



Choosing surrogates for biodiversity conservation in complex planning environments

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ABSTRACT: The coarse filter/fine filter hypothesis suggests that by conserving high-quality examples of all ecological systems along with imperiled species and communities, we could protect the majority of native biodiversity. Given the cost of data collection, conservation planners might wonder how close they could get using alternatives to the ideal data (i.e., surrogates). We conducted an analysis of the sensitivity of surrogate options on reserve selection in Napa County, California, USA. We evaluated the extent to which representation goals for the coarse/fine-filter elements were met by surrogates and whether the same general locations were being selected. Napa County represents a data-rich setting, whereas the test surrogates portrayed a range of circumstances where less data are available. A worst (data-poor) case, based only on landscape condition with no biological data, was tested to identify the value of improved information. Our results suggest that in complex planning environments, there are no simple shortcuts in collecting data. None of the surrogate sets was particularly effective at meeting all the goals for the full set of baseline elements. There was also relatively low spatial congruence between the various test solutions and the baseline. However, we did find that all combinations of surrogates provided some degree of protection, suggesting that in less complex planning problems, simpler surrogates can serve a useful function. Studies like this will help planners gauge how much effort would be prudent to spend in compiling spatial data relative to the risks to, and irreplaceability of, native biodiversity.

Keywords: conservation planning, reserve selection, surrogates, sensitivity analysis, coarse-filter, fine-filter, Napa County

INTRODUCTION

Central to most conservation planning approaches is the identification of the features to be conserved (Margules and Pressey 2000, Groves et al. 2002), which we refer to here as “biodiversity elements” or more simply “elements.” These elements could include plant and animal taxa, such as threatened and endangered species, or local environments, such as wetlands that fall under environmental regulation. In some cases, land use planning might be directed at conserving *all native biodiversity* in a given area. This more comprehensive approach could allow for better long-term conservation – helping avoid the circumstances where new species and habitats would need to be regulated in the future. However, planning for all biodiversity is still far beyond our grasp because of the monumental task to collect all the relevant data on every element (Groves et al. 2002).

This ideal – *preserving all native biodiversity* – can be pragmatically if imperfectly addressed, however, through careful selection of biodiversity elements that would serve as “surrogates” around which to craft a network of protected areas. Selection criteria may include all characteristic, or representative, ecological systems, then compliment those with rare and vulnerable communities, species assemblages, and species. These criteria reflect what is known as the “coarse filter/fine filter” hypothesis (Jenkins 1976, Noss 1987, Noss and Cooperrider 1994). This hypothesis suggests that by setting and meeting coarse-filter goals to conserve multiple, high-quality examples of all ecological systems, we can also sustain the majority of native biodiversity. Because this coarse-filter approach might not adequately represent all biodiversity, special attention is also needed for communities and species that are rare or vulnerable – the “fine filter.” Experience suggests that this is a very workable approach for selecting a network of reserves (e.g., Noss 1987, Kintsch and Urban 2002, Groves 2003). These methods may need to be supplemented with population viability assessments, particularly to ensure persistence of vulnerable and/or migratory species (Carroll et al. 2003).

Planners might naturally wonder how large this set of coarse- and fine-filter elements should be. Their concern is whether the cost of data collection (related both to the number of elements and the precision of mapping) would be so prohibitively great that it would be beyond the means of many jurisdictions or land conservancies to plan effectively for biodiversity conservation. What set of features would effectively serve as “surrogates” (Andelman and Fagan 2000) for all biodiversity? Could either the coarse-filter or fine-filter alone suffice? How coarse can the coarse-filter be in terms of the level of classification and its biological relevance? Which groups of fine-filter elements must be included? Three important factors influence the effectiveness of surrogates: the choice of surrogates themselves, the spatial data used to represent their distributions (e.g., choice of predictive distribution model, Loiselle et al. 2003), and the representation goals set for each element.

Several previous studies have evaluated the ability of sets of surrogates to adequately represent other elements in the reserve system when they were not explicitly targeted, i.e., a “sweep analysis” (Kiestler et al. 1996) or “incidental representation” (Warman et al. 2004). Most of these have either investigated the use of coarse-filter surrogates to sweep or represent other taxa, such as the use of land classes to sweep birds, mammals, or reptiles into the reserve network (Lombard et al. 2003), of one indicator taxa (e.g., birds) to sweep another (e.g., mammals) (Warman et al. 2004), or of taxa to represent at-risk species and vice versa (Lawler et al. 2003). Others have explored the ability of umbrella and flagship species to represent other taxa (Andelman and Fagan 2000).

This paper presents an analysis of the sensitivity of the selection of a reserve network to the choice of surrogates. The original data and representation goals for coarse- and fine-filter elements from a recent study conducted by NatureServe on behalf of the Land Trust of Napa County (LTNC), California (Riordan and Barker 2003), were used to define a baseline. Different sets of surrogates of these elements were systematically removed or substituted, and alternative reserve networks were generated to

achieve representation goals for the surrogates. We compare the results of each variation to the baseline sets in two analyses: 1) the incidental representation of goals for the full set of elements, and 2) the spatial congruence of each reserve solution to the solution for the baseline set. All parameters were maintained across all tests so that the only difference in the results was due to the choice of surrogates. We address two questions through this sensitivity analysis: How successful are simpler sets of surrogates in meeting basic representation goals? Or stated more pragmatically from a planner's perspective, what is the tradeoff between data collection effort and achieving goals? We divide this question into two parts. First, how well do coarse- and fine-filter surrogates represent each other and how well do simpler land cover types, subsets of fine-filter surrogates, and/or models of landscape condition represent the original set of surrogates. Second, do these simpler sets of surrogates identify the same general locations for conservation as the baseline set? We believe our study is the first to simultaneously consider full coarse- and fine-filter sets and compare various surrogates with fewer elements or less precise data against this combination.

METHODS

Napa Study Area

Napa County in northern California (Figure 1, page 29) lies in one of the hotspots of imperiled biodiversity in the United States (Chaplin et al. 2000). Its location also makes it extremely attractive for vineyard and residential development. Moreover, land stewardship occurs in a complex pattern of public and private lands, with approximately 25% of the county in some level of conservation lands (Figure 1). The LTNC works to conserve the county's bountiful natural and cultural heritage. Fortunately for planners, the distribution of biodiversity in Napa is relatively well-documented. Because of this convergence of conservation need and data availability, NatureServe and partners recently undertook a conservation planning exercise in Napa on behalf of the LTNC (Riordan and Barker 2003). The data

compiled for that planning effort were used in the present study. Relative to other parts of the nation, Napa represents a complex planning situation with the high end in data quantity and quality and provides a suitable site for this sensitivity analysis on the effects of biodiversity surrogates.

Surrogates Tested

For the Baseline coarse-filter/fine-filter scenario, element selection criteria included 1) all types of upland and wetland ecological systems as defined by NatureServe (Comer et al. 2003, freshwater and coastal marine types were not addressed in this study); 2) rare plant community types as defined by the U.S. National Vegetation Classification (NatureServe 2003), and using conservation status ranks defining them as globally rare (G3) to critically imperiled (G1) under the NatureServe ranking system (Brown et al. 2004); and 3) all plant and animal species listed as globally rare (G3) to critically imperiled (G1) under the NatureServe ranking system or federally and state listed species. Regional and local experts reviewed lists and recommended additional species of concern, based on knowledge of their vulnerable conservation status. The resulting 104 elements were categorized into four groups: 23 ecological systems (SYSTEMS, i.e., the coarse-filter elements), 17 federally and state listed species and communities (LISTED), 43 imperiled species and communities that are not listed (IMPERILED, i.e., those that are globally ranked as G1 or G2), and 21 other species and communities of concern (CONCERN) (Table 1, page 30). LISTED, IMPERILED, AND CONCERN elements constituted the full set of fine-filter elements.

Different combinations of groups of surrogate elements were evaluated in the tests (Table 1). The Baseline elements form the "best-case" or "data-rich" benchmark against which the other sets were compared. At the other extreme, a "worst case" or "data poor" benchmark was simulated. The "data poor" test (T6, Intact landscapes) assumed that a planner has no information about patterns of biodiversity, and only knows something about

FIGURE 1 Location map of Napa County study area.

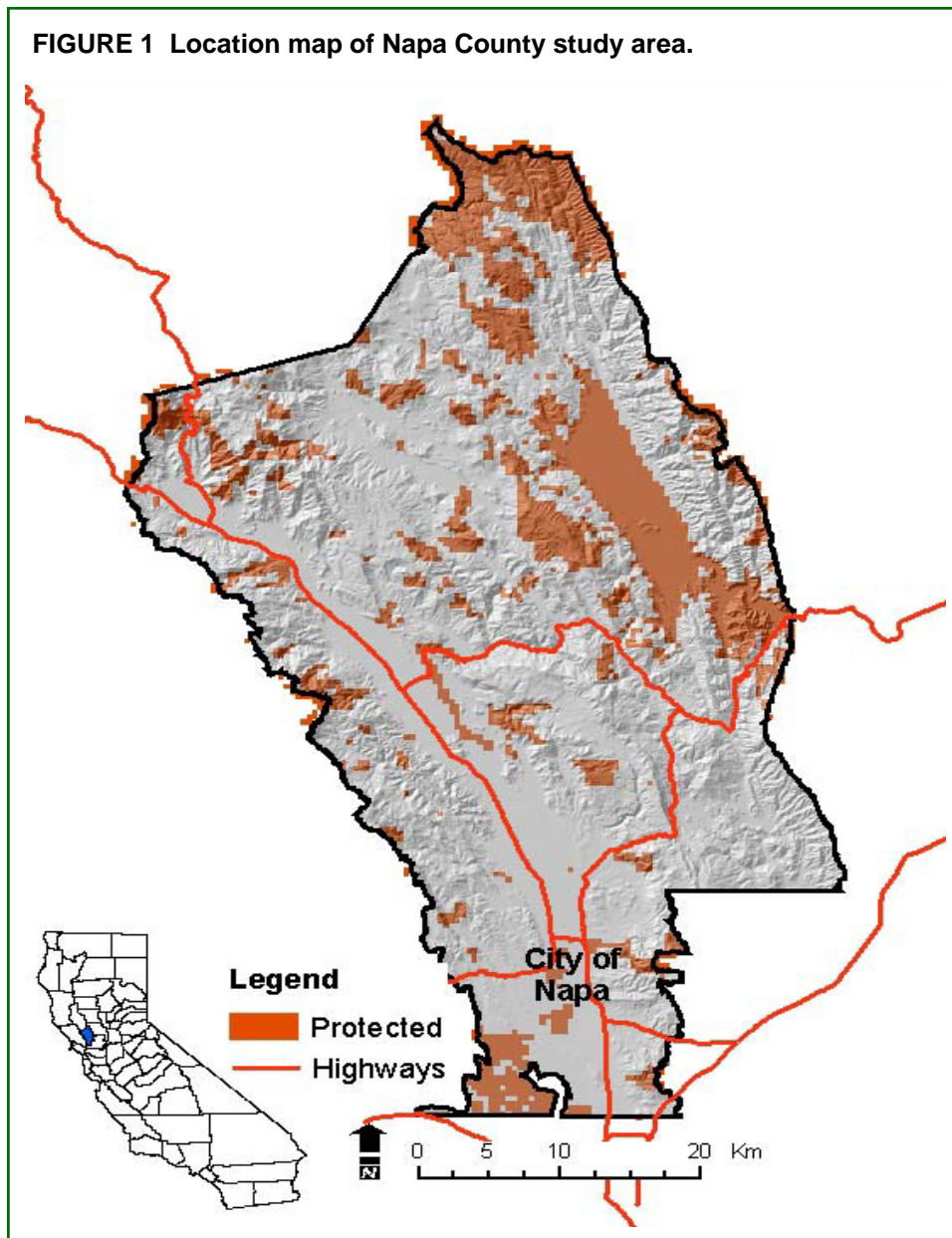


TABLE 1 Surrogate Sets Used in the Sensitivity Analysis Tests

Test	COARSE-FILTER		FINE-FILTER			COST
	SYSTEMS	HABITATS	LISTED	IMPERILED	CONCERN	LANDSCAPE CONDITION
B. Baseline	•		•	•	•	•
T. Systems only	•					•
T2. Species / Communities only			•	•	•	•
T3. Habitats only	•					•
T4. Habitats plus listed	•	•				•
T5. Habitats plus listed and imperiled	•	•	•	•		•
T6. Intact Landscapes						•

landscape condition, land use, roads, and land management, derived from commonly available spatial data. This approach is similar to trying to protect biodiversity in “wilderness areas” (Dobson et al. 2001). Between the best-case and worst-case benchmarks, five additional sets of surrogates were evaluated. T1 included only the SYSTEMS coarse-filter elements, while T2 used only the full set of fine-filter elements (LISTED, IMPERILED, and CONCERN). High-resolutions maps of ecological systems do not yet exist everywhere, but most areas (at least in developed countries) have been mapped with some type of moderate-resolution habitat or vegetation classification. In some tests, a land cover map with this simpler classification and lower spatial resolution [HABITATS] was used as a surrogate for SYSTEMS as the coarse-filter. T3 simply used HABITATS to represent SYSTEMS. T4 added LISTED baseline elements, along with HABITATS, as a surrogate for the full set of fine-filter elements. T5 added IMPERILED elements as additional fine-filter surrogates to those in T4. Thus T3-T5 represent plausible subsets of surrogates that planners may wish to use instead of investing in collecting the ideal database required in the Baseline.

The project team derived a map of ecological SYSTEMS from a recent vegetation map of Napa County (Thorne et al. 2004). The original map was produced through photo-interpretation of digital aerial photography, then field

verified. Minimum map units are approximately 0.5 hectare (mean of 12 hectares). Thematically, the map depicts composition and density of woody vegetation and categorizes vegetation cover types according to a commonly used California classification system. These types were then ‘crosswalked’ to NatureServe’s nationally standardized classification of upland and wetland ecological systems (Comer et al. 2003). Locations of vernal pool systems were inserted from an independent source (Barbour et al., unpublished data).

HABITATS was based on the Multi-Source Land Cover Data (MSLC) map, which classified Landsat and other imagery of the state of California into wildlife habitat types with a minimum mapping unit of 1 hectare (mean of 17 hectares) (California Department of Forestry and Fire Protection 2002). Twenty-one native habitat types were mapped for Napa County. The classification of types was designed to describe vegetation types important to wildlife vertebrate species. The MSLC map is typical of data that is almost universally available to planners in the United States, whereas maps such as SYSTEMS, with some specialized classes and high spatial resolution, are still less common today.

Maps of fine-filter elements were compiled from several existing sources, including the California Natural Diversity Data Base (CNDDDB; a NatureServe member program)

and the California Native Plant Society. Patches of rare plant communities were acquired from CNDDDB or extracted from the detailed vegetation map. Where needed, existing NatureServe standards for documenting discrete occurrences were applied to non-standard location data.

Establishing quantitative representation goals for biodiversity elements is a recent and still controversial area of conservation science (Soulé and Sanjayan 1998). However, they are central to many conservation plans, and we applied common approaches for this study. Representation goals for coarse-filter elements are commonly expressed as areal extent, and are directed towards maintaining representative ecological processes and environmental settings that support the majority of non-target communities and species (Groves et al. 2002). Areal measures have been commonly applied to representation goal-setting at national scales using theory from island biogeography and species-area relationships (MacArthur and Wilson 1967, Wilcox 1980, Rosenzweig 1999). Representation goals were specified for each coarse-filter element (either SYSTEMS or HABITATS) as a percentage of estimated area circa 1850, or the time period immediately prior to wide-spread European-American settlement of Napa County. The 1850 time period marks the beginning of rapid and transforming, human/technology-driven changes to California ecosystems, but is recent enough to reflect vegetation patterns under modern climatic conditions. It therefore provides a useful and important reference point (Awimbo et al. 1996) though we acknowledge that selecting historic reference points is controversial (Noss 1985). For most well-understood ecological systems, the presettlement extent can be estimated with acceptable precision from current land use/land cover data and knowledge of the biophysical setting. As in many regional planning processes (Groves 2003), we selected an initial objective of 30% of historic extent for each system or habitat type.

Representation goals established for SYSTEMS and HABITATS had a comparable total area to be conserved. Therefore, any difference in the achievement of representation goals using different coarse-filter

surrogates should be due to their mapped patterns and spatial resolution and not from some difference in overall area conserved.

Representation goals for fine-filter elements area were directed at protecting sufficient numbers of extant populations to support species recovery and/or maintenance. Goals were expressed as a percentage of the number of known locations (“occurrences”) where the element is found within the county, in rough proportion to the county’s known share of the global distribution. That is, goal percentages were set highest for elements that are narrowly endemic to Napa County. This provides a simple and practical mechanism for establishing initial objectives in the absence of sophisticated population viability analyses. Experience suggests that, for imperiled species, nearly all extant occurrences are needed for recovery and continued viability. Therefore the goal was set at 90% of the known occurrences, which permits a small degree of flexibility for common circumstances where individual occurrences cannot be practically conserved and restoration in other locations is more likely to succeed. For at-risk and declining/vulnerable species categories (ranked G3 and G4, respectively), there are typically more occurrences to choose from, and the rangewide proportion of occurrences found within a given county is smaller than for imperiled species. This greater degree of conservation options is reflected in lower proportional goals. Here percentages were set at 60% of the occurrences for at-risk (G3) elements, and 30% for declining/vulnerable elements.

Reserve Selection Model

We applied a reserve selection program (Sites 1.0, Andelman et al. 1999) to select a (near) minimum set of planning units that met the representation goals of each set of surrogates. GIS operations calculated the amount of each element in a set of 13,124 spatial analysis units (16 hectares in size) that covered the entire county. In addition, each analysis unit was assigned a “cost,” derived from the landscape condition map, which penalized units that were highly degraded by intensive

land uses. A small but equal weight was applied in all tests to influence solutions towards larger contiguous areas of reserves, all else being equal (Andelman et al. 1999). In all tests, approximately 48,000 hectares of existing conservation areas (Figure 1) were pre-assigned into all solutions. This simulates common conservation strategies where conservation hubs or cores can be integrated into a “green infrastructure” (Weber and Wolf 2000).

Sites employs a simulated annealing algorithm to select an initial random set of analysis units, and then iteratively chooses units at random for addition or deletion from the current set (Possingham et al. 2000). If a change is satisfactory, it is accepted by the algorithm. Because of these stochastic procedures, repeated runs of the algorithm can create different solutions. For each test, Sites generated ten runs with one million iterations each. We only report the run that was the most efficient for each test.

Analyses

Two sets of analyses were performed to answer the questions of how well the “complete” set of baseline elements were represented by subsets of surrogates (Table 1) and how similar the geographic areas were that were selected for a reserve system. The Sites model reported on the area conserved for each Baseline element for every scenario, even though it was generated for a different set of surrogates. The number of Baseline elements in each group for which the representation goals were achieved were totaled for each scenario. This binary either/or classification masks additional detail about how close the solution came to the goals of the remaining elements. Therefore we also examined the proportion of surrogates in each group by categories of level of goal achieved (i.e., 100% of goal met or exceeded, 90-100% of goal met, 50-90%, 1-50%, and 0%).

To investigate the spatial congruence of test solutions with the Baseline, a modified Jaccard similarity coefficient

(van Jaarsveld et al. 1998, Gladstone 2002, and Warman et al. 2004) was calculated. The version of the coefficient, J , used here, following Gladstone (2002), is:

$$J = \frac{a}{(a + b + c)}$$

where a is the number of selected analysis units common to the Baseline and the test, b is the number of analysis units unique in the Baseline, and c is the number of units unique to the test run. Analysis units that correspond to existing conservation areas were not included in a , so that the comparisons for spatial congruence are only in reference to additional analysis units selected to achieve representation goals. The tests were only compared to the Baseline, not to each other. We also computed J for the other nine Sites solutions for the Baseline against the best Baseline solution to determine the amount of spatial congruence created solely by the stochastic nature of the simulated annealing algorithm. Low congruence between runs would suggest that the analysis units in the best solution were relatively replaceable.

RESULTS

The Sites model reports the total boundary length (perimeter) and area of selected planning units in each scenario, which provide a metric of compactness and contiguity. A set of small reserves will have a greater boundary length than a set of large reserves of the same total area. The perimeter:area ratio was calculated in order to compare the compactness of each scenario. For reference, the minimum perimeter:area ratio would be found for a single circular reserve.

The Baseline solution would increase the conservation area of Napa County by 59,165 hectares over existing protected areas and would achieve all coarse- and fine-filter representation goals except for five ecological systems. These five exceptions occurred where there

was an insufficient amount of the system remaining to meet a goal of 30% of its historical extent.

The additional area captured in each of the other scenarios ranged from 58,631 hectares, in the intact landscapes scenario, down to just 19,603 hectares, for the scenario including just LISTED, IMPERILED, AND CONCERN species. Neither the coarse-filter nor the fine-filter surrogates fully met the representation goals of the other (Table 2). SYSTEMS alone, while they protected some 54,228 additional hectares, only incidentally represented the goals for 6 of 17 LISTED elements, 15 of 43 IMPERILED elements, and 12 of 21 elements of CONCERN. All fine-filter elements together only protected an additional 19,603 hectares, which has enough area to incidentally represent the goals for 5 of

the 23 SYSTEMS (or of the 18 systems fully represented in the Baseline).

The tests that used HABITATS added 20% less area than the Baseline scenario, and did as poorly at representing SYSTEMS as fine-filter surrogates alone did, but were very similar to the systems-only test (T1) in representing fine-filter surrogates. Interestingly, the “intact landscape” test (T6) was quite similar to the test using just habitat types as surrogates with regard to the number of Baseline surrogates fully represented.

Counting numbers of surrogates with full representation is a rather conservative measure of success for a test scenario. Some surrogates may have relatively large fractions of their goals met that would not be counted by this method. Therefore we also examined the degree of

TABLE 2 Comparison of Results of Tests

Test	COARSE-FILTER			Number of Surrogates with Goals Met			
	Additional area conserved (hectares)	Spatial congruence Jaccard coefficient ^a	Ratio of total perimeter: total area ^c	SYSTEMS (of 23)	LISTED (of 17)	IMPERILED (of 43)	CONCERN (of 21)
B. Baseline	59,165	0.56 ^b	1.13	18	17	43	21
T. Systems only	54,228	0.50	1.17	18	6	15	12
T2. Species / Communities only	19,603	0.29	1.49	5	17	43	21
T3. Habitats only	47,267	0.32	1.15	6	6	15	13
T4. Habitats plus listed	47,672	0.30	1.13	8	17	14	14
T5. Habitats plus listed and imperiled	54,228	0.40	1.14	9	17	43	17
T6. Intact Landscapes	58,631	0.35	0.98	7	6	17	15

^a The Jaccard coefficient, J, ranges from 0 (no overlap) to 1.0 (perfect overlap).

^b Compares mean of the other nine baseline solutions against the best Baseline solution.

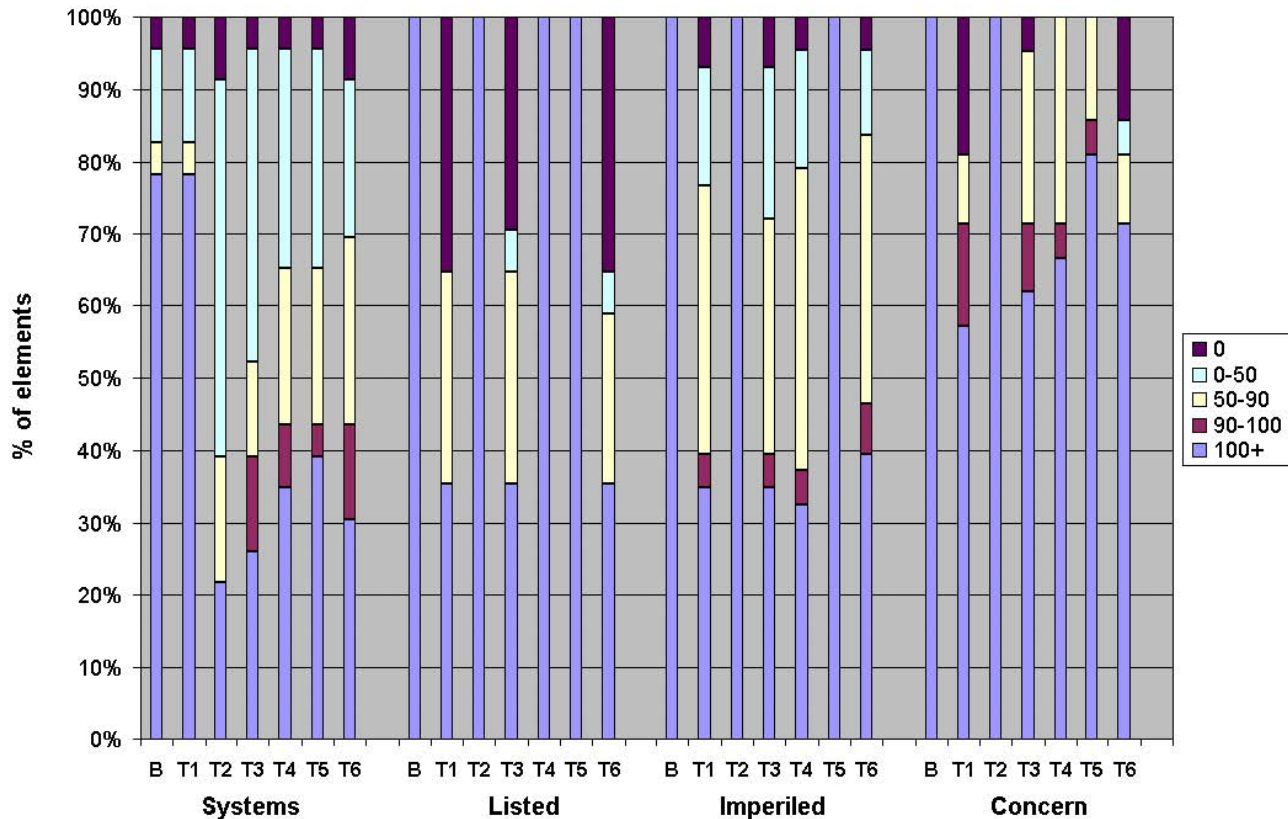
^c The lowest possible perimeter:area ratio for a reserve system with same total area as Baseline = 0.11, based on a circle.

representation achieved for each surrogate by group (Figure 2). In all tests where SYSTEMS were not explicitly targeted, less than half of the systems achieved 90% of their goals, and at best, only two thirds had even 50% of their goals met. Fine-filter elements alone did the poorest job representing systems, and once again, the “Intact Landscape” test (T6) did as well or better than the other tests. When listed elements were not explicitly targeted, none of the tests did well at representing them. All tests only met the 50% goal level or higher for about two-thirds of these elements, and approximately one-third had no representation at all. Less than half the imperiled group was represented at the 90% or better level, and approximately three-fourths at the 50% or better level. The “Intact Landscape” test actually outperformed the other surrogate tests for the imperiled group. All tests

provided 50% or better representation for most elements of concern, although the test with systems surrogates alone was slightly worse than the “Intact Landscape” (T6) test.

We examined patterns of spatial congruence (using the Jaccard coefficient) of the tests to the Baseline solution to determine if the solutions for different surrogates are concentrated in the same geographic locations. We excluded existing conservation areas from this calculation because these correspond to past decisions based on criteria other than meeting the representation goals of this analysis. The highest congruence of any test was 0.50 for SYSTEMS (T1) (Table 2), meaning only half of the analysis units between this test and the Baseline were the same. The fine-filter surrogates had the lowest

FIGURE 2 Bar plot of level of achievement for baseline element groups (SYSTEMS, LISTED, IMPERILED, and CONCERN) using test surrogate combinations. The Test numbers correspond to the tests in Table 1.



congruence of 0.29, largely because it had the least total area selected, but 90% of the selected units in T2 nest within the Baseline. The T3 and T4 surrogate tests had slightly higher congruence with the Baseline. T5 surrogates and the “Intact Landscape” (T6) test had an intermediate congruence of 0.4 and 0.35, respectively. Except for T2, the tests were not highly nested subsets of the Baseline. Most tests had a large proportion of their selected analysis units outside of the Baseline solution.

How much of the incongruence in the tests was the result of the stochastic nature of the simulated annealing algorithm? The ten alternative runs for each test differed because each began with a random starting set with random additions and deletions at each iteration. We examined the congruence of all ten runs for each test against the Baseline, and although there were some differences, the mean congruence within test runs was close to the congruence of the best test solution with small standard deviation. However, the variation within the Baseline runs was relatively large. The mean congruence of the other nine runs with the best Baseline was only 0.56, with a standard deviation of 0.18. Combining this result with the finding that the fine-filter (T2) test was highly nested within the Baseline solution, we conclude that sites with fine-filter elements tend to be relatively irreplaceable whereas some coarse-filter elements, especially those that are most abundant and likewise had proportionally larger representation goals can be represented in Napa County in many good combinations of analysis units. That is, the relatively low congruence in many of the tests is due in large part to flexibility in representing coarse-filter surrogates (Pressey et al. 1993).

Most scenarios had a ratio of total perimeter to total reserve area near 1.15 km/km² (Table 2). The exceptions were scenario T2 (fine-filter only) with a higher ratio and T6 (intact landscapes) with a lower ratio. Higher ratio values would be caused by small, isolated reserves. T6 was not required to include the many small, isolated fine-filter elements as the other scenarios were, and therefore it could find the most compact reserves. This result indicates that the Baseline scenario could protect a

full set of conservation elements without compromising on compactness relative to scenarios that did less well at meeting representation goals.

DISCUSSION

We posed two research questions to be addressed in this paper. How effective are simpler sets of surrogates in meeting basic representation goals? And do these simpler sets of surrogates identify the same general locations for conservation as the Baseline set? There are two parts to the first question. First, how well do solutions designed to achieve goals for coarse- or fine-filter elements coincidentally achieve goals for the other? In this study, neither was particularly successful in sweeping or incidentally representing the other. Neither set of surrogates achieved even 50% of the goals for all elements. One-third of LISTED elements received no incidental protection from meeting goals for ecological SYSTEMS. In Napa County, underlying assumptions of the coarse-filter/fine filter approach were supported in the sense that the two sets of surrogates are quite complementary and both are required to achieve conservation at the level specified for the Baseline. The second part of the representation question asks whether more commonly-available land cover maps, in conjunction with subsets of fine-filter elements, can represent native biodiversity as effectively as more detailed SYSTEMS maps. The answer in Napa County appears to be mixed. HABITATS were poor surrogates of ecological systems types under any scenario, but did no worse than systems at independently capturing fine-filter elements. However, most sets of surrogates provide at least some representation to all elements in each group, typically meeting at least 50% of stated representation goals (Figure 2). Only the LISTED group had several elements completely unprotected by surrogates.

It was interesting that the “Intact Landscape” (T6) test, based on no biological distribution data, performed relatively well compared with many of the other tests with biological data. This test assumed a planner only had commonly available GIS data related to landscape

condition, such as roads, land use, and pollution sites, and thus was treated as a benchmark of the most data-poor location in the United States and most developed countries. An index based on landscape condition was used as a cost attribute for analysis units, and the algorithm was instructed to minimize the total costs (or degradation) in selected units while selecting an area comparable to the Baseline. We expected that this test would be the least effective at meeting baseline goals and could be used as a benchmark for estimating the value of additional biological information on surrogates was added. Therefore we were somewhat surprised that the T6 test performed as well or better at representing ecological SYSTEMS than any of the tests using HABITATS as surrogates and was comparable to SYSTEMS or HABITATS alone at representing fine-filter elements. Only the Baseline with the full set of elements substantially outperformed the T6 test. Our results support the conclusions of Dobson et al. (2001) that a mix of strategies is necessary to conserve biodiversity and that simply conserving “wilderness” (such as our intact landscapes) is unlikely to protect the most imperiled species.

In answer to the second question, there was a relatively low degree of spatial congruence between the test solutions and the baseline. The fine-filter surrogate (T2) test solution was essentially nested within the Baseline solution. The coarse-filter surrogates using ecological SYSTEMS alone had the highest congruence index, but even this indicated only 50% overlap. The T6 test had moderate congruence with the Baseline, comparable to many of the biologically-based tests. This suggests that landscape degradation, used here as a cost, was a strong driver in finding cost-effective solutions. That is, given a choice between a degraded and an intact site with the same amount of a surrogate, the reserve selection algorithm would favor the intact site, even without knowing of its biological composition.

Our findings about surrogates are generally consistent with previous studies, although most studies were at much broader spatial scales with very large analysis units. Lombard et al. (2003) tested the ability of reserves

selected to represent Broad Habitat Units to sweep protea and vertebrates in 40 km² analysis units. The habitat units were ineffective at sweeping species that were rare, had limited ranges, or required specialized habitats. Kiester et al. (1996) found that vegetation classes did not effectively sweep listed species and vice versa, even when the representation goals were a single occurrence of each element. Ward et al. (1999) caution that the most cost-effective choice of surrogates may well depend on the level of the representation goals. For instance, in a coastal marine context, habitat types were the most efficient surrogates tested when total area goals exceeded 40%, whereas fish and invertebrate assemblages were more efficient with low area goals of 10-20%.

More commonly, sweep analysis studies have had a slightly different focus than ours. They have often concentrated on the ability of one taxa to sweep another (Pharo et al. 2000, Gladstone 2002), of taxa to sweep at-risk species (Lawler et al. 2003), or of environmental (land, vegetation, or habitat) classes to sweep vertebrate or other taxa (Kiester et al. 1996, Lombard et al. 2003). Andelman and Fagan (2000) showed that common shortcuts in selecting surrogates, such as flagship and umbrella species or biodiversity indicators of high species richness, were not significantly better than randomly selected species in sweeping other biodiversity elements, despite their appeal in generating popular support for conservation programs.

It should be noted that the classification of ecological systems, as defined by NatureServe (Comer et al. 2003), is relatively new. Consequently, their effectiveness as coarse-filter surrogates, relative to habitat types or land classes, to allow persistence of more widespread species has not yet been formally tested and was not the focus of this study. Brooks et al. (2004) recently voiced concern about using environmental classes (e.g., vegetation, habitat, or land types) as biodiversity surrogates because they often do poorly at sweeping other surrogates and are not evaluated against a null hypothesis of random selection. We heartily concur that habitat or land type classifications as coarse-filter surrogates are insufficient

to sweep fine-filter species and communities, as corroborated in our study. On the other hand, we conclude that ecological systems are a valuable complement to fine-filter surrogates in protecting native biodiversity. We did not test a truly random selection to estimate the value of biological information in reserve design. Planners in developed countries have access to spatial data related at the very least to landscape condition, which was found in Napa County to be comparable to other subsets of surrogates in sweeping biodiversity elements. Therefore we felt that landscape condition made a better data-poor baseline than a null hypothesis based on no data whatsoever.

CONCLUSION

Napa County is a relatively “data-rich” area, with a very detailed map of terrestrial ecological systems and detailed (though incomplete) occurrence data on 81 elements that are listed, imperiled, or of special concern. Many areas may not be fortunate enough to possess this quantity and quality of spatial data on the distribution of the types of coarse- and fine-filter biodiversity surrogates. In these “data-poor” regions, data collection represents a potentially significant investment of time, money, and human resources. It is of great practical importance, therefore, to have some sense of the effects of taking shortcuts. That is, how successful might a plan be in protecting all native biodiversity if planners used subsets of the Baseline surrogates and/or more commonly available maps of land cover? We performed a sensitivity analysis comparing alternative reserve networks based on different sets of surrogates. Although this study represents just one example in developing general guidelines, we believe the results are informative and reinforce lessons from similar studies.

Based upon our premise that a combination of coarse-filter and fine-filter elements of biodiversity are an effective set of surrogates for planning for the conservation of all native biodiversity, our case study found no simple information shortcuts that will likely achieve the desired baseline level of conservation. The

only way we could select a potential set of reserves to satisfy these goals was to explicitly include each species, natural community, or ecological system in the reserve selection process. As others have found, fine-filter elements are typically rare and generally inhabit small, isolated fragments of the landscape that, by themselves, are insufficient to conserve the broad suite of biodiversity one intends to capture with coarse-filter surrogates. Conversely, at this level of goals, the coarse-filter alone could not incidentally represent all fine-filter elements. The latter tend to occur in fragmented and disturbed conditions that would not be selected for coarse-filter elements when there are options in better condition. And last, ecological systems, as classified by NatureServe (Comer et al. 2003), integrate greater ecological information on factors that influence species’ habitat needs than traditional vegetation-based land cover or habitat type maps.

From our results, we would not suggest delaying conservation planning until the ideal quality or quantity of biological data has been developed. All combinations of the surrogates we tested achieved some portion of the “true” representation goals, which is certainly better than not acting at all. Rather, it is important to assess each planning setting, and understand what the potential surrogates and available data may or may not provide relative to the representation goals for the area. There is a broad spectrum of circumstances that define the relative complexity of most conservation planning problems. Ecological complexity, such as the number and type of ecosystems and species of concern, can vary considerably between planning areas. Socioeconomic complexity among planning areas varies from relatively simple (limited economic interests and stakeholders open to exploring multiple land use options) to complex (virtually all land use decisions require substantial tradeoffs and decisions are closely scrutinized; if not contested). Similarly, planning areas range from no conservation where any intelligent new designations could be effective to places with an extensive network of conservation lands already in place and therefore relatively narrow gaps to fill. If few lands are currently under conservation and threat is low, planners could

afford to start with relatively limited data (e.g., a generalized habitat map and a model of landscape condition) and be confident that important conservation decisions could be supported while developing information for additional surrogates.

Napa County presents a relatively complex planning environment that is typical of many regions of the world, with well-documented richness in endemic and sensitive biodiversity, a complex mixture of existing conservation lands, intense land-use pressures, and high land values. In this type of situation, a full set of biodiversity surrogates is likely required for effective conservation decisions that capture the breadth of biodiversity. The fine-filter elements in particular tend to occur in disturbed sites that are not adequately represented by coarse-filter elements. Without rapid conservation action, these are particularly vulnerable to extirpation. We hope that studies like this one will help planners gauge how much effort is prudent to spend in compiling spatial data relative to the risks to and irreplaceability and native biodiversity.

ACKNOWLEDGEMENTS

We thank many NatureServe staff that compiled the GIS data for this study, especially Larry Master, Linda Evers, Lynn Kutner, and Mike Tuffly. The California Natural Diversity Data Base, California Native Plant Society, and the Information Center for the Environment at the University of California Davis generously contributed spatial data for this project. Funding from the Doris Duke Charitable Fund is gratefully acknowledged. The present study could only have been undertaken because the Land Trust of Napa County boldly and generously volunteered to participate in the original pilot project. We also thank the three reviewers for helpful comments on the content and Alyssa Krogstad for editorial assistance in cutting down the jargon.

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