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Apples, oranges, and probabilities: Integrating multiple factors into biodiversity conservation with consistency

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We explore the problem of integrating some of the many factors involved in conservation planning by focusing on their effects on a common currency of conservation success, the probability of persistence. This approach has the potential to reduce many of the difficulties inherent in combining different pattern and process factors. For handling information expressed as probabilities, five area-selection methods are compared.

Keywords: biodiversity, probability of persistence, efficiency, area-selection methods

1. Introduction

Identifying the best networks of areas for conserving biodiversity is a problem that depends upon many different biological and social factors [1]. Biological factors include: diversity (of genes, species, assemblages of species, ecosystem processes, etc.), rarity, endemism, viability, vulnerability to threat. Social factors include: human-induced threats, cost of acquiring areas, cost of management, opportunity costs, and other social and political interests. The problem is that when accommodating multiple factors, area-selection methods often rely on arbitrary weightings that are easily challenged. We argue that more defensible solutions could be obtained if we integrate these factors by examining their effects on conservation success, measured as the probability of persistence for valued features. We proceed to compare five methods for using estimates of probability of persistence when selecting networks of important areas in the face of social costs and constraints. We then discuss some of the many challenges that have to be met in estimating probabilities of persistence and in treating inter-dependencies in probabilities among areas.

1.1. Quantitative methods

Faced with many factors, decisions could be reached using an entirely political process of negotiation. However, the danger is that solutions reached in this way might reflect the relative influence of pressure groups over the decision makers, rather than the relative biological merits of their cases. Instead, when there is sufficient political stability and social cohesion, quantitative assessment can provide what has been described as the “highest form of rationality” [2]. We see quantitative methods not as an attempt to provide a technical fix for encompassing the entire political decision-

making process, but as a way of formalizing what are legitimately technical issues within the biological component. At the very least, these methods may be useful for comparing and assessing alternative plans proposed by others.

Suitable models for quantitative assessment of multiple factors already exist in the operations research literature, although conservation has perhaps been slow to benefit from this expertise [3]. Previous quantitative assessments for biodiversity have usually accommodated multiple factors by using one of two approaches [4]: either by using compensatory methods, which combine scores for factors, often by summation; or by using non-compensatory methods, often by treating factors sequentially, in an ordered series of decisions. We consider how the advantages of both of these approaches might be exploited while avoiding their more serious disadvantages. We do this by looking at some of the underlying relationships among the many factors, and where possible, by using these relationships to integrate factors within a common currency of conservation success: *the probability of persistence for valued features*. This should provide improved consistency when integrating factors, which would contribute ultimately to a more accountable decision process. More consistent and accountable solutions are preferable because they are repeatable and because they can be more robust to legal challenges from groups whose interests conflict with biodiversity conservation [5].

1.2. Compensatory methods

Compensatory methods seek to combine scores for multiple biological and social factors into a single score for an area. They are referred to as “compensatory” because an increased contribution from one factor can appear to balance or offset a reduction in another. Examples of combinatorial techniques range from simple summation [6], to multivari-

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ate weighting techniques [7], to embedding combinatorial functions within iterative area-selection algorithms [8]. The attraction of the method is that single combined scores may appear to be much simpler to compare when assessing the conservation value or priority of areas.

Whichever combinatorial method is used, the problem is that the approach is difficult to defend when the different factors are measured in different currencies, which is usually the case. Because these different currencies are incompatible and non-interconvertible (i.e., incommensurate) [9], there is no uniquely justifiable way of weighting them for compensation against one another [10]. For example, using standardization of score ranges and of score frequency distributions would necessarily imply a particular conversion factor, although ultimately this would still lack any uniquely defensible philosophical justification [3]. The fundamental problem in these cases is how to address questions like: how much of a decrease in diversity might legitimately compensate for a particular increase in rarity?; or how much extra diversity would be a worthwhile benefit for accepting a particular increase in threat? Such factors are often described as being “not additive”. However, unless an underlying relationship between these factors can be found, the same problem would apply to any other form of combinatorial function. Consequently any combinatorial system for disparate factors is likely to be essentially arbitrary and idiosyncratic. Thus, in a recent review [1], Margules and Pressey concluded (p. 250) that *“Planning for both representation of patterns and persistence of species and natural processes requires planners to compare apples and oranges. There are no guidelines for optimizing the outcome. . .”*

The techniques used traditionally by economists to treat “apples and oranges” conversion problems do not solve the consistency problem. The first technique, plotting trade-off curves between factors, can be used to find a series of different “best” solutions when a series of different inter-conversion weightings is supplied. However, it does not solve the problem of which inter-conversion weighting should be used. For example, this approach has been used to examine trade-offs between biodiversity and cost in the selection of protected areas [10]. The second technique involves making the process explicitly subjective, by polling public opinion for an average view of the relative weightings. When using this technique, it is recognized that the weightings given may differ among people not only between studies, but also within studies (where circumstances might be expected to be more similar) [11], thereby causing severe difficulties for accountability. Different weightings are also very likely to result in different priorities, which may then be favored by different interest groups. In effect, this would move aspects of the assessment into the political arena, even when they involve legitimately biological decisions. These kinds of problems could be avoided if certain ways of relating factors were shown to be more biologically defensible, which should help to unify support at least among biological interest groups.

1.3. Non-compensatory methods

Non-compensatory methods deal with each of the different factors so that an increased contribution from one factor cannot balance or offset a reduction in another. An example is the sequential treatment of the selection of areas by biodiversity value, at one step of the analysis, and the prioritizing of areas for management action by the urgency of the threats they face at a subsequent step. Variations on this stepwise approach [1,4,12] have become popular for quantitative conservation assessment because they can avoid the need to attempt direct conversion between some incommensurate currencies (see sections 2.3 and 4.3).

There are two problems with the sequential approach. First, sequential treatment imposes an order of precedence (importance) among the factors and this order may not always be easy to justify. The order may be viewed as a form of weighting. Second, when a sequential treatment is applied as a series of filters, it may restrict decisions to a simplistic yes or no, thereby losing much of the quantitative information. Examples include most previous treatments of information relating to species’ local probabilities of occurrence or of persistence, which have usually excluded any areas from consideration where species’ scores fall below some threshold [12–15]. In effect, applying a threshold converts probability data into presence–absence data, but at the cost of ignoring the uncertainties.

1.4. Using probabilities

The most direct and consistent way of dealing with multiple biological and social factors would be to seek a common currency through which all of their effects might be expressed. Our approach differs from a simple compensatory approach in that we seek to discover how the various factors interact with one another to affect conservation outcomes. To this end, we develop the idea of persistence, which has been much discussed before as an ideal for conservation [4,14,16–21]. But so far none of the area-selection studies has taken a consistently probabilistic approach to persistence, which we see as the ultimate currency of conservation success.

There is an analogy with the consistency problem from another field of biodiversity research, where measures of biodiversity value have been sought in terms of the variety of the different organisms. In this case, the two different properties of interest are, first, the number of organisms in each biota, and second, how different those organisms are from one another. The two properties could have been measured separately and combined, but this would have led to apples-and-oranges consistency problems. Instead, the approach was to seek to identify a single currency of value that underlies both aspects [22,23]. This underlying value is taken from an economic concept of the option value (for future use or evolution) associated with the different genes or characters of the organisms. Techniques were developed for comparing the relative variety value of different biotas,

based on the degree of relatedness, that avoided consistency problems by using this single unified currency.

Apples-and-oranges consistency problems in area selection might be reduced if we could relate the many factors affecting decisions to the over-arching idea of long-term conservation success. Seeking these inter-relationships is not an attempt to deny the complexity of the problem, but a way to try to reduce it to a form that is more easily comprehended [3] and which might then be solved using relatively simple techniques. One starting point is the idea expressed by Margules and Pressey [1] that the two primary roles of conservation areas are (i) to achieve representativeness of biodiversity elements or features (be they genes, species, or ecosystem processes) and (ii) to ensure persistence of these valued features. Unfortunately, decision makers assessing alternative plans do not know in advance with certainty which alternatives will yield persistence for the largest number of valued features. However, it is usually possible to make at least approximate estimates of probabilities of persistence. If the features of biodiversity value to be represented could be treated as equivalent for the purposes of a conservation study (as the valued “beans” to be counted), and if the probabilities of persistence for these features could be estimated in a consistent way, then these probabilities could be treated as a consistent and uniform currency. This would allow them to be combined for area-selection, thus providing the potential for overcoming the apples-and-oranges problem for representativeness and persistence.

Looking at this another way, using probabilities of persistence provides a solution, at least in part, to the apples-and-oranges problem of seeking to conserve both valued patterns and processes. Biodiversity has often been viewed from either a compositionalist (emphasizing pattern) or a functionalist (emphasizing process) standpoint [24]. It is now becoming widely recognized that, for conservation to be successful, the two aspects have to be linked. Persistence of species and sustainability of ecological processes (including “ecological services”, such as providing clean water, or pollination of crops) are largely dependent upon one another, even though the two are not wholly interchangeable. One way of addressing the linkage is to begin from the compositionalist approach. This requires that we treat the probabilities of conserving the components (valued biodiversity features) as depending upon maintaining the processes that support them [25]. It provides the potential for extending assessment studies to include as many of the inter-dependencies between features and processes as may be considered important, or as resources permit (see section 4.2). Studies using probabilities may also be extended more easily to take account of the contribution of all areas within the entire landscape matrix.

In this paper, we use previously published estimates of probabilities of occurrence, which are expected to be related positively to persistence [15], in order to compare five heuristic area-selection methods. Most previous area-selection methods dealing with information relating to prob-

ability of occurrence or persistence have applied thresholds in order to reduce probabilities to presence-absence data [12–15]. We use two of these methods and another based on presence data alone. In contrast, Margules and Nicholls [26] proposed an area-selection method that used probability estimates directly. However, as we have shown elsewhere [27], their algorithm is even less efficient (in terms of the mean among species of the combined probability achieved for a given area required) than using a simple complementarity algorithm and the original presence data. This is important, because inefficiency means lost opportunities for protecting more of the valued biodiversity [28]. So for our fourth method, we include an improved algorithm for handling all of the differing levels of probability directly. The fifth method combines this direct probability-based approach with the threshold approach [29].

2. Methods

2.1. Area-selection problems

We consider a simplified form of conservation problem, in which just some areas are selected for conservation management. This is unrealistic to the extent that we make no allowance for the contributions to species’ probabilities of persistence made by areas outside the selected-area network. For our analysis, the contribution of these areas is regarded as an unknown bonus, but one upon which we do not rely. Ultimately, it should be possible to integrate the full range of land uses within the analysis by including expected contributions to probabilities of persistence from all areas, even those that are not selected (see section 4.2).

Most previous studies have considered two common forms of area-selection problems [30]. First is the minimum-set problem, such as “what is the minimum-cost set of areas required to represent all species with a probability of greater than 0.95?” Second is the maximum-coverage problem, such as “for a given budget, which set of areas could represent all species with the largest minimum probability?” (Other variations on these goals are possible, but are not considered here.) Any approximation to a minimum-set method that selects more areas might be expected to result in higher probabilities simply because including more areas is likely to include more representations of species. Maximum-coverage solutions provide a means of making comparisons between approximate methods when either the same number of areas is selected, or the same combined cost of areas is expended.

Araújo and Williams [15] have described a framework for estimating probabilities of persistence for use in area selection. For most species, the best information available is likely to be presence data from atlases [31]. In this situation, one first step is to estimate species’ local probabilities of occurrence, by modeling habitat suitability and species’ local potential for dispersal.

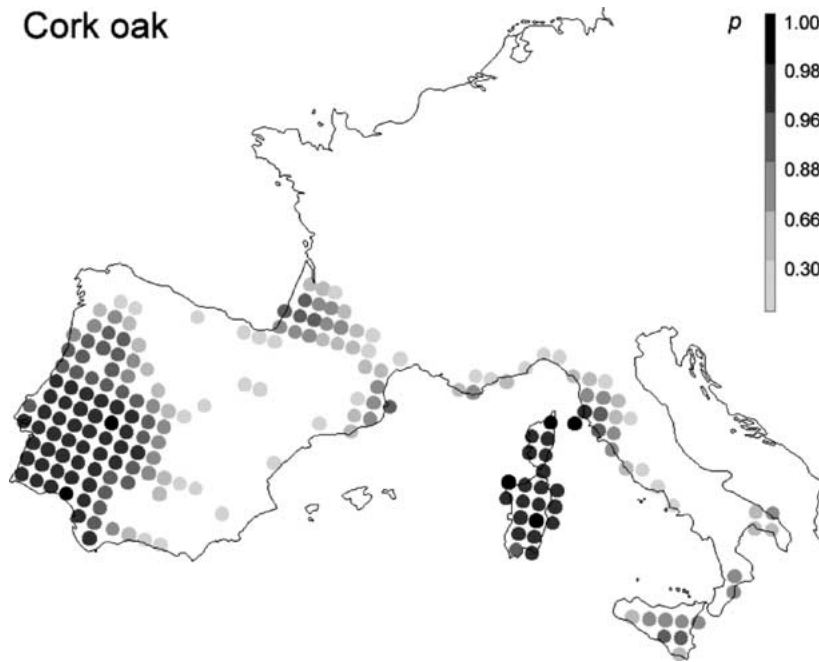


Figure 1. Example map showing probability of occurrence for a single species of tree (*Quercus suber*) obtained using a prototype model. This example is based on logistic regression between environmental and spatial data and records of the tree from the *Atlas Florae Europaeae* on a 50×50 km grid [32]. Probability estimates are shown (in shades of gray) only for grid cells within which the tree has been recorded.

2.2. Occurrence, habitat suitability, and dispersal

Our analysis began with records of species' presence from a distribution atlas. We used records for 148 species and subspecies of native European trees (hereafter referred to as "species"), which include most of the important timber species. These are a subset of the *Atlas Florae Europaeae* (AFE) data, mapped on the 50×50 km cells of a modified version of the Universal Transverse Mercator (UTM) grid [32] (hereafter referred to as "areas"). The region considered covers 2405 grid cells in western Europe, excluding most of the former Soviet Union, but including the Baltic States, because here sampling effort has been relatively intensive and uniform [33]. Logistic regression models were used to estimate species' probabilities of occurrence within grid cells from their association with explanatory variables [15]. The explanatory variables used included six environmental factors to represent aspects of habitat suitability (mean annual precipitation; mean temperature in January and July; mean potential evapotranspiration in January and July; altitude above sea level). In addition, a measure of spatial aggregation among neighboring records within the distribution of each species was used as an explanatory variable to represent species' potential for dispersal among areas. Ideally human impacts and other dependencies would also have been included, but this information was not available to us (see section 4.2). The resulting estimates of probabilities differ both (i) within species among areas, and (ii) among species within areas. Estimated probabilities are considered for area selection only within areas where records were present in the original atlas data (observed occurrence), and are interpreted as representing the

probability that an area meets the habitat and dispersal requirements that a species needs to occur there in the near future (figure 1).

2.3. Threat and vulnerability

Converting estimates of occurrence probabilities into estimates of persistence probabilities requires, at the least, including the time dimension. This extends probability of occurrence under present conditions, if they were to continue unchanged, to persistence to a particular time horizon in the future. Probabilities of persistence also require some consideration of the added risk that comes from the combination of any extrinsic threats that might be expected during the specified time period and each species' corresponding vulnerabilities [15]. Some aspects of threat and vulnerability can be estimated or modeled [34,35]. However, while this is potentially the most direct approach, even when considering single species there are still many difficulties [36–38].

Alternatively, we need not attempt difficult estimations of added risk, if we accept two assumptions. First, we might assume that we could reduce substantially the added risk from threats by applying appropriate conservation management. Second, we might assume that vulnerabilities to all threats under consideration are similar among all species. Both assumptions are crude simplifications. But with these assumptions, after selection we could use threat scores to prioritize (rank) selected areas for the urgency with which ameliorating management needs to be applied. This approach relies upon a relative rather than an absolute estimation of the added risk from extrinsic future threat. Furthermore, because this (sequential, non-compensatory) treatment of

Table 1

An algorithm for selecting areas using binary data for minimum-set or maximum-coverage goals.^a Used for the presence method, simple threshold method, and re-scaled threshold method (see text for data modifications).

Step	Rule
1	Select all areas for species that are more restricted than the representation goal (for representing all species at least once, this means selecting all areas with unique species records)
2	The following rules are applied repeatedly until all species are represented: (a) select areas with the greatest complementary richness in just the rarest species (ignoring less rare species), or if cost data are available, choose the area with the highest (rarest-species richness)/cost ratio; (b) if there are ties (areas with equal scores), select areas among ties with the greatest complementary richness in the next-rarest species (or (rarest-species richness)/cost ratio); (c) if there are persistent ties, select areas among persistent ties at random (this is an arbitrary rule; other criteria, such as proximity to previously selected cells, or number of records in surrounding cells, could be substituted); (repeat steps 2(a)–(c) until all species are represented).
3	Identify and reject any areas that in hindsight are unnecessary to represent all species (this includes a fast check of whether pairs of selected areas can be replaced by a single area).
4	Repeat steps 1–3 for representing every species at least once, twice and so on, until the required number of areas, n , is attained or exceeded, disregarding the results of one iteration of steps 1–3 before moving on to the next.
5	The following rules are applied repeatedly until all selected areas are re-ordered by complementary richness: (a) choose the previously selected area with the greatest complementary richness; (b) if before all areas are re-ordered the maximum complementary richness increment declines to 0, continue to re-order areas (step a above) after re-setting the cumulative richness to 0, but with starting scoring complementary richness again from the current position on the area list (ignoring: previously re-ordered areas; species more restricted than the current multiple representation target; and species that are already represented the required number of times within a smaller number of areas); (repeat steps 5(a)–(b) until all previously selected areas are re-ordered).
6	Choose the first n areas from the re-ordered area list.

^a Rules 1–3 are used to select a near-minimum-cost set of areas to represent all species at least once. Rules 4–6 are added to select a near-maximum-coverage set for any given number of areas (or budget), including multiple representations.

threat does not attempt to combine value, threat, and vulnerability estimates directly, there is no problem of incommensurate currencies. Therefore, because we plan to treat threat through prioritizing areas for management, we expect probabilities of persistence (from intrinsic population processes under conditions continuing as now, but with protection), to be correlated with probabilities of occurrence under these current conditions. Thus we use these latter probabilities as first-approximation surrogates. Preliminary empirical results show that in the absence of major catastrophes, correlations between probabilities of occurrence and probabilities of persistence can be very high [29]. Any differences between these probabilities that still retained the same rank order of values would affect the number of areas required for minimum sets (see section 2.1), but not the choice of areas for maximum-coverage solutions. However, changes in climate are likely to affect range edges first, which might make our lowest estimates of persistence probabilities particularly imprecise (with broader confidence intervals) because some marginal populations are expected to become more likely to persist while others might become less likely. Therefore the lower probabilities, which tend to be associated with range edges, would be less reliable for use in area selection and might be excluded by applying thresholds (see section 2.5).

2.4. Area costs

The cost constraint on conservation can be accommodated within quantitative area selection by maximizing the ratio of conservation value (benefit) to cost when considering each candidate area (tables 1 and 2) [4]. This approach

to cost is consistent, because the conversion relationship is supplied empirically from the common link via particular areas of both the costs and the incremental probabilities for valued biodiversity. “Costs” may include not only the obvious financial costs of acquiring and managing areas, but also the opportunity costs that are incurred from the income foregone when excluding other incompatible land uses, such as some forms of logging, agriculture, or other commercial development [10]. In the absence of good cost data, we treat all areas as having identical cost, so that the number of areas is used as a surrogate for monetary cost.

2.5. Complementarity methods

For both minimum-set and maximum-coverage problems (as defined in section 2.1), we compare five heuristic methods for dealing with probability data. All five methods exploit complementarity among biotas to increase efficiency of representation [28,39]. We assess the results of these methods against the results of selecting areas at random. For all of the methods used here, probabilities of persistence are treated as though they were independent of one another when selecting areas (but see section 4.2).

2.5.1. Presence method

The first method treats all non-zero probabilities as presence data (equivalent in this case to using the original atlas data). The algorithm used is based on a popular heuristic technique of selecting those areas richest in the rarest species at each step [40], a form of so-called “greedy algorithm”. Checks to exclude redundant areas have been added to im-

Table 2
A “goal-gap” method to select areas using probability data for minimum-set or maximum-coverage goals.^a

Step	Rule
1	Select all irreplaceable areas: (a) select all areas with species that have a total combined ^b probability (p_i) less than the representation goal ($p_{g(i)}$); (b) calculate the combined representation probability of species among selected areas (p_i) ^b ; (c) all data (p_{ij}) for any species that have reached their realizable representation goal, and all data for any selected areas, are set to zero (to ensure complementarity).
2	The following rules are then applied repeatedly until all species are represented: (a) calculate the potential contribution of each record in the matrix to increasing the combined representation probability above the current combined representation probability; (b) calculate the part of the potential contribution of each record in the matrix to filling the gap between the current combined representation probability and the representation goal; (c) sum these goal-gap contributions for all species yet to be fully represented for each area; (d) select the area with the highest summed goal-gap contribution, or if cost data are available, choose the area with the highest (summed contribution)/cost ratio; (e) if there are ties (areas with equal scores), select the area with the largest sum of probabilities across all species without complementarity (total p_j); (f) calculate the combined representation probability of species among selected areas (p_i) ^b ; (g) all data (p_{ij}) for the species that have reached their representation goal, and all data for any selected areas, are set to zero (to ensure complementarity); (repeat steps 2(a)–(g) until all species meet the representation goal).
3	For maximum-coverage problems, the set of selected areas from steps 1 and 2 may be re-ordered by re-applying the rules in step 2(a)–(g) to produce a series of approximate solutions for maximizing mean probability across all species.
4	For maximum-coverage problems, choose the required number n (or cumulative cost) of areas starting from the beginning of the re-ordered area list.

^a Rules 1 and 2 are used to select a near-minimum-cost set of areas to represent all species with a combined probability of at least $p_{g(i)}$, using probability data (p_{ij}) for species i in area j . Rules 3 and 4 are added to select a near-maximum-coverage set for a given number of areas or budget up to the number of areas required for the specified probability goal.

^b Probabilities are combined using $p_i = 1 - \prod_{j=1\dots n} (1 - p_{ij})$ (see section 2.5).

prove efficiency [41], together with a re-ordering procedure that provides approximate solutions to maximum-coverage problems (table 1). Once areas have been selected using the presence data, the results can be assessed for the combined probability of persistence (p_i) for each species i calculated across the entire network of selected areas. To give these area-network probabilities (p_i) for each species, local probabilities (p_{ij}) for species i in area j are combined among the n selected areas by using the product of probabilities of local non-persistence (extirpation):

$$p_i = 1 - \prod_{j=1\dots n} (1 - p_{ij}).$$

2.5.2. Simple threshold method

The second method is a modified form of the presence method (above). It differs in that it applies a higher threshold to the probabilities so that only the higher values are treated as presence data [14]. The effect is that the selection algorithm (table 1) “sees” only the areas with the higher species’ probabilities. The advantage is that it avoids selecting only one area with a low probability to represent a species, where it is unlikely to persist. Here we use the presence method for data above a threshold of $p_{ij} > 0.95$. The choice of threshold will affect the comparison of results, but this has not been investigated.

2.5.3. Re-scaled threshold method

The third method is a slightly modified form of the simple threshold method (above) that has also been used with

probability data [15]. The probabilities for species in areas (p_{ij}) are re-scaled to scores (s_{ij}) in the range 0–1 within each species before a threshold (here, $s_{ij} > 0.95$) is applied. This device is used simply to ensure that all species have at least some areas with re-scaled scores above the threshold, with the effect that the selection algorithm (table 1) “sees” the best areas for all species, even if their maximum absolute probabilities are low. The consequences of selecting areas by this method are compared with those of the other methods using the original (untransformed) probability estimates (p_{ij}), without the re-scaling applied for the area-selection procedure. Again, the choice of threshold will affect the comparison of results, but this has not been investigated.

2.5.4. Goal-gap method

The fourth method differs in that it is designed specifically to use the probability information directly in order to seek solutions requiring less area to represent species with high combined probabilities of persistence [27]. The goal ($p_{g(i)}$) was set here for representing all species (i) with $p_{g(i)} > 0.95$ where this is attainable. Any local estimates of $p_{ij} < 0.05$ are excluded, so that the selection algorithm (table 2) “sees” only the areas with the higher probabilities for each species. This avoids selecting many areas with very low probabilities for any one species, which would be undesirable if the lowest probability estimates were particularly imprecise (see section 2.3). The selection procedure is described in table 2. In outline, the method begins by selecting all of the completely “irreplaceable” [42] areas (ta-

Table 3
Species-representation results for near-minimum-area sets.

Area-selection method	Number of areas selected	Mean ^a among all species of combined probability within areas selected	Lower-upper quartile range among all species of combined probability within areas selected
Presence method	19	0.77	0.43
Simple threshold method	29	0.86	0.02
Re-scaled threshold method	40	0.94	0.02
Goal-gap method	79	0.97	0.01
Goal-gap threshold method	72	0.97	0.01
All areas with records above the quasiextinction threshold	2203	0.97	0.00

^a Means are used for comparison of central tendency because the probability distributions are too highly skewed for medians to be informative.

ble 2, step 1). These include all of the areas for any species with total combined probabilities among areas of less than the representation goal. The method then chooses one area at each iteration (table 2, step 2), by examining how much choosing each area would contribute incrementally to reaching the combined representation goal for each species, and choosing the area that contributes the most to this “goal gap” across all species. If ties occur for any choice, then the area with the highest sum of probabilities across all species is selected. A previous preliminary study [27] suggested that for addressing the maximum-coverage problem, using the first n areas from the re-ordered selected-area set can provide a good approximation to adjusting the probability goal. This is explored further here.

2.5.5. Goal-gap threshold method

The fifth method is a modified form of the goal-gap method (above). It differs in applying a much higher threshold to the probabilities, so that here we exclude the lower 50% of the observed range of probability data for each species. These areas would be better avoided if more of the lower probability estimates were expected to be imprecise (see section 2.3). The choice of threshold will affect the comparison of results, but this has not been investigated in more detail.

2.5.6. Random method

To assess the success of the five area-selection methods above relative to the lower bound of performance expected with these data [43], 1000 area sets were chosen by random draws without replacement for each number of areas required. For each of these area sets, we calculate the combined probabilities for each species represented, and then calculate the mean among all of the species represented. When these 1000 set means had been ranked in ascending order, the 951st value was used as an estimate of the threshold for whether observed set means were greater than expected by chance from the data. All area-selection methods were automated using the WORLDMAP software [44]. Because the analysis is used purely as an example to compare the consequences of using species’ local probability estimates

in area selection, the results should not be interpreted as an attempt to propose a new protected area network for Europe.

3. Results

3.1. Minimum-set problem

The species’ probabilities (central tendency and variation) achieved when seeking minimum-area sets by the five area-selection methods are shown in table 3. Means are used here for comparison of central tendency because the probability distributions are so highly skewed that medians are uninformative. The goal-gap method and the goal-gap threshold method succeed in achieving a higher probability across all species than the other methods, but also require 2–4 times as many areas. The re-scaled threshold method does almost as well as the goal-gap method in terms of (untransformed) probabilities, but requires approximately half the number of areas.

For the goal-gap method, figure 2(A) shows that the benefit from increasing the probability goal between 0.1 and 0.99 is a nearly linear increase in the mean probability among tree species combined among the selected areas. Oscillations in the results for lower probability goals occur because the goal is set for the minimum probability among species, not the mean, and the resulting changes in small numbers of areas have relatively large effects on the mean. The upper limit to the combined probability is constrained for these data by the 7% of species that would have a probability of less than 1, even if all areas were selected. However, because the cost of near-minimum sets in terms of numbers of areas required increases more rapidly and at an increasing rate (figure 2(B)), the relative efficiency (the benefit-to-cost ratio) of these area sets declines monotonically as probability goals increase (figure 2(C)). This shows that reducing the uncertainty about conservation success becomes disproportionately more expensive as the uncertainty is reduced.

3.2. Maximum-coverage problem

The central tendency in species’ probabilities achieved when seeking maximum-coverage sets of from 1 to 50 areas is shown in figure 3. All five methods represent species with

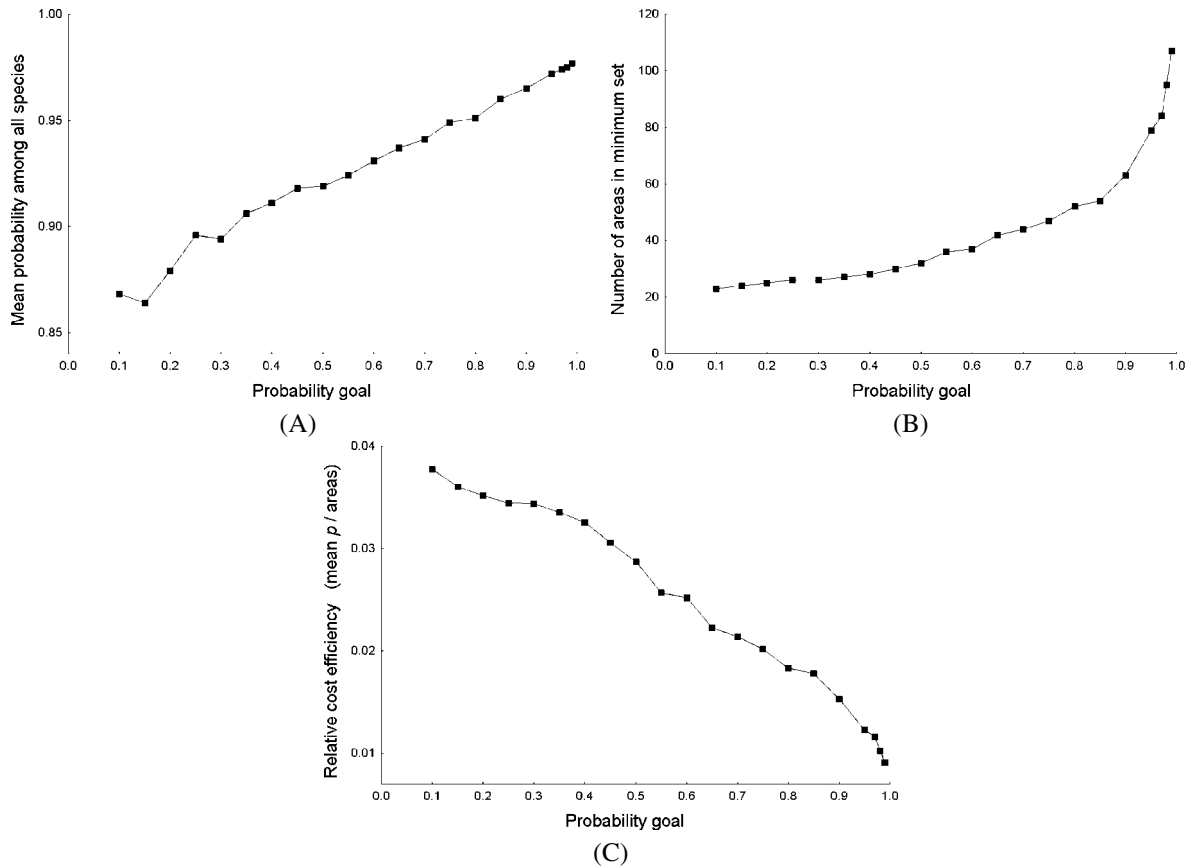


Figure 2. Consequences of selecting near-minimum-area sets for different probability goals ($p_{g(i)}$) by applying the goal-gap probability method (table 2) to the probability estimates for 148 species and subspecies of trees: (A) mean of the combined probabilities among all species among selected areas; (B) number of areas required for the near-minimum sets; (C) relative cost-efficiency of the area sets measured as mean species' probabilities (benefit, from graph A) divided by the number of areas required ("cost", from graph B). Areas are 50×50 km cells of the *Atlas Florae Europaeae* grid.

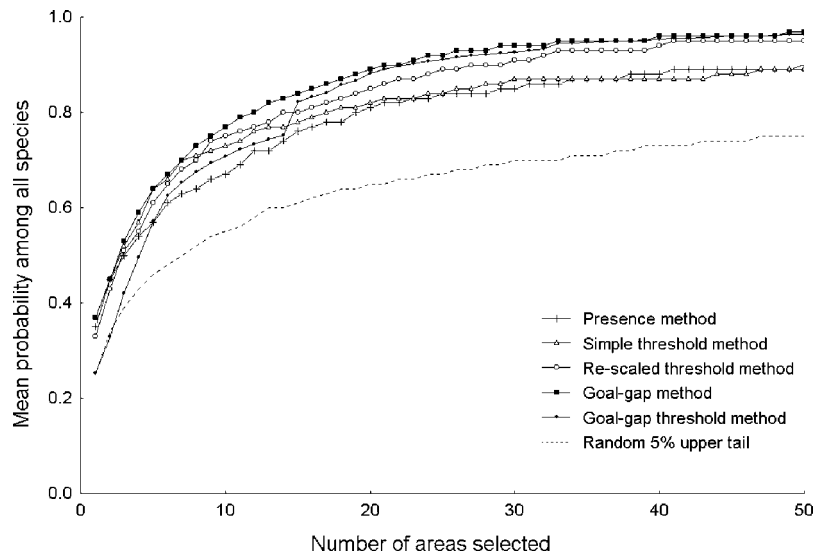


Figure 3. Comparison of the mean combined probabilities among all 148 species and subspecies of trees when 1–50 areas are selected for maximum coverage using five methods: *presence method* – treating all records as equivalent presences (table 1); *simple threshold method* – as above (table 1), but using records for species (i) in an area (j) only where $p_{ij} > 0.95$; *re-scaled threshold method* – as above (table 1), but after re-scaling probabilities for each species to scores (s_{ij}) in the range 0–1, then using records only where $s_{ij} > 0.95$; *goal-gap method* – for a goal of representing species with a probability goal of $p_{g(i)} > 0.95$, and taking the first 50 re-ordered areas that contribute to this goal (table 2); *goal-gap threshold method* – as above (table 2), but using records for species (i) in an area (j) only where the species' local probability p_{ij} is greater than 50% of the maximum p_{ij} for each species; and compared with the upper 5% tail of the distribution from drawing 1000 sets of 1–50 areas at random, so that scores below the dashed line are within the range expected when choosing areas at random. Areas are 50×50 km cells of the *Atlas Florae Europaeae* grid.

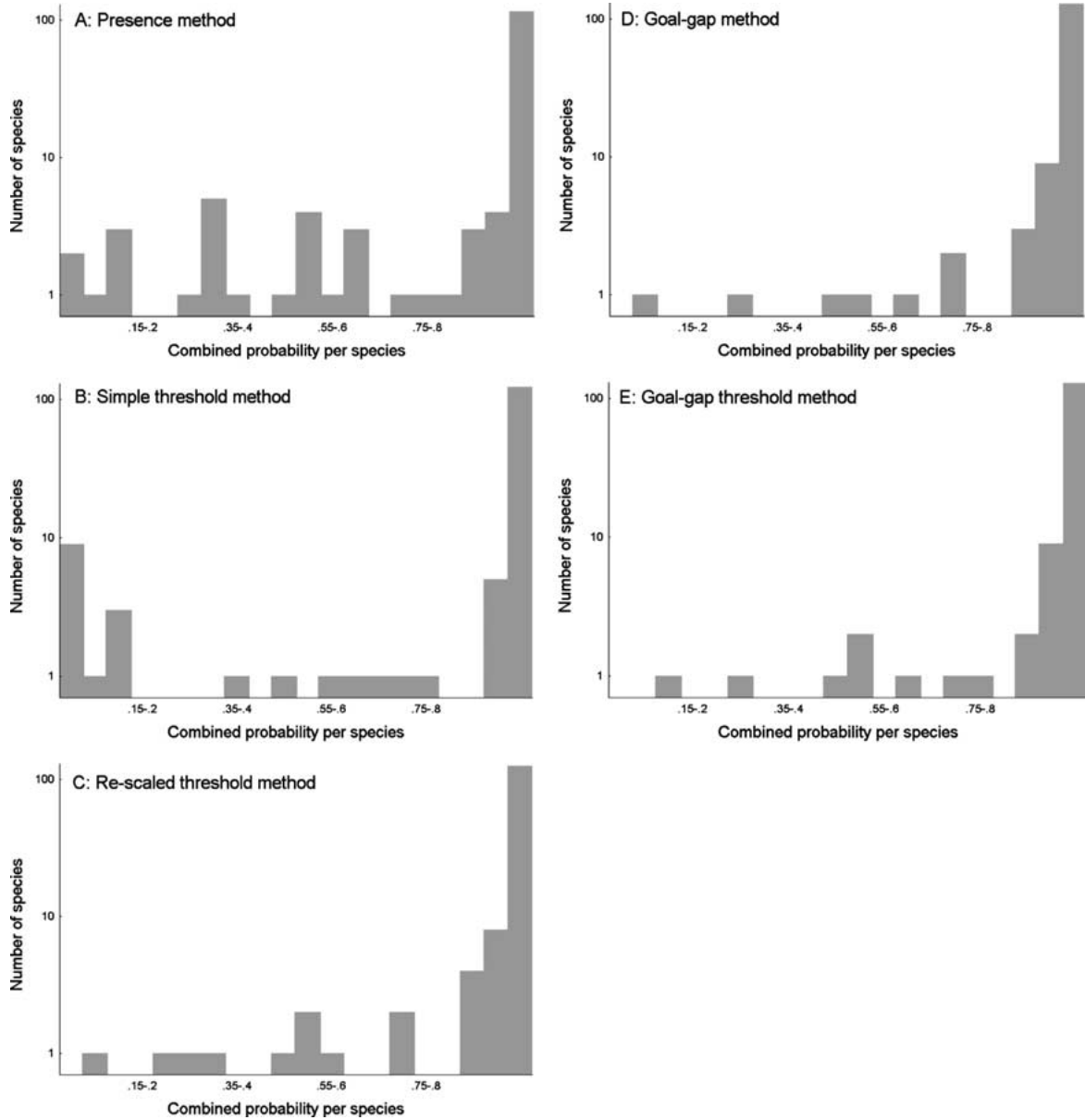


Figure 4. Frequency distributions of the combined probabilities for the 148 species and subspecies of trees from near-maximum-coverage solutions for 50 areas selected using five methods (see legend to figure 3).

a significantly higher mean probability than would be expected from selecting areas at random, except when choosing one or two areas with the goal-gap threshold method. The goal-gap threshold method performs so poorly when selecting only a few areas because it ignores many co-occurrences of species where the probabilities are below the threshold. Within the range of 1–50 areas selected, the relative performance of the five methods in terms of mean probability is predominantly: goal-gap > re-scaled threshold > simple threshold ≥ presence method, with the goal-gap threshold method moving from worst to joint best. The simple threshold method does relatively well for small numbers of areas, but becomes progressively worse as the number of areas increases. Again, the re-scaled threshold method does almost as well as the best goal-gap method. Com-

pared to using the presence method (at least when 5–50 areas are selected), the best probability method (goal-gap) usually gives an improvement of more than 10% in the mean among all species for the probability achieved in the areas selected.

A similar pattern of relative performance among five of the methods for the variation among species in their probabilities when selecting 50 areas is shown in figure 4. For this number of areas, the goal-gap, goal-gap threshold, and re-scaled threshold measures succeed in representing all but a very few species with high probabilities, where the other two methods represent more species with low probabilities. This is because the two latter methods either do not discriminate levels of probability and may therefore select areas with only very low probabilities

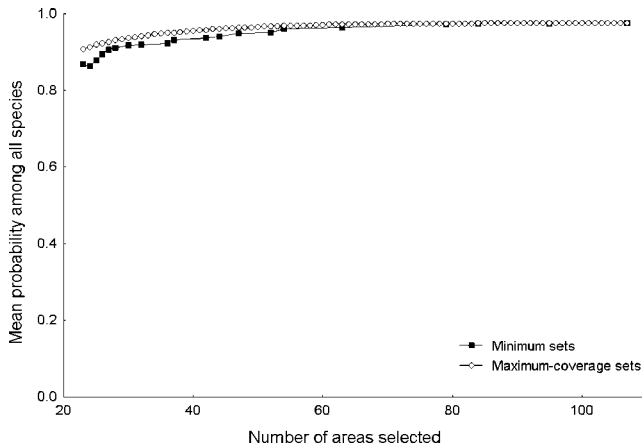


Figure 5. Comparison of the mean combined probabilities among all 148 species and subspecies of trees between two approximations to maximum coverage using the goal-gap method: by selecting near-minimum sets of areas (table 2, rules 1 and 2) for different probability goals ($p_{g(i)} > 0.1, \dots, 0.99$, see figure 2); and by selecting a near-minimum set for a probability goal of $p_{g(i)} > 0.99$ and then re-ordering the areas as a series of near-maximum-coverage solutions (table 2, rules 1–4).

for some species (the presence method), or else are completely “blind” to species with probabilities that nowhere exceed the threshold used in the method (the simple threshold method).

To address maximum-coverage problems for different numbers of areas, two different approximations based on the goal-gap method may be used: re-ordering, or changing the probability goal. Figure 5 shows that mean probabilities among species are slightly higher when a minimum set selected for a high probability goal is re-ordered (table 2, rules 1–4), compared to changing the probability goal to achieve minimum sets of different sizes (table 2, rules 1 and 2). This difference is small compared to many of the differences among methods in figure 3, and decreases as the number of areas selected by changing the goal converges on the re-ordered minimum set. On the other hand, figure 6 shows that the disadvantage of the re-ordering procedure is that it gives lower probabilities for a few of the species with the lowest combined probabilities, and that this persists over a broad range of probability goals. However, the re-ordering procedure is also much quicker and more convenient to use than searching for the most appropriate goal in terms of probability.

4. Discussion

4.1. Probability methods

The principal challenge for the probability approach is whether useful estimates of species’ probability of persistence can be obtained [36,37]. We often lack knowledge as to which factors govern species’ probabilities of persistence at any particular time and place, as well as lacking good data for quantifying these factors. Furthermore, not all aspects of the external threat or of the internal dynamics of populations

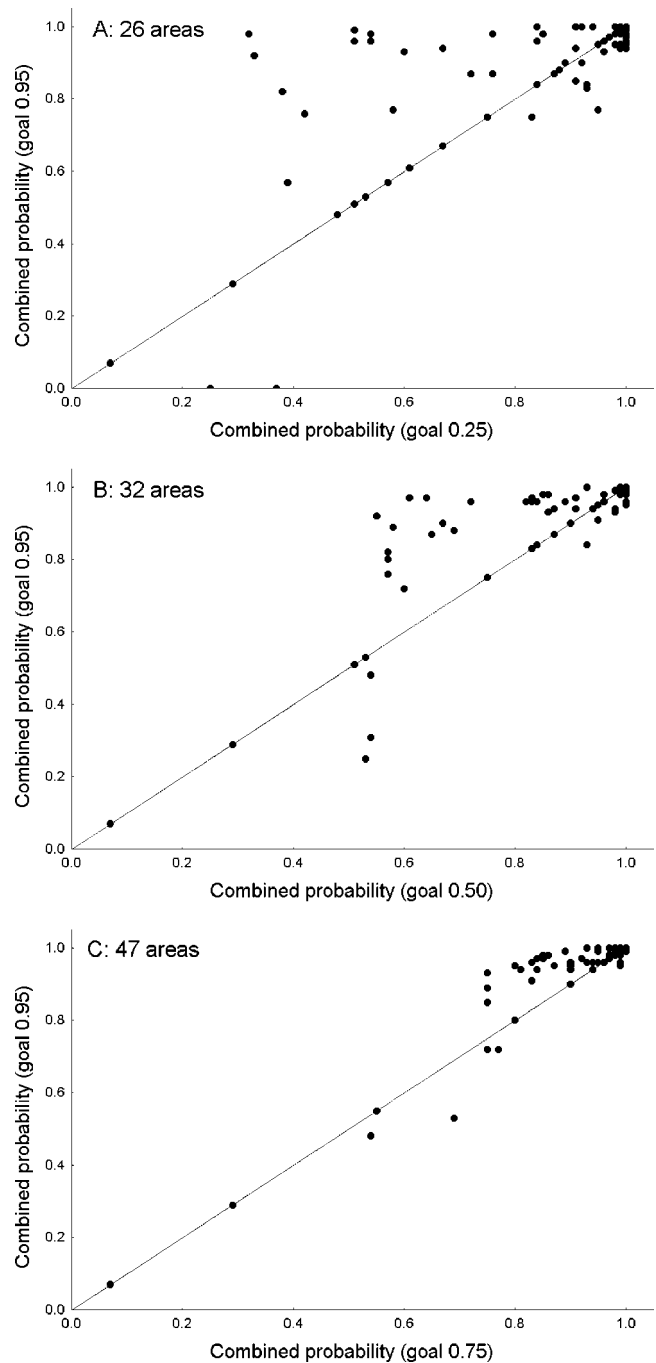


Figure 6. Variation in combined probabilities among all 148 species and subspecies of trees between two approximations to maximum coverage using the goal-gap method, plotted: (x axis) by selecting near-minimum sets of areas (table 2, rules 1 and 2) for different probability goals ($p_{g(i)} = 0.25, 0.5, \text{ and } 0.75$); and (y axis) by selecting a near-minimum set for a probability goal of $p_{g(i)} > 0.95$ and then re-ordering the areas as a series of near-maximum-coverage solutions (table 2, rules 1–4) and selecting the corresponding numbers of required areas (26, 32, and 47 areas). The diagonal lines represent equal probability in the results from the two methods.

will be predictable. The probability models used here are crude because they include only a few of what we believe to be the most important factors, although more inclusive models could be substituted when they become available. These difficulties should not prevent efforts for trying to reach use-

ful predictions now, particularly when enough is known at least to exclude the worst options. Consequently, it should be possible to reach estimates of probability of persistence that improve upon the current practice of treating all species' presence records as equivalent [15].

Empirically, comparisons of bird atlas data from Britain for two time periods 20 years apart have confirmed that short-term local persistence can be predicted from relatively simple habitat-suitability models [29,45]. Whether longer-term persistence will be as predictable remains to be seen, particularly when it is affected strongly by rare and unpredictable catastrophic events [38] or by fast rates of climate change. In principle, environmental change scenarios could be included within the suitability models, for example by using models of climate change with dispersal constraints [46].

Our results show that one advantage of using probabilities as a unifying currency for pattern and process factors in area selection is a greater expectation of conservation success: when using this more inclusive information, the species' combined estimated probabilities of persistence among the areas selected are higher. In particular, the increases in probabilities tend to be highest for the least widespread species [15]. This occurs because there tends to be a lower proportion of occupied grid cells with high probabilities within the ranges of the less widespread species. Consequently, even if areas were in effect selected at random by the presence method from within the ranges of these restricted species, then these areas would be expected to yield lower probabilities for this reason alone.

We find that the re-scaled threshold method and the goal-gap method are nearly equally area-efficient in representing species with high probabilities from the tree data. Of these methods, the re-scaled threshold method is simpler to implement. However, when inter-dependencies among areas are considered (see section 4.2), only the goal-gap method will be suitable.

4.2. *Extending the methods to include inter-dependencies*

The probability approach lends itself to a more realistic re-formulation of two aspects of the problem of how to select networks of conservation areas for biodiversity:

First, estimating probabilities of persistence opens the door to a more inclusive quantitative treatment of ecological dependencies when selecting area networks. These ecological dependencies might include the effects of: (i) connectivity and dispersal among areas for population and metapopulation processes; (ii) any requirements for more distant feeding, migration, and over-wintering areas; and (iii) inter-species interactions. Using probabilities that take account of dependencies within species among areas and dependencies among species within areas should select directly for networks of areas with beneficial characteristics where the models show that this would increase the combined probability of success. This should reduce the need for relying on simplistic "rules of thumb", which may not have the same value in all situations. Examples of such rules include the

debate on the relative merits of single-large-or-several-small reserves [47] and the discussion on the relative merits of selecting areas within the cores versus peripheries of species' ranges [48].

Second, it may be possible to predict the likely consequences for species' persistence of land uses in areas outside the network of areas selected as the primary reservoirs of biodiversity [17]. This could take account of the additional contributions that all other areas within the broader landscape matrix could make to species' persistence. It would be a useful step towards addressing the need to integrate biodiversity conservation within the broader pattern of other land uses within a region [49].

Ideally, networks of inter-dependent areas for optimal persistence of biodiversity would be sought by comparing all possible networks. Unfortunately, the problem will usually be too large computationally for complete enumeration of the possibilities. Similarly, the complexity of inter-dependencies among areas is likely to make branch-and-bound techniques with modeling at each step too time-consuming. Therefore, a simpler heuristic technique will be needed, in which areas are chosen in a series of steps, even though the result will provide only an approximation to the mathematically optimal solution [27].

Among heuristic techniques, the goal-gap method is much better suited than simple threshold methods for use in selecting inter-dependent areas, because it deals directly with the continuous scale of probabilities. As before, a single area would be chosen at each step, by comparing scores for candidate areas. The aim would be to find which area would make the largest incremental contribution towards increasing the probability of persistence across all species (or other valued features) for reaching the chosen goal. But when taking account of inter-dependencies, the probabilities of persistence would need to be re-estimated dynamically at each step of selection. This would involve two calculations. First, probabilities of persistence for each species would have to be estimated for the combination of previously selected areas, including the effects of any inter-dependencies among these areas (this calculation is needed only once for each step in area-selection). Second, and for each candidate area in turn, probabilities of persistence for each species would have to be estimated for the combination of the previously selected areas plus the candidate area. This would need to include any inter-dependencies among previously selected areas and the candidate (this calculation is needed for every candidate area at every step). As mentioned above, if the additional information were available, then both sets of probability estimates should ideally include the contributions of all remaining unselected areas and their interactions, but discounted appropriately for land uses that are not aimed primarily at managing for conservation. For the goal-gap method of area selection, a candidate area's score is expressed as the sum across all species (or other valued features) of the incremental changes in probability between the two sets of probability estimates. Thus the goal-gap method would still be applicable to this more complex and realistic

problem, and it is only the modeling part of the procedure that would need to be modified in order to integrate the inter-dependencies among species and areas.

4.3. Apples and oranges

We argue in the introduction that many of the biological and social factors that have to be considered in decision-making for conservation can potentially be integrated with consistency within fewer currencies to make the inter-conversion problems more defensible. Examples of integrating related factors include: (i) accommodating diversity, range-size rarity and endemism, by using the complementary value of local biota [39]; (ii) accommodating complementary value (in the broadest non-monetary sense) with habitat suitability, dispersal, vulnerability, and threat, by using probabilities of persistence (see sections 1.4, 2.2, and 2.3); and (iii) accommodating probabilities of persistence with other social factors, such as the cost of acquiring areas, cost of management, and opportunity costs, by using the conservation benefit-to-cost ratio (see section 2.4). If some of the social and political constraints [50] could be expressed in terms of their consequences for a common "cost" currency by economists, then this would be one way of integrating these factors within area selection with consistency. Clearly, an appropriate formulation of costs presents a challenge (for economists), both in deciding how factors should be included, and in acquiring appropriate data.

4.4. Putting methods into practice

Prendergast et al. [51] have suggested that the greatest problems for applying quantitative methods to practical conservation stem from a lack of communication and funding. We suspect that there may be even greater difficulties in persuading many interest groups to forego direct influence over a political decision-making process in favor of merely influencing the goals of a quantitative process, or of choosing among alternative solutions. This may be particularly difficult if the quantitative results thwart the interests of these groups. Such a position is perfectly rational from a political perspective, if not from a biological perspective [2]. But this should not prevent research into improving biological methods for use when opportunities arise.

Nonetheless, many land managers may indeed be either unaware of quantitative methods, or at least unaware of how these methods could be used to get the most from their expert local knowledge. While more biological surveys are certainly needed, quantitative methods also need to be passed to land managers in a form that can help them explore and communicate their wealth of existing knowledge. This process might benefit from easy-to-use decision-support software (DSS), if it could make area-selection procedures more accessible for application to large numbers of species (the conservation analogue of an easy-to-use word-processor program replacing earlier desktop-publishing systems of similar power that once required expensive specialist machinery

and staff). Combining these resources would go some way towards improving the chances of conserving biodiversity, even when using very simple surrogates for the major factors affecting species' persistence.

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