
The Boundary-Quality Penalty: a Quantitative Method for Approximating Species Responses to Fragmentation in Reserve Selection

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Abstract: *Aggregation of reserve networks is generally considered desirable for biological and economic reasons: aggregation reduces negative edge effects and facilitates metapopulation dynamics, which plausibly leads to improved persistence of species. Economically, aggregated networks are less expensive to manage than fragmented ones. Therefore, many reserve-design methods use qualitative heuristics, such as distance-based criteria or boundary-length penalties to induce reserve aggregation. We devised a quantitative method that introduces aggregation into reserve networks. We call the method the boundary-quality penalty (BQP) because the biological value of a land unit (grid cell) is penalized when the unit occurs close enough to the edge of a reserve such that a fragmentation or edge effect would reduce population densities in the reserved cell. The BQP can be estimated for any habitat model that includes neighborhood (connectivity) effects, and it can be introduced into reserve selection software in a standardized manner. We used the BQP in a reserve-design case study of the Hunter Valley of southeastern Australia. The BQP resulted in a more highly aggregated reserve network structure. The degree of aggregation required was specified by observed (albeit modeled) biological responses to fragmentation. Estimating the effects of fragmentation on individual species and incorporating estimated effects in the objective function of reserve-selection algorithms is a coherent and defensible way to select aggregated reserves. We implemented the BQP in the context of the Zonation method, but it could as well be implemented into any other spatially explicit reserve-planning framework.*

Keywords: boundary length, connectivity, edge effect, fragmentation, habitat model, model averaging, reserve selection, site-selection algorithm, Zonation

La Sanción Calidad del Lindero: un Método Cuantitativo para Aproximarse a las Respuestas de Especies a la Fragmentación en la Selección de Reservas

Resumen: *La agregación de redes de reservas generalmente es considerada deseable por razones biológicas y económicas: la agregación reduce los efectos de borde negativos y facilita la dinámica de la metapoblación, que plausiblemente beneficia a la persistencia de las especies. Económicamente, la gestión de redes agregadas es menos costosa que la de redes fragmentadas. Por lo tanto, muchos métodos para el diseño de reservas utilizan heurísticas cualitativas, tales como criterios basados en la distancia o sanciones de la longitud del lindero, para inducir la agregación de reservas. Diseñamos un método cuantitativo que introduce agregación a las redes de reservas. Denominamos al método sanción de la calidad del lindero (SCL) porque el valor biológico de una unidad de terreno (celda de la rejilla) es sancionado cuando la unidad ocurre tan cerca del borde de una reserva de tal modo que una fragmentación o el efecto de borde podría reducir la densidad de las poblaciones en la celda reservada. La SCL puede ser estimada para cualquier modelo de hábitat que incluya efectos de vecindad (conectividad), y que pueda ser introducida en software de selección de reservas de manera estandarizada. Utilizamos la sanción de la calidad del lindero en un estudio de caso de diseño de*

reservas en Hunter Valley, en el sureste de Australia. La SCL resultó en una estructura de red de reservas mucho más agregada. El grado de agregación requerida fue especificado por respuestas biológicas a la fragmentación observadas (aunque modeladas). La estimación de los efectos de la fragmentación sobre especies individuales y la incorporación de efectos estimados en la función objetiva de algoritmos de selección de reservas es una forma coherente y defendible de seleccionar reservas agregadas. Implementamos la SCL en el contexto del método de Zonación, pero bien pudo haber sido implementado con cualquier otro marco de referencia para la planificación de reservas espacialmente explícito.

Palabras Clave: algoritmo para la selección de sitios, conectividad, efecto de borde, fragmentación, lindero, modelo de hábitat, promedio de modelos, selección de reservas, Zonación

Introduction

Fragmentation influences species distributions via metapopulation dynamics and edge effects (e.g., Hanski 1998; Debinski & Holt 2000). When aiming at long-term persistence of species within reserves (e.g., Vane-Wright 1996; Margules & Pressey 2000; Cabeza & Moilanen 2001), it is important to account for the biological consequences of fragmentation. Nevertheless, doing so is hard because of high computational demands of spatial population modeling and lack of knowledge concerning species responses to fragmentation (Moilanen & Wintle 2006).

Aggregation of reserve networks is desirable to mitigate known and unknown effects of fragmentation (see Williams et al. 2005; Moilanen 2005 for references). Thus, various heuristics have been developed to induce aggregation in reserve networks. These include distance criteria, core-area methods, and boundary-length penalties (BLPs). Examples of distance criteria include selecting sites nearest to already selected sites (Nicholls & Margules 1993), minimizing the diameter of the reserve network (Önal & Briers 2002a), and minimizing the sum of inverse interpatch areas (Rothley 1999). Area and core-area methods set requirements for the minimum areas or minimum effective areas of reserve sites, accounting for buffer zones (e.g., Batisse 1990; Kunin 1997; Clemens et al. 1999; Burgman et al. 2001).

Boundary length penalties (BLPs) are perhaps the most widespread way of inducing aggregation in reserve networks (e.g., Possingham et al. 2000; Nalle et al. 2002; Önal & Briers 2002b). A BLP is simply a penalty term inserted into the objective function of the reserve selection. The term gives a high penalty when the ratio of reserve edge to reserve area is high. When the reserve is highly aggregated, the penalty is low. As a consequence of having the penalty term in the objective, the reserve network proposed by the reserve-selection algorithm becomes aggregated. The most appropriate value for the BLP is usually determined by an arbitrarily weighted trade-off between apparent conservation value and reserve aggregation. Notably, a very high value for the penalty may force the inclusion of significant amounts of low-quality habitat into

the reserve, reducing the biological value that can be obtained otherwise for a given reserve area (or expenditure). Many researchers have found that significant reserve aggregation can be obtained with little extra cost (e.g., McDonnell et al. 2002; Fischer & Church 2003; Cabeza et al. 2004).

In addition to qualitative heuristics, a few studies have included explicit, species-specific effects of fragmentation (connectivity) into reserve selection (e.g., Cabeza 2003; Westphal & Possingham 2003; Moilanen 2005; van Teeffelen et al. 2006). These studies account for the influence of connectivity on predicted numbers of individuals or populations, and they essentially have implemented inside the reserve-selection software a statistical model of the effects of landscape structure on species occurrence. On the downside including connectivity effects in large problems can be computationally expensive. A computationally efficient technique, distribution smoothing (Moilanen et al. 2005), approximates the connectivity requirements of species by including a species-specific scale of landscape utilization into the reserve-selection process, inducing aggregation in reserve design. Other methods that attempt to optimize species persistence by incorporating spatially explicit population models in the reserve-selection process are extremely demanding of data and computation time, making them impractical in most situations (Moilanen & Cabeza 2002; Westphal et al. 2003).

Negative edge effects (Debinski & Holt 2000; Gaston et al. 2002) and metapopulation dynamics (Hanski 1998) are perhaps the two most important factors that could lead to decreased conservation value of cells that are close to the edge of a reserve network. These effects are implicitly apparent in statistical habitat models, which often include neighborhood measures or buffer variables in the best-fitting models (e.g., Wintle et al. 2005). The presence of a buffer variable (such as the amount of forest within a given radius) in a habitat model implies that the species may respond negatively to nearby habitat loss. Here we describe use of the *boundary-quality penalty*, a novel quantitative way to induce aggregation into reserve networks. First we estimated how species-specific probabilities of occurrence are influenced by the proportion of

good habitat in the neighborhood of the focal cell. Essentially, the neighborhood effects present in a habitat model are condensed to one response function, which can be used efficiently in a reserve-selection algorithm. We then implemented this effect in a recently developed conservation-planning algorithm, Zonation (Moilanen et al. 2005, 2006; Moilanen & Wintle 2006; Moilanen 2007), which produces a hierarchy of conservation priority throughout the landscape. We demonstrated our approach in the context of a case study in which the aim was to identify suitable habitat to be conserved for priority fauna in the Hunter Valley, Australia.

Methods

Adding the Boundary-Quality Penalty to the Zonation Algorithm

We used the Zonation algorithm, which is summarized briefly here (see Moilanen et al. [2005] for details), to identify potential conservation priority areas. Zonation produces a hierarchy of conservation priority throughout the landscape. Starting from the full landscape, Zonation iteratively removes cells from the edge of the remaining area, and the rank of removal gives the priority for the cell (most important cells remain until last). Cell removal is done in a manner that minimizes biological loss by picking an edge cell i that has the smallest δ value:

$$\delta_i = \max_j \frac{Q_{ij}(S)w_j}{c_i}, \quad (1)$$

where w_j is the weight (or priority) of species j , c_i is the cost of adding cell i to the reserve network, and $Q_{ij}(S)$ is the proportion of the remaining distribution of species j present in cell i , calculated for the set of remaining cells S .

The critical element in Eq. 1 is $Q_{ij}(S)$. When a part of the distribution of a species is removed, the proportion of the distribution located in each remaining cell goes up. This means that Zonation tries to retain core areas of all species until the end of cell removal even if the species is initially widespread and common. The min-max structure of Eq. 1 also indicates a strong preference for retaining the best locations with the highest occurrence levels—Zonation does not treat probabilities of occurrence as additive. Ten locations with $p = 0.099$ are not the same as one location with $p = 0.99$.

In Zonation cell removal continues until all cells have been removed from the landscape. A best $x\%$ solution (where x represents a given proportion of habitat allocated to reserve) can be obtained by simply taking $x\%$ of the cells retained last in the process of cell removal. Thus, a single run produces a hierarchy of conservation priority in the landscape: the best 5% of the landscape is within the best 10% and so on. It is an important feature of

Zonation that the entire hierarchy of solutions (different cut levels) can be visualized in a single graph. The fact that Zonation removes cells only from the edge of the remaining landscape means that a degree of structural connectivity is retained in the solution even when no special measure to induce aggregation is used. Removal from the edge also makes the algorithm efficient with large data sets because only cells at edges are candidates for removal. A simple variant of Zonation allows removal of cells from anywhere within the landscape, but in our experience this has had little effect on the results, especially for a region like Hunter Valley, where there is plenty of low-quality edge. (The importance of edge-removal is case-specific and should be separately investigated with each new data set.)

We introduce a variant of the Zonation algorithm, which explicitly considers the boundary-quality penalty (BQP). The effect of the removal of a cell is not only the loss of the value in the cell itself but also a (potentially species-specific) reduction in quality in the neighboring cells:

$$\delta_i = \max_j \frac{w_j}{c_i} \left\{ H_j \left(\frac{n_{ij}}{n_{ij}^*} \right) Q_{ij}(S) + \sum_{k \in N_j(i)} Q_{kj}(S) \left[H_j \left(\frac{n_{kj}}{n_{kj}^*} \right) - H_j \left(\frac{n_{kj} - 1}{n_{kj}^*} \right) \right] \right\}, \quad (2)$$

where w_j , c_i , and $Q_{ij}(S)$ are as in the basic Zonation algorithm. The remaining symbols are defined as follows: $N_j(i)$ is the neighborhood of cell i for species j , the set of cells remaining within the species-specific radius (buffer) around cell i . Denoting with b the fraction of original neighbors that have been lost from within the species-specific buffer around the site, $H_j(b)$ is the proportion of the original value of a cell remaining for species j when the focal cell has fraction b of its neighbors remaining. The fraction of cells remaining is simply $b = n_{kj}/n_{kj}^*$, where n_{kj} is the number of neighbors remaining for cell k within buffer radius of species j and n_{kj}^* is the original number of neighbors the cell had.

The loss term in braces is divided into two, local loss and loss in the neighborhood of the focal cell due to decreased connectivity of neighboring cells. Local loss is the fraction remaining of the original value of the focal cell i . If many of its neighbors have already been lost, the value of $Q_{ij}(S)$ is reduced. Loss in the neighborhood is mediated via the loss of one cell from the number of neighbors, which goes down from n_{kj} to $n_{kj} - 1$. We explain below how the function $H_j(b)$ was derived. The size of the neighborhood of a cell and the magnitude of the effects of habitat loss are defined separately for each species according to habitat models, which themselves mediate the BQP.

For the sake of comparison, we implemented a qualitative BLP into the Zonation process by adding a penalty

term, $b\Delta(\text{BL}/A)$, to Eq. 1, where b is the penalty parameter and $\Delta(\text{BL}/A)$ indicates the change in the boundary-length to area ratio of the remaining set of cells when focal cell i is removed from the landscape. When calculating $\Delta(\text{BL}/A)$, the area of the reserve goes down by one and the effect of removal on boundary length depends simply on the number of immediate neighbors the cell has. For example, if the cell has zero neighbors, BL goes down by 4 with the removal of the cell. Solutions obtained via the BLP are evaluated in two different ways in our comparison, either assuming no influence of fragmentation or assuming a reduction of quality near edges as defined by the BQP.

Approximating Species-Specific Responses to Habitat Loss and Proximity to Edge

Quantifying the effects of local habitat loss or fragmentation is difficult because of the complexity of species responses to the local spatial arrangement of habitats and the lack of data available for making inference about such processes. We approximated species responses to local neighborhood habitat loss with a combination of expert opinion and modeled species-habitat relationships (Wintle et al. 2005). The approximation was based on the average predicted reduction in habitat quality of focal cells that resulted from a given loss of forest cover within a given radius of the focal cell. The size of the radius used depended on the home range size of the individual species. For example, the Sooty Owl (*Tyto tenebricosa*) model included the buffer variable "proportion of unmodified forest within 2 km" (unmod2km) as an independent predictor variable (Wintle et al. 2005). It is possible to investigate the influence of neighborhood habitat loss on the Sooty Owl based on the predictions from a fitted habitat model. Our approach was to simulate a gradual reduction in unmod2km at all survey locations and predict (with the original fitted model) the probability of Sooty Owl occurrence after each reduction. This allowed us to construct a profile of the proportional reduction in probability of occurrence resulting from reductions in the proportion of unmodified forest in the local (2-km radius) neighborhood. This approach can be applied with any model that incorporates buffer variables such as unmod2km.

Experts helped us identify the model variables most likely to influence the neighborhood habitat quality for each species and the appropriate neighborhood to be considered for each species. The neighborhoods for each species closely matched species home ranges. We adjusted independent buffer variables to approximate species home ranges. For example, buffer variables such as unmod2km were used for large home-range species such as the Powerful Owl (*Ninox strenua*), whereas buffer variables with smaller radii (500 m) were considered more likely to explain variation in squirrel glider (*Petaurus norfolcensis*) occupancy (home range < 8 ha; Quin 1995).

The species' occurrence data and environmental variables described by Wintle et al. (2005) were used to develop models for this study; however, the actual method of model fitting was altered slightly. We fitted and assigned posterior-mode probabilities to a suite of models for each species with a Bayesian model-averaging algorithm called BMA.GLM (Wintle et al. 2003), which is implemented in S-PLUS 6 (Insightful 2001). We generated a suite of plausible models for each species, rather than identify a single best model because the estimated loss of conservation value was sensitive to the choice of habitat model. In cases where no buffer variables made it into the best model for a species (e.g., the model with the lowest value for Akaike's information criterion: see Wintle et al. 2003 for details), that species would appear to be unaffected by the loss of neighboring habitat cells. Nevertheless, if plausible alternative models, with similar explanatory power, did contain buffer variables, there would be at least some empirical evidence that the amount and quality of surrounding habitat influenced the habitat value of the focal cell. This situation represents a form of model uncertainty, wherein it is unclear which model should be used as a basis for inference (Draper 1995; Hoeting et al. 1999). Model averaging provides a convenient framework for incorporating such evidence in inference and prediction when there exists model uncertainty (Hoeting et al. 1999; Burnham & Anderson 2002; Wintle et al. 2003).

For each species j , the average expected loss of conservation value resulting from a proportional loss of habitat in the surrounding area was estimated as

$$H_j(b) = 1 - \frac{\sum_i p_{ij}(b)}{\sum_i p_{ij}^*}, \quad (3)$$

where p_{ij}^* is the model-averaged prediction of the habitat value of cell i for species j within its present habitat context and $p_{ij}(b)$ is the predicted value of cell i for species j after the loss of a proportion b of its originally present neighbors from within the buffer radii (given in Table 1). We decreased the values of relevant buffer variables in the cell for that species by a fraction b and then used the suite of habitat models for each species to make a model-averaged prediction of the new probability of occurrence for the cell. We calculated $H_j(b)$ as a fraction of sums rather than as an expected value over cell-specific fractions $E[p_{ij}(b)/p_{ij}^*]$. This was done because $E[p_{ij}(b)/p_{ij}^*]$ would be dominated by large fractional errors in small probabilities, and locations with low habitat value would dominate the analysis. In contrast Eq. 3 gave implicitly higher weight to effects of habitat loss at the best locations (with highest probabilities), which are the ones most important for conservation planning.

Case-Study Location and Species

We applied our methods to a reserve-selection case study in the Hunter Valley in eastern Australia. The objective of the conservation plan was to identify a conservation

Table 1. Competing models derived from the BMA.GLM algorithm (Wintle et al. 2003) for each of the seven species in the Hunter region.

Species	Competing models: logit($pr[occupancy]$) ^a	Postprob ^b
Powerful Owl	rain+poly(cold,3)	0.50
	powlexp2000+rain+poly(cold,3)	0.20
	poly(rain,2)+poly(cold,3)	0.08
	rain+poly(cold,3)+unmod2000	0.05
Sooty Owl	rain+poly(cold,3)+dry2000	0.05
	poly(rain,2)+terr1000	0.18
	+rugg500+unmod2000	
	wet2000+poly(rain,2)	0.13
	+terr1000+rugg500	
	rain+terr1000+rugg500+poly(sowlexp2000,2)	0.11
	+unmod2000	
wet2000+rain+terr1000	0.09	
+rugg500		
rain+rugg500+poly(sowlexp2000,2)	0.09	
+unmod2000		
Masked Owl	poly(mowlexp2000,3)	0.58
	+unmodexp2000	
Koala	unmodexp2000	0.31
	temp+poly(rugg500,2)	0.38
Yellow-bellied glider	+poly(dryexp2000,2)	
	temp+rugg500	0.31
	null model	0.30
	rain+rf2000+ybglexp2000	0.72
Tiger quoll	+unmod2000+percnonfor2k	
	rain+rf2000+ybglexp2000	0.23
	+unmod2000	
Squirrel glider	rain+rf2000+poly(ybglexp2000,2)	0.04
	rain	0.27
	temp+rain	0.22
	rugg500+rain	0.068
	temp	0.057
Squirrel glider	percnonfor2k+temp+rain	0.049
	sqglexp500+rugg500	0.62
	rugg500+percnonfor2k	0.28
	rugg500+unmod500	0.07
	rugg500	0.04

^aA maximum of five competing models for each species are shown for compactness. The expression poly(variable, n) in the competing model's column indicates variables included as a polynomial term with n degrees of freedom. All independent variable names are defined in Table 2 in Wintle et al. (2005).

^bThe posterior model probabilities returned by the BMA.GLM algorithm (Wintle et al. 2003) for each of the competing models. The best model is defined as the model with the highest posterior probability.

network that would provide maximum habitat protection for the priority fauna species in a given fraction of the landscape. This objective was approached in an indirect manner via the stepwise minimization of loss strategy employed in Zonation. The case-study area was composed of large patches of contiguous forest (>10,000 ha) and forest fragments of varying quality and size (10 - 1000 ha)

interspersed in an urban-agricultural matrix. The study area was 160 × 120 km including 369,253 1-ha cells of habitat with forest cover.

For the sake of demonstrating the BQP method, we used only the seven priority fauna species modeled by Wintle et al. (2005) to identify habitat priority areas. Those species were the Sooty Owl, Powerful Owl, Masked Owl (*Tyto novaehollandiae*), yellow-bellied glider (*Petaurus australis*), tiger quoll (*Dasyurus maculatus*), koala (*Phascolarctos cinereus*), and squirrel glider. In practice vegetation maps and a range of other biological, social, and economic considerations and constraints would be incorporated in the development of comprehensive reserve network options for Hunter Valley. For the sake of demonstrating the method compactly, however, here we focused only on one component of the biodiversity analysis: fauna habitat. We used the method described in the previous section to determine the degree to which each of the seven species was affected by neighborhood habitat loss, in terms of probability of occurrence. Species-specific radii used in Eq. 3 were chosen to correspond to approximate home range sizes for the species. We used a 2-km radius for the larger home-range species in the study and smaller radii of 1 km and 500 m for species with smaller ranges. These radii were also entered as the neighborhood size into the Zonation computations (Eq. 2).

Results

The Models

There was a substantial degree of uncertainty about the best model for all species (Table 1), confirming the importance of considering more than just a single best model when making inference about species habitat relationships, including the effects of neighborhood composition. For several species habitat buffers were not included in the best model but were included in plausible competing models. Several of the competing models for a given species gave contradictory impressions about the influence of neighborhood habitat quality.

For most species improved explanatory power was achieved when buffer variables with large buffer radii were included, indicating that processes beyond home range use of habitat influenced habitat occupancy. The proportion of deviance reduction achieved by fitting models was generally quite low.

Predicted Response of Species to Neighborhood Habitat Loss

There were substantial differences between species in the inferred influence of neighborhood habitat integrity (Fig. 1). The Sooty Owl and the yellow-bellied glider had the strongest negative response to reductions in forest cover in the local neighborhood, whereas the Masked

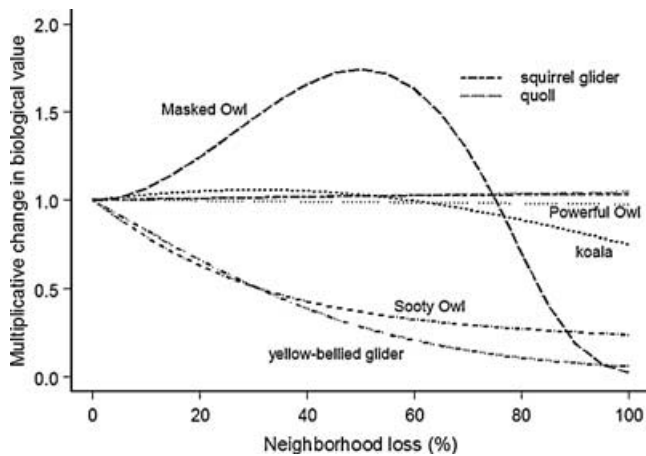


Figure 1. Responses of seven species to neighborhood habitat loss. The response axis represents the proportional multiplicative change in the habitat value of local cell resulting from a given loss in neighboring forest, $H_i(h)$ in Eq. 3.

Owl appeared to benefit from an intermediate level of fragmentation but demonstrated a low tolerance to high levels of fragmentation. The positive response of the Masked Owl to intermediate levels of disturbance was discussed with experts who indicated that it may reflect edge-hunting preferences or that it may be an artifact of the recent fragmentation of its core habitat. The koala was moderately affected by higher levels of local habitat loss, and the remaining three species showed relative indifference to varying levels of reduction in neighborhood forest cover. Because of the usual levels of uncertainty associated with wildlife habitat models (Elith et al. 2002), the influence of local neighborhood habitat integrity on habitat quality for each species was, at best, an approximation.

Use of the original probability of occurrence surfaces in reserve selection resulted in a convoluted (and impractical) reserve network structure with a high boundary-length to area ratio (Fig. 2). When the BQP was included in the Zonation process (via Eq. 2 and the functions shown in Fig. 1), the reserve network for the seven priority fauna changed (Fig. 3). The recommended reserve solution became more aggregated; thus, accounting for species-specific response to habitat loss, and proximity to edge had a significant effect on the spatial structure of the reserve network.

Comparison between the Boundary-Quality Penalty and the Boundary-Length Penalty

We compared the BQP solution to one generated via the use of a BLP. Figure 4 shows what happens to the conservation value of the solution when the BLP is increased. With no penalty, 30% of Hunter Valley included 38.3% of the original distributions of all species at a boundary-

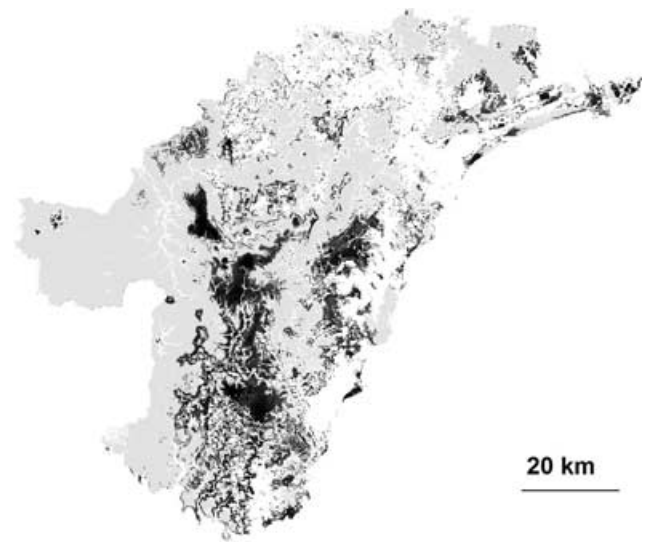


Figure 2. The basic Zonation solution for the top 30% of area of the Hunter Valley when no neighborhood effects are accounted for in Zonation (Eq. 1). The best 30% of area is shown in, dark gray or black, and the areas outside the top 30% fraction are shown in light gray.

length to area ratio (BL/A) of 1.1. A reduction of BL/A to 0.7 was achieved with essentially no decrease in conservation value. When the penalty was increased, there was a drop to 32% of distributions reserved with BL/A < 0.4.

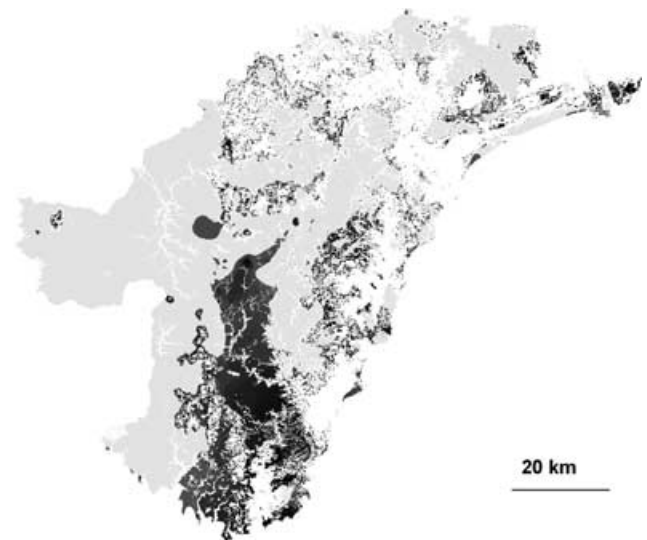


Figure 3. A top 30% reserve structure for the Hunter Valley obtained with the boundary-quality (BQP) penalty in Zonation (Eq. 2). The BQP approximates the functions given in Fig. 1. The solution is more aggregated than the one in Fig. 2. Light gray indicates areas outside the top 30% fraction. Dark gray to black indicates the top 30% of area, with the most important areas shown in black.

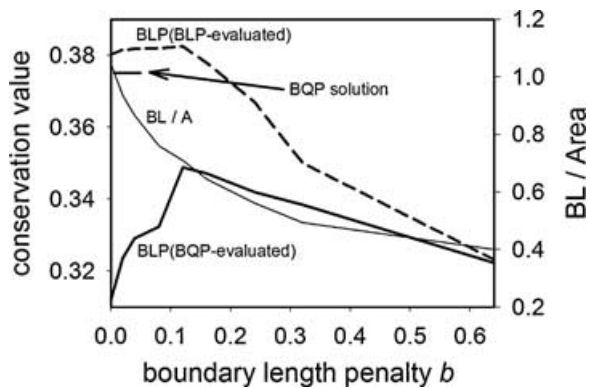


Figure 4. A comparison between how the boundary length penalty (BLP) and the boundary-quality penalty (BQP) evaluate a solution generated with the BLP technique for the top 30% fraction of Hunter Valley. The conservation value (across species minimum proportion of original distributions remaining in the cells) is shown as a function of the BLP parameter b (thick lines). Only the BL/A ratio curve (thin solid line) relates to the right axis. The solution obtained with the BLP is evaluated in two different ways in the figure. The thick dashed line gives the performance of the BLP solution when evaluated without effects of fragmentation (ordinary BLP optimization). The thick solid line gives the performance of the same BLP solutions when evaluated with the BQP reduction in habitat value close to reserve edges, marked BLP (BQP). The arrow indicates the performance of the solution calculated with the BQP (Eq. 2). This BQP solution has no associated BLP parameter value, which is why it is marked by a level instead of a point in the figure.

Nevertheless, the BLP solutions were derived via qualitative aggregation because the model has no explicit biological effects of fragmentation in it, and the effects are not species-specific. Our perception of the situation changed when the BLP solutions were evaluated with the BQP. (The solution was calculated via the BLP, but the BQP was accounted for in evaluating the conservation value of it.) Now it was seen that aggregation was indeed beneficial. With no BLP, the solution was fragmented (Fig. 2), and the BQP evaluation gave a solution value of only 31% of original distributions remaining, as compared with 38.3% assuming no effects of fragmentation when evaluating the solution (Fig. 4). Thus, there was an ~20% discrepancy in the estimated value of the solution when the solution was evaluated with and without the BQP. When the BLP was increased, the value of the solution increased to ~35% at BLP 0.12 to 0.16; thereafter, the solution became too aggregated and its value went down due to suboptimal areas being included in the solution. (The optimal value for the BLP would generally not be known and here we know it only because we can eval-

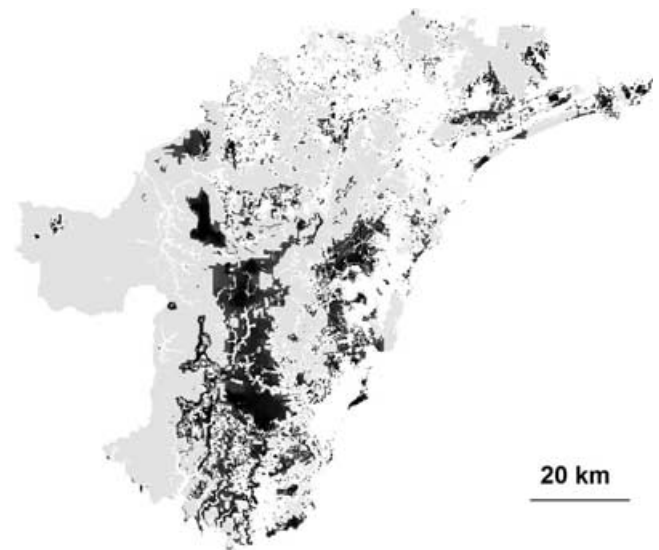


Figure 5. A Hunter Valley top 30% Zonation solution generated with the boundary-length penalty to induce aggregation (BLP = 0.16 solution of Fig. 4). Shadings are as in Fig. 3.

uate BLP solutions with the BQP.) The Zonation solution calculated directly with the BQP achieved a conservation value of ~37.5% (Fig. 4) at BL/A = 0.90. This showed that aggregation generated via the BLP was beneficial for the species but that the BLP solution was inferior to a solution computed directly with the BQP.

There is an interesting difference in the spatial patterns generated via the BQP (Fig. 3) and BLP (Fig. 5). The solutions differed subtly in two ways. First, the BLP achieved aggregation by dropping many small fragments from the top center and right center parts of the region. The BQP solution retained these areas because they were predicted to be good habitat for the sugar glider and Masked Owl. The BQP solution included an almost completely continuous block of habitat in the lower-central part of the region – this area is good for the Sooty Owl and yellow-bellied glider, both of which appear to be averse to fragmentation. The BLP solution allowed some fragmentation of this center block, which was the biggest reason the solution was evaluated as inferior to the BQP solution (when evaluating with the BQP). Consequently, even though the BLP solution was more aggregated than the BQP in some parts of the region, it was predicted to have lower conservation value. Essentially, the BLP solution took aggregation where it could be obtained most easily from a structural standpoint, and not necessarily taking it where it was beneficial to a specific species. In other words, the BLP forced aggregation for species that did not benefit from it, potentially unnecessarily sacrificing good-quality habitat to obtain unneeded aggregation. In contrast the BQP solution generated aggregation for those species and locations that were estimated to benefit from it according to the

original habitat models (with connectivity effects) and the BQP calculated from them (Fig. 1).

Discussion

In the absence of qualitative or quantitative factors favoring reserve network aggregation, a typical "optimal" reserve network will be severely fragmented. In the present case (Fig. 2), fragmentation was caused by the fact that many of the species (e.g., the Sooty Owl) are predicted to occur along convoluted valley bottoms, which lead to a fragmented reserve selection unless neighborhood effects were accounted for.

Decreased habitat value at edges can be explicitly included in a reserve-selection algorithm, which then leads to aggregated reserve structures that account for species-specific responses to habitat loss. Applying such a BQP is different from using the BLP, which penalizes for long borders (indicating low compactness) but does not explicitly consider what kind of habitat occurs near the boundary (the border could be placed right next to very good habitat). If habitat cells near reserve boundaries are less valuable, it pays to buffer the best areas so that they are far enough from the reserve edge so as not to incur significant biological loss. Thus, an aggregated patch network is produced, but this network is different from the one obtained by the use of the BLP (see Figs. 3a & 5). The BQP is not a simple edge effect; rather, it is the joint effect of edge avoidance, spatial population dynamics, and lowered local-population persistence in small habitat fragments. These effects are not modeled explicitly or separately; their joint effect is estimated statistically from habitat models that include neighborhood effects. Use of the BQP is not restricted to the Zonation algorithm we used here. It could be incorporated into the utility or objective function of other spatial reserve-selection algorithms.

Our proposed approach can be seen as a standardized approximation of the nonlinear effects of landscape structure (including connectivity) on reserve selection when using habitat model predictions. Such effects could possibly be implemented directly into reserve-selection algorithms by internal replication of the statistical habitat model occupancy (or abundance) prediction process. Problems with this approach include the computational cost of predicting the model value of habitat at each step in the reserve-selection algorithm and the difficulties involved in generalizing the reserve software to allow for the many statistical modeling methods available for fitting and predicting habitat models (Guisan & Thuiller 2005; Elith et al. 2006). The BQP exploits the existing habitat model structure to obtain a once-off estimate of the local abundance or probability of occurrence of the species in each cell in the landscape and the average effect of neighborhood habitat loss on the habitat quality (or con-

servation value) of each species. This simplification of the effects of landscape structure can be implemented efficiently in a spatial reserve-planning framework.

The reserve network we present (Fig. 3) would require all of the usual error checking and socioeconomic analyses before it could be realistically considered a reserve-planning option. Nevertheless, it represents a more biologically realistic reserve structure than the one that would be proposed by considering habitat quality in isolation of nonlinear interactions between habitat quality and landscape structure. One particular fact to check before Fig. 3 could be accepted as a basis for a conservation planning is the apparent indifference (or even preference) of the squirrel glider, Powerful Owl, and Masked Owl to fragmentation of habitat. This feature of the data and the BQP curves (Fig. 1) lead to the selection of some fragmented areas in Fig. 3. In the case of the squirrel glider and the Masked Owl, it is possible that the best remaining habitat for the species is in fragmented areas, in which case, the identification of those areas in reserve selection is not only justified, but central to their persistence. In the case of the Powerful Owl, the low explanatory power of the fitted habitat model made it difficult to make strong inference about the effects of fragmentation. It is possible that strong fragmentation effects in the model were masked by the poor quality of the survey data. In cases involving inadequate survey data, modeling may well benefit from the introduction of expert knowledge via Bayesian methods.

Interpretation of our results is influenced by the assumption implicit in Zonation, that all unreserved land units ultimately will be lost. This assumption is not unreasonable in landscapes where substantial land-use pressures exist or where substantial uncertainty about the future of unreserved lands warrants a precautionary approach. In the Hunter Valley region off-reserve conservation is likely to contribute to the long-term persistence of some species, so the assumption of complete loss is possibly overconservative. If land-use projections are available, the assumption of full loss outside reserves could be relaxed by allowing an option that all conservation value is not lost in some parts of the landscape, even if no reservation action is taken. In this way the analysis is based on retention rather than reservation (Pressey et al. 2004). The method could also be used to compare the utility of habitat restoration options by choosing the restoration options that lead to the greatest boundary-quality score.

If a reserve network proposed by a BLP method is analyzed with the boundary-quality criterion, two observations are likely to follow. First, for the species suffering a reduction in habitat quality when neighborhood cells are lost, the boundary-quality criterion will predict a decrease in the overall habitat value of a given reserve-network solution near the edges of the reserve (compared with the BLP solution based on raw predicted habitat value). Consequently, the BQP will give an overall lower estimate

for the biological quality of the reserve than would be indicated from the solution proposed by BLP that is evaluated with raw, predicted habitat value (Fig. 4) without any boundary effects. Second, under the BQP, there will be a predicted optimal aggregation level, in which local and neighborhood habitat quality balance (Fig. 4).

Adding a BQP term directly into the reserve-selection objective function (as in Eq. 2) makes it possible to identify a network of aggregated reserves that gives the best conservation value based on species-specific responses to neighborhood habitat loss. The BQP term complicates computations somewhat because the reserve-selection problem becomes mildly nonlinear (i.e., the conservation value of a cell will be influenced by the number of neighbors remaining). Calculations also slow down significantly, especially if some species have large neighborhood areas with many cells in them.

The proposed method takes the advantage of statistical habitat models to quantify the effects of neighborhood habitat loss. When these are not available, it would be possible to use expert biological knowledge or models for qualitatively similar species to parameterize the BQP. In the absence of expert opinion, using the qualitative BLP is likely to be better than doing nothing to discourage fragmentation in reserve solutions.

It is interesting to compare the present solution (Fig. 3) to reserve networks suggested by another recently introduced method that generates aggregated reserves (i.e., distribution smoothing; Moilanen et al. 2005, 2006; Moilanen & Wintle 2006). Distribution smoothing favors areas with relatively continuous high levels of occurrence for a species and thus discounts the value of fragmented areas. Consequently, a fragmented area (top of Fig. 3) is not included in a solution obtained by distribution smoothing. In contrast, large areas of fragmented habitat (top and right Fig. 3) are included in the solution because of a high estimated level of occurrence (in the case study the squirrel glider and Masked Owl in these regions). The relationship between distribution smoothing, the BQP, and the BLP is another topic for further research. We hypothesize that the BLP and distribution smoothing may be ill suited for problems where some species naturally occur in small fragments, although this hypothesis needs to be tested explicitly.

The incorporation of species-specific responses to fragmentation in reserve planning is a major challenge. We present the BQP as a reasonable approximation that is easily implemented and includes the advantage of a quantitative and transparent representation of fragmentation effects.

Acknowledgments

This study was funded by the Academy of Finland project 1206883 to A.M., the Finnish Centre of Excellence

Programme 2000–2005, grant 44887, and Australian Research Council grant LP0347473 to M. Burgman. We thank M. Burgman, the University of Melbourne, and the Australian Mathematical Sciences Institute for the MASCOS working group meeting during which this work was initiated. We thank three anonymous reviewers for constructive comments.

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