Biological Reserves, Rare Species and the Opportunity Cost of Diversity

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Abstract

The preservation of species diversity generally suggests protection of either the greatest number of species possible or all species. Requiring representation of each species in at least one parcel in the system and seeking the minimum number of parcels in the reserve system to achieve this requirement is termed the Species Set Covering Problem (SSCP). Nonetheless, it is important, as well, to consider the rarest of species, as their populations are the most in need of protection to assure their survival. This paper uses zero-one programming models and an existing data set to study species protection, rarity and the opportunity costs of diversity.

We employ for this purpose an integer programming model that uses the SSCP format to require at least one representation of each and every species, but that seeks in addition protection of the rarest species. This is achieved by maximizing redundant coverage of those species designated as rare. Results are then compared to those of the SSCP.

Recognizing that resources available for conservation purchases could well be insufficient to represent all species at least once, we structure a model aimed at trading-off first coverage of the greatest number of species against redundant coverage of rare species. We develop a tradeoff curve for this multi-objective problem in order to evaluate the opportunity cost of covering more species as redundant coverage of rare species decreases –and vice versa.

Finally, various possible rarity sets and various budget proxies are considered along with their impacts on conservation policies, Pareto optimality and on the opportunity cost of diversity.

Keywords: 0-1 programming models, nature reserve selection, rare species, opportunity costs, conservation policies

1. Introduction

The Convention on Biological Diversity was opened for signature at the United Nations Conference on Environment and Development in Rio in 1992 and entered into force at the end of the following year. The ratifying nations committed to achieve a significant reduction of the current rate of biodiversity loss by 2010.

One of the important strategies to conserve biodiversity is the setting aside of (public and private) land for the creation or enlargement of biological reserves to preserve key habitat and species living within those reserves.

Over the past twenty years, an increasing amount of research has aimed at delineating nature reserves for promoting the conservation of biodiversity. The preservation of species diversity often suggests protection of the greatest number of species, of all species and/or of rare species.

This new field of "reserve selection and design science" strongly parallels another, older, field, that of "facility location science" (see ReVelle et al., 2002). As a matter of interest, locating the least number of facilities (say, fire stations), such that all demand nodes (say households) are covered by stations within a certain distance or time standard, is methodologically identical to selecting the least number of eligible land parcels for a nature reserve such that all species in need of protection are present in at least one parcel. Facilities and land parcels, like households and species are indivisible or integer variables. Similarly, as financial resources may be insufficient to cover all demand nodes or all species, another problem is to protect respectively as many demand nodes or species as possible with a limited number of facilities or of land parcels. The two location science models explained above are named the LCSP – for Location Set Covering Problem – and the MCLP – for Maximal Covering Location

Problem – and were elaborated in the seventies by Toregas et al. (1971) and Church and ReVelle (1974). More recently, these same ideas have been applied to reserve selection and design science. First, Kirkpatrick (1983) and Margules et al. (1988) articulated the first models later recognized and developed as the counterpart model of the LSCP by Possingham et al. (1993) and Underhill (1994). Next, Church et al. (1996) and Camm et al. (1996) formulated the counterpart species protection model of the MCLP, although, in general, the original species protection researchers did not recognize the antecedent models of location science.

These models were later refined in different ways. Ando et al. (1998) and Polasky et al. (2001) considered the difference in land values and formulated budget-constrained models. Probabilistic models with an uncertain incidence of species within sites and no guarantee of survival have been set up (e.g., Haight et al, 2000 and Camm et al., 2002). Models with spatial attributes, requiring , for example, land parcels to be selected in a compact and/or contiguous way have recently been proposed, among others, by Nalle et al. (2002) and Mc Donnell et al. (2002). Reserve design science, that is the science of nature reserves with spatial characteristics, has been thoroughly reviewed by ReVelle et al. (2002) and Williams et al. (2004).

All the above models focus on protecting either all or the greatest number of species although some of the models add spatial considerations as well. If we interpret the achievement of biodiversity as the need to protect as many species as possible, it follows that populations of the rarest species are in critical need of protection. Indeed, species richness and the presence of rare species are the most frequently cited criteria for site selection by conservationists (Prendergast et al., 1993). Recently, Arthur et al. (2004) took rare species into account by using a probabilistic formulation for maximizing expected coverage while ensuring that recognized endangered species meet a minimum coverage probability threshold. The purpose of this paper is to explicitly consider protection of “rare” species and to determine the opportunity cost of diversity in a deteministic setting. The former is obtained by maximizing the parcel appearances of those rare species. Coverage of all species is then traded off against representation of rare species in order to determine the opportunity cost of diversity.

The remainder of the paper is organized as follows. The next section details the data set which will be used to implement and exercise the models. Section 3 reviews the counterpart problem of the LSCP. Section 4 presents a model of redundant coverage of rare species given coverage of all species. Section 5 details the multi-objective problem of preserving as many species as possible and preserving rare species in as many parcels as possible. The tradeoff between the two objectives is evaluated and the opportunity cost of diversity is explored. Section 6 discusses both impacts of refinements in the rarity definition and the influence of various conservation budgets on the solutions, and Section 7 concludes.

2. The Data Set

The State of Oregon has been divided in 441 identical 635 square kilometers hexagonal sites. These hexagons, completely or partially overlapping the political boundaries of Oregon (White et al., 1992) were originally developed for the US Environmental Protection Agency.

Data mapping terrestrial vertebrates for each hexagon have been developed for the Biodiversity Research Consortium. This study is limited to terrestrial vertebrates: bird, mammalian, reptilian and amphibian species breeding in the State of Oregon, which add up to a total quantity of 426 species. Data on the occurrence of these species and the research methodology are obtained from and are developed in Master et al. (1995) and Master (1995).

Species are assigned to hexagons on the basis of both known records of occurrences and known habitat preferences and on known or suspected habitat occurrence within an hexagon.

This means that few hexagons have been comprehensively surveyed; hence, the data base represents known and predicted distributions by hexagon, ranked into one of the four following categories. Species' presence in a site is confident or certain if verified sightings of the species in each of the hexagons have occurred in the past two decades. It is probable or predicted if the hexagon contains suitable habitat for the species, if there have been verified sightings in adjacent hexagons and if a local expert believes it is highly probable that the species occurs in the parcel. Occurrence is possible if no verified sightings have occurred in the parcel, if the habitat is of questionable suitability for the species and if a local expert believes it is possible that the species occurs in the parcel. When species' likelihood of occurrence does not fall into one of the three above categories, the population is considered as absent from the hexagon because the habitat is unsuitable for the species in question.

As the ranking of "possible" is speculative, only the categories "confident" and "probable" were used to assign the presence of each 426 species in each of the 441 hexagons.

The complete set or partial sets of the Oregon's species occurrence data have recently been used for implementing various models such as those described in Csuti et al. (1997), Haight et al. (2000), Polaski et al. (2001), Camm et al. (2002) and Arthur et al. (2004). The next three sections develop various integer-programming formulations for representing all species in the smallest number of hexagons (section 3), for favoring the occurrence of rare species in a predefined number of selected parcels (section 4) and for trading off redundant coverage of rare species with primary coverage of all species (section 5). The models are solved as linear programming with branch and bound and the outcomes based on the complete data set are discussed in each section.

3. The Species Set Covering Problem

The Species Set Covering Problem (SSCP) introduced as a formal model by Possingham et al. (1993) and Underhill (1994) parallels in structure the Location Set Covering Problem (LSCP) (Toregas et al., 1971). The model requires representation of each species in at least one parcel in the system and seeks the minimum number of parcels in the reserve system to achieve this requirement.

Let there be n parcels of land eligible for selection and indexed j and m species that all need to be represented in the system, indexed i, with J and I representing the sets of parcels and species.

The problem is formulated as an integer program:

$$\text{Min } Z_1 = \sum_{j=1}^{n} x_j \tag{1}$$

$$\text{s.t.} \quad \sum_{j \in N_i} x_j \geq 1 \qquad \forall i \in I \tag{2}$$

$$x_j \in \{0,1\} \qquad \forall j \in J \tag{3}$$

where x_j=1 if parcel j is selected for inclusion in the reserve and zero otherwise and where N_i represents the set of parcels j that contain species i.

The objective (1) seeks to minimize the number of land parcels in need of preservation while requiring that each species is represented somewhere in the system at least once. Indeed, equation (2) states that, for each species i, the sum of parcels containing that species must be greater or equal to 1; that is, at least one parcel x_j (for $j \in N_i$) must be equal to 1, or equivalently, species i must be contained in the system.

The solution to this integer program gives a number $Z_1 = p^*$ representing the minimum number of parcels necessary to represent all species that are in need of protection. This result can be obtained by solving the model as a linear program with branch and bound if it is required. Alternatively, heuristics have been developed for solving these problems. Heuristics have the disadvantage of finding possible local instead of global optima. Their advantage is i) usually a faster time for solution than a linear programming with a branch and bound add on and ii) relative transparency of the methodology employed.

This particular model and formulations in subsequent sections are solved as linear programming problems with branch and bound using Xpress MP (2003) and GAMS/Cplex (1990). The minimum number of hexagons to set aside as biological reserves for protecting all the 426 terrestrial vertebrate species is 23 ($Z_1=p^*=23$). It means that if only a little more than 5 percent of the complete land surface of the State of Oregon were set aside as a nature reserve, all species would be protected.

4. Redundant Coverage of Rare Species

Here, we aim at enhancing species diversity by structuring another integer programming model that still requires at least one representation of each and every species, but now favors additional protection of the rarest species.

There does not seem to be any strong consensus about the definition of rare species. Rarity is a measure of extinction risk and provides a basis to identify threatened species. In general, species characterized by small geographic range, habitat specialization and low abundance are at higher risk of extinction than a widely distributed, habitat generalist with high abundance.

Even though frameworks exist for classifying rare species (used for example in Hannon et al., 2004), rarity is often defined arbitrarily: by expert opinion, by deciding that half or a quarter of the species are rare, or by making the distinction between low and high abundance species and between species with narrow versus wide geographic range at the median values for each variable (Cofre and Marquet, 1999). These subjective methods will guide the reserve selection procedure, and for this reason, a sensitivity analysis will be undertaken in section 6, for determining the impact of various subjective definitions on the results.

Here, the set of species I will be partitioned into two distinct subsets R for rare species and C for common species ($\{R\}=\{I\}\backslash\{C\}$). Like Malcolm and ReVelle (2004), it is assumed that i) each species is likely to sustain itself in each parcel where it appears if the parcel is preserved, ii) the degree of viability is indistinguishable no matter the parcel in which the species is present and iii) survivability is independent of co-location with other species.

Church et al. (1996) and Storch and Sizling (2002) recently found out that, in general, most species are either relatively infrequent or very common in terms of the number of occupied sites (that is in terms of N_i). The frequency distribution of species' area of occupancy is thus often bimodal, as it is for the Oregon data set, as shown in Figure 1.

Figure 1

The rarest among the 426 species of the Oregon data set are present in a single hexagon whereas the most common individuals occur in all parcels; that is, the cardinality of N_i varies from 1 to 441 over all species. Figure 1 also shows that 114 species occupy less than 10 percent of the sites and 89 are present in at least 90 percent of the parcels. The latter can be considered very common and the former are relatively infrequent.

As rarity is a measure of extinction risk, it is plausible to assume that, among the infrequent species, those appearing in less than 1 percent of the surface of the State of Oregon (4 parcels or less) are rare and threatened for their survival in the region. As illustrated in Figure 2, which is a development of the first frequency bar of the bimodal distribution of Figure 1, there are 22 rare species among the 426 terrestrial vertebrates. Said differently, the set of rare species is defined as $R=\{i: |N_i| \le 4\}$ with $|R|=22$.

Figure 2

Having identified which species are rare, the model can now be modified to require not only coverage of each and every species as before, but also to maximize the number of parcel appearances of rare species within the reserve system selected by the SSCP. Mathematically, the model can be formulated as such:

$$\text{Max } Z_2 = \sum_{i \in R} \sum_{j \in N_i} x_j = \text{cumulative parcel appearances of rare species} \tag{4}$$

$$\text{s.t.} \quad \sum_{j \in N_i} x_j \ge 1 \qquad \forall i \in I \tag{5}$$

$$\sum_{j \in J} x_j = p^* \tag{6}$$

$$x_j \in \{0,1\} \qquad \forall j \in J \tag{7}$$

where R is the set of rare species ($R \subset I$). The constraints ensure that all species are covered at least once (equation 5) and that p^* parcels are selected in the reserve system (equation 6) or said otherwise, that the quantity of parcels preserved corresponds to the minimum number of land parcels needed to cover all species, as deduced from the SSCP. The objective (4) maximizes the total number of occurrences of rare species in the system of chosen parcels. In other words, within all the sets of parcels containing each species i (within N_i), only those parcels x_j containing rare species ($i \in R$) are maximized. Solutions to this model select from among the alternate optima to the SSCP with preference placed on repeated coverage of rare species.

For illustration purpose, suppose that there are 9 parcels to choose from, labeled x_1 to x_9 and that 5 species are present in various parcels according to the following: $N_1=\{x_1, x_2, x_4, x_6\}$, $N_2=\{x_2, x_5, x_7, x_8\}$, $N_3=\{x_3, x_4\}$, $N_4=\{x_1, x_5, x_7, x_8, x_9\}$ and $N_5=\{x_3\}$. Suppose further that species are qualified as rare if they occur in two or fewer parcels. This means that species 3 and 5 are rare as they respectively appear in 2 and 1 parcels, whereas the number of occurrences of species 1, 2 and 4 are respectively 4, 4 and 5 or the cardinality of N_i for each i. Therefore, the parcels that appear in the objective function are only those including these two rare species, that is x_3 and x_4 for rare species 3 and x_3, for rare species 5. The objective of maximizing the number of parcel occurrences of these two rare species is thus: Max $Z = 2x_3 + x_4$ subject to constraints (5) to (7). Equation (4) is thus equivalent to Max $Z = \sum_{j \in J} a_j x_j$ where a_j is the number of rare species represented in parcel j, since it is equivalent to Max $Z = \sum_{i \in R} \sum_{j \in J} x_j$.

When the model described in equations (4) to (7) is solved on the Oregon data, the maximal value of the objective is Z_2=24, which means that there are 24 parcel appearances of rare species. Said differently, each selected parcel contains in average one rare species (in fact, at most two rare species appear in a selected parcel; hence, some parcels do not contain any rare species).

Figure 3

Interestingly, parcel occurrences of rare species are exactly the same with the redundant coverage model (equations 4 to 6) and all of the SSCP runs (equations 1 to 3). This peculiar result can be explained by the conjunction of various factors. First, the rare species set is a very small group (22 individuals out of 426). Second, no parcel contains more than 2 rare species, thereby equating redundant coverage to simple second coverage (see Hogan and ReVelle, 1986, for back-up coverage formulations and applications). Third, 7 out of the 22 rare species only occur in one parcel and therefore cannot even benefit from back-up coverage. And fourth, the number of selected parcels is only 23 and these must cover all (rare and common) species.

Suppose that the redundant coverage model would now be changed to accommodate more parcels in the reserve system. As shown in Figure 3, each additional hexagon would be chosen among those with the highest number of parcel occurrences of rare species. Indeed, the first 5 additional parcels (p* increases incrementally from p*=23 to p*=28) bring about 2 additional appearances per hexagon. Further increases in the number of parcels selected only add up one rare species occurrence per additional hexagon up to a point where no more rare species are present in the remaining unchosen parcels (as of p*=52).

5. Species Coverage Versus Redundant Coverage of Rare Species

Departing from an ideal world, it is recognized that resources available for conservation purchases could well be insufficient to cover all species at least once. Hence, a smaller than optimal number of parcels is available to set aside ($p^{**}<p^*$) and the purpose is to have as many species covered as possible.

This MSCP, for Maximal Species Covering Problem, defined as the MCLP counterpart, was first established by Church et al. (1996) and does not ensure that rare species will be represented in the chosen parcels. For that reason, objective (4) is maximized, thereby favoring not only the presence of rare species but also their redundant coverage (i.e. their inclusion in more than one parcel). This objective is added to the MSCP objective.

This bi-objective formulation is written:

$$\text{Max } Z_3 = \sum_{i \in I} y_i = \text{number of species represented at least once} \qquad (8)$$

$$\text{Max } Z_4 = \sum_{i \in R} \sum_{j \in N_i} x_j = \text{number of parcel occurrences of rare species} \qquad (9)$$

$$\text{s.t.} \qquad y_i \leq \sum_{j \in N_i} x_j \qquad \forall i \in I \qquad (10)$$

$$\sum_{j \in J} x_j = p^{**} \tag{11}$$

$$x_j \in \{0,1\}, y_i \in \{0,1\} \qquad \forall i \in I, \forall j \in J \tag{12}$$

where y_i is equal to 1 if species i is represented in at least one parcel selected in the set N_i and is zero otherwise.

As financial resources are assumed to be insufficient to cover all species, objective (8) maximizes the number of species that will be represented in the system. Objective (9) maximizes the number of times rare species are represented by favoring selection of parcels in which they are present. The juxtaposition of these two objectives is particularly important because protection of the greatest number of species as the sole objective (objective 8) may disadvantage the protection of rare species (objective 9). Indeed, many species rich areas often do not coincide for different taxa and many rare species frequently do not occur in most species-rich areas[1] (Prendergast et al., 1993). Therefore, species at risk of extinction may not be likely to be included in sites selected to protect indicator groups (Lawler et al., 2003) or common species. Conversely, maximizing the occurrence of rare species alone may drastically reduce the protection of all the other species.

The first constraint (equation 10) ensures that species i is covered (y_i=1) only if there is at least one parcel containing i in the reserve system ($\sum_{j \in Ni} x_j \geq 1$). Constraint (11) states that only a smaller than optimal number of parcels (p^{**}) is available for selection due to budgetary limitations.

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[1] However, Cofre and Marquet (1999) found that conservation of species-rich areas in their data set also protects large population of rare and threatened Chilean mammals even though it does not offer protection for Chilean endemic species. And to a certain extent, it also seems to happen in the Oregon data set (see infra, section 6).

There exists various methods for solving multi-objective programs, one of them being the weighting method (Cohon, 1978). It simply places a weight w ($0 \le w \le 1$) to each objective so as to solve the model as a single objective integer program:

$$\text{Max } w\sum_{i \in I} y_i + (1-w)\sum_{i \in R}\sum_{j \in N_i} x_j \tag{13}$$

subject to constraints (9) to (12). By varying the weight given to each objective, a set of Pareto optimal results (sometimes also called the non-inferior or non-dominated set in the multicriteria optimization literature) can be generated. One objective is thus traded off against the other, and yields solutions different from the solution given by optimizing a single objective. This enables us to determine, for example, the impact of an increase in the number of occurrences of rare species (equation 9) on the total numbers of species covered. In other words, the opportunity cost of species diversity, defined here and as of now, as increased occurrences of rare species, can be computed. Conversely, one can estimate the opportunity cost of covering additional species in terms of diversity loss, or said another way, the opportunity cost of further coverage of all species as redundant coverage of rare species decreases.

Suppose that the available conservation budget enables us to set aside 15 parcels of land instead of the 23 required to protect all species ($p^{**}=15$). Solving the multi-objective problem by the weighting method with a weight $w=0$ would be equivalent to solving the single objective redundant coverage model for rare species with a limited number of parcels (15) to be selected. All species would not be represented in this solution since the number of parcels is insufficient. In other words, only Z_4 (equation 9) would be maximized. Conversely, setting w equal to 1 would be equal to the Maximal Coverage Species Problem, that is the counterpart of the Maximal Covering Location Problem, and would not consider the rare species to be of any special importance. As weights are gradually varied from 0 to 1, both competing objectives are considered and their relative importance increases with their respective weights.

Figure 4

Figure 4 depicts the tradeoff curve for the above-mentioned objectives. If w=0, parcel appearances of rare species amount to Z_4=24, like the redundant coverage model (equations 4 to 7) where Z_2=24. This means that the more limited number of parcels selected (15 instead of 23) does not decrease parcel occurrences of rare species because the multi-objective program does not require that all species be covered. Hence, the 15 parcels including the rarest species are only considered and by chance in this case, they amount to the same number as the redundant coverage model[2]. When w increases from 0.3 to 0.4, 8 additional species are covered (404 to 414) to the expense of four representations of rare species (24 to 20). In that case, the opportunity cost of protecting one additional species in terms of biodiversity loss is 0.5. The law of increasing opportunity cost shows that it costs more and more to increase one objective in terms of the other one. Indeed, increasing w to 0.6 and 0.7 enables to cover one additional species in each case and this costs respectively 1 and then 3 parcel disappearances of rare individuals (19 and 17 occurrences respectively). Up to now, all the points illustrated in Figure 4 are Pareto optimal but increasing w to 1 (going to the bottom right point of Figure 4) would be Pareto inferior as parcel occurrence of rare species would go down from 17 to 14 without any gain on species coverage.

Reading the graph the other way around enables us to determine the opportunity cost of diversity. As biodiversity is enhanced by selecting parcels in which rare species are present, i.e. as w goes down incrementally, less common species are protected with a fixed budget. The

[2] Parcel occurrences of rare species would of course increase if more parcels were to be selected, without requiring that all species be covered, as shown later in Figure 7.

opportunity cost of diversity – 1 additional parcel appearance of rare species – is valued at 0.5, 1 and 2 species lost as *w* changes from 0.7 to 0.6, 0.4 and 0.3 as it respectively induces an increase of 2, 1 and then 4 additional parcel occurrences of rare species (17 to 19, 20 and 24) at the expense of 1, 1 and 8 primary coverage (416 to 415, 414 and 406). In other words, if both objectives are given at first an equal weight and if the conservation agency later desires to favor rare species (increasing *w* from 0.5 to 0.6), it in fact accepts to trade 1 additional parcel appearance of rare species for 1 common species. Placing a further weight on rare species (*w*=0.7) would be equivalent to accepting the loss of 2 species for an additional parcel appearance of a rare species.

6. Refinements: reconsidering rarity definition and budget proxy

The rarity measure used here is subjective, as are all rarity measures. Its definition is very strict in this context as species are said to be rare when they appear in less than 1 percent of the hexagons (that is in 4 parcels or less). Only 22 species out of 426 individuals correspond to such a definition. A wider set would increase the number of rare species and compared to what is said in the literature (e.g. Cofre and Marquet, 1999; Storch and Sizling, 2002), it is not inconceivable to estimate that species occurring in less than 10 percent of the study area are relatively infrequent or rare.

Three new rarity sets, based on relative rarity (see Figure 2) are thus defined: a) $R' = \{i: |N_i| \leq 12\}$, b) $R'' = \{i: |N_i| \leq 24\}$ and c) $R''' = \{i: |N_i| \leq 43\}$. The first new rarity set R' includes 51 species ($|R'|=51$) appearing in 12 parcels or less; that is, the first three bars of Figure 2 compared to the original rarity set corresponding to the first bar of the figure. The cardinality of the next rarity set is $|R''|=86$; it is more lenient as it corresponds to species appearing in at the most 24 parcels and is represented in the first six bars of Figure 2. The final rarity set shows that 114 species ($|R'''|$=114) appear in less than 10 percent of the parcels (the whole of Figure 2), or said differently, some 27 percent of all species of the Oregon data set are relatively rare, which is illustrated by the binomial distribution of species frequency: this final rarity set is the first bar of Figure 1.

Figure 5

Figure 5 depicts the tradeoff curve of the multi-objective formulations with the three new rarity sets and 15 parcels to be selected as biological reserve, as in the previous section. When Z_3 only, the total number of species, is maximized (w=1), rare species are not considered differently than regular species, hence, 416 individuals are protected in all cases. The rarity set is therefore not critical when the sole objective is to protect as many species as possible with a given budget. However, when Z_4 only, the parcel occurrences of rare species, is maximized, parcel appearances of rare species increase more than proportionally with an expanded rarity set. Said differently, the magnitude between the top-left points of the tradeoff curves increases as the rarity sets get larger (see Figures 4 and 5). As a matter of fact, the value of Z_4 increases from 24 for the original rarity set ($|R|$=22, Figure 4) to 82 when $|R'|$=51, 206 when $|R''|$=86 and 337 when $|R'''|$=114 (Figure 5). Hence, if parcel occurrences of rare species only amount to 24 with the original rarity set comprising 22 species, they increase with the rarity sets to reach the value of 337 when 10 percent of the species are qualified as rare.

This means that defining a rarity set is not a trivial enterprise. A conservation policy aimed at enhancing parcel appearance of rare species cannot be effective if the very few species appearing in one or two parcels only are defined as rare; and a contrario, biodiversity can be greatly and effectively promoted with a set of "relatively rare" or "infrequent" species, including those individuals appearing in, for example, less than 10 percent of the study area. And in that case, at least for the Oregon data set, protecting those rare species only, by setting *w* equal to zero in equation (13) with a limited budget (p^{**}=15) enables coverage of 373 out of the 426 species with 337 parcel occurrences of rare species. This seems to be a counterexample to Prendergast et al.'s (1993) statement that many rare species – at least for this last rarity set *R*''' definition – often do not occur in most species-rich areas.

Modifying the rarity sets also imply important changes in the opportunity cost of diversity. Obviously, as shown by the shape of the tradeoff curves of Figure 5, the law of increasing opportunity costs is still valid, but their magnitude changes dramatically. Starting to consider rare species by incrementally decreasing *w* from 1 yields a respective gain of 13 to 23 occurrences for 1 species lost with *R*' and *R*'' to be compared with a smaller gain of 5 occurrences for 1 species lost in the original rarity set. This means that one additional occurrence of rare species is cheaper in terms of species lost when the rarity set expands. In other words, the opportunity cost of diversity is lower with a larger rarity set, which is expected, since those rare species as defined by the new hypothetical sets are present in 51 to 114 hexagons; hence, increasing their occurrence has a smaller impact on species lost.

Figure 6

This is illustrated in Figure 6 where the opportunity cost of diversity is computed and graphed for the original rarity set *R* as well as for *R*' and *R*''. It indeed shifts outwards as the rarity set is expanded. Nonetheless, giving additional weight to rare species does contribute to lose protection of common species, no matter the rarity set; but that loss varies negatively with the magnitude of the rarity set. In all cases, the opportunity cost is exponential, as already deduced from the shape of the tradeoff curves (Figures 4 and 5).

Figure 7

Figure 8

The number of parcels selected is a very gross budget proxy. Obviously, a higher conservation budget enables the purchase and maintenance of additional land parcels, thereby increasing the number of parcels, p. Inversely, a budget limitation decreases the number of parcels that can be afforded. But these basic statements indirectly suppose two strong conditions: first, each parcel is de facto supposed to have a similar cost than another parcel and second, the value of protecting each species is similar to the value of protecting another species (ReVelle et al., 2002). Clearly, land value is not uniform in a large area such as the State of Oregon: for example, values are likely to be higher in parcels close to urban areas (Polasky et al., 2001; Arthur et al., 2004). Species are valued differently as well: for example, well-known, popular or endangered species, especially the "charismatic megafauna", typically benefit from a higher willingness-to-pay than more common species. Notwithstanding these caveats and understanding the caution needed in interpreting the results, more parcels will nevertheless require, on average, a higher budget than less parcels and vice-versa. For that reason, it is interesting to estimate the impact of a steady increase in the number of parcels protected (as a budget proxy) on the coverage of all (rare and common) species and its tradeoff with maximizing parcel occurrences of rare species. The budget has been increased marginally by increments of one parcel – that is, the model is run with number of parcels to be selected, p^{**}, augmented by 1 at each run until p^* is reached.

Loosening the budget constraint obviously increases primary coverage as well as parcel appearances of rare species. Figure 7 depicts Pareto-optimal[3] tradeoff curves with budget increases (that is with $p^{**}=16$ to $p^{**}=22$) and indeed shows that any increase in budget shifts the

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[3] Points that are not Pareto-optimal (or not part of the non inferior set) are not drawn on this graph.

tradeoff curve outwards, to the east. Contrary to a "north-eastern" movement, this "east" movement indicates that a larger budget always increases at least one objective but not necessarily both. Therefore, even though most budgetary increases reflect a Pareto efficient move from one frontier to another one, it cannot be generalized to all conservation budget augmentations.

Figure 8 depicts the opportunity cost of diversity at various budget levels (p^{**}=15, 17, 19 and 21) for the original and an expanded rarity set ($|R|$=22 and $|R'|$=51). The two bold lines represent the opportunity cost curves detailed in Figure 6. An increase in budget enabling preservation of 17 instead of 15 parcels for the original rarity set brings about a lower opportunity cost, as expected. Indeed, increased appearances of rare species are cheaper in terms of more abundant species preserved with a larger budget. However, a further rise in budget increases the opportunity cost. This unexpected outcome is likely to be due to a relative measure. If Z_3 only, species coverage, is maximized (w=1), parcel appearances of rare species increase by about 50 percent when budget moves from p**=15 to p**=19 or 21 (these two budgets leading to the same results). Moreover, any increase in parcel occurrence of rare species is very limited for $|R|$=22 (see above, Section 4). Therefore, any further increase in the presence of rare species with a larger budget might cost more in terms of common lost species. This unexpected result does not appear anymore when considering budgetary changes with a larger rarity set (dotted lines in Figure 8). Opportunity cost of diversity decreases as budget is larger – the dotted lines are below the original solid line – and it is especially true as redundant coverage of rare species goes up.

7. Conclusion

The models we have presented consider protection of rare species as well as common species. At first, a modified Species Set Covering Problem is formulated to protect all species and to favor parcel occurrences of rare species.

It is then recognized that budgetary limitations may prevent protection of all species. Therefore, another model is set up with the objectives of both protecting as many species as possible and favoring parcel appearances of rare species. These two conflicting objectives enable us to determine a tradeoff curve and to provide decision makers the opportunity to choose among a set of Pareto optimal solutions. The tradeoff curve is developed by use of the weighting method of multi-objective programming. These choice options determine the opportunity cost of diversity, defined as increased appearances of rare species in terms of species lost, and conversely, the opportunity cost of primary coverage, defined as increased numbers of protected species in terms of biodiversity loss.

Another implication of this analysis is the fact that a Pareto optimal choice for one budget and another Pareto optimal choice for a larger budget cannot always be compared on Pareto grounds as it is possible, in restricted cases, that the move between two Pareto optimal points, when budget is relaxed, may not provide advantage to both primary coverage and redundant coverage of rare species.

Finally, the importance of the subjective definition of rarity is underlined. As a matter of fact, a very strict determination of rarity (e.g. rare species are those inhabiting less than 1 percent of the total surface area) may not be compatible with a policy aimed at enhancing parcel occurrences of rare species as these will be too infrequent to be favored – and thus too costly in terms of loss of primary coverage – even without budget limitations. However, with larger but obviously credible rarity sets (e.g. rare species are present in 5 or 10 percent of the area of analysis at the most), such policies may have large and positive impacts on biodiversity, even when the budget is limited. The opportunity cost of diversity therefore varies negatively with a larger rarity set and – to a smaller extent – with a larger available conservation budget.

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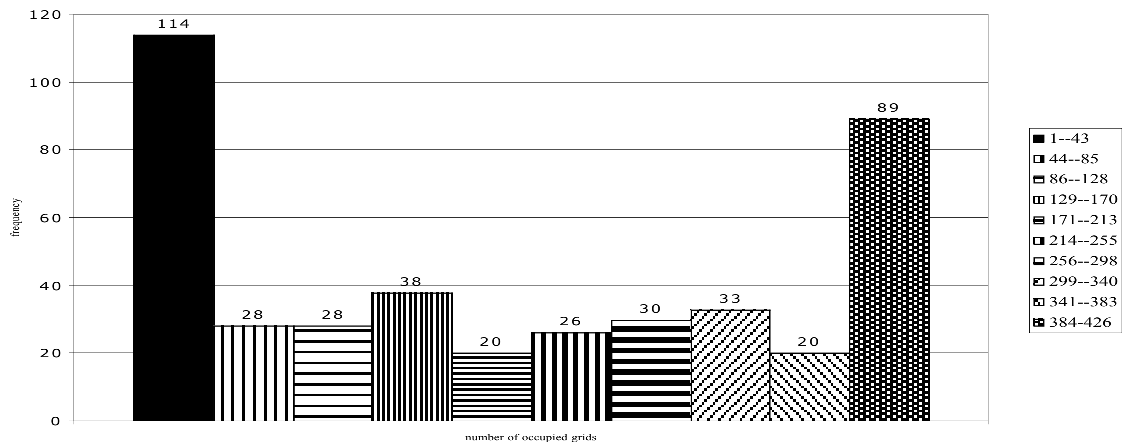

Figure 1: Species Frequency per occupied parcels

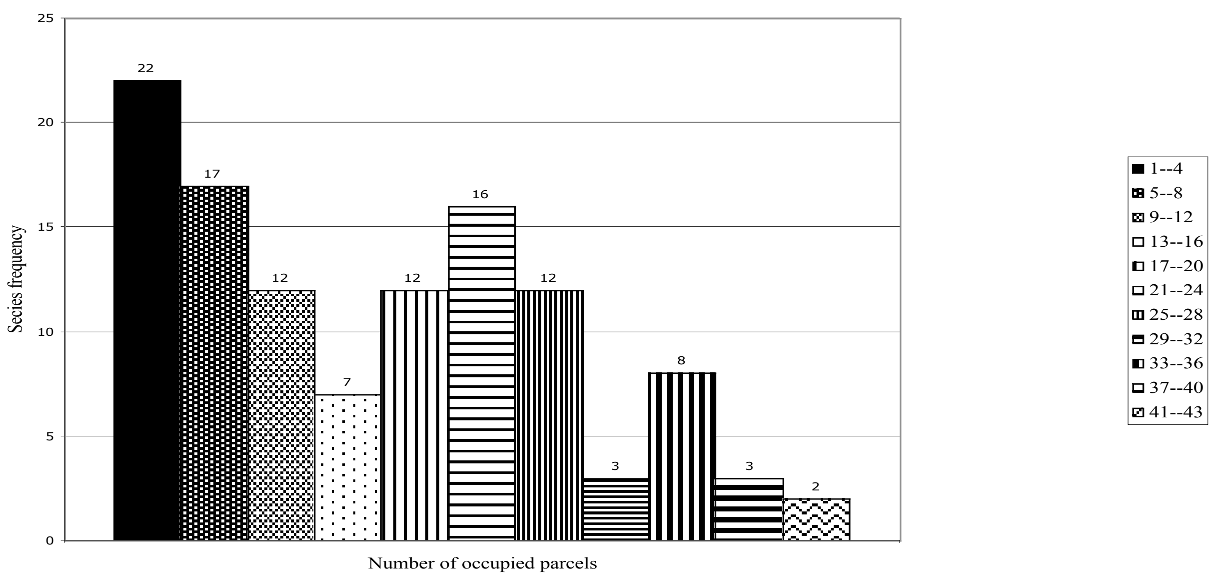

Figure 2 : Frequency of relatively infrequent species (present in 10% of the parcels at the most)

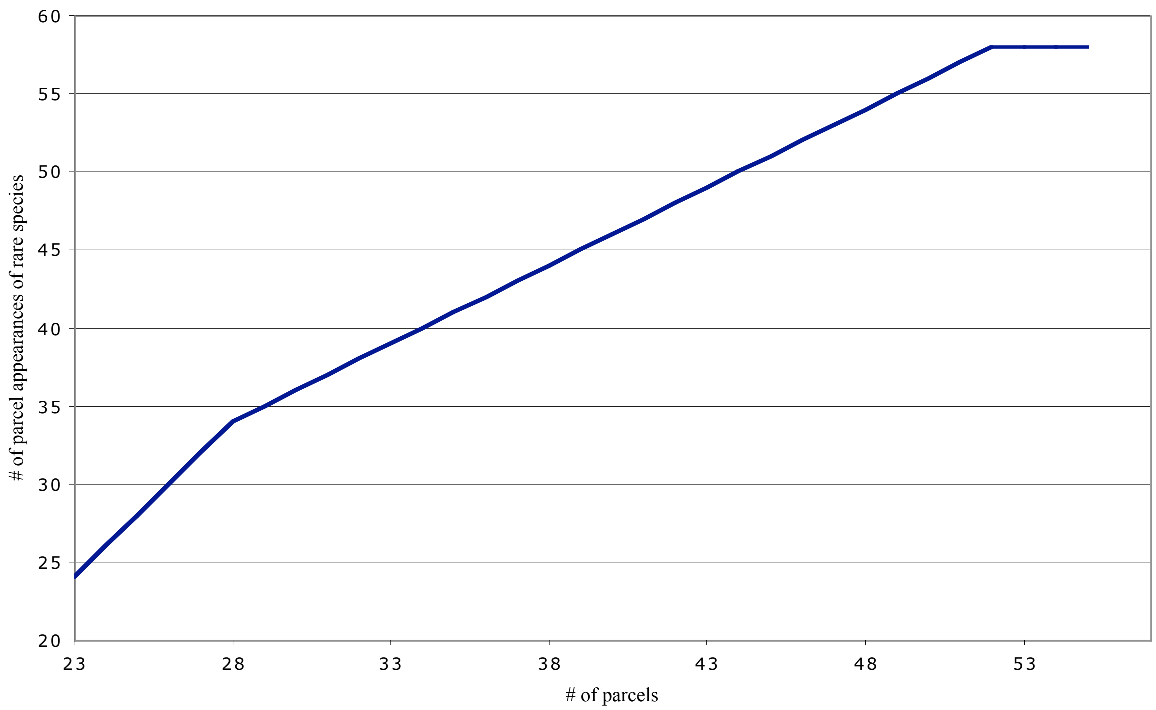

Figure 3: Parcel occurrences of rare species

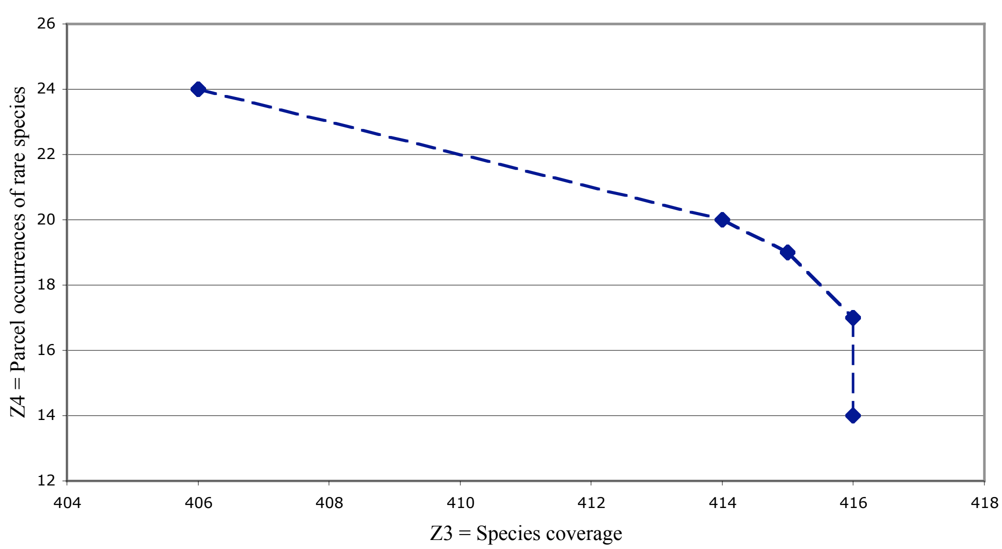

Figure 4 : tradeoff curve

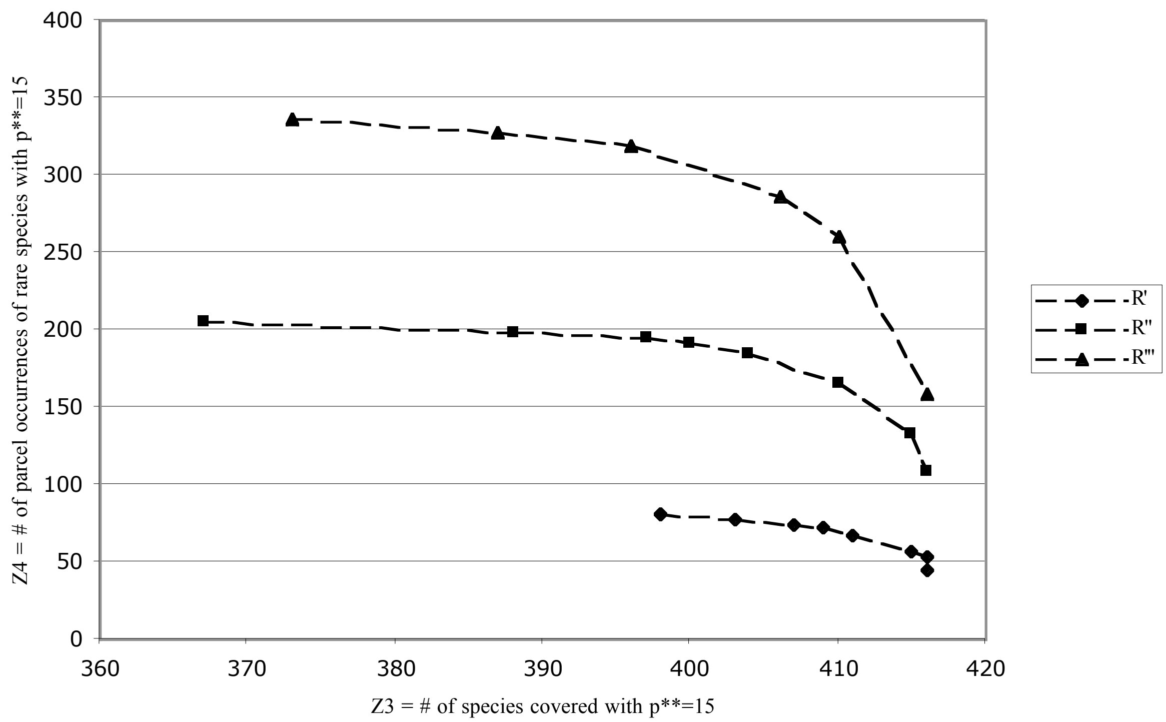

Figure 5: tradeoff curve with the new rarity sets

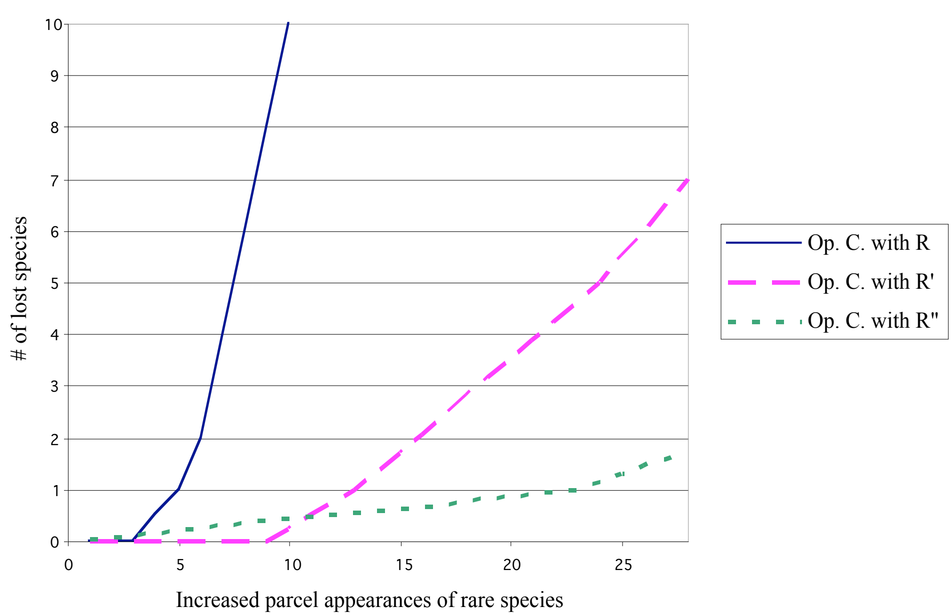

Figure 6: the opportunity cost of diversity

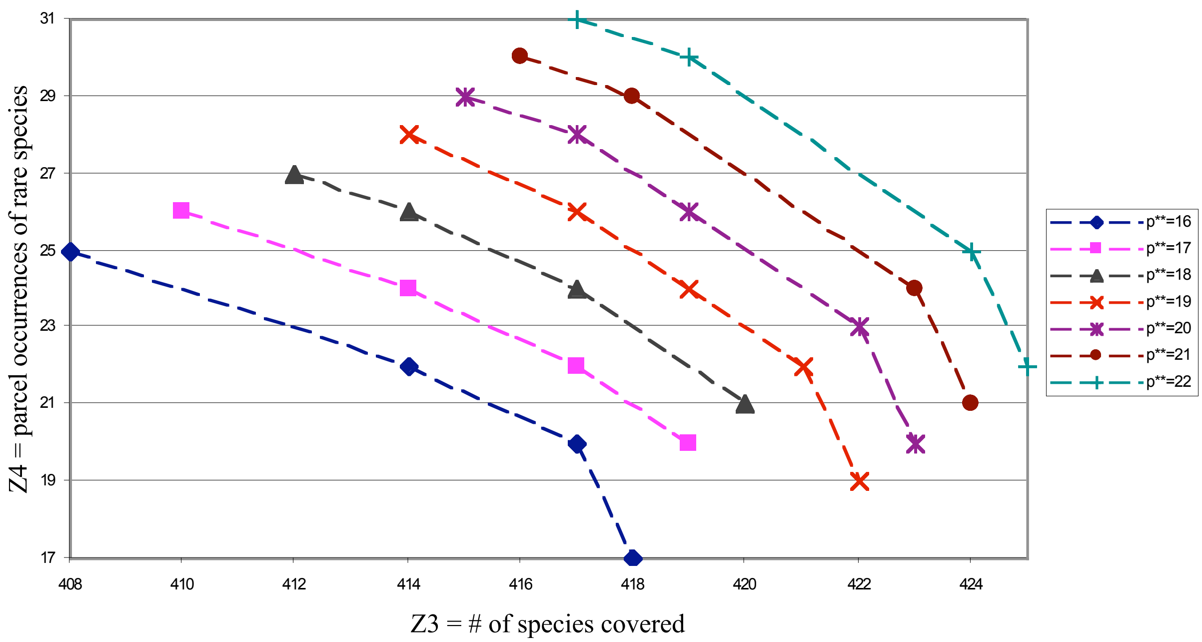

Figure 7: Tradeoff curves with budget increases

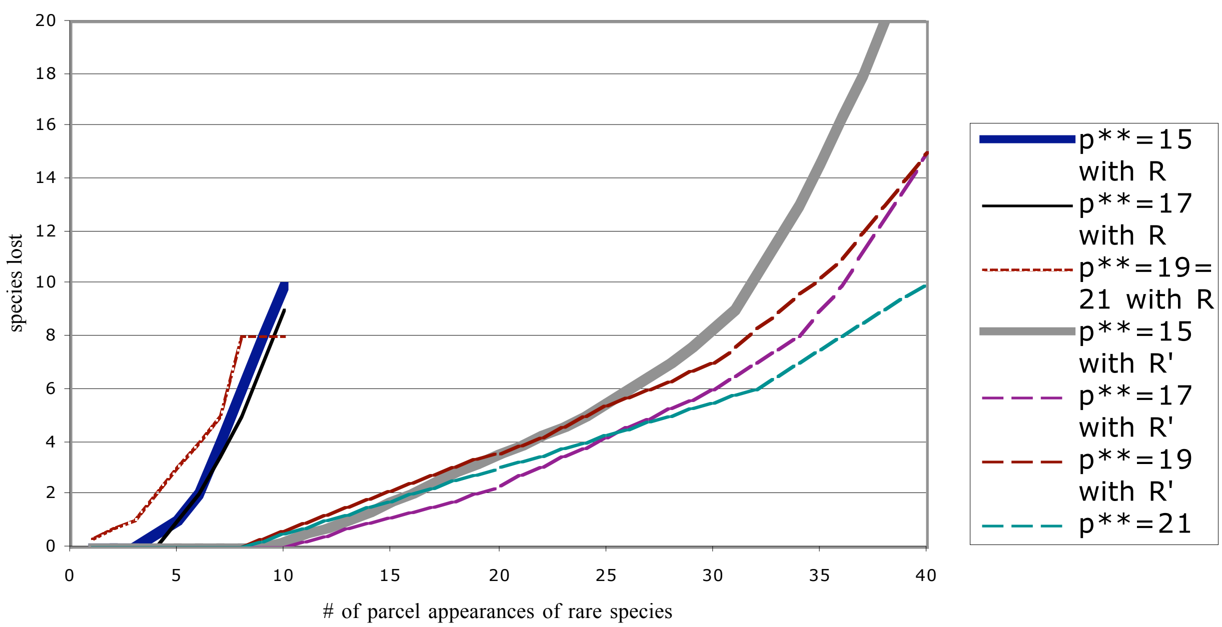

Figure 8: The opportunity cost of diversity for various rarity sets and budgets