage target level of representation (same for all species), and $\mathbf{p} = \{p_{ij}\}, p_{ij} \in U(\alpha, \tilde{p}_{ij})$, which is the uncertainty bound for the probabilities of species *j* (Eq. (2)). Eq. (4) states that the robustness of a reserve structure is the maximal α , $\hat{\alpha}$, with which all species are still represented at least at a level of T, given the most adverse choices of probabilities within the bounds specified by Eq. (2).

The robustness function is used to identify the favoured reserve structure as follows: When evaluating a reserve structure, it is assumed that all non-reserved habitat is eventually lost. Accordingly, the proportion of neighbours lost to each cell (L_i) is calculated (from within a given radius) and the most adverse p_{ij} is then computed according to $p_{ii} = \tilde{p}_{ii} f(\alpha L_i)$. Then, by evaluating Eq. (3), it can be found what the minimum fraction of species distributions is, that can be expected to be in the proposed reserve network candidate X with any given uncertainty level α . Increasing α decreases the target that can be achieved robustly. Note that a minor adjustment to the algorithm would allow the assumption of complete habitat value loss outside of reserve to be relaxed. An alternative approach would be to allow the cells outside of the reserve to maintain some biological value with a level of uncertainty commensurate with the tenure.

2.2. Reserve selection methods: the Zonation algorithm and distribution smoothing

The method used in this study to generate aggregated reserve networks is distribution smoothing (Moilanen et al., 2005). The smoothing can be interpreted as a connectivity computation (Hanski, 1994; Moilanen and Nieminen, 2002), where the connectivity value of a cell is proportional to the number of immigrants predicted to come to the cell. Technically, distribution smoothing is a two-dimensional kernel smoothing (or moving weighted average), where the width of the smoothing kernel is determined by the estimated dispersal ability of the species in question. Smoothed distributions result in more aggregated reserve networks (Moilanen et al., 2005).

Spatial reserve design was done using the Zonation algorithm, which is only summarized briefly here (see Moilanen et al., 2005 for details). Commencing with all cells available for addition to the reserve system, Zonation removes cells iteratively from the landscape. Cell removal is done in a manner that minimizes biological loss by selecting cell i that has smallest biological value according to

$$\delta_i = \max_j \frac{\mathsf{Q}_{ij}(\mathsf{S})\mathsf{w}_j}{\mathsf{c}_i},\tag{5}$$

where w_j is the weight (or priority) of species j and c_i is the cost of adding cell i to the reserve network. The critical part of the equation is $Q_{ij}(S)$, the proportion of the remaining distribution of species j located in cell i for a given reserve network S. (S includes the cells that have not been removed yet.). When a part of the distribution of a species is removed, the proportion located in each remaining cell goes up. This means that, while considering complementarity, Zonation tries to retain core areas of all species until the end of cell removal even if the species is initially widespread and common.

There is one further significant detail in the operation of Zonation, it only removes cells from the edge of the remaining landscape (these are cells that have not been removed but which have a neighbour that has been removed). This way of removing cells promotes a degree of structural connectivity in the solution even when smoothed distributions are not used. In a Zonation run, a best Z% solution can be obtained by simply taking the Z% of cells retained last in the cell removal process. Thus, a single optimisation run produces a nested hierarchy of conservation priority in the landscape: the best 5% of the landscape is nested within the best 10% and so on. To provide sufficient starting points (edge) for the cell removal, urban and intensive agriculture areas can be removed from the landscape prior to the main Zonation run.

2.3. Estimating effects of habitat loss on the priority fauna

Quantifying the effects of local habitat loss or fragmentation is difficult due to complexity of species' responses to the local spatial arrangement of habitats and the lack of data available for making inference about such processes. Here species responses to local neighbourhood habitat loss were approximated using habitat models developed for a planning exercise in the Hunter Valley region of south-eastern Australia (Wintle et al., 2005). The following approximation is based on the average predicted reduction in habitat quality of focal cells that results from a given loss of forest cover in a 2 km radius immediately surrounding the focal cell. For example, most of the models described by Wintle et al. (2005) include the buffer variable 'proportion of unmodified forest within 2 km' as an independent variable (or predictor). It is possible to investigate the effects of habitat loss around a focal cell by modifying the value of the buffer variable, in this case, by decreasing the amount of unmodified forest in the 2 km radius around model fitting locations and recalculating the predicted probability of occurrence for the species using the model.

For each species *j*, the average expected loss (over all cells) of biological value resulting from a proportional loss of habitat in the surrounding area was estimated as:

$$H_j(h) = 1 - \sum_i p_i(h) / \sum_i p_i^*,$$
 (6)

where p_i^* is the predicted habitat value of a cell with all neighbours intact. To calculate $p_i(h)$, the predicted value of cell i after the loss of h% of its neighbours, the values of relevant buffer variables in the cell are first decreased by a fraction h, and then the habitat model is used to predict a new probability of occurrence for the cell. Note that $H_j(h)$ was calculated as a fraction of sums rather than as an average over cell-specific fractions $E[p_i(h)/p_i^*(h)]$. This is because $E[p_i(h)/p_i^*(h)]$ would be dominated by large fractional errors in small probabilities, and locations with low habitat value would dominate the analysis. In contrast, Eq. (6) gives higher weight to effects of habitat loss at the best locations (with highest probabilities), which are the ones most important for conservation planning.

The estimated loss of biological value is naturally sensitive to the choice of habitat model. In cases where no buffer variables made it into the best model for the species, the value of a cell for the particular species will appear to be unaffected by the loss of neighbouring habitat cells. This represents a limitation of the approach chosen to estimate effects of neighbourhood fragmentation in this study, especially in cases where plausible alternative models may contain buffer variables. Future implementation of this approach might search a wider range of candidate habitat models for buffer effects that are not incorporated in the best model.

The uncertainty analysis is applied to the Hunter Valley area, which includes large patches of contiguous forest (>10,000 ha) as well as forest fragments of varying size (10– 1000 ha) and quality interspersed in an urban-agricultural matrix. The study area is 160 by 120 km including 369,253 one-hectare cells of habitat with forest cover. Seven priority fauna species modelled by Wintle et al. (2005) were used to evaluate different reserve structures. They included the sooty owl (Tyto tenbricosa), powerful owl (Ninox strenua), masked owl (Tyto novaehollandiae), yellow-bellied glider (Petaurus australis), tiger quoll (Dasyurus maculatus), koala (Phascolarctos cinereus) and squirrel glider (Petaurus norfolcensis).

3. Results

Fig. 1 demonstrates the difference in a probability of occurrence map (Fig. 1(a)), a smoothed map (Fig. 1(b)) and reserve network structures arising from the use of original (Fig. 1(c))



Fig. 1 – (a) A probability of occurrence map for the sooty owl predicted using a logistic regression habitat model (Wintle et al., 2005). Dark colour indicates relatively high probability of occurrence. (b) A smoothed version of the same map assuming a negative exponential smoothing (dispersal) kernel with a mean dispersal distance of 2 km (α = 0.5). (c) The best 20% of Hunter Valley as defined using the Zonation algorithm (Moilanen et al., 2005) and probability of occurrence maps for seven priority fauna (Wintle et al., 2005). (d) An aggregated 20% reserve structure generated using smoothed distributions for the same seven fauna.

and smoothed distributions (Fig. 1(d)) for many species. There is a marked difference in the aggregation levels of the networks. For example, the scattering of tiny areas in the upper middle area are included in the fragmented solution due to high predicted occurrence levels for the sugar glider. These areas do not come out as important when distribution smoothing is applied. The uncertainty analysis that evaluates the effects of reserve network fragmentation (Section 2.1) can be applied to any reserve structure irrespective of the method used to generate it.

Fig. 2 shows how the estimated biological value of a reserve network may depend on a potential decrease in biological value close to a reserve boundary, as analysed via the info-gap uncertainty analysis here. If the nominal estimates are fully trusted (info-gap uncertainty $\alpha = 0$, all p_{ij} are exactly at their best estimates \tilde{p}_{ij}), then the fragmented solution (1C) starts from a biological value of at least 25.9% of the distributions of all species. The solution based on smoothed distributions (1D) starts from 23.9%, when evaluated by the original best estimates \tilde{p}_{ij} . Thus, the extra aggregation comes with an apparent cost of 2% of the full distributions of the species.

The curves in Fig. 2 have been generated by increasing the value of the uncertainty parameter α (Eq. (2), allowing true p_{ij} to take values from within an increasingly wide interval). In (2B) reserve value is plotted against the assumed maximum

level of biological loss resulting from a given loss of neighbours $(1 - f(\alpha, L_i)$ in Eq. (2)). Different buffer sizes $(3 \times 3, 5 \times 5)$ and 7×7) in Fig. 2 simulate the impact of varying ranges of edge-effect. Species impacted further away suffer potentially more from habitat loss around the reserve area. Consequently, the larger buffers produce lower overall biological value. Locations where solid and dashed lines cross give the point where the conservation decision would reverse if the goal was to maximise remaining biological value. Left of the crossing point (i.e. at lower estimates of biological loss associated with neighbourhood loss) the fragmented solution (1C) is preferable. To the right of the crossing point the more aggregated solution is estimated to be better. For example, the curves cross at 20% when the proportion of lost neighbours is calculated from a 3×3 buffer. The curves cross at 15% when using a 7×7 buffer.

The same figure could also be plotted against a different interpretation for the loss axis. The respective curves cross at 40% (3×3 buffer) and 25% (7×7 buffer) when looking at the level of biological loss with the loss of all neighbours (not shown). The curves cross at 7% (3×3) and 4% (7×7) when looking at biological loss with the loss of only one neighbour out of eight (not shown). The question is, how should these values for crossing points be interpreted biologically?

Intuitively, one would expect all species that are reliant on 'internal' forest (edge avoiders) to be located on the right side



Fig. 2 - Effects of decreased biological value at edges on reserve network performance. The same data has been plotted twice with different interpretations on the x-axis. (a) Decline in reserve performance as uncertainty (a) increases (Eq. (2)). (b) As (a), but plotting $1 - f(0.5\alpha)$, the proportion of cell value lost with the loss of one half of the neighbouring sites within a given buffer. Solid and dashed lines are for the fragmented and aggregated reserve structures shown in Fig. 1(c) and (d), respectively. The analysis was replicated three times using varying buffer sizes for looking at the proportion of habitat lost near the focal cell. These buffer sizes are 3 × 3 (corresponding to topmost lines in the figure), 5 × 5 (middle lines), and 7 × 7 (bottommost lines), respectively. The crossing point of the respective solid and dashed lines indicates a reversal of preference concerning which reserve structure is estimated to be better. To the left of the crossing point the fragmented reserve holds higher biological value and to the right the aggregated reserve is better.

of the crossing points in Fig. 2. For example, a 25% biological loss following the loss of all immediate neighbours is likely to be an underestimate for such species. Similarly, a 20% biological loss following the loss of one half of the neighbours of the focal cell would underestimate the effects of fragmentation on edge-averse species (Weins, 1989). The buffers used in the analysis of Fig. 2 are rather small (cells are 1 ha in size), and loss of neighbouring habitat is likely to impact easily disturbed species such as the sooty owl to distances much further away from the edge. Thus, for the Hunter Valley, one would prefer (1D) to (1C). Another way of interpreting Fig. 2 is that the aggregated reserve is never much worse than the fragmented reserve. On the other hand, it can be much better than the fragmented one if there are any moderate edge effects. Thus, the aggregated reserve structure seems a comparatively safe investment. Safe meaning that known and unknown negative effects of fragmentation would have relatively minor effects on reserve (1D) whereas the true biological value of (1C) could turn out to be much less than that expected based on the original probability of occurrence estimates.

It is also possible to test for edge effects explicitly in the case of the Hunter Valley, because the original habitat models contain neighbourhood measures. Table 1 gives the proportional loss of habitat value resulting from a given decrease in the neighbouring habitat cells for each species. The impact of neighbourhood fragmentation was dramatic for both the yellow-bellied glider and the sooty owl, both of which loose substantial biological value with a relatively small loss of neighbouring habitat. The koala responded negatively to large (75%) or extreme (100%) loss of neighbouring habitat, but was relatively indifferent to moderate losses. The other species were either unaffected or showed slightly positive effects of neighbourhood fragmentation. The sooty owl and the yellow-bellied glider results indicate that they are positioned on the right side of the crossing point in Fig. 2, meaning that the aggregated reserve (Fig. 1(d)) would be a much safer investment than the fragmented one (Fig. 1(c)) for these species. Based on the current results, the other species would be largely indifferent to the reserve options.

4. Discussion

The present analysis describes a quantitative argument that can be used for evaluating uncertain effects of fragmentation on the biological value of a reserve network. Two reserve network structures are compared, a fragmented one and an aggregated one, which apparently has slightly lower biological value because connectivity has been purchased via the inclusion of biologically suboptimal cells into the reserve. The aggregated solution could have been obtained using any reserve selection algorithm that aggregates the reserve in a qualitative sense, e.g. using a boundary length penalty. The present analysis is based on uncertainty analysis and it can answer the question, "how great a decrease in biological value of cells close to the border of the reserve can be assumed before the aggregated reserve is preferable to the more fragmented one"? The present uncertainty analysis helps in identifying reserve structures that are more robust to longterm degradation of the habitat outside the selected reserve areas because it ensures a degree of connectivity in the reserve system itself that might not be there if the reserve was structured on high quality habitat alone.

The analysis of species-specific responses to habitat loss (Table 1) shows that the aggregated reserve network obtained via the use of smoothed distributions (Fig. 1(d)) is a much safer investment than the fragmented one (Fig. 1(c)). These results can be understood by examining the habitat models of Wintle et al. (2005). Of the seven species modelled by Wintle et al. (2005), only one (the powerful owl) contained no vegetation buffer variables, though other topographic buffer

Table 1 – Estimated mean proportion of value (probability of occurrence) remaining in a cell after the loss of a given fraction of suitable habitat from within a 2 km buffer The mean proportion of value remaining in a cell following neighbourhood loss					
Sooty owl	0.350	0.092	0.02	0.01	0.01
Masked owl	-	-	-	-	-
Powerful owl	-	-	-	-	-
Yellow bellied glider	-	0.941	0.266	0.045	0.006
Squirrel glider	-	-	-	-	-
Spot-tailed quoll	-	-	-	-	-
Koala	_	-	-	0.869	0.321

For example, with 50% forest loss, the sooty owl loses 98% of the original probability of occurrence. This data can be used for validating the results of the uncertainty analysis in Fig. 2.

25%

Proportional loss of forest in neighbourhood

variables were included in the best model. For three species, buffer variables were included, indicating the species favoured at least some level of fragmentation in the landscape. There are three possible explanations. First, some species may favour environments with at least a moderate amount of 'edge' habitat for hunting or foraging (e.g. the masked owl showed a positive response to the proportion of cleared land in a 2 km buffer). Second, there may be a correlation between some environmental attributes favoured by the species and fragmentation (e.g. the apparent propensity of koalas to exist in partially fragmented areas is probably because of their reliance on high nutrient locations). Finally, sampling biased toward human inhabited areas may result in a relatively high proportion of observations in those areas, especially if for some reason species are more detectable in such areas (e.g. the squirrel glider). Alternative plausible models containing other buffer variables could be considered.

10%

In the data used here, the yellow-bellied glider and the sooty owl showed a clear and very strong aversion to areas with moderate levels of disturbance and fragmentation. Also, the koala appeared to tolerate only minor to moderate amounts of fragmentation. Furthermore, the Hunter Valley area is likely to include other species that are more sensitive to fragmentation than the ones for which models exist presently. The uncertainty analysis strongly suggests that an aggregated reserve network, as obtained via Zonation and distribution smoothing (Fig. 1(d)), is a safe investment compared to the fragmented one (Fig. 1(c)).

It is known that many species avoid edges due to changes in abiotic conditions or increased predation. However, explicit modelling of the effects of fragmentation has large data demands and is difficult for many species. For example, species interactions, spatially correlated stochasticity and the effect of landscape structure on movement are difficult to model accurately based on typically available sparse data. Furthermore, the modelled species often are a small subset of (indicator) species occurring in the candidate set of sites. Consequently, there is substantial uncertainty about the effects of reserve network fragmentation on the occurrence of all species in the reserve network. The present uncertainty analysis based on information-gap decision theory is a suitable tool for spatial reserve planning when there are severe uncertainties concerning negative effects of fragmentation.

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