Uncertainty Analysis for Regional-Scale Reserve Selection

ATTE MOILANEN,* BRENDAN A. WINTLE,† JANE ELITH,† AND MARK BURGMAN†

*Metapopulation Research Group, Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014, University of Helsinki, Finland, email atte.moilanen@helsinki.fi
†School of Botany, University of Melbourne, Parkville, VIC 3010, Australia

Abstract: *Methods for reserve selection and conservation planning often ignore uncertainty. For example, presence-absence observations and predictions of habitat models are used as inputs but commonly assumed to be without error. We applied information-gap decision theory to develop uncertainty analysis methods for reserve selection. Our proposed method seeks a solution that is robust in achieving a given conservation target, despite uncertainty in the data. We maximized robustness in reserve selection through a novel method, "distribution discounting," in which the site- and species-specific measure of conservation value (related to species-specific occupancy probabilities) was penalized by an error measure (in our study, related to accuracy of statistical prediction). Because distribution discounting can be implemented as a modification of input files, it is a computationally efficient solution for implementing uncertainty analysis into reserve selection. Thus, the method is particularly useful for high-dimensional decision problems characteristic of regional conservation assessment. We implemented distribution discounting in the zonation reserve-selection algorithm that produces a hierarchy of conservation priorities throughout the landscape. We applied it to reserve selection for seven priority fauna in a landscape in New South Wales, Australia. The distribution discounting method can be easily adapted for use with different kinds of data (e.g., probability of occurrence or abundance) and different landscape descriptions (grid or patch based) and incorporated into other reserve-selection algorithms and software.*

Keywords: distribution discounting, distribution smoothing, information-gap decision theory, reserve-network design, site-selection algorithm, spatial reserve design, zonation

Análisis de Incertidumbre para la Selección de Reservas a Escala Regional

Resumen: *Los métodos para la selección de reservas y la planificación de conservación a menudo ignoran la incertidumbre. Por ejemplo, las observaciones de presencia-ausencia y las predicciones de los modelos de hábitat son utilizadas como datos, pero comúnmente se asume que no tienen errores. Aplicamos la teoría de decisiones con vacío de información para desarrollar métodos de análisis de incertidumbre para la selección de reservas. El método que proponemos busca una solución que sea robusta en el logro de una determinada meta de conservación, a pesar de la incertidumbre en los datos. Maximizamos la robustez de la selección de reservas mediante un método novedoso, "descuento de la distribución," en el que la medida del valor de conservación de un sitio o especie (relacionado con las probabilidades de ocupación específicas) era penalizado por una medida de error (en nuestro estudio, relacionado con la precisión de la predicción estadística). Debido a que el descuento de distribución se puede implementar como una modificación de los archivos de datos, es una eficiente solución computable para la inclusión del análisis de incertidumbre en la selección de reservas. Por lo tanto, el método es particularmente útil para problemas de decisiones de altas dimensiones característicos de la evaluación regional de la conservación. Implementamos el descuento de distribución en el algoritmo zonation para la selección de reservas que produce una jerarquía de prioridades de conservación en el paisaje. Lo aplicamos a la selección de reservas para siete faunas en un paisaje en New South Wales, Australia. El método de descuento de la distribución se puede adaptar fácilmente a diferentes tipos de algoritmos (basados*

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en cuadrículas o parches) y se puede incorporar a otros algoritmos y datos de software (e.g., probabilidad de ocurrencia o abundancia) para la selección de reservas, así como a diferentes descripciones del paisaje.

Palabras Clave: algoritmo para la selección de sitios, atenuación de la distribución, descuento de distribución, diseño de redes de reservas, diseño espacial de reservas, teoría de decisiones con vacío de información, zonación

Introduction

Reserve-selection algorithms are decision-support analyses for conservation planning (reviewed by Pressey 1999; Margules & Pressey 2000; Cabeza et al. 2004*a*; Williams et al. 2004). The question is which areas (land parcels) should be protected or targeted for conservation management or restoration? The reserve-selection process can be divided into the definition of a conservation goal (the objective, defining what needs to be optimized) and to the construction of a numerical solution method, which is often called a site-selection algorithm, reserve-selection algorithm, or an area-prioritization method. Different reserve-selection objectives include (1) finding the least expensive solution (e.g., in terms of money, area, effort) that gives at least one population per species with a given aggregate probability of occurrence ("probabilistic representation"; e.g., Haight et al. 2000; Williams & Araújo 2000; Camm et al. 2002), (2) finding the least expensive solution that includes a given proportion of the distribution of a species ("proportional coverage"; e.g., ReVelle et al. 2002; Cabeza 2003; Moilanen 2005), or, similarly, (3) finding the least expensive solution that includes a given proportion of each land-cover type in a region (e.g., Pressey & Tully 1994; McDonnell et al. 2002; Leslie et al. 2003), and (4) maximizing the number of biodiversity features that are adequately reserved given a limit to available resources ("maximum coverage"; e.g., Csuti et al. 1997; Polasky et al. 2000; Arponen et al. 2005).

In contrast to the variety of reserve-selection objectives and solution algorithms, a feature common to all implementations is the acceptance of biological data at face value. An observed absence is treated as a true absence, and a predicted probability of occurrence is treated as a certain estimate, without error. Nevertheless, data have known and unknown errors. For example, a probability of occurrence predicted by a statistical habitat model has an associated 95% confidence interval (Hosmer & Lemeshow 1995). Observation error such as false absences is common in habitat studies (Tyre et al. 2003; Wintle et al. 2005*b*), and numerous other uncertainties are embedded in prediction surfaces, many of which are difficult to quantify statistically (Elith et al., 2002). Uncertainty could arise, for example, from scarce or outdated observational data, anthropogenic land-use changes, or climate change (e.g., Thomas et al. 2004). Consequently, predictions and reserve-selection solutions are clouded by statistical uncertainty in habitat models and by a host of pervasive, nonstatistical uncertainties (Elith et al. 2002).

We describe how such errors may be accounted for in reserve selection. The need to treat uncertainty has been established in the context of population-viability decision analyses (e.g., Maguire 1986; Possingham et al. 2001; Drechsler & Burgman 2004). Nevertheless, uncertainty analysis is by and large missing from most regional-scale reserve-selection methodologies, which need to address high-dimensional optimization problems that can be difficult to solve even without the extra complications introduced by uncertainty analyses.

Taking into account both conservation value and uncertainty creates a prospect of four scenarios: (1) areas with high estimated conservation value and high certainty often are important for conservation, (2) areas with low estimated conservation value and high certainty ordinarily rank low among conservation priorities, (3) areas with high estimated conservation value but low certainty may produce negative surprises for conservation, and (4) areas with low estimated conservation value and high uncertainty may produce positive surprises (e.g., large areas of inexpensive and poorly surveyed land have potential for positive surprises if the absence of observations has been equated to the absence of conservation value). The question confronting the planner is which network of sites is the best solution? To approach this question we used information-gap decision theory (Ben-Haim 2001). In the context of this theory, *best* means the most robust solution, the one most likely to achieve given conservation targets given a level of uncertainty in species distributions. Such a solution is called robust-optimal solution.

Essentially, uncertainty analysis in reserve selection evaluates trade-offs between conservation value and the certainty of information. Moilanen et al. (2006) applied information-gap decision theory (Ben-Haim 2001; Regan et al. 2005) to develop uncertainty analysis methods for the comparison of individual conservation scenarios. They addressed the question of how robustly a particular reserve network achieves a conservation target, given uncertainty in species distributions. Here we focus on how to find a robust-optimal reserve network from a very large set of alternatives. We show how information-gap uncertainty analysis can be made computationally efficient in many site-selection algorithms by simple modification of species-specific distribution data matrices. We demonstrate the proposed technique, which we call *distribution discounting*, by implementing it in a reserve-selection algorithm suitable for large, grid-based data sets (zonation; Moilanen et al. 2005). We applied it to models for seven priority fauna in a 570,000-ha region containing approximately 370,000 ha of partially fragmented forest in New South Wales, Australia (Wintle et al. 2005*a*).

Methods

Information-Gap Decision Analysis for Linear Reserve-Selection Models

Information-gap decision theory (Ben-Haim 2001) utilizes a performance measure (in our case, conservation value) and a model for uncertainty. The aim of the analysis is to find solutions that are robust to the presence of uncertainty. The robust-optimal solution is the one that achieves given performance goals with highest robustness (Ben-Haim 2001). In the present case we wished to achieve conservation targets despite the possibility of there being smaller populations or fewer occurrences in the areas than expected based on the best biodiversity prediction models. The robust-optimal solution was the reserve network that maximized the horizon of uncertainty up to which the reserve network achieved given conservation targets.

We assumed there was a grid-based landscape containing probabilities of occurrence for each species s in each grid cell c. We mark by $\tilde{p}_{sc}$ the nominal (best estimated) probabilities, which in the present case were based on logistic regression habitat models (Wintle et al. 2005*a*). The information-gap formulation states that these probabilities are uncertain and that the true probability $p_{sc} \in [0,1]$ is likely to differ from $\tilde{p}_{sc}$. In the simplest case p_{sc} could be within an interval specified by an envelope bound (Ben-Haim 2001)

$$\max\{0, \tilde{p}_{sc} - \alpha E_{sc}\} < p_{sc} < \min\{1, \tilde{p}_{sc} + \alpha E_{sc}\}, \quad (1)$$

where α is a horizon of uncertainty and E_{sc} is any error weight related to the accuracy of $\tilde{p}_{sc}$. Because the probabilities of occurrence used come from logistic regressions, we used a plausible alternative for the uncertainty model, which defines the uncertainty interval (Eq. 1) in logit space:

$$|\text{logit}(p_{sc}) - \text{logit}(\tilde{p}_{sc})| < \alpha E_{sc}, \quad (2)$$

where E_{sc} is the standard error for the linear predictor of a logistic regression. Equations 1 and 2 state that the true probability p_{sc} could be either higher or lower than the estimate $\tilde{p}_{sc}$, with the bounds for p_{sc} determined by α and the relative error measure E_{sc}.

We denoted a reserve network (set of grid cells) by $\boldsymbol{X}$, making it possible to calculate the representation, $R_s(\boldsymbol{X}, \boldsymbol{p}_s)$, of species s in $\boldsymbol{X}$ given a vector of probabilities $\boldsymbol{p}_s = \{p_{sc}\}$. For the expected number of occurrences, the representation $R_s(\boldsymbol{X}, \boldsymbol{p}_s) = \sum_{c \in X} p_{sc}$. If a species-specific level of target representation is T_s then the requirement for reserve selection is $R_s(\boldsymbol{X}, \boldsymbol{p}_s) > T_s$ for all species. Whether targets are satisfied depends on $\boldsymbol{X}$ and $\boldsymbol{p}_s$, and $\boldsymbol{p}_s$ is bounded by Eq. 2 at any given horizon of uncertainty α.

In information-gap terminology (Ben-Haim 2001) the robustness of a reserve design $\boldsymbol{X}$ is the largest horizon of uncertainty, $\hat{\alpha}$, up to which given targets are satisfied given the most adverse choice of probabilities allowed by Eq. 2. Importantly, given our definitions, the most adverse choice of probabilities always occurred when all probabilities were at their lower bounds (i.e., when the lowest expected number of populations were obtained),

$$\text{logit}(p_{sc}) = \text{logit}(\tilde{p}_{sc}) - \alpha E_{sc}. \quad (3)$$

The robust-optimal reserve design, $\boldsymbol{X}^*$, is by definition the one that achieves given targets T_s while allowing for the highest possible level of uncertainty, α, in Eq. 3. In other words a robust reserve network would achieve the given conservation targets even if there is substantial error in the nominal probability of occurrence estimates. Formally, the information-gap definition of robustness $\hat{\alpha}$ is

$$\hat{\alpha} = \max\left\{\alpha : \min_s \left[\min_{\boldsymbol{p} \in U(\alpha, \tilde{\boldsymbol{p}})} R_s(\boldsymbol{X}, \boldsymbol{p}) - T_s\right] \geq 0\right\}, \quad (4)$$

where $U(\alpha, \tilde{p})$ is the uncertainty interval defined by Equation 2 and R_s and T_s are the representation and target for species (biodiversity feature) s, respectively.

Directly following from the information-gap formulation, one could implement the following algorithm to find the robust-optimal reserve network:

1. Set highest obtainable robustness $\alpha^* = 0$.
2. Repeat (e.g., by a using a stochastic optimization process).
   2.1. Generate a new candidate reserve design, $\boldsymbol{X}$, that does not exceed a limit, $C_{\max}$, for reserve cost, $\text{cost}(\boldsymbol{X}) < C_{\max}$.
   2.2. Calculate highest α, $\hat{\alpha}$, that still allows $R_s(\boldsymbol{X}, \boldsymbol{p}_s) > T_s$ for all species s, given the most adverse choice of probabilities as defined by Eq. 3.
   2.3. If $\hat{\alpha} > \alpha^*$, replace $\boldsymbol{X}^*$ with $\boldsymbol{X}$ and α^* with $\hat{\alpha}$.

This way of searching for robust optimal reserves is not convenient because of item (2.2), which requires finding the highest α that allows the targets to be met. The critical level of α can be found by a divisive search strategy (e.g., binary search) along the α-axis, which iteratively places α into a decreasingly short interval. In 20 iterations $\hat{\alpha}$ can be determined to a very high precision. Even so, the calculations of Eq. 3 would need to be repeated many times.

An alternative is that the performance of each solution (each alternative reserve network is represented by a line in Fig. 1) can be examined as uncertainty increases. Some

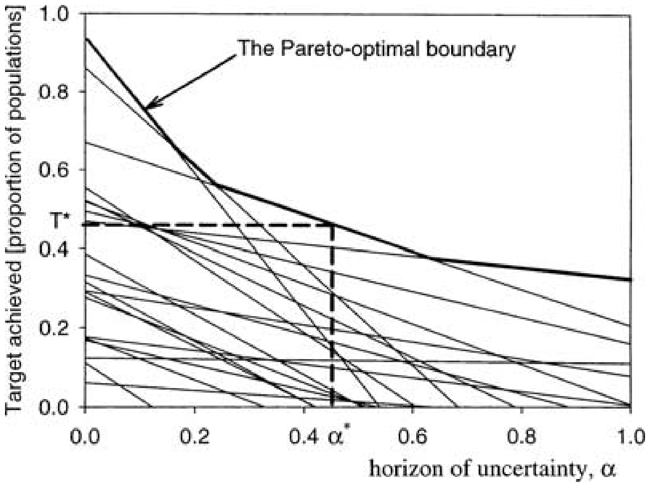

Figure 1. Conceptual scheme for the inclusion of uncertainty analysis in reserve selection. Each thin line represents one solution (reserve-network spatial structure). The thick line is the Pareto-optimal boundary, which represents solutions that are optimal in the sense that increased conservation value can only be obtained with the cost of lowered robustness, and vice versa. An increasing robustness requirement (α) implies that a decreasing conservation target can be achieved. For any given level of uncertainty α^*, there corresponds a maximal target T* *that can be achieved.*

designs are always bad, and some are good according to nominal habitat-model predictions but bad if uncertainty in models is incorporated. Other designs have intermediate nominal performance but have good robustness to uncertainty. Importantly, when searching for the robust-optimal design, only a small subset of all possible reserve designs is of interest. These designs are at the Pareto-optimal boundary with respect to the target. To achieve greater robustness one must sacrifice conservation value, and vice versa. A Pareto-optimal reserve network has the highest possible robustness α^* that can be obtained for any given target level T^*. From a computational perspective it is relevant that a Pareto-optimal design also achieves the highest possible target T^* for any given robustness requirement α^*. Therefore, we used the following algorithm (called distribution discounting) for finding information-gap, robust-optimal reserve designs:

1. Specify robustness requirement α^*.
2. Perform distribution discounting. Read in species information. For every species and cell, set $\text{logit}(p_{sc}) = \text{logit}(\tilde{p}_{sc}) - \alpha^* E_{sc}$ and calculate p_{sc} from the logit value.
3. Use any (linear) reserve-selection algorithm to search over spatial patterns. The robust optimal design $\boldsymbol{X}^*$ is the one that achieves the highest possible conservation target with the given α^*, assuming a limit to reserve network cost.

Thus, the optimization is changed to a maximization of the target achievable through the use of discounted distributions. The advantage of this approach is that the worst-case probability set has to be calculated only once (in item 2); thereafter, the contributions of cells to representation levels, p_{sc}, do not change. This means that distribution discounting can be done as a preprocessing step before using any existing reserve-selection software to do the optimization. Naturally, different optimization runs are necessary to find maximal target levels and corresponding designs for different robustness requirements.

With nonlinear reserve-selection formulations (Moilanen 2005) information-gap analysis can be substantially more complicated than described here. In these formulations the spatial structure of the candidate reserve network explicitly affects the conservation value in selection units. Consequently, finding the most adverse set of conditions (the minimization within Eq. 4) within the uncertainty bounds (analog of Eq. 3) defined by the robustness requirement is no longer simple. Reserve-selection objectives that seek to delineate aggregated reserves often display nonlinear characteristics. We generated reserve aggregation via a procedure, distribution smoothing, in the context of which information-gap analysis can be implemented in a linear manner.

The Zonation Algorithm and Distribution Smoothing

The search for robust-optimal solutions is essentially a search for a solution over all feasible reserve networks, and with many selection units (L) this is an enormous search space. We were interested in landscapes at typical management scales that potentially have hundreds of thousands of grid cells. Searching such a space requires specialized methods because common approaches are limited computationally (e.g., integer-programming formulations reach their limit at approximately 10,000 landscape units due to the combinatorial explosion of the search space [Williams et al. 2004]). Here we selected reserves through a method called zonation, which uses a reverse stepwise heuristic approach to produce a hierarchy of conservation priorities throughout the landscape (Moilanen et al. 2005). Distribution smoothing (Moilanen et al. 2005) is a method that can be used in conjunction with zonation to identify reserve areas that are aggregated at a scale relevant for the focal species.

Zonation starts from the full landscape and cells are removed stepwise to minimize loss of conservation value. Thus, the least important areas are removed first, leaving the most important areas that remain, with each cell allocated a score based on its rank order of removal. In the basic zonation algorithm (Moilanen et al. 2005), cells are only removed from the edge of the remaining area, which makes the procedure computationally efficient and promotes structural connectivity in the remaining landscape.

Site cost and species weights are considered in zonation in the equation determining the removal order of grid cells. The cell *i* to remove next is the one with the smallest maximum conservation value across species, δ_i:

$$\delta_i = \max_j \frac{Q_{ij}(\boldsymbol{S})w_j}{c_i}, \qquad (5)$$

where w_j is the weight of species *j* and c_i is the cost of cell *i*. A critical part of Eq. 5 is $Q_{ij}(\boldsymbol{S}) = p_{ij} / \Sigma_{i \in S}\, p_{ij}$, which is the proportion of the remaining distribution of species *j* located in cell *i* in the set of remaining cells $\boldsymbol{S}$. When part of the distribution of a species is removed (via iterative removal of cells from $\boldsymbol{S}$), the proportion present in each remaining cell goes up. This means zonation retains core areas of all species until the end of cell removal, even if the species is initially widespread and common. A zonation solution is nested (i.e., the best 5% is within the best 10% and so on). A single optimization run produces a removal rank surface that can be cut at any given level (e.g., 20%) to give the set of cells belonging to that fraction of the landscape.

Moilanen et al.'s (2005) variant of zonation operates linearly in the sense that the structure of the remaining landscape does not affect the occurrence of species in cells. Nevertheless, it is well known that linear reserve-selection models may lead to excessively fragmented reserve structures, which is evident from a comparison between methods that either use or do not use a mechanism, such as the boundary-length penalty, for inducing aggregation into reserve networks (e.g., Possingham et al. 2000; Nalle et al. 2002; Fischer & Church 2003; Cabeza et al. 2004*b*). When effects of landscape structure are considered explicitly (assuming habitat loss outside reserve areas), optimal reserve networks become aggregated (e.g., Cabeza 2003; Moilanen 2005; van Teeffelen et al. 2006).

We used the distribution smoothing technique of Moilanen et al. (2005) to generate aggregated reserve networks. In distribution smoothing a connectivity surface is calculated based on the original distribution (here probability of occurrence) map for the species. We calculated this surface by applying a negative exponential (dispersal) kernel on the landscape, assuming that the probabilities represent source population sizes (Moilanen 2005; Moilanen et al. 2005). In the smoothed surface the value of a grid cell is proportional to the expected number of migrants potentially using the cell. In practice, the distribution of the species in the landscape becomes smoother and populations in fragmented areas have less value relative to continuous areas with the same average probability of occurrence. Essentially, we sought to identify continuous habitat areas with high, reliably predicted population occurrences for all species, so we replaced the original distribution maps of the species with the discounted and then smoothed surface for the purposes of reserve selection.

Distribution smoothing is relevant only when selection units are small relative to the scale of population dynamics of the focal species. This is the case with our application, in which all species may move at a scale much larger than the 1-ha grid cells used in the habitat modeling.

Distribution Data for Priority Fauna

Distribution data used in the analysis came in the form of seven raster habitat maps, in which each element of each map (cell) represents the predicted probability of occurrence for one of seven fauna species. All maps have a cell size of 1 ha. Predictions of the probability of occurrence were derived from logistic regression models developed for seven priority fauna species in the Lower Hunter-Central Coast (LHCC) region of southeastern Australia for use in regional conservation planning (see Wintle et al. 2005*a* for a detailed description of the models and model validation). Habitat modeling was based on variables such as temperature, rainfall, elevation, terrain ruggedness, and the amounts of dry, wet, and unmodified forest in 500-m or 2-km circles around the focal site (Wintle et al. 2005*a*).

The priority fauna were seven vertebrate species: 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*). Habitat distribution maps for each species contained approximately 370,000 individual grid-cell predictions. Areas without forest cover (approximately 200,000 ha) were considered to have no habitat value for the species and were not considered in the analysis. For the purpose of demonstrating our approach, we did not include the other biological, social, or economic values and constraints that would normally be considered in a full conservation planning effort (e.g., Cowling et al. 2004).

Results

Distribution-discounted maps give insight into the trade-offs between predicted probabilities and errors (Fig. 2). For Sooty Owls, areas that combined high nominal predictions with low error, such as the region close to the center of the Hunter Valley, emerged with highest conservation values (Fig. 2). Other areas had high estimates and high error. For example, one area (top right, Fig. 2) had relatively high probabilities of occurrence for the owl (Fig. 2a), but when high uncertainty (Figs. 2b & 2c) and effects of fragmentation (via distribution smoothing, Fig. 2d) were considered, the area had low certainty of being an important habitat for the owl. Distributions for the other species had similar characteristics (not shown). We expect the trade-off between the probability of occurrence and the

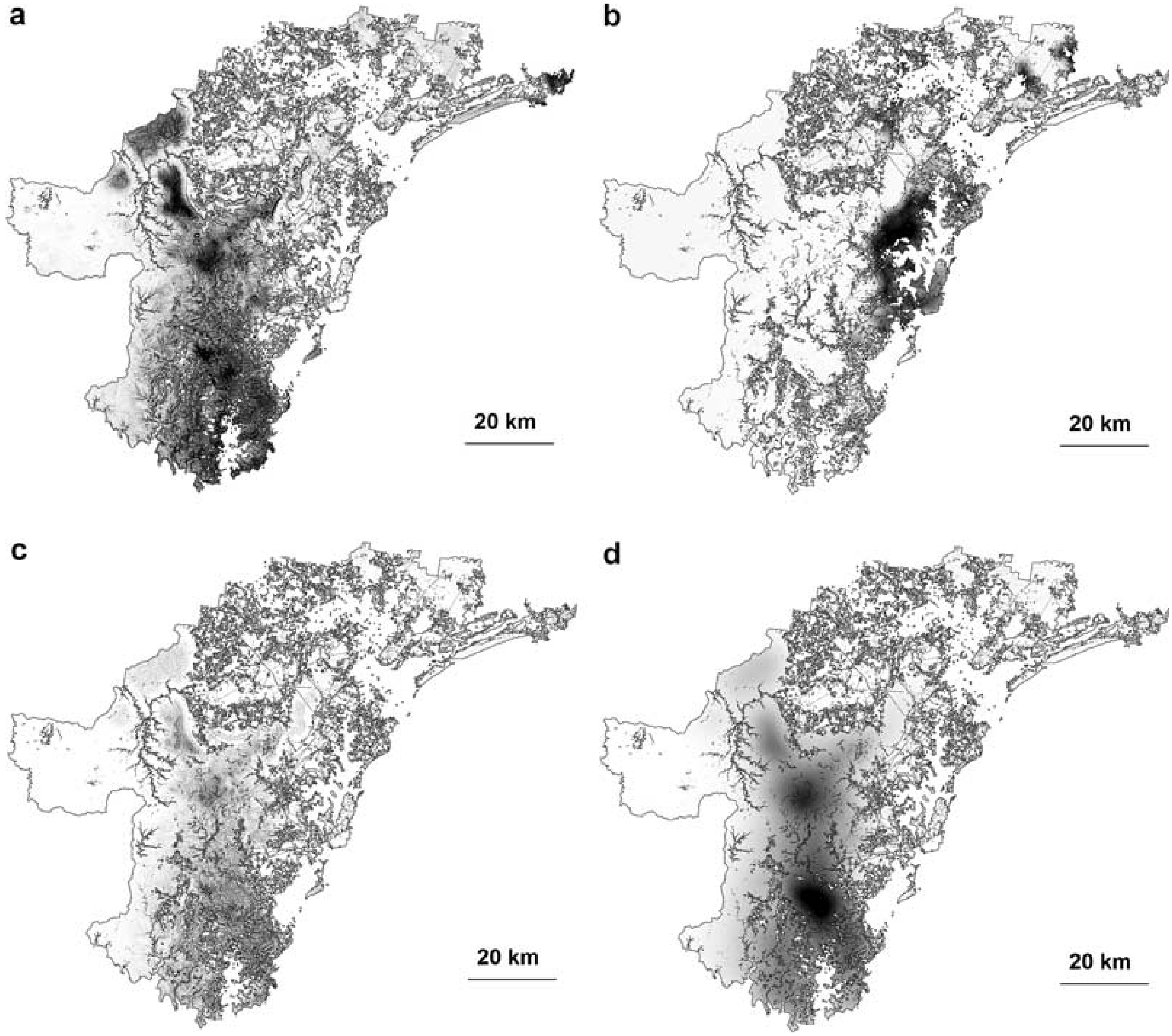

Figure 2. Reserve selection and uncertainty analysis based on discounted distributions as applied to the Sooty Owl in the Hunter Valley region: (a) probability of occurrence predictions from a habitat model (Wintle et al. 2005a) (dark area, probabilities close to one; white areas, probability of zero); (b) respective error distribution, with dark shading corresponding to high relative error in predictions; (c) discounted distribution according to Eq. 3, essentially a multiple of (b) has been subtracted from (a) in logit space; (d) connectivity distribution calculated by distribution smoothing on (c) assuming the species has an average annual dispersal distance of 2 km.

certainty of the estimate will be relevant for many if not most species.

We investigated consequences of varying the levels of distribution smoothing and distribution discounting in the Hunter Valley data (Fig. 3). The smoothing parameter was varied from zero to values corresponding to double the annual dispersal distances. The robustness requirement was assigned values of 0, 1, and 2, which corresponded to subtracting the respective number of standard errors from the linear predictor value of each grid cell in logit space, after which the link function was applied to obtain probabilities. The greatest differences arose from distribution smoothing. Solutions that were not smoothed (row 1) differed in that they included large numbers of small fragments. In contrast, the large features of the solutions were relatively unaffected by the robustness requirement (Fig. 3 compare panels within each row). This suggests that the distribution uncertainty is not a major consideration in reserve selection for these species in the Hunter Valley.

A moderate robustness requirement (−1 SD) and smoothing corresponding to estimated annual dispersal distances yielded a potentially "reasonable" solution (third row, second column, Fig. 3). Nevertheless, the

Figure 3. Effects of distribution smoothing and uncertainty analysis on reserve solutions for the Hunter Valley (black, spatially distinct areas included in the best 20% of the landscape according to the zonation applied on the species distributions; gray scale, outside the best 20% of the landscape; light shading, least important areas). Species distributions were treated with uncertainty analysis (see Fig. 2) and distribution smoothing (by row: 1, no smoothing; 2, halved dispersal distances; 3, normal dispersal distances; and 4, double dispersal distances; by column: 1, no robustness requirement; 2, α = 1; 3, α = 2).

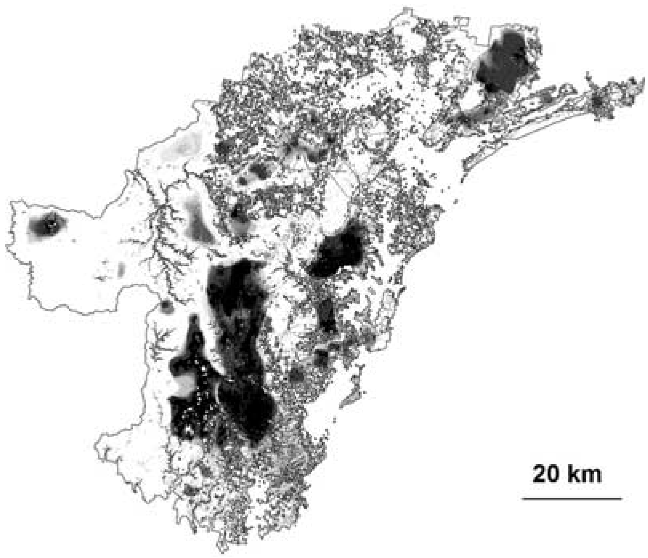

Figure 4. A summary of the results shown in Fig. 3. The gray scale indicates frequency of inclusion into the best 20% from 1 (light gray) to 12 times (black) in the panels shown in Fig. 3. Dark regions are thus the areas most reliably important for the priority fauna.

correct amounts of distribution smoothing and discounting were unknown. Even so, an analysis of selection frequency provided some insight into the best possible reserve network for these species in the Hunter Valley. A cumulative analysis indicated that 61% of the landscape was never selected in any of the 12 analyses (Fig. 4), showing that these are areas of relatively low value irrespective of the assumptions made concerning distribution smoothing and uncertainty analysis. The remaining 40% of the landscape was selected in at least 1 of the 12 analyses, and 5% of the landscape was selected in all 12 analyses. Three comparatively large areas were selected consistently (Fig. 4; the largest one in the middle, one in the east, and one in the northeast). These areas are likely to be the robust core areas for the distributions of these fauna in Hunter Valley.

Discussion

Data for conservation assessment are never complete or without error. Some species are not surveyed and some populations and occurrences remain unobserved (e.g., MacKenzie et al. 2002; Tyre et al. 2003; Wintle et al. 2005*b*). Distribution modeling introduces additional error, and habitat models naturally explain only a part of the variance in the distributions of species. There is uncertainty, for example, in the structure of the habitat model, in the variables included, and in the coefficients fitted for different variables (Elith et al. 2002). Information-gap theory can accommodate nonstatistical uncertainties such as the subjective choice of candidate variables and the structural assumptions embedded in spatial analysis.

We focused on uncertainty in predicted probabilities of occurrence. One site (grid cell) may have a high probability, and this information may be certain because the nominal estimate is based on conditions that are statistically confidently associated with a high occurrence probability. Another area may have an equally high probability of occurrence, but the estimate may be based on an environmental condition (variable) with a large standard error. In many cases one might be willing to forego aspirations (in the nominal estimates) in favor of a reserve network that is more robust to uncertainty in distribution estimates. The trade-off between estimated conservation value and the certainty of the information may lead to qualitatively different planning objectives that reflect the planner's attitude toward risk. Choosing sites that have lower, more certain estimates would reflect aversion to risk.

Other sources of uncertainty, not addressed in this study, may affect the value of a site. For example, a site may not retain its value in the face of urban expansion (e.g., Pressey et al. 2004), populations may not persist (Cabeza & Moilanen 2001), and correlated spatial dynamics may cause synchronous fluctuations in occupancy, resulting in the loss of populations living in a small group of cells (Moilanen & Cabeza 2005). Climate change may cause regional-scale changes in environmental conditions, leading to the loss of apparently large and stable populations (e.g., Thomas et al. 2004). Socioeconomic factors influencing site availability and future land use might also be treated as forms of uncertainty in reserve selection. To accommodate such factors in the information-gap model would require one to build a model of these uncertainties (resulting in relative error weights at selection units) and then to analyze the model as we did for the confidence intervals here in this study. The intervals could be based on subjective judgment or on models that predict the kind and variability of responses to ecological pressures such as urban development and climate change.

Here we identified core areas for protection of priority fauna in the Hunter Valley. We located three relatively large and continuous blocks that were robustly included in the most important 20% of the landscape, irrespective of the choices of assumed scale of habitat use of the species and of the chosen horizon of uncertainty. Similarly, some 60% of the landscape was never chosen under any assumptions, suggesting that these areas should not be priorities in conservation planning (for the best 20% of the landscape for the priority fauna).

The present application of the distribution discounting method applies to the envelope-bound model (Eqs. 1 & 2) of the information-gap formulation. Other error structures, such as the proportional bound (Ben-Haim 2001), only require changes to Eq. 2. Distribution discounting can be applied to abundance-based distribution models by penalizing nominal abundance with a multiple of an error measure. Similarly, distribution discounting is also applicable in the context of patch-based reserve-selection algorithms, although then it is necessary to consider carefully the effect of patch size on the error weight assigned to the patch. Furthermore, distribution discounting could be easily implemented in the context of other reserve-selection algorithms and software than zonation, which we used here.

The steps we developed here are among the first of many that can be taken to develop uncertainty analysis methods for reserve selection. For example, we looked at the search for robust solutions, but ignored another aspect of decision theory—opportunity (Ben-Haim 2001). In this context opportunity means areas that have high potential of proving better opportunities for conservation than is apparent, based on available information. In addition, one could explore the robustness of an individual site being included in an optimal solution, the robustness of the persistence of a metapopulation, or the effects of assumed dispersal distances on optimal reserve networks. Much work in uncertainty analysis for reserve selection remains. The reward will be improved confidence in efficient, robust, and defensible conservation decisions.

Acknowledgments

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