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Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies

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ABSTRACT

The most widespread reserve selection strategy is target-based planning, as specified under the framework of systematic conservation planning. Targets are given for the representation levels of biodiversity features, and site selection algorithms are employed to either meet the targets with least cost (the minimum set formulation) or to maximize the number of targets met with a given resource (maximum coverage). Benefit functions are another recent approach to reserve selection. In the benefit function framework the objective is to maximize the value of the reserve network, however value is defined. In one benefit function formulation value is a sum over species-specific values, and species-specific value is an increasing function of representation. This benefit function approach is computationally convenient, but because it allows free tradeoffs between species, it essentially makes the assumption that species are acting as surrogates, or samples from a larger regional species pool. The Zonation algorithm is a recent computational method that produces a hierarchy of conservation priority through the landscape. This hierarchy is produced via iterative removal of selection units (cells) using the criterion of least marginal loss of conservation value to decide which cell to remove next. The first variant of Zonation, here called core-area Zonation, has a characteristic of emphasizing core-areas of all species. Here I separate the Zonation meta-algorithm from the cell removal rule, the definition of marginal loss of conservation value utilized inside the algorithm. I show how additive benefit functions and target-based planning can be implemented into the Zonation framework via the use of particular kinds of cell removal rules. The core-area, additive benefit function and targeting benefit function variants of Zonation have interesting conceptual differences in how they treat and trade off between species in the planning process.

1. Introduction

The framework of systematic conservation planning (Margules and Pressey, 2000) specifies components needed in properly done quantitative conservation decision-making. The second of these components is the specification of species-specific conservation goals, which would often be given as representation targets levels. Following the specification of representation targets, site selection algorithms can be used to find flexible solutions that achieve these targets. Two common formulations for the target-based site selection problem are the minimum set formulation and the maximum coverage formulation. The minimum set formulation seeks the least expensive site that achieves the given targets (e.g., Underhill, 1994; Pressey et al., 1997; Polasky et al., 2000). The maximum coverage formulation (e.g., Church and ReVelle,

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1974; Camm et al., 1996; Snyder et al., 1999) starts from the situation where there is a given amount of resource (money) available and not all targets can be met. The goal then is to meet as many of the targets as possible. Both the minimum set and maximum coverage formulations operate very specifically in terms of the given representation targets.

The benefit function formulation to reserve selection (Arponen et al., 2005, 2007; Cabeza and Moilanen, 2006) operates very differently. In this formulation targets are also given, but the targets are seen as soft quantities and the value of the representation of a species is a continuously increasing function of representation. In particular, it makes a difference how much below or how much above a nominal target level the representation is; both under- and overrepresentation are valued. The value of a reserve network candidate is then a sum over the species-specific values of representation in the network. In this additive formulation species can compensate for each other: losing some representation for a species leads to a loss of value for that species, but the loss may be at least partially compensated via increased representation for other species elsewhere. This is different from target-based planning where the explicit aim is to achieve the targets for all species.

In target-based planning and in the benefit function formulation of Arponen et al. (2005) as well, the solution is computed at one specific resource level, which is either given (with maximum coverage or benefit function formulations) or which comes out as a result of meeting the given targets (minimum set). The Zonation algorithm (Moilanen et al., 2005) is different as it generates a hierarchy of conservation priority through the entire landscape. The hierarchy is generated via a strategy of minimization of marginal loss, the iterated removal of that cell whose loss causes smallest decrease in the conservation value of the remaining reserve network. As an advantage of the Zonation method, any given most important fraction (1%, 2%, 5%) of the landscape can be picked later based on the cell removal order which is recorded during the iterative cell removal. See, e.g., Moilanen et al. (2005) for examples of priority hierarchies produced using Zonation.

While the Zonation meta-algorithm is simple, there are many additional features that can be implemented into it. Really poor areas of the landscape or areas that cannot be had for conservation can be cut out of the landscape before starting the iterative cell removal (Moilanen et al., 2005). Cell removal can be restricted to the edge of the remaining landscape for computational efficiency (Moilanen et al., 2005). Methods for generating aggregation into the reserve network proposed by Zonation include distribution smoothing (Moilanen et al., 2005; Moilanen and Wintle, 2006), the boundary quality penalty (Moilanen and Wintle, 2007) and the boundary length penalty (e.g., Possingham et al., 2000; Nalle et al., 2002; Cabeza et al., 2004). Then there is a method, distribution discounting, for uncertainty analysis with the aim of going for robust reserves at areas where the predictions of species occurrence levels are reliably high (Moilanen et al., 2006a; see also Moilanen and Wintle, 2006 and Moilanen et al., 2006b). Replacement cost analysis (Cabeza and Moilanen, 2006) is a practical method, applicable in the context of both Zonation and other reserve selection frameworks, for evaluating the value of proposed reserve areas or loss from areas that cannot be had due to other land-use pressures.

The original version of the Zonation algorithm has a cell removal rule that emphasizes the areas with highest occurrence levels for each species separately. From hereon I call this algorithm variant the core-area Zonation. In this study I explain how the original Zonation algorithm (Moilanen et al., 2005) should be separated into the Zonation meta-algorithm and the cell removal rule. I show how both the additive benefit function formulation and target-based planning can also be implemented within the Zonation framework via the choice of particular mathematical forms for the cell removal rule. Each of the cell removal rules treats tradeoffs between species very differently, for which reason the variants are best suited for different planning situations. I also demonstrate differences in the average and variance of proportions of species distributions retained between different cell removal rules, and differences in the quality of cells selected by different cell removal rules.

Finally, it is proposed that benefit functions, or utility functions using the terminology of economics and decision theory, can be seen as a general framework to reserve selection. When defining benefit functions one needs to quantitatively describe how species trade off against each other and how the value of the reserve network is aggregated over species. Specification of these two components results in a clear description of the priorities of the planner.

2. Methods

2.1. *Zonation as a reserve selection meta-algorithm*

The Zonation algorithm (Moilanen et al., 2005) is intended for reserve planning using species distributions predicted on large grids. It produces a hierarchical prioritization of the conservation value of a landscape. By hierarchical, I mean that the most valuable 5% is within the most valuable 10%, the top 2% is in the top 5% and so on. At a high level, Zonation is simply an iterative removal of all cells one by one from the landscape, using minimization of marginal loss as the criterion to decide which cell is removed next. The order of cell removal is recorded and it can later be used to select any given top fraction, like best 10%, of the landscape.

2.1.1. *The Zonation meta-algorithm*

1. Start from the full landscape. Set rank $r = 1$.
2. Calculate marginal loss following from the removal of each remaining site i, d_i.
3. Remove the cell with smallest d_i, set removal rank of i to be r, set $r = r+1$, and return to 2 if there are any cells remaining in the landscape.

That there is a very particular reason why cells are removed from the landscape instead of added there. This has to do with effects of connectivity. If cells were to be added starting from the most valuable cell, then add the second most valuable cell and so on, this leads to a problem when trying to account for connectivity in the process. The reason is, that starting a new cluster will be seen as having low value due to the fact that a single isolated cell will necessarily have very low connectivity. And consequently, existing clusters will tend to be overextended into poor areas before starting new clusters. The reverse removal algorithm does not suffer from this problem. There the initial landscape includes all clusters with maximal possible connectivity, and cell removal will proceed in a manner that maintains maximal value and connectivity for remaining areas. Thus there is not a problem in identifying multiple spatially distinct important regions (at any given fraction of cell removal).

Whether the Zonation algorithm makes any sense at all depends on the definition of marginal loss, step 2 in the algorithm above. The original Zonation variant, core-area Zonation (Moilanen et al., 2005), uses a particular way of calculating this quantity. Below, two other ways of calculating this quantity will be introduced. These are based on an additive benefit function formulation (Arponen et al., 2005; Cabeza and Moilanen, 2006) and on a benefit function variant intended for target-based reserve selection. I emphasize that most properly the Zonation meta-algorithm and the cell removal rule should not be confounded, but that the cell removal rule should be seen as a separate component with several alternatives that have different interpretations.

2.2. Core-area Zonation cell removal rule

In core-area Zonation cell removal is done in a manner that minimizes biological loss by picking cell i that has the smallest δ, where:

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

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 in the remaining set of cells, S. When a part of the distribution of a species is removed, the proportion located in each remaining cell goes up. This means 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. (1a) also indicates a strong preference to retaining the best locations with highest occurrence levels – core-area Zonation does not treat probabilities of occurrence as additive; ten locations with $p = 0.099$ is not the same as one location with $p = 0.99$. The weight w_j in Eq. (1a) can be used to decide how important a species is with respect to other species. A high weight means that a relatively high fraction of the distribution of the species will be retained at any level of cell removal. Moilanen et al. (2005) demonstrates clear effects of weighting for butterflies of UK.

Note that Eq. (1a) can alternatively be expressed as (Moilanen et al., 2005)

$$\delta_i = \max_j \frac{q_{ij}w_j}{Q_j(S)c_i}, \qquad (1b)$$

where q_{ij} is the fraction of the original full distribution of species j predicted to reside in cell i, and $Q_j(S)$ is the fraction of the original distribution of species j in the remaining set of cells S.

2.3. Additive benefit functions in Zonation

Arponen et al. (2005) introduces (non-spatial) benefit-function based reserve planning where the value, V_j, of a species in a reserve network is an increasing function of its representation level, R_j. The total value of a reserve network is simply a sum over species-specific values – thus the qualifier additive, which emphasizes the linearly additive manner in which value is summed over species. It turns out that benefit-function based planning can be implemented into Zonation easily.

Fig. 1 shows a typical benefit function. Following Fig. 1, the value of the cell removal index (marginal loss) is simply a sum over species-specific declines in value following the loss of cell i:

$$\delta_i = \sum_j \Delta V_j = \sum_j [V_j(R_j(S)) - V_j(R_j(S - i))], \qquad (2)$$

in which $R_j(S)$ is the representation of species j in remaining set of sites S, and $\{S - i\}$ indicates the set of remaining cells minus cell i. V_j will be some increasing function of representation, for which typical alternatives include convex, sigmoid and ramp functions, see Arponen et al. (2005).

When using a mathematically smooth benefit function form Eq. (2) can actually be made computationally much more efficient by noting that $\Delta V_j \approx V'_j(R_j)\Delta R_j$. Assuming we use a power function for value, we have $V_j(R_j) = w_j R_j^x$. Then $V'_j(R_j) = w_j x R_j^{(x-1)}$ – this is a quantity that needs only be computed once for any set of remaining cells S; it does not depend on the representation level of the species in the focal site to be removed, i. In contrast, term $V_j(R_j(S - i))$ in Eq. (2) depends on the identity of the site and would need to be calculated separately for each cell that is candidate for removal. Finally, marking by q_{ij} the proportion of the original distribution of species j in cell i, we have $\Delta V_j \approx w_j x R_j^{(x-1)} q_{ij}$. This approximation is quite accurate due to the fact that the distribution of the species would typically be divided between many cells each of which contain a minute fraction of the full distribution of the species.

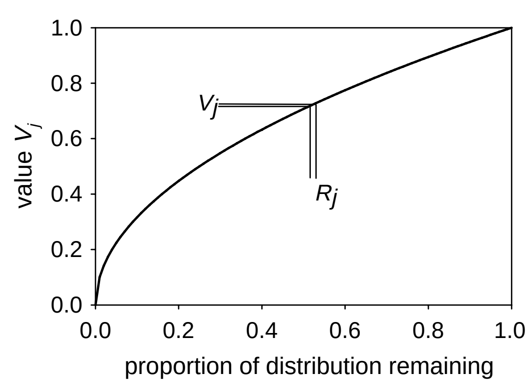

Fig. 1 – Using an additive benefit function in Zonation. The benefit function is an increasing function of representation. When a grid cell is removed from the landscape, the representation of each species occurring in the cell goes down by a small fraction ΔR_j and the respective value for that species goes down by ΔV_j. The total marginal loss in value is simply a sum over species-specific losses.

It is computationally very advantageous if one can use the additive benefit function formulation with a smooth convex function for value (as in Fig. 1). Such a formulation falls into the realm of convex optimization, where an optimal or very near optimal solution can be achieved with a simple iterative search strategy (e.g., Bazaraa et al., 1993, pp. 99–102). In principle, it is possible to optimize a convex function to an arbitrary precision using a simple gradient-ascent type algorithm. In fact, when applying a convex benefit function formulation to a restoration application, van Teeffelen and Moilanen (unpublished) found that an iterative heuristic was able to identify in simulated problems the single global optimum out of millions of possible solutions with a success rate of >85%. This suggests that a reverse iterative heuristic (Zonation) could indeed find the global optimum for the additive benefit function formulation. This assumption is based on the fact that in a large landscape any one cell includes a minute fraction of the full distribution of the species. Thus, one is for practical purposes doing convex continuous optimization.

2.4. *Implementing target-based planning into Zonation with benefit functions*

The Zonation algorithm is implicitly aiming at a maximum coverage type solution; by minimizing marginal loss one maximizes conservation value remaining at any specific level of cell removal. This objective may seem to be at odds with minimum set coverage, where the aim is to find the smallest solution (in terms of area, money, etc.) that can satisfy given targets for all species. But in fact this is not so. A minimum set coverage type optimization can be implemented inside the Zonation algorithm in the following manner.

I propose that target-based planning could be implemented in Zonation using a very particular type of benefit function (Fig. 2a). In this function value V_j is zero until representation R_j reaches the target T_j. Then there is a step with the height of $(n+1)$, where n is the number of species. When R_j increases above T_j and approaches 1, there is a convex increase in value, with a difference in value $[V_j(1) \quad V_j(T_j)] = 1$. This means that the loss in value from dropping any one species below the target is higher than any summed loss over multiple species that stay above the target. The idea is that species representations will approach the species-specific targets from above, and that the functional form with increasing marginal loss when approaching the target will maintain all species above target as long as possible. Then, at some point it will not be possible to remove any more cells without violating the target for at least one species. The solution at this point is what I propose to be the solution for a targeting benefit function Zonation. Note that this solution is supposed to be (near)optimal only in the minimum set sense, another solution (like the additive benefit function one) could have higher mean representation over species at the same fraction of cell removal.

Target-based planning with partial target achievement valued can be implemented with a similar function defining cell value at the removal step (Fig. 2b). Above the target the function is the same as in Fig. 2a. However, at the target level there is no step, but rather, a (linear) decline to zero value at zero representation. With this functional form species above and below target can compensate for each other especially after several species have dropped below targets, which is a major difference to the function of Fig. 2a, using which a species never drops below target as long as it can be avoided in the cell removal step.

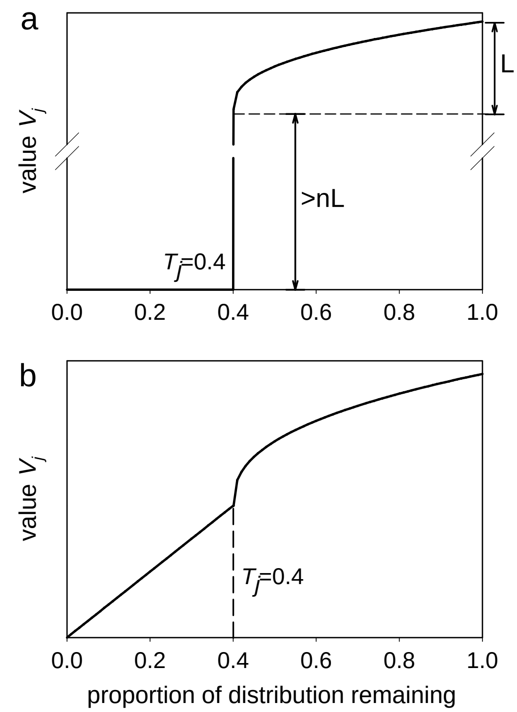

Fig. 2 – (a) Implementing target-based planning into Zonation can be done using a specialized form for the specification of marginal loss. Value is zero up to the target T_j and then it jumps to $(n + 1)L$, where n is the number of species. When R_j increases from T_j to 1.0, the benefit function has a strongly concave form, and the increase in value for this increase in representation is L. It follows that the marginal loss in value when breaking a target is so large, that no species will ever be let below the target as long as there are other cells to remove that do not lead to a target violation. (b) This general functional form for marginal loss implements target-based planning with fractional target achievement valued.

2.5. *Benefit functions as a general approach to reserve planning*

Benefit functions can actually be seen as a general framework within which reserve selection goals can be formulated. Fig. 3 illustrates the concept. Fig. 3a shows the conservation value of a reserve network as a function of the representation levels of two species in target-based planning. The value surface essentially consists of steps – each target achieved raises value one step higher. Fig. 3b shows the value surface for target-based planning where partial target achievement is calculated. This surface has

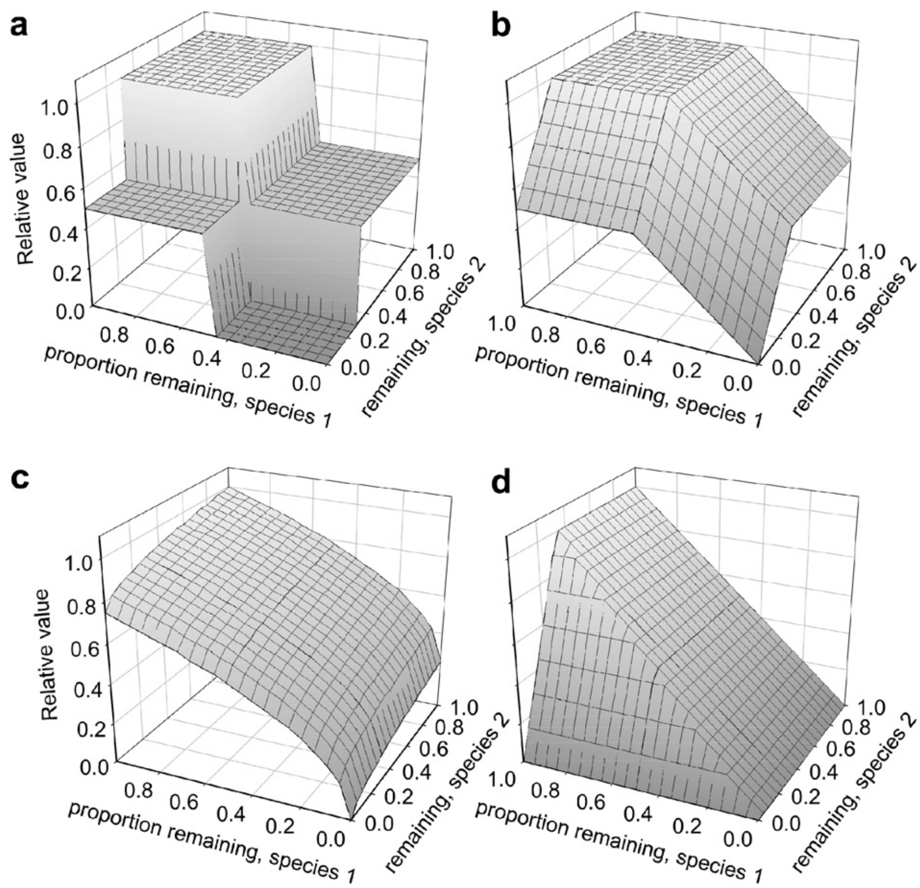

Fig. 3 – Some forms for benefit functions showing how species trade off against each other. (a) The step function; target-based planning with hard targets $T_1 = 0.2$ and $T_2 = 0.4$. (b) The ramp function; target-based planning with fractional target coverage valued. (c) An additive benefit function (here square root) with $w_1 = 1$ and $w_2 = 3$. (d) An approximation of the core-area Zonation benefit function, see text.

the appearance of a ramp. Fig. 3c shows the value surface of the additive benefit function. This surface is a continuously increasing smooth convex surface, increasing the representation of either species always generates more value. Surfaces like in (b) and (c) are much more convenient for optimization than a discontinuous surface such as in (a).

Fig. 3d shows an approximation of the value surface of core-area Zonation, calculated from Eq. (1b) under assumption of having equal q_{ij} and c_i for all sites. It follows that the value is approximately $\min[Q_1(S), w_1Q_2(S)/w_2]$. However, this is a simplification of the benefit function of core-area Zonation, in which the definition of optimality arises indirectly via the iterative minimization of marginal loss. The definition of marginal loss is such that locations with high occurrence levels are emphasized. This means that the value of a core-area Zonation solution depends not only on the proportion of distribution obtained for species, but also on what kinds of sites with what kinds of occurrence levels have been chosen. Even so, Fig. 3d illustrates the idea that species representation levels must raise in a kind of synchrony (influenced by species weights) for value to increase. In a sense core-area Zonation is closer to target-based planning than to the additive benefit function (c) or the partial target achievement (b).

3. Results

Fig. 4 illustrates some differences between the core-area Zonation, the additive benefit function formulation and the targeting benefit function (Hunter Valley priority fauna data by Wintle et al., 2005; data variant of Moilanen, 2005). The figure has been calculated as a function of the fraction of landscape remaining. At any fraction, there is a particular spatial pattern (set of cells) remaining, and from this set the fraction remaining of the original full distribution of each species was calculated ($Q_j(S)$ in Eq. (1b)). It is instructive to look at the minimum proportion over species and average proportion over species distributions remaining.

First, the additive benefit function has highest average proportion over species retained, but it simultaneously has the smallest minimum proportion retained. Core-area Zonation has a high minimum proportion combined with a relatively low average. The targeting benefit function does well in terms at finding the highest level of cell removal without having any species violate a target. However, when further away from the target it does relatively poorly in terms of the minimum fraction over species retained. The problem with the targeting benefit function is that it is aimed at good performance at one particular set of targets, but the hierarchy of solutions

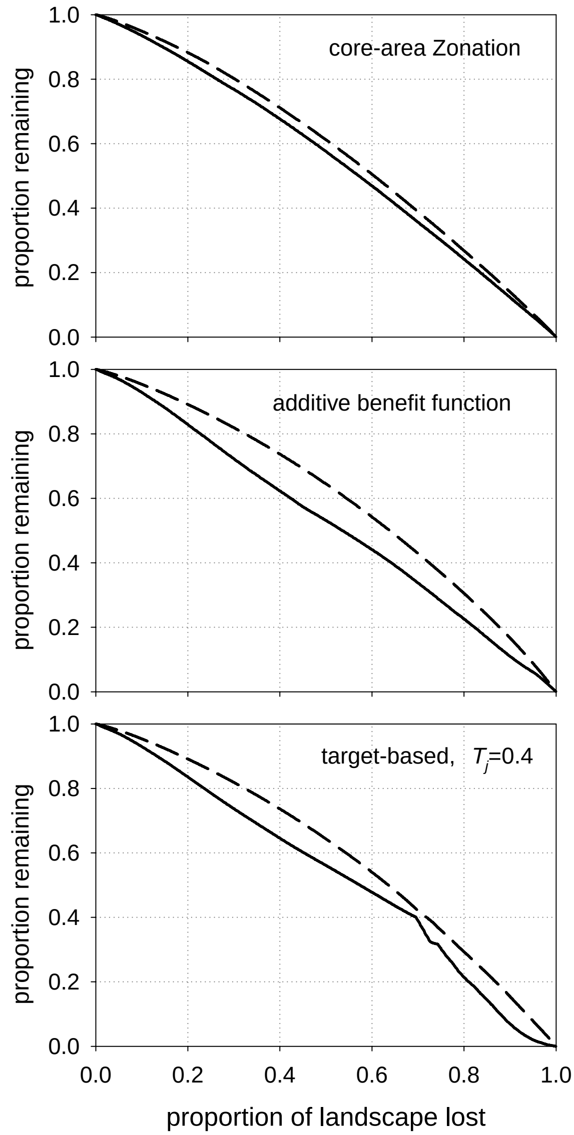

Fig. 4 – Results from Zonations using different cell removal rules for the Hunter Valley (data of Moilanen, 2005). The figures show the minimum (solid line) and average proportion (dashed line) over species of the original distribution retained as a function of proportion of landscape lost. Core-area Zonation, the additive benefit function and the targeting benefit function display differences in solutions that can be expected to occur in other data sets as well.

is missing in the sense that good overall performance at other levels of cell removal, especially at a level where targets have been violated, cannot be guaranteed.

Table 1 gives statistics about Zonation solutions using different cell removal rules on the same data that was used to generate Fig. 4. The overall conclusion of this comparison is that core-area Zonation demonstrably selects cells with higher probabilities of occurrence per species but with generally less overlap between species distributions, compared to either additive or targeting benefit functions. For example, looking at a solution with on average 30% remaining of the original distributions of species, it can be seen that core-area Zonation requires on average 5770 cells per species to get half of the remaining (30%) distribution of the species, whereas the benefit function variants require 6300 and 6353 cells. This indicates a 10% difference on species-specific probability of occurrence levels in cells. On the other hand, the total area over all species needed to achieve this representation is higher for core-area Zonation (24,924) compared to benefit function variants, 21,616 and 22,608. This shows that core-area Zonation solutions have higher occurrence levels but less overlap between species distributions than the benefit function variants. This phenomenon is further illustrated with a simple example in Fig. 5.

4. Discussion

Conservation priorities should be set and reserve networks designed based on approaches that integrate both costs and benefits of conservation. Of these, costs might be more easily described than benefits, and it has been observed that accounting for spatial heterogeneity of cost allows either more efficient planning or higher targets to be met with a given resource (Ando et al., 1998; Polasky et al., 2001; Balmford et al., 2000, 2003; Moore et al., 2004). Benefit is more complicated as one needs to decide how various protection levels for biodiversity elements jointly translate into conservation value. This work concerns the translation from representation to conservation value. Benefit could also be defined in terms of other variables, for example, Nicholson and Possingham (2006) describe various ways of aggregating (valuing) extinction probabilities over multiple species. Ultimately, minimizing the extinction risks of species should be the primary goal of conservation planning (e.g., Margules and Pressey, 2000; Cabeza and Moilanen, 2001; Nicholson and Possingham, 2006). When there is not sufficient information available to translate representation into extinction risk, one would base planning on maximizing representation and connectivity, indirectly aiming at species persistence, as is done in the Zonation approach. A third way of defining benefit is in direct economic terms, when species presence/abundance has a definable economic value (e.g., Nunes et al., 2003; Naidoo and Adamowicz, 2005a,b). Note that in terms of terminology, benefit, value, and utility would mean essentially the same thing, how a planning option is evaluated in terms of conservation value. Therefore, the broadest mathematical framework into which the present work could be placed is the utility maximization framework of decision theory and economics (see e.g., Aleskerov and Monjardet, 2002; Hammond et al., 2003). Further study of the functional form and estimation of biodiversity benefit functions will be needed for deeper understanding of the application of utility theory to conservation planning.

I suggest that different reserve selection frameworks can be understood and profitably defined under the general concept of benefit functions. Here, it has been shown how both additive benefit functions and target-based planning could be implemented within the Zonation reserve selection framework. Thus, three on the surface very different approaches to reserve selection (target-based planning, additive benefit functions and core-area Zonation) could be operationally uni-

Table 1 – Difference in selected cells in a 30% cut (33,085 cells) of the Hunter Valley Moilanen (2005)

Method	Remaining			Cells in distribution	
	Area	Min.	Mean	90%	50%
For 30% of landscape remaining					
Core-area Zonation	33,085	0.357	0.389	18,848	7638
Additive benefit function	33,085	0.338	0.428	21,349	8885
Target 0.4	33,085	0.391	0.421	20,923	8863
For average 30% remaining per species					
Core-area Zonation	24,924	0.272	0.300	14,153	5770
Additive benefit function	21,616	0.221	0.300	14,786	6300
Target 0.3	22,608	0.221	0.300	15,198	6353

Min. and mean columns are for minimum and average proportion of species distributions retained. Columns 90% (50%)-cells give the average number of cells needed to represent 90% (50%) of the distribution remaining for each species at that level of cell removal. Note that core-area Zonation uses fewer cells indicating that they must have relatively higher occupancy levels to achieve the same proportion retained.

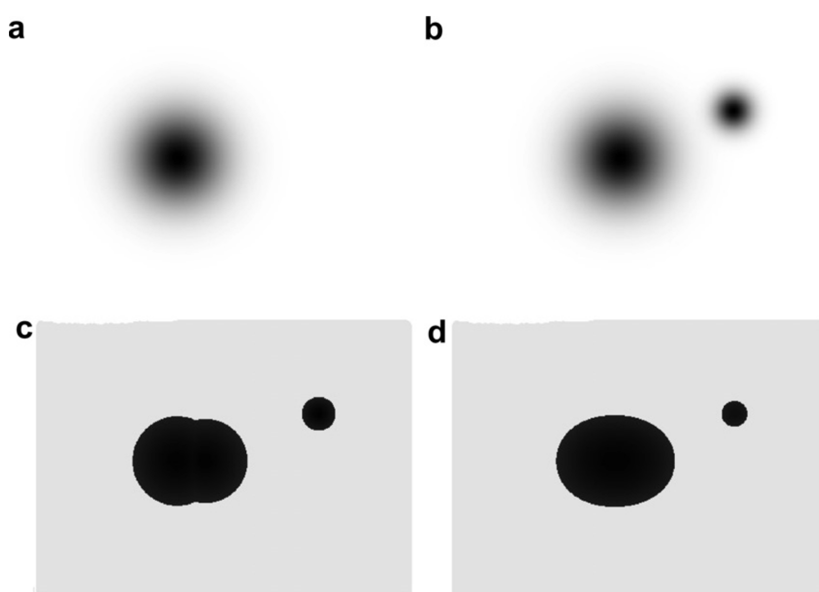

Fig. 5 – Differences in areas selected by the core-area Zonation and the additive benefit function. Panels (a) and (b) show hypothetical distributions for two species, with black corresponding to a probability of occurrence of 1.0 and white a probability of occurrence of zero. Panels (c) and (d) are 10% top fractions for the core-area Zonation and benefit function solutions, respectively. Core-area Zonation (c) gives relatively more weight to the isolated high-quality spot for species B. The benefit function solution (d) expands around the edges of the big spot, where both species occur with middle to low densities.

fied under a generalization of the Zonation algorithm. Each of these frameworks makes certain explicit and implicit assumptions and they are thus suited for somewhat different situations. The main properties of each method are summarized next.

In the additive benefit function formulation reserve network value is a sum over species, which means that the absence of a species from a reserve network can be compensated by having more of the distributions of other species. Free tradeoffs between species are fully allowed. This may be appropriate if the set of species is seen as a sample from a larger regional species pool. If this is the case, not all species will be equally covered in any case and thus representation for one species could be sacrificed if adequately high compensation can be obtained elsewhere. What exactly is adequate compensation will be defined via the weights and benefit function forms used for different species. The additive benefit function allows natural species weighting and the formulation is computationally advantageous due to the smooth and possibly convex form of the value surface. This formulation generates the hierarchical solution and it will achieve high average value of representation but it may have the tendency to abandon species that occur in species-poor regions. Value over species and occurrence levels (probabilities of occurrences, abundances, etc.) in cells are both treated as additive.

Target-based planning is very different in that a given representation level is explicitly requested for each species. Species weighting is not easy as it needs to be done via the setting of differential targets for species. In the Zonation context the method does not produce a good hierarchical solution because it is aimed at high performance only at the particular target level – a species may be abandoned when it drops below its target representation. Occurrence levels are treated as additive.

The core-area Zonation is different from both the additive benefit function and target-based planning in that probabilities are not treated as additive, but rather, locations with high occurrence levels are specially emphasized. Core areas for all species will be retained according to the cell removal rule, in which respect the method resembles target-based planning. Core-area Zonation allows natural weighting of species and a proper hierarchy of solutions is generated. Note that when land cost is used with core-area Zonation, the interpretation of the analysis output is complicated by the fact that it is not known whether an area is an important core-area due to biological features or if it appears to be a core area just because land cost is very low. This complication is not relevant with the additive benefit function or targeting benefit function formulations because there occurrences are additive in any case.

In general, core-area Zonation can be expected to (i) require more area to achieve a given proportional representation level, but (ii) this representation will be achieved with relatively higher local occurrence levels compared to the benefit function variants. The benefit function variants will have higher average representation per species, but with lower occurrence levels and higher variance among species – for example, a species occurring in a species-poor region could end up with very low representation. All these differences are such that they can logically be expected to occur in any other data set, with the magnitude of differences depending on the nestedness of species distributions. Differences would be largest when there are both (i) substantial regional differences in species richness combined with (ii) a generally low overlap between species distributions. In this case core-area Zonation could catch cores of species occurring in species-poor areas whereas the additive benefit function would concentrate the solution more towards species-rich locations, where cells have high aggregate value over species.

The Zonation method is applicable to relatively large landscapes, with current software limits (when using a PC) being around 700 species occupying a 1 million (effective) element grid, or equivalently 70 species modeled in a 10 M element grid. The ability to combine different cell removal rules with the Zonation meta-algorithm provides improved possibilities for choosing a reserve selection framework that is well suited for the planning needs of the particular situation. Zonation version 1.0 (Moilanen, 2006) is downloadable from the MRG web pages, www.helsinki.fi/science/metapop.

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