

IDENTIFYING GAPS IN CONSERVATION NETWORKS: OF INDICATORS AND UNCERTAINTY IN GEOGRAPHIC-BASED ANALYSES

CURTIS H. FLATHER,¹ KENNETH R. WILSON,² DENIS J. DEAN,³ AND WILLIAM C. MCCOMB⁴

¹*U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado 80526 USA*

²*Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523 USA*

³*Department of Forest Sciences, Colorado State University, Fort Collins, Colorado 80523 USA*

⁴*Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA*

Abstract. Mapping of biodiversity elements to expose gaps in conservation networks has become a common strategy in nature-reserve design. We review a set of critical assumptions and issues that influence the interpretation and implementation of gap analysis, including: (1) the assumption that a subset of taxa can be used to indicate overall diversity patterns, and (2) the impact of uncertainty and error propagation in reserve design. We focus our review on species diversity patterns and use data from peer-reviewed literature or extant state-level databases to test specific predictions implied by these assumptions. Support for the biodiversity indicator assumption was varied. Patterns of diversity as reflected in species counts, coincidence of hot spots, and representativeness were not generally concordant among different taxa, with the degree of concordance depending on the measure of diversity used, the taxa examined, and the scale of analysis. Simulated errors in predicting the occurrence of individual species indicated that substantial differences in reserve-boundary recommendations could occur when uncertainty is incorporated into the analysis. Furthermore, focusing exclusively on vegetation and species distribution patterns in conservation planning will contribute to reserve-design uncertainty unless the processes behind the patterns are understood. To deal with these issues, reserve planners should base reserve design on the best available, albeit incomplete, data; should attempt to define those ecological circumstances when the indicator assumption is defensible; should incorporate uncertainty explicitly in mapped displays of biodiversity elements; and should simultaneously consider pattern and process in reserve-design problems.

Key words: biodiversity mapping and disclosure of uncertainty; cartography and error propagation; conservation network, gaps in; conservation reserves, designing of; gap analysis; indicator taxa, reliability of; landscape conservation; reserve design, role of ecological processes in; species diversity and richness; species–habitat relationships.

INTRODUCTION

Protecting biological resources often has been accomplished by establishing national parks, refuges, wilderness areas, or other reserves that are managed to preserve their natural condition. Although reserve establishment is a common conservation strategy, protected areas managed strictly for biological conservation comprise only a small proportion ($\approx 3\%$) of the terrestrial land base worldwide (McNeely 1994b). Such a limited land area can be expected to maintain only a small proportion of the globe's biota. As our biological heritage is further eroded by land-use intensification, there is a growing demand and urgency for extending the network of conservation areas (Ehrlich and Wilson 1991). Compounding this urgency is a recognition that many past efforts dedicating land to reserves have been ad hoc (Pressey and Tully 1994), and that increasing competition among alternative land uses is limiting future opportunities to extend conservation networks.

Consequently, when there is a choice of areas to add to a network, selection should be judicious and in some sense optimal (Pressey et al. 1993, Lomolino 1994).

Unfortunately, we do not yet know how to allocate limited conservation resources in a manner that guarantees comprehensive protection of the biota. Evidence of this uncertainty is implicit from the various strategies that have been proposed to guide nature-reserve selection (see Margules and Usher 1981, Rapoport et al. 1986, Burgman et al. 1988, Erwin 1991, Vane-Wright et al. 1991, Given and Norton 1993, Solow et al. 1993, Noss and Cooperrider 1994). Despite this variation, a concept that has emerged as a general strategy for reserve planning is gap analysis (Burley 1988)—a process whereby cartographic techniques are used to identify underrepresented elements of biological diversity (i.e., gaps) in an existing network of protected areas. Gap analysis has been used in conservation planning for >25 yr (see Specht et al. 1974, Crumpacker et al. 1988, Keel et al. 1993), and has recently been formalized as a program to complete a comprehensive evaluation of biodiversity conservation in the United States (Scott and Csuti 1992). As de-

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scribed by Scott et al. (1993), the Gap Analysis Project uses state or regional maps of vegetation and animal distributions to determine if vegetation types are inadequately represented or if centers of species richness fall outside areas currently managed for biodiversity protection. Vegetation, vertebrate, and butterfly distributions are used as indicators of overall biodiversity. Vegetation data are obtained from satellite imagery, while species distributions are predicted from distribution maps and models of habitat affinity. By overlaying maps of land ownership and management status on vegetation and species distributions, "gaps" in the extant conservation network can be determined in a geographically explicit manner.

Burley (1988:227) cautioned that gap analysis is deceptively simple, and Scott et al. (1993) noted that it should be followed by detailed biological examination prior to setting conservation priorities. These caveats notwithstanding, there is a tendency for map users to impute credibility to mapped information indiscriminately (Bailey 1988, Monmonier 1991), which can lead to uncritical acceptance of assumptions underlying map generation. It is our purpose to review a set of assumptions and issues that we feel is critical to the implementation and interpretation of gap analysis. Specifically, we review two issues that we state as questions: (1) Is there support for using biodiversity indicators to reflect overall diversity patterns?, and (2) What is the implication of uncertainty in delineating reserve boundaries? We used published data and the literature to address these questions. Although we recognize that biodiversity conservation spans multiple levels, from genetic to ecosystem diversity, we focus primarily on the species level because of the species orientation of gap analysis.

INDICATORS OF BIOLOGICAL DIVERSITY

Will managing for vertebrate diversity . . . assure protection for the invertebrate component of biotic diversity as well? (Murphy and Wilcox 1986:287)

The concept of "indicators" has received much attention in the areas of environmental risk assessment, biological monitoring, and conservation biology (Cairns 1986, Landres et al. 1988, Graham et al. 1991, Kremen 1992). In general, indicators represent key attributes that are monitored under the assumption that they reflect the condition and trend of some ecological property that is too difficult or expensive to monitor directly (Noss 1990). The concept is frequently cited in reserve-selection problems because basic inventory data for most taxa are lacking (Raven and Wilson 1992). Consequently, conservation planners must often assume that diversity patterns for well-studied taxa (e.g., vertebrates, butterflies) indicate biodiversity in general (Scott et al. 1987, Sisk et al. 1994). If some carefully chosen subset of data-rich taxa does indicate the overall pattern of biological diversity within a re-

gion (see Roberts 1988), then the problems with incomplete and taxonomically biased inventories are moot. If, however, indicator taxa do not reflect diversity in general, then there is concern that reserve-selection decisions will be suboptimal (Conroy and Noon 1996) and may unknowingly lead to further loss of biological resources.

Testing the veracity of the biodiversity indicator assumption is difficult for a number of reasons. First, a true test requires a complete biotic inventory for a region of interest—a data set that will remain unavailable in the near future even for relatively small regions. A second difficulty concerns the ambiguity inherent in defining test measures for indicators. For example, should one test for correlated species counts among different taxa, or should one focus on distribution extremes and test for overlap in areas supporting the highest richness of various taxa? A final difficulty is the issue of scale. Ecological investigations directed at conserving biological diversity span global, continental, regional, and local scales (Humphries et al. 1995), which raises questions about the appropriate scale for reserve planning. To address the first problem we only tested predictions among taxa for which adequate distribution data exist in the peer-reviewed literature. To address the second problem we chose not to focus on any single indicator measure, but rather examined three common test measures of indicators from the literature—namely correlated species counts, coincidence of species "hot spots," and representativeness of species composition. And finally, rather than trying to define a priori the "most appropriate scale," we review published data collected at several spatial scales.

Correlated species counts

The simplest test of the indicator status of a particular taxon is to examine species counts among sites for some pattern of covariation. If species counts for the indicator taxon are strongly correlated with other taxa, then, on average, regions where many species of the indicator taxon occur will also be characterized by high species counts in other taxa. Despite the simplicity of this test, we found few examples where this test was completed.

In a continental-scale test of whether tiger beetles (*Cicindelidae*) could serve as an indicator taxon, Pearson and Cassola (1992) observed significant ($P < 0.01$) positive correlations in species counts among tiger beetles, birds, and butterflies across North America, Australia, and the Indian subcontinent. The mean correlation among taxonomic comparisons was 0.66 (range: 0.37–0.87). Although these statistics indicate a broad pattern of concordance in species counts, the strength of the association was often weak, with species counts in any one taxon accounting for <50% of the variation in other taxa.

In addition, we found that much of the covariation in species counts could be accounted for by the general

pattern of increasing diversity with decreasing latitude (Begon et al. 1990:831). We reanalyzed the data from North America and used partial correlation analysis (Draper and Smith 1981:265) to statistically remove the influence of latitude on species counts for all taxa. We assigned each 275×275 km grid from Pearson and Cassola (1992:Figs. 2 and 3) to a latitude based on the location of the grid center. Partial correlation coefficients indicated much weaker patterns of association among taxa (Table 1). The correlation between tiger beetle counts and bird counts was no longer different from 0 ($P = 0.20$), and the association between tiger beetles and butterflies was considerably weaker once covariation with latitude had been removed. Although significant associations remain (e.g., strong association between birds and butterflies), these results do not support a general expectation of concordant species counts among taxa.

Although continental-scale analyses can be used to define regions of conservation priority, it is unlikely that reserve boundaries will be defined at such scales. However, species-count data at finer geographic scales also raise questions as to the generality of the biodiversity indicator assumption. We used the data reported in Debinski and Brussard (1994) to ask if bird and butterfly diversity covaried among sites within Glacier National Park, Montana, USA. We estimated Spearman's rank correlations (Conover 1971:245) between total butterfly and total bird species counts among sites where both taxa were surveyed. Correlations in species counts for 1988 ($r_s = -0.29$, $P = 0.33$, $n = 13$ sites), 1989 ($r_s = 0.49$, $P = 0.11$, $n = 12$ sites), and averaged across years to control for temporal variation ($r_s = 0.13$, $P = 0.68$, $n = 11$ sites), did not show evidence of concordance between species counts.

In a study that specifically addressed how correlation among species counts varies with the spatial scale of investigation, Murphy and Wilcox (1986) observed that the magnitude of the concordance varied greatly with scale. Correlations between butterfly and bird species counts were weak ($r = 0.496$, $P < 0.05$, $n = 13$ sites) at a biogeographic scale (species counts within boreal islands atop mountain ranges within the Great Basin, USA); were stronger ($r = 0.786$, $P < 0.01$, $n = 11$ sites) at an intermediate scale (riparian canyons within a single mountain range), and showed no relation ($\tau = -0.047$, $P = 0.42$, $n = 17$ sites, Kendall's rank test) at a fine spatial scale (1-ha plots within a subset of canyons). These results, along with those reviewed previously, indicate that species counts of one taxa sometimes covary with other taxa at certain scales.

Coincidence of hot spots

Under circumstances where the conservation objective is to select areas that will maximize the number of species, evaluating the indicator status of a particular taxon based on correlated counts is a conservative test. It is not critical that the full range of species count

distributions covary, but rather that there is some degree of spatial concordance among areas that are particularly rich in species (i.e., hot spots) for different taxonomic groups. The appropriate test becomes one of examining the data for evidence of geographic coincidence between hot spots of an indicator taxon and other taxa.

The classic zoogeographic literature offers a continental-scale test of geographic overlap among centers of species richness for different taxa. We examined published species-richness maps for the United States and Canada for mammals (Simpson 1964); breeding birds, excluding seabirds (Cook 1969); amphibians, reptiles, and indigenous trees (Currie 1991); and tiger beetles (Pearson and Cassola 1992) for evidence of coincidence. We used the criteria in Prendergast et al. (1993) to define diversity hot spots as the richest 5% of the area of interest. Because we chose not to interpolate areas from the original maps, our estimate of the upper 5th percentile was not exact—on average we delineated areas that comprised the richest 5.6% of the mapped area (Fig. 1). A qualitative visual inspection of species-richness centers among taxa indicated that while the overlap was high for some taxa (e.g., amphibians and trees), this was not a general pattern. Regions rich in mammals were not the same regions rich in birds, reptiles, or amphibians at this scale.

A more quantitative assessment of hot-spot overlap was completed by Prendergast et al. (1993) based on an extensive data base of British plants and animals on a scale of 10×10 km sample grids. Distribution data for birds, butterflies, dragonflies, liverworts, and aquatic plants revealed that species-rich areas frequently did not coincide among taxa. The percentage overlap in the richest areas between all pairs of taxa averaged only 15% (range: 0–34%).

We found similar results at finer geographic scales. Again, using the data from Debinski and Brussard (1994), there was little geographic correspondence in sites supporting a rich bird or butterfly fauna. Of the 25 sites that had both bird and butterfly surveys, no overlap in species-rich sites were observed under the Prendergast et al. (1993) criterion, assuming that survey sites were of similar area. Site overlap was not observed until the upper 20th percentiles were compared.

These published data illustrate that centers of species richness for a chosen indicator taxon are not likely to coincide with centers of species richness for other taxa. This finding should not be surprising. The species pool inhabiting a region will contain a mix of species with varying habitat preferences, migratory habits, reproductive strategies, and other life-history characteristics (Hansen and Urban 1992). Consequently, factors affecting the distribution of different taxa, and the scales over which species assess habitat suitability, are expected to vary (Kolasa 1989, Hoekstra et al. 1991).

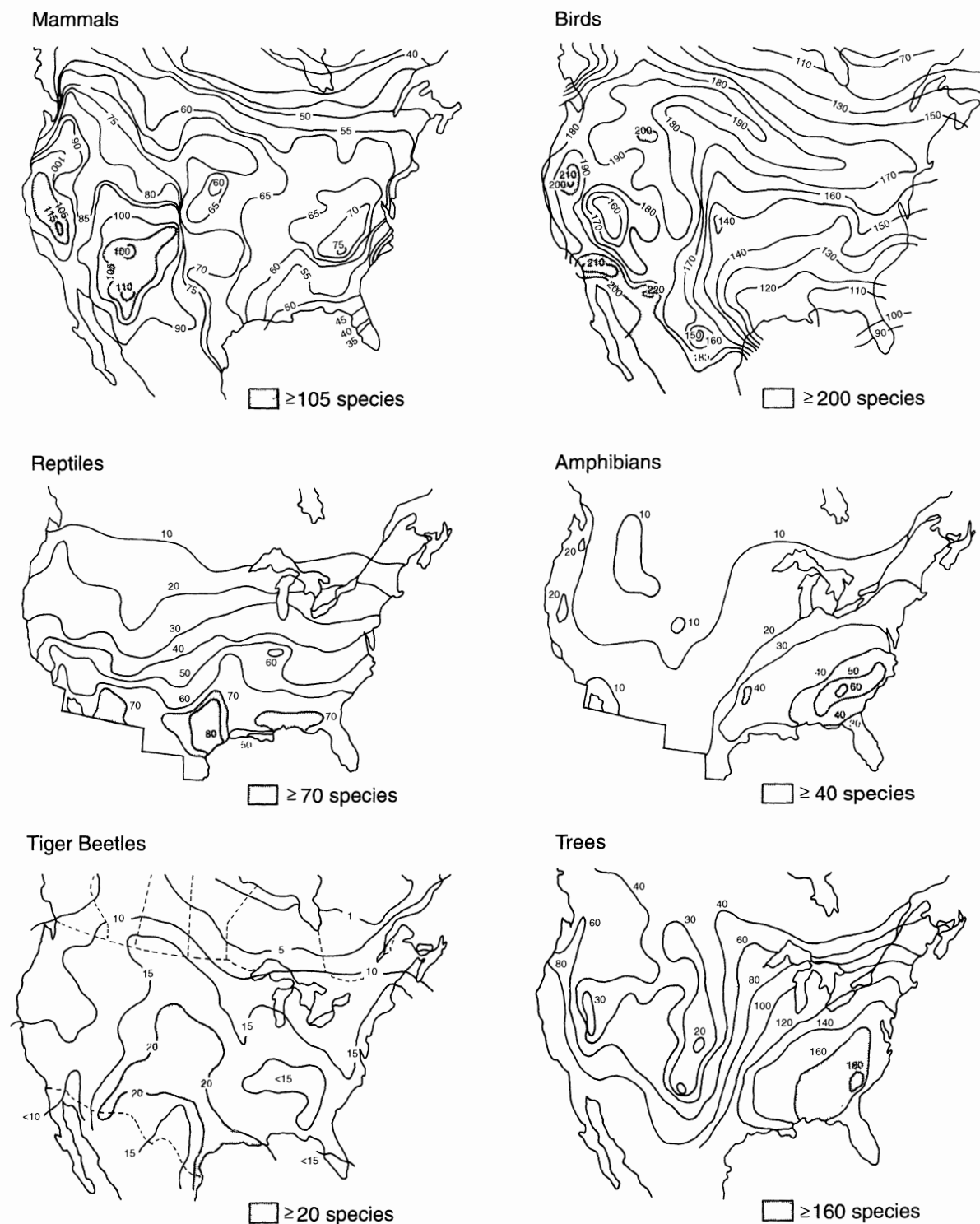


FIG. 1. Species richness maps for the United States and southern Canada for mammals (Simpson 1964:60 [Fig. 1]), breeding birds (Cook 1969:65 [Fig. 1]), reptiles, amphibians, trees (Currie 1991), and tiger beetles (Pearson and Cassola 1992:385 [Fig. 6]). Shaded areas represent, approximately, the richest 5% portion of each map. Reprinted with permission of *Systematic Zoology* (for mammals, breeding birds), University of Chicago Press (for reptiles, amphibians), *Nature*, Macmillan Magazines, Ltd. (for trees), and Society for Conservation Biology and Blackwell Scientific, Inc. (for tiger beetles).

TABLE 1. Pearson product-moment correlations (r) of species counts among taxa and with latitude, from Pearson and Cassola (1992). Based on species counts within 207 grid cells (275 km on a side) overlaid on North America. Correlations below the diagonal (italicized) are partial correlations after removing the effect of latitude. Probabilities that $r = 0$ are reported parenthetically.

	Tiger beetle	Bird	Butterfly	Latitude
Tiger beetle		0.37 (<0.01)	0.75 (<0.01)	-0.80 (<0.01)
Bird	0.09 (0.20)		0.74 (<0.01)	-0.40 (<0.01)
Butterfly	0.42 (<0.01)	0.71 (<0.01)		-0.72 (<0.01)

Note: We eliminated a single observation from Pearson and Cassola (1992: Fig. 2, row 2, column 2 from the northwest-most corner) because of a reporting error in the number of bird species occurring in that particular grid cell. Consequently, our correlations do not match exactly those reported by Pearson and Cassola (1992:386–387).

Representativeness and minimum sets

One difficulty in ranking candidate reserves based on some index (e.g., species richness) is that areas with similar ranks may differ substantially in species composition. This makes it impossible to evaluate areas based on their net contribution to the conservation of some regional species pool. The most species-rich area would not necessarily be the optimal choice for reserve status if its species composition is similar to those in existing reserve systems, or if the area's richness is attributed to invasion of non-native species.

One solution to this problem is to supplant index-based criteria with rules based on "representativeness"—a measure of how completely the species pool for a region is included within a reserve system (Margules and Usher 1981). The critical question is: What minimum number of areas is needed to conserve the maximum number of species? (Margules et al. 1988). With regard to the indicator assumption, one presumes that a set of reserves guaranteeing representation for sampled taxa also guarantees representation of uninvetered taxa.

Tests of the indicator assumption under representativeness criteria are rare. Prendergast et al. (1993) did observe that if all hot spots of bird richness could be protected then 100% of butterfly species, and >90% of dragonflies, liverworts, and aquatic plants would also be represented. Curiously, only 87% of the bird species were represented in bird species hot spots. In a more direct test—one where the initial selection of protected areas was based on representativeness criteria rather than species counts—Game and Peterken (1984) found that selecting reserves to include all rare plants in central England also included 99% of all other plant species. Similarly, Launer and Murphy (1994) found that if all sites where a rare butterfly occurred were preserved, guaranteeing genotypic representation,

>98% of native spring-flowering forbs would also receive some measure of protection.

Although these results do support some optimism that comprehensive biodiversity protection may be attained by targeting a subset of taxa, there are difficulties and conflicting evidence. Representativeness can be an expensive reserve-planning criterion. Achieving representation of target taxa can require an extensive land area (Lomolino 1994). In addition, Bedward et al. (1992) noted that reserve selection using representativeness criteria can result in a fragmented or diffuse reserve network, which could significantly increase management costs. Apart from these logistic difficulties, some investigators have found that representativeness can also suffer from a lack of congruence among taxa. If the most species-rich wetlands from each of nine wetland types were selected as reserves, thus guaranteeing full representation of major wetland habitat types in northern New South Wales, Australia, only 67% of the native wetland plant species would also occur (Margules et al. 1988). Similarly, Sætersdal et al. (1993) found that the minimum set of 32 areas with complete representation of plants only shared 5 sites with the minimum set of 12 areas with representation of birds.

Limitations associated with the use of indicators in conservation science (see Landres et al. 1988) and gap analysis (see Scott et al. 1993:8) have been recognized, but the assumption is still invoked as a practical necessity (see Roberts 1988). Results for the three test measures we examined (i.e., correlated species counts, coincidence of hot spots, and representativeness) all demonstrated that support for the biodiversity indicator assumption is not general. Although our literature review was limited, we found few published studies that have attempted to test this assumption directly or that provided data to support reanalysis. Nonetheless, failure of the indicator assumption in one case is sufficient to caution against indiscriminate use. This is not to say that the biodiversity indicator assumption is indefensible. Rather, our review points to an important research question—Are there ecological circumstances where diversity patterns of a few taxa do reflect the pattern of other taxa? Several cases where the indicator assumption appeared to hold involved taxonomically similar species (e.g., rare plants reflecting plants) or species where a strong functional relationship existed (e.g., butterflies indicating flowering plants). However, in another case evidence supporting the indicator assumption was observed among taxonomically dissimilar species (Prendergast et al. 1993). Research directed at defining those circumstances where the indicator assumption is tenable would provide a valuable standard for gauging the confidence that should be placed on conservation plans or reserve recommendations based on distributional patterns from a small subset of taxa.

TABLE 2. Observed error rates in predicting species occurrence based on habitat characteristics. Errors of commission were calculated as (number of species not observed but predicted) $\div$ (number of species predicted). Errors of omission were calculated as (number of species observed but not predicted) $\div$ (number of species observed).

Source	Taxon	Error rate (%)	
		Commission	Omission
Scott et al. 1993	Amphibians	20	13
	Reptiles	13	3
	Birds	16	12
	Mammals	34	11
Block et al. 1994	Amphibians†	75–100	0–75
	Reptiles†	40–88	0–25
	Small mammals†	50–90	0–66
	Birds	20–44	6–39
Timothy and Stauffer 1991	Birds	‡	54–70
Dedon et al. 1986	Birds	22–75	‡
Raphael and Marcot 1986	Combined§	11	14
Waldon et al. 1993	Amphibians	66–70	0–33
	Reptiles	50–53	4–25
	Mammals	49–57	3–26
	Birds	60–68	9–40

† Based on small sample sizes, ≤ 14 species predicted, ≤ 7 species observed.

‡ Not reported.

§ Includes amphibians, reptiles, mammals, and birds.

UNCERTAINTY AND RESERVE BOUNDARIES

Considerable quantities of ecological survey data have accumulated over the last few decades, but there is little information on its reliability.

(Cherrill and McClean 1995:6)

Conservation-reserve problems are inherently spatial and, as such, lend themselves to cartographic analysis techniques. Geographic information systems (GIS) are powerful tools in cartography and offer much flexibility in the analysis, manipulation, display, and synthesis of spatial data. However, operations within a GIS are often implemented with little regard for the types and magnitudes of error in the input data (Veregin 1989).

In conservation-reserve applications, species distributions constitute the fundamental input data. Because basic distribution data for most taxa are lacking (Nicholls 1989), biologists have supplemented deficient inventories by predicting species distributions based on habitat associations (Scott et al. 1993). Naturalists have been predicting occurrence of vertebrates based on habitat characteristics for decades (Morrison et al. 1992), and such models are common in GIS applications (Cocks and Baird 1991). However, the confidence that should be placed in predictions of species presence or absence has remained largely unexamined and undetermined.

Error in habitat-based predictions

Uncertainties surrounding the characterization of species habitats cannot be interpreted as flaws in the methods used to identify gaps in conservation networks per se (Nicholls and Margules 1993). Rather, the issue is with data quality, how to quantify the uncertainty

associated with predicting species occurrence, and how to incorporate error information into the decision-making process. The argument is often made that many urgent problems of applied ecology require that decisions be made with available information and models so that "... the choice is between crudely imperfect advice and none at all" (May 1984:14). Although many applied ecological problems will be burdened with primitive and incomplete data, Slobodkin (1988:341) argued that one should not assume that crude advice is better than no advice. Although this latter view could be considered extreme, it does stress the critical need for addressing the implication of error in resource conservation decisions (see MacDougall 1975, Briggs 1995).

Quantification of imprecision in predictions of species distribution has not received much empirical investigation (Block et al. 1994). Of the few validation efforts that have been attempted, error rates vary considerably among studies and taxa (Table 2). The expected pattern of lower error rates for well-studied taxa (e.g., birds) relative to other taxa (e.g., amphibians) was not consistently observed in the literature we reviewed.

Although reported error rates appear high, numerous factors that are not often incorporated into simple habitat-association models can interact to elevate uncertainty. For example, intra- and interspecific interactions (Hildén 1965, Fretwell 1972), the spatial arrangement of habitat patches (Helle 1986, Kratz et al. 1991), and the temporal heterogeneity of habitat (Southwood 1977) can each cloud the observed affinity between a species and a particular vegetation type. Furthermore, species presence or absence has an ambiguous interpretation. Observing a species in a given vegetation

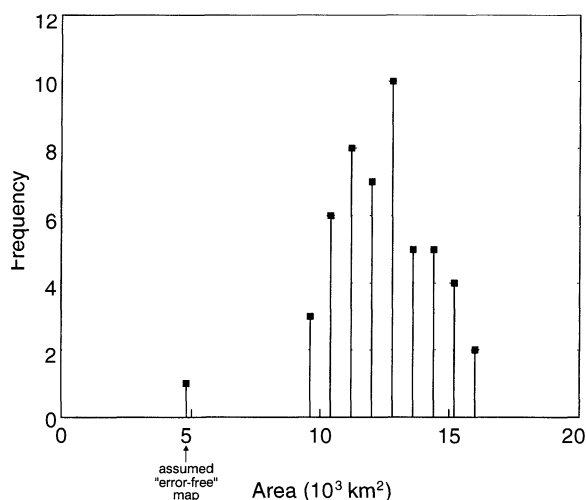


FIG. 2. The impact of simulated errors of 5% omission and 5% commission on the distribution of 10 rodent species in southeastern Oregon, USA. The total area supporting five rodent species (a hypothetical hot spot) in the original map (assumed error-free) is compared to the distribution of total area supporting five rodent species under 50 realizations of error.

type is a necessary but not a sufficient condition for defining habitat capable of supporting populations in the long term (Van Horne 1983, Pulliam 1988). Similarly, the failure to detect a species in a vegetation type could be associated with sampling error or could reflect the transitory nature of habitat use observed in metapopulation dynamics (Hanski 1991). Consequently, defining and characterizing the geographical range of a species is controversial and very imprecise (Rapoport 1982).

A particularly important issue in gap-analysis applications is the accumulation of error through the process of overlaying many species-distribution maps to depict patterns of species richness. How errors in individual species maps propagate when generating composite maps of species richness has not been examined (Stoms and Estes 1993). If composite map accuracy declines exponentially with increasing number of data layers (see Verigin 1989), then species-specific habitat models with acceptable error (as defined by the user) will not guarantee an acceptable composite richness map. We addressed this latter issue in a case study of several small-mammal species that inhabit southeastern Oregon, USA.

Case study: small mammals in southeastern Oregon

Data on vegetation cover types and vertebrate species-habitat associations were obtained from the Oregon Department of Fish and Wildlife (T. O'Neill, *personal communication*). The data consisted of a digital vegetative-cover-type map (delineated from satellite imagery) and habitat-affinity matrices based on vegetative cover, physiographic province, and county-of-

occurrence range information. Combining these data permitted the construction of species-specific distribution maps that indicated presence or absence of species in each habitat type, which we used to generate a composite map of species richness that was assumed to be error-free.

Monte Carlo methods (Manly 1991) were used to simulate the effects of prediction errors on species-distribution maps (see Dean et al. [1996] for details). Each iteration of the Monte Carlo simulation randomly introduced a predefined error level and assumed that errors were independent among species. Because these error simulations were extremely time consuming and required extensive computer resources, we used a subset of the original data in our analysis. We arbitrarily selected a taxonomically similar set of species (10 rodent species) that are expected to occur in southeastern Oregon. For illustrative purposes we introduced 5% errors of commission and 5% errors of omission—error rates that are conservative compared to those reported in Table 2. If a species does not occur at a site but a model predicts presence, then an error of commission occurs. An error of omission occurs if a species is in fact present but the model predicts absence. Our Monte Carlo approach mimicked these errors by giving each habitat polygon where species *X* was in fact absent a 5% chance of having species *X* erroneously predicted (error of commission) and each habitat polygon where species *X* did in fact occur a 5% chance of having species *X* erroneously omitted (error of omission). A total of 50 realizations of omission and commission error were generated, and each realization produced a map of species richness.

We examined the total area supporting five species for each error-filled map as an arbitrary criterion for defining a species-richness hot spot. The distribution of total area for the error-filled maps was compared against the total area estimate for the original map, which was assumed to be an error-free map (Fig. 2). The total area supporting five species under errors of commission and omission was much greater (median = 12 479 km², $n = 50$ simulations) than that observed for the assumed error-free data (4836 km²). Much of the area that supported five species under the error-free map was also found to support five species in the error-filled maps in a majority of the error simulations (i.e., in ≥ 25 [50%] of the 50 realizations, Fig. 3). However, there were areas adjacent to the actual richness hot spot, and diffuse throughout the study area, that also supported five species in 26–48% of the simulations. This simple error analysis indicated that reserve-system design could vary greatly if uncertainty is explicitly incorporated into the analysis.

Three limitations associated with this exercise warrant remark. First, we have not considered error in the vegetation map, which is the basis for the species occurrence predictions. Uncertainty with habitat mapping

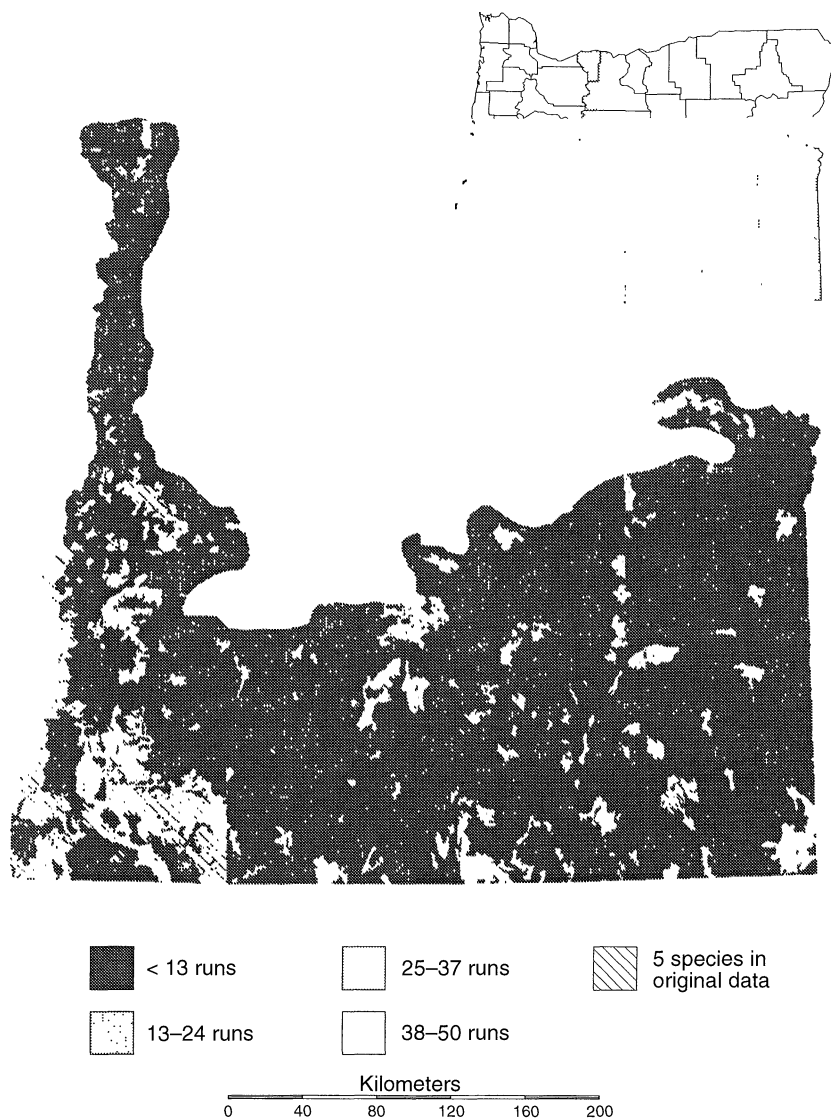


FIG. 3. Geographic distribution of 10 rodent species in southeastern Oregon after simulating errors of 5% omission and 5% commission. Crosshatching indicates the region that supported five species (a hypothetical hot spot) in the original (assumed error-free) map. The number of realizations supporting five species when error was introduced are shaded (maximum of 50).

can be substantial (see Cherrill and McClean 1995, Edwards et al. 1995) and should be incorporated into error analyses of this type. Second, because species exhibit patterns of co-occurrence and avoidance, error is likely correlated among species. Therefore, because we have treated each species independently, our analysis likely reflects a worst-case estimate of composite map error (MacDougall 1975, Veregin 1989). Third, this exercise only considered 10 species. Comprehensive diversity-conservation issues will consider hundreds, if not thousands, of species. It is critical that more research on error propagation be completed to estimate how cumulative error varies with number and kind (i.e., species with certain life-history characteristics) of species.

Ecological process as a source of uncertainty

Patterns in biological diversity have been the primary focus of geographic-based approaches to conservation planning, and data on the distribution of species and ecosystems are clearly fundamental to reserve-design problems in general (Humphries et al. 1995). However, it is equally clear that documenting vegetation and species distributional patterns must be complemented with an understanding of the ecological processes generating those patterns. Without commensurate consideration of process, there is no guarantee that those biological attributes used to justify reserve establishment will be conserved over time (McNeely 1994a). Consequently, failure to consider process will

contribute to the uncertainty in recommending location, size, and shape of reserves.

As currently conducted, gap analyses consider a static landscape. Given the certainty of continued natural and anthropogenic change across large regions, what may be a desirable landscape pattern today may result in a less desirable landscape pattern in the future. The potential problems associated with reserve designs that disregard ecological process have been recognized. Scott et al. (1993:6) noted that "[e]cological and evolutionary processes ultimately are as much a concern in a biodiversity conservation strategy as are species diversity and composition." Furthermore, Scott et al. (1993) cautioned that gap analysis should be regarded as an initial step in the development of a comprehensive conservation program. However, if as "an initial step" conservation planners use patterns in vegetation and species distribution to highlight areas that warrant further study, then they are assuming that pattern-defined boundaries also define the boundary within which the pattern-generating processes operate—an assumption that is increasingly difficult to defend (Janzen 1983, Ricklefs 1987, Cale et al. 1989). For example, if diversity patterns are generated by processes that operate at a broader scale, then areas outside the pattern-defined boundary may be important to the maintenance of the diversity pattern observed (see Shmida and Wilson 1985:6–7, Botkin 1990:53).

These concerns are leading to increased attention to the question of how to incorporate important ecological processes in protected-areas management (McNeely 1994b). Recommendations are now being made for less reliance on the presence or absence of biological elements and more emphasis on the organizational processes that generate and maintain biological elements (Angermeier and Karr 1994). Gap analyses could incorporate process concerns by determining if desirable landscape patterns based on static analyses are likely to persist as desirable patterns into the future, given knowledge of long-term ecosystem dynamics and current land-management policy. In doing so, analysts may not only identify a desirable landscape pattern for the long term, but they may also be able to have a positive influence on land-management activities.

CONCLUSIONS AND RECOMMENDATIONS

Approaches used to select and design conservation areas are diverse because of the variation in ecological and socioeconomic circumstances surrounding reserve-selection problems. This variation notwithstanding, gap analysis has emerged as a general strategy for comprehensive (i.e., multi-species) conservation of biological diversity. The appeal of mapping the distribution of floral and faunal elements as a way of identifying places warranting conservation efforts derives largely from the approach's simplicity. However, we identified two critical issues that increase the complexity of gap-analysis interpretation and implementation.

First, because comprehensive inventories of the distribution of species are lacking for most taxa, gap analyses often assume that data for a small subset of taxa are reflective of overall diversity patterns. Data bearing on this so-called biodiversity indicator assumption do not support its general applicability. Second, mapped vegetation and species distributions have an error component that may be acknowledged but has not been incorporated into reserve-boundary analyses. We found that simulated errors of omission and commission could significantly alter the reserve-boundary recommendation even when using error rates that were more conservative than those reported in the literature. In addition, uncertainty in reserve-boundary definition can be further complicated by focusing on diversity patterns without an understanding of the processes that have generated the pattern.

These findings suggest a number of recommendations and research needs for further evaluation and modification of the gap-analysis approach. First, because we did not find broad support for the biodiversity indicator assumption, gap analyses should simply acknowledge that conservation strategies will use the best information available rather than implying that inventoried taxa have the potential to reflect the diversity pattern of the regional species pool. The absence of general support notwithstanding, there were specific cases in the literature where the assumption did appear to hold. In particular, results based on the representativeness criterion seemed to support the indicator assumption more frequently than other test criteria. Research is needed to determine if there are ecological circumstances where the assumption is tenable so that conservation decisions can take into account the added benefits conferred by biodiversity indicators.

A second recommendation concerns data uncertainty. Any database encompassing the type and amount of information incorporated into a gap analysis is bound to have errors, and thus uncertainty. Error sources include gross errors, such as recording errors or misidentification; systematic errors, such as instrument imperfections; and random errors, due to natural variation and sampling (Khagendra and Bossler 1992). Without evaluating the potential effects of these errors on a gap analysis, the utility of the results will be suspect. No matter how accurate the data, providing analysts and planners with the capability to assess and display the impact of errors through sensitivity analysis and error-propagation routines (e.g., Stoms et al. 1992, Lanter and Veregin 1992) would greatly increase the value of species maps for making conservation decisions.

Addressing the limited focus on ecological process in gap analysis is the most difficult. Although it is simple to recommend that ecological process consideration be incorporated into reserve design, process-oriented research at large spatial scales is difficult (Hargrove and Pickering 1992). Despite these difficulties,

nontraditional research approaches for macroecology are developing and could provide important insight into the ecological mechanisms behind biodiversity patterns. Included among these are the developing discipline of landscape ecology with its focus on spatial pattern and the generative processes behind that pattern (Hansson and Angelstam 1991); the evolving non-equilibrium ecological paradigm (Pickett et al. 1992); the statistical analysis of unreplicated large-scale quasi-experiments (Carpenter 1990); and the synthesis of smaller scale experiments to infer large-scale phenomena through meta-analysis (Mann 1990).

Mapped vegetation and species distributions represent basic ecological information required in any reserve selection effort. Once compiled, these data place conservation planners and researchers in a unique position to describe biodiversity patterns, to propose and test hypotheses regarding the processes behind the pattern, and to delineate those regions where such research may be the most fruitful. Such compilation and synthesis has the potential to be extremely useful in a wide range of natural-resource and conservation-management issues. Whether this potential is realized will depend, in part, on how issues of biodiversity indicators, uncertainty, and ecological process are addressed.

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