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MAPPING OF SPECIES RICHNESS FOR CONSERVATION OF BIOLOGICAL DIVERSITY: CONCEPTUAL AND METHODOLOGICAL ISSUES[1]

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Abstract. Biodiversity mapping (e.g., the Gap Analysis Program [GAP]), in which vegetative features and categories of land use are mapped at coarse spatial scales, has been proposed as a reliable tool for land use decisions (e.g., reserve identification, selection, and design). This implicitly assumes that species richness data collected at coarse spatiotemporal scales provide a first-order approximation to community and ecosystem representation and persistence. This assumption may be false because (1) species abundance distributions and species richness are poor surrogates for community/ecosystem processes, and are scale dependent; (2) species abundance and richness data are unreliable because of unequal and unknown sampling probabilities and species-habitat models of doubtful reliability; (3) mapped species richness data may be inherently resistant to "scaling up" or "scaling down"; and (4) decision-making based on mapped species richness patterns may be sensitive to errors from unreliable data and models, resulting in suboptimal conservation decisions. We suggest an approach in which mapped data are linked to management via demographic models, multiscale sampling, and decision theory. We use a numerical representation of a system in which vegetation data are assumed to be known and mapped without error, a simple model relating habitat to predicted species persistence, and statistical decision theory to illustrate use of mapped data in conservation decision-making and the impacts of uncertainty in data or models on the decision outcome.

Key words: biological diversity; conservation; decision theory; gap analysis; GIS; landscape modeling; mapping; population modeling; reserve design; sampling; scaling.

INTRODUCTION

Concern over loss of biological diversity has stimulated efforts in the cartographic analyses of species distributions and landscape characteristics. For example, the Gap Analysis Program (GAP; Burley 1988, Scott et al. 1988, 1993) has among its objectives the delineation of maps of biodiversity (i.e., animal species richness), vegetation communities, and land-use classifications. Animal species richness is predicted from actual observation, distributional data (range maps), or inferred from vegetation (habitat) maps and models relating abundance or presence/absence to vegetation cover attributes and physical features (Scott et al. 1993). Proponents suggest that maps of the distribution of species richness can be used as a first approximation for identification and selection of reserves and corridors, and other land-use decisions directed at the conservation of biological diversity (Scott et al. 1993). They suggest that knowledge of ecological systems, and conservation of their biodiversity, can be gained in a hierarchical manner, using "coarse filters" such as GAP to capture community types and processes (Noss 1987); the process identifies species-rich areas as candidate reserves, from which an optimal reserve placement and design can be selected.

We approach the problem of conservation planning by first exploring population processes at the habitat-patch scale, and then examining the consequence of "scaling up" these processes to landscapes. If the "filter" analogy is appropriate, information essential to conservation will be preserved at broader scales. The above assumes that mapped vegetative communities and animal distributions are known without error. Unreliability in data and models further detracts from the utility of mapped presence/absence or abundance information for conservation decisions. We suggest that biodiversity "inventory" be approached in the context of multistage sampling, with clear exposition of objectives, quantification of uncertainty, and application of optimality rules for decision-making. Finally, we end with a plea for experimental studies at the population-landscape interface, explicitly directed to the development of linkages across disparate spatiotemporal scales.

A CONCEPTUAL MODEL FOR MAPPING HABITAT SUITABILITY

We use a multispecies generalization of Pulliam's (1988) source-sink model to illustrate the conse-

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quences of two types of information loss in mapping biodiversity. A more general, spatially explicit model is derived from Appendix 1. In the model, the determining processes are habitat-specific growth rates and dispersal.

Consider a hypothetical landscape **R** of area *A*, and an animal community comprising *S* different species, each having unique habitat affinities and demographic and movement responses to habitat variation. In our example, there are two habitat types, "forest" (*F*) or "opening" (*O*) that jointly define the landscape, so that $\boldsymbol{R} = \boldsymbol{R}(F) \cup \boldsymbol{R}(O)$; edge effects are not considered (Appendix 1). Within each habitat type a vector of habitat attributes (**z**) is unchanging, so that in $\boldsymbol{R}(F)$, $z(x, y) = \mathbf{z}(F)$, and in $\mathbf{R}(O)$ $z(x, y) = z(O)$. The respective areas of each region are $A(F)$ and $A(O)$, where $A(F) + A(O) = A$. The community is composed of *S* species' populations, occupying $\boldsymbol{R}$, characterized by their annual rates of population change (λ) in $\boldsymbol{R}(F)$ or $\boldsymbol{R}(O)$, $\lambda_i(F)$, and $\lambda_i(O)$. For species 1, . . . s_k we assume forested habitat is suitable [source; $\lambda_i(F) = \lambda_i(1) > 1$] and open habitat is unsuitable [sink; $\lambda_i(O) = \lambda_i(2)$; $0 \leq \lambda_i(2) < 1$]. The converse relationship holds for species $s_{k+1} + 1, \ldots, S$ [i.e., $\lambda_i(F) = \lambda_i(2)$; $0 \leq \lambda_i(2) < 1$, $\lambda_i(O) = \lambda_i(1) > 1$]. Within a source patch, we assume each species to be numerically limited by the total area of suitable habitat [$A_i(1)$], e.g., density limitation in a territorial species. The area of unsuitable habitat for each species, $A_i(2)$, is obtained by subtraction, since $A_i(1) + A_i(2) = A$.

The equilibrium abundance for each species in its source habitat, $\hat{N}_i(1)$, is determined by the area of habitat suitable for that species. The equilibrium abundance in sink habitats, $\hat{N}_i(2)$ is determined by

$$\hat{N}_i(2) = \hat{N}_i(1) \left[\frac{\lambda_i(1) - 1}{1 - \lambda_i(2)}\right] \tag{1}$$

(Pulliam 1988; see Appendix 1). By definition, equilibrium source and sink densities are

$$\hat{D}_i(j) = \frac{\hat{N}_i(j)}{A_i(j)}, \qquad j = 1, 2 \tag{2}$$

and proportional, equilibrium densities are

$$\frac{\hat{D}_i(2)}{\hat{D}_i(1)} = \left[\frac{\lambda_i(1) - 1}{1 - \lambda_i(2)}\right] \frac{a_i}{1 - a_i}, \tag{3}$$

where $a_i = A_i(1)/[A_i(1) + A_i(2)]$, the proportion of the landscape availability as source habitat for species *i*. We assume all dispersers to have equal access to all habitat patches within the landscape; thus, the model is not spatially explicit with respect to dispersal. However, each species is unique with respect to how landscape composition (availability of source or sink habitats) affects density (see Appendix 1). We also assume, except for density limitation in source habitat, that demographic rates and movement are independent of density. Given these assumptions, densities can become unrealistically high in sink habitats, particularly if $1 - a_i$ is small. Therefore, in the analyses to follow we constrained $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$ to [0, 6] to avoid unrealistically high sink densities.

Loss of information in summary metrics

It is difficult to estimate directly the demographic processes that determine the above relationships; instead we usually measure habitat-specific pattern of abundance and density, $N_i(j)$ and $D_i(j)$, or simply species presence/absence distributions. There is an obvious loss of information moving from demographic processes to summary statistics. For example, consider equilibrium source-sink densities as a response surface to variation in $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$, and proportional amounts of source habitat (Fig. 1; Eq. 3). We observe first that a given combination of $\lambda_i(1)$ and $\lambda_i(2)$ yields an equilibrium density of 1 for source habitats, but densities ranging from < 1 for some sink habitats, to >1 for others, dependent both on (1) the ratio $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$, and (2) the relative amounts of source (a_i) and sink ($1 - a_i$) habitat in the landscape. Thus, data on abundance or density are inadequate to reflect underlying demographic process; neither are necessaryily related to habitat quality, a fact recognized by previous workers (e.g., Van Horne 1983, Pulliam 1988, Van Horne and Wiens 1991). Further, the distribution of individual species' abundance and density in multispecies communities is confounded by the species-specific nature of the parameters. Thus, the relative densities of two species within a habitat type may reflect both their unique demographic and movement parameters, as well as differences in the amounts of either source or sink habitat available for each species. Therefore, statistics such as abundance, density, or species richness are by themselves inadequate predictors of persistence of species assemblages under different landscape configurations, as might occur through management.

Transfer of information across spatial scales

We have assumed habitat patches to be identifiable, and the relevant demographic statistics known for each patch type. To meet these assumptions requires a spatial resolution at which each identified habitat type *j* has homogeneous $\lambda_i(j)$. If we assume an arbitrary spatial scale, then it is of interest to inquire about the consequences of observing abundance, density, and related statistics at coarser scales of resolution.

Consider the above landscape/community scenario, and define "habitat suitability" for species *i* as the expected fitness (Southwood 1977, 1988) of all individuals of species *i* animals comprising the population over a defined region ($\boldsymbol{R}$). If $\boldsymbol{R}$ is partitioned into patches within which fitness is homogeneous, as above, then

$$\bar{\lambda}_i = \sum_j \lambda_i(j)\beta_i(j), \tag{4}$$

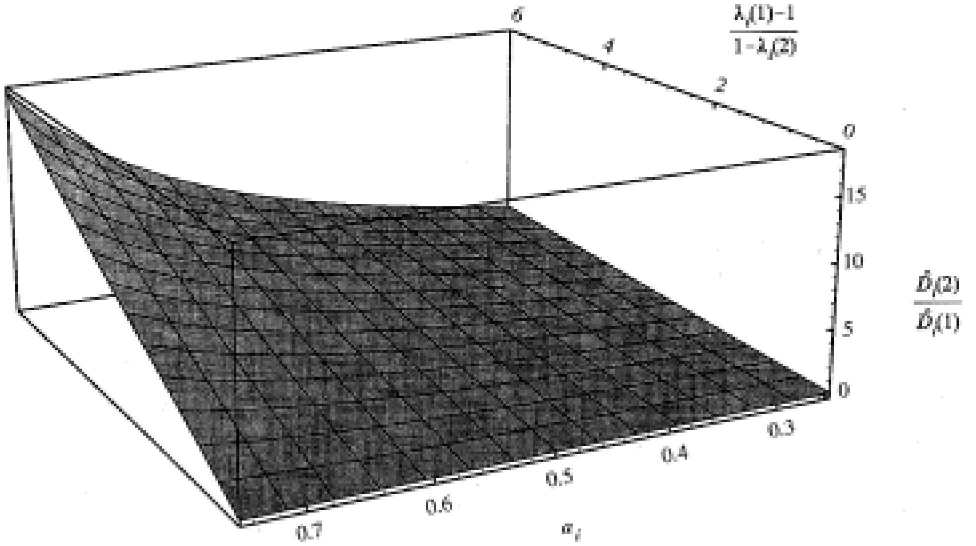

FIG. 1. Relationship among ratio of equilibrium sink-to-source densities [$\hat{D}_i(2)/\hat{D}_i(1)$, vertical axis], ratio of source surplus to sink deficit finite rates of increase ($[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$), and proportion of area in source habitat (a_i).

where ($\beta_i(j)$ represents the proportion of the population of species i in habitat j. For each species, assume an initial, equal density D_i (say 1), providing abundance $D_i A(j) = A(j)$ for each habitat, and equilibrium densities provided by Eq. 2. Expected fitness in each habitat type is $\lambda_i(j)$. Average, initial net growth across all habitat types is given by Eq. 4. In particular, if there are two habitat types, source (1) and sink (2), then

$$\begin{aligned}\bar{\lambda}_i &= \lambda_i(1)\frac{A_i(1)}{A} + \lambda_i(2)\left(1-\frac{A_i(1)}{A}\right)\\ &= a_i\left[\lambda_i(1)-\lambda_i(2)\right]+\lambda_i(2).\end{aligned} \tag{5}$$

Overall growth ($\bar{\lambda}_i$), initially defined by Eq. 4, will [given temporally constant $\lambda_i(j)$] reach equilibrium with $\bar{\lambda}_i = 1$ and density

$$\hat{D}_i = \frac{\hat{N}_i(1)+\hat{N}(2)}{A} = \frac{\hat{N}_i(1)+\hat{N}_i(1)\left[\frac{\lambda_i(1)-1}{1-\lambda_i(2)}\right]}{A}$$

or

$$\hat{D}_i = \frac{\hat{N}_i(1)}{A}\left[\frac{\lambda_i(1)-\lambda_i(2)}{1-\lambda_i(2)}\right] \tag{6}$$

If density in the source is arbitrarily set equal to 1 (e.g., the carrying capacity is 1 individual/ha), then $\hat{N}_i(1) = A_i(1)$ and

$$\hat{D}_i = a_i\left[\frac{\lambda_i(1)-\lambda_i(2)}{1-\lambda_i(2)}\right] = a_i\left[1+\frac{\lambda_i(1)-1}{1-\lambda_i(2)}\right] \tag{7}$$

By substitution of $\bar{\lambda}_i$ (Eq. 4) in Eq. 7 we have

$$\hat{D}_i = \frac{\bar{\lambda}_i - \lambda_i(2)}{1-\lambda_i(2)} \tag{8}$$

For a fixed relationship between fitness in, and movement among, habitat types, determined in a source-sink model by $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$, density at the "landscape" scale is monotonically related to the proportion of suitable habitat a_i (Eqs. 6-8, Fig. 2). This scaling relationship is dependent on the life history attributes (sensu Stearns 1976) of each species.

Further, the map scale at which the above theoretical relationship operates is itself dependent on the species' life history. This is so because varying $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$ affects the extent to which dispersal to sink habitats will occur, and thus the extent to which it is important to delineate these habitats. For species 2 and 4, where this ratio is low, there is little dispersal to sink habitats, and thus little need to delineate them. Species 1 and 3, however, have much greater potential for dispersal, and their densities cannot be predicted without delineating unsuitable habitats as well. As map scale broadens we become forced to assume that λ is homogeneous over a wider range of habitat variation, and equilibrium density for all species is predicted by a simple linear relationship to overall habitat suitability (Eqs. 5 and 8). At finer map scales, equilibrium density in habitat types (now delineated as source or sink) is no longer predicted by this simple relationship, but requires the more complex predictions of Eqs. 2-3. Given a suitably broad map scale that "averages" over source and sink habitats, there is an apparent simplification of the association between habitat and demography. The difficulty is, it is impossible to know a priori what that scale should be, without knowledge of the demographic rates $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$ and the relative areas of source habitat a_i. Further, because of the species-specificity of the above parameters, no single map scale will suffice for all species of interest, unless these have identical dispersal characteristics.

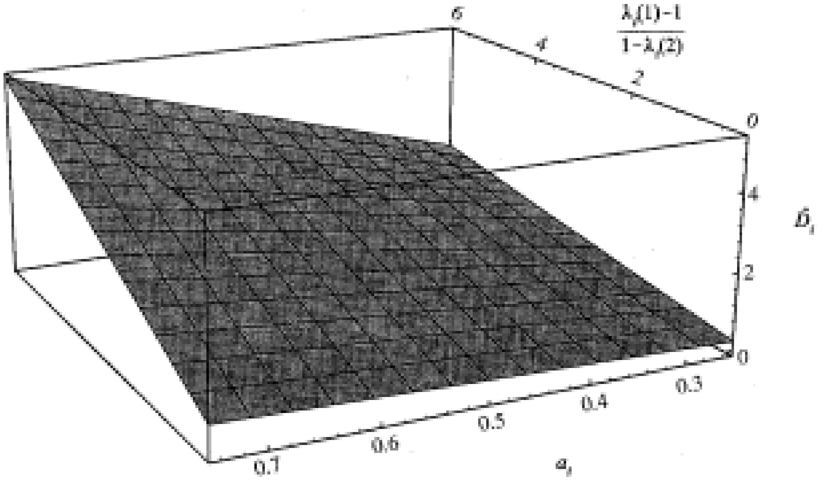

FIG. 2. Relationship between predicted landscape (across habitat patches) density ($\hat{D}_i$) under model depicted in Fig. 1 vs. ratio of source surplus to sink deficit finite rates of increase ($[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$) and proportion of landscape in source habitat (a_i).

Clearly, mapped community metrics cannot be interpreted in terms of expected fitness or persistence, without knowledge of the underlying demographic processes and the spatial scale of the assessment. Even if landscape patterns and population processes are simple, as above, information is irretrievably lost in summary statistics. One purpose of GAP and other "coarse filters" is to assist with the identification of potential reserves (Scott et al. 1993; J. M. Scott, *personal communication).* The above results suggest that caution is needed even at the "coarse filter stage," because patterns observed at an arbitrary map scale do not necessarily correlate in a predictable fashion with processes important to species persistence, presumably the goal of reserve identification, selection, and design (e.g., Bedward et al. 1992, Pressey and Nicholls 1989).

The point of this exercise is *not* the degree to which *any* of these models is true (they are all "wrong" to some degree), but how starting from first principles of population dynamics can lead to divergent, scale- and metric-dependent results and inferences. Other authors have made this same point; for example it is widely acknowledged that various landscape "diversity" measures are scale dependent, a motivation for their replacement with fractal dimension analysis (e.g., Saxon and Dudzinski 1984, O'Neill et al. 1988). However, the focus of our analyses on processes fundamental to populations clarifies the potential loss of information in a way not obvious in other approaches.

RELIABILITY AND UTILITY OF MAPPED DIVERSITY DATA

We have assumed that the species abundance distribution and its derivative statistics are known and mapped without error. This assumption is clearly false. Here we consider how statistical unreliability in spatially referenced data may affect the utility of mapped species richness patterns for decisions such as reserve selection and design. We argue below that this problem remains, even if the issues of metric and scale dependence identified earlier are resolved.

Reliability of species distributional data

The terms "inventory" and "census" suggest perfect knowledge of the kinds and abundances of species present. Inventory data of this quality are seldom available, and instead sample data are used to make inference about a *target population,* based on probability sampling. However, maps of species distribution data are often from disparate sources, and of questionable reliability. In contrast, some surveys, (e.g., Pospahala et al. 1974) are based on statistical sampling principles (Cochran 1977), and the resulting estimates have known statistical properties, the results are repeatable, and measures of reliability are available.

Other surveys are not based on probability sampling, are biased with respect to the target population (e.g., many indices and roadside surveys), or are simply compilations of occurrence records (e.g., museum records; various atlas projects). These data, while valuable for some purposes, have unknown reliability, because of sampling probabilities that are unknown but likely vary among taxa and habitats (Davis et al. 1990) and fortuitously (e.g., intense sampling near universities). Also, rare species are more likely to be missed than common ones (e.g., Sanders 1968, Hurlbert 1971, Heck et al. 1975, Smith and Grassle 1977, Sudman et al. 1988, Green and Young 1993). Finally, the detection of ≥ 1 individual of a species provides affirmative evidence of occurrence (presence), but the failure to detect an individual (absence) does not necessarily provide any information (e.g., Belbin 1993).

Using mapping data in decision-making

A further difficulty with many biodiversity inventory and monitoring data, including cartographic approaches, is lack of a clear connection to the use of these data for decision-making. For example, in lieu of the "emergency room" approach typical of much endangered species conservation, GAP (Burley 1988, Scott et al. 1988, 1993) is viewed as a proactive approach, enabling judicious decisions to be made about habitat protection, land-use designations, and reserve design. However, the published literature on GAP provides an incomplete consideration of uncertainty, and no methodology for the objective discrimination among competing proposals for conservation action that takes into account uncertainty.

Decision theory can be used to evaluate alternatives (e.g., different reserve designs) when the consequences of each (e.g., the number of species persisting in a landscape of area A) are uncertain. The decision process is (Lindley 1985): (1) list all possible decisions $\{d_1, d_2, \ldots, d_m\}$; (2) list uncertain events or outcomes that can occur $\{\theta_1, \ldots, \theta_n\}$; (3) assign prior probabilities to outcomes $\{p(\theta_1), \ldots, p(\theta_n)\}$. As will be seen, these probabilities may depend on models, data, or both; (4) assign utilities $u(d_i, \theta_j)$ to outcomes for each decision; and (5) choose the decision that maximizes expected utility:

$$\bar{u}(d_i) = \sum_{j=1}^{n} u(d_i, \theta_j)p(\theta_j). \tag{9}$$

Utilities are scaled to the unit interval, with $u = 1$ "best" and $u = 0$ worst; $\bar{u}(d_i)$ is the expected or average utility for decision i, over the probability space of the uncertain outcomes. While "utility" is arguably subjective in specific instances, certain outcomes (e.g., the total loss of species richness) are unequivocally the worst possible [$\bar{u}(d_i) = 0$] and others (e.g., the persistence of all species with no economic trade-offs) are the best [$\bar{u}(d_i) = 1$].

CASE STUDY: RESERVE DESIGN UNDER SOURCE SINK DYNAMICS

Scenario

Consider four species capable of occupying a landscape of 100 ha. The landscape is composed of a proportion (f) of forested (F) and ($1 - f$) of unforested (O) habitat, each habitat type in turn source or sink for a given species. Assume forested habitat is source for species 1 and 2, with $\lambda_1(F) = 1.3$, $\lambda_1(O) = 0.85$, $\lambda_2(F) = 1.01$, $\lambda_2(O) = 0.01$, and open habitat is source for species 3 and 4, with $\lambda_3(F) = 0.85$, $\lambda_3(O) = 1.3$, $\lambda_4(F) = 0.01$, and $\lambda_4(O) = 1.01$. In actuality the relative fitness in each habitat may be sufficient information, because the source-sink model is fully specified by the ratio $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$.

The decision problem

Our decision set is the area A ($0 \le A \le 100$ ha) that is conserved, with fA maintained as forested habitat and $(1 - f)A$ as nonforested habitat; thus, rather than being fixed as above, A and f are varied by management. For simplicity we assume that all area not conserved ($100 - A$) will become totally unsuitable for all four species; in general this need not be the case, i.e., partial suitability for nonconserved areas could be allowed. The decision space $d_i \in \{A, f;\ 0 \le A \le 100,\ 0 \le f \le 1\}$ is composed of combinations of area conserved and proportion of area forested. The operational decisions of reserve identification, selection, and design can be represented within this general framework (e.g., Pressey and Nicholls 1989, Bedward et al. 1992). Other decision scenarios are special cases, for example the total area of a reserve is fixed at $A = A_0$, but the composition (f) varies subject to management or reserve placement.

Because the reserve size (A) and habitat mix (f) necessary to sustain equilibrium populations of all four species are unknown, there are five eventual, uncertain outcomes for species richness, having probability of occurrence, $p(S = s)$, $s = \{0, 1, 2, 3, 4\}$. Each combination of decision (choice of A and f) and species richness outcome has a utility. We specified the utility obtained from conserving S species as $u(S) = S/4$, which is 1 at $S = 4$ (i.e., all four species conserved) and 0 at $S = 0$ (none conserved). Utility also may depend on the cost or effort expended on conservation, proportional to A. For simplicity, we have specified this as $u(A) = 1 - A/100$, 0 when the entire area is used in the reserve, and 1 when no area is used, and given all values of f of equal utility. In general, more realistic economic functions might be used to express the relationship between area conserved and cost, and forested and nonforested lands assigned different utilities. Finally, we define overall utility by the relationship $u(A,S) = u(A)u(S)$, that is, the joint utility of the decision-species richness outcome. Overall utility is 0 when either no species persist or all available land is used in the reserve, implicitly creating a trade-off between costs (resources forgone) and benefits (species conserved).

Expected species richness in a reserve area of size A and composition f is

$$\bar{S}(A, f) = \sum_{S=1}^{4} Sp(S = s). \tag{10}$$

Expected, overall utility is given by

$$\bar{u}(A, f) = u(A)\sum_{S=1}^{4} u(S)p(S = s), \tag{11}$$

and the optimal decision is to select A and f such that $\bar{u}(A, f)$ is maximized.

To make the optimal reserve decision based solely on distributional data requires an implicit assumption that $\bar{s}(A,f)$ will remain constant, that is, the S species included within $\{A,f\}$ must persist through time. However, because species persistence, and thus species richness, is uncertain, to arrive at an optimal decision we must estimate the probability density function (pdf) of species richness outcomes, $p(S = s)$, as a function of the species and habitat-specific fitness parameters and dispersal rules (Eqs. 1-8). We use our previous model and parameters, along with a simple persistence model (Appendix 2). First, we considered a model that perfectly predicted persistence for all species; any uncertainty was conditional on demography and initial population size.

Then, we conditioned persistence probabilities on observed data (X), rendering decisions subject to uncertainty from statistical sampling errors, model inadequacies, or both. We generated the response surfaces for $\bar{s}(A, f \mid X)$ and $\bar{u}(A, f \mid X)$, under a range of assumptions about the influence of data on the pdf of species richness, ranging from no influence ($L = 1$, Appendix 2, Eq. 2) to strong influence ($L = 20$, Appendix 2, Eq. 2) of a binary data outcome, $X = 0$ or $X = 1$. For example, $X = 0$ might represent the outcome that average, estimated abundance from surveys of the four species has declined over a period of interest, whereas $X = 1$ represents no decline over the same period. The contribution of data to the species richness pdf is represented by the likelihood ratio, L, where $L = 1$ implies no contribution of data (X); $L > 1$ implies that the data (in this example, the event $X = 0$) support a hypothesis of lower persistence probabilities than that predicted by a simple relationship to abundance (Eq. 1, Appendix 2). We then numerically maximized the utility response surface to select the optimal decision, conditioned on X, and calculated the expected utility averaged across the uncertain data outcomes, $X = 0$ or $X = 1$, as $\sum_{X=0}^{X=1} \bar{u}(A, f \mid X)p(X = x)$. For all cases we took the data outcomes as equally likely [$p(X = 0) = p(X = 1) = 0.5$]; in general these would be determined empirically, as would the likelihoods. Finally, we calculated the expected value of partial information (EVPI) for each value of L as

$$\text{EVPI} = \sum_{X=0}^{1} \bar{u}(A, f \mid X) - \bar{u}(A, f) \qquad (12)$$

(Lindley 1985). Because of the complexity of the response surfaces, for this analysis we considered a restricted decision set, in which f was fixed a priori, and A was varied to maximize utility. We considered values of $f = 0.5$ (equal proportions of forest and open habitat), $f = 0.25$ (predominately open), and $f = 0.75$ (predominantly forest). All expressions were coded and graphics generated using Mathematica (Wolfram 1991).

Results

Fig. 3a and b represent model outcome not conditioned on data. The expected number of species persisting, $\bar{s}(A, f)$, responded predictably to increases in A: as proportion of the landscape in the reserve approached 1, $\bar{s}(A, f)$ approached, but remained <4 (maximal S) for all cases (Fig. 3a) and was symmetric about optimal values for $f = 0.5$, representing equal proportions of forested and nonforested land conserved. Likewise, expected utility was highest for intermediate size ($A \approx 0.50$) and composition ($f \approx 0.5$) reserve designs (Fig. 3b). The key result of these analyses is that even under optimal decision making [$\bar{s}(A,f)$ maximized], the value of S at equilibrium (Fig. 3a) declines from $S = 4$ of initial conditions. The loss in S reflects the failure to fully incorporate stable source populations of all species when the reserve is constrained by economic costs.

However, optimal reserve design also was highly dependent on the empirical evidence in favor of the hypotheses underlying models used to predict outcomes under various management scenarios, and thus potentially on observed data (Table 1). When the data did not contribute to discrimination between these hypotheses ($L = 1$), optimal reserve area was identical, regardless of observations. As the ability of the data to distinguish hypotheses increased ($L = 2.5$-20), the results of data gathering began to have a profound influence on the optimal reserve decision, with optimal reserve areas differing by as much as 2:1, and corresponding differences in the expected utility of these decisions. Further, the expected utility of decisions averaged across the uncertain data outcomes also increased, resulting in a greater value of the data to decision-making, relative to decision-making in the absence of data (EVPI).

DISCUSSION

In the above, simple population models were used to make decisions about reserve design that take into account the stochastic nature of species persistence. Depending on the quality of the data (i.e., ability to discriminate between alternative predictions), observations from surveys, monitoring, and research may contribute to decision-making. In some cases, the data will contribute little or nothing to reaching an optimal decision, but it may be possible to collect additional data that do assist with decision-making. Decisions made without reference to data, or that use data based on poor survey or experimental designs, may lead to suboptimal decisions (choice of A and f), resulting in a loss of utility because of lower expected species richness, inappropriate use of resources, or both.

This approach also provides an explicit valuation of data in a decision-making context, and could be used to rank priorities for surveys and research. Of course, in many instances it will be impractical to significantly expand upon current research and monitoring efforts. Nonetheless, the inherent uncertainty in model predictions must be conveyed to decision-makers. Often data are absent, or if available, are poor or support conflict-

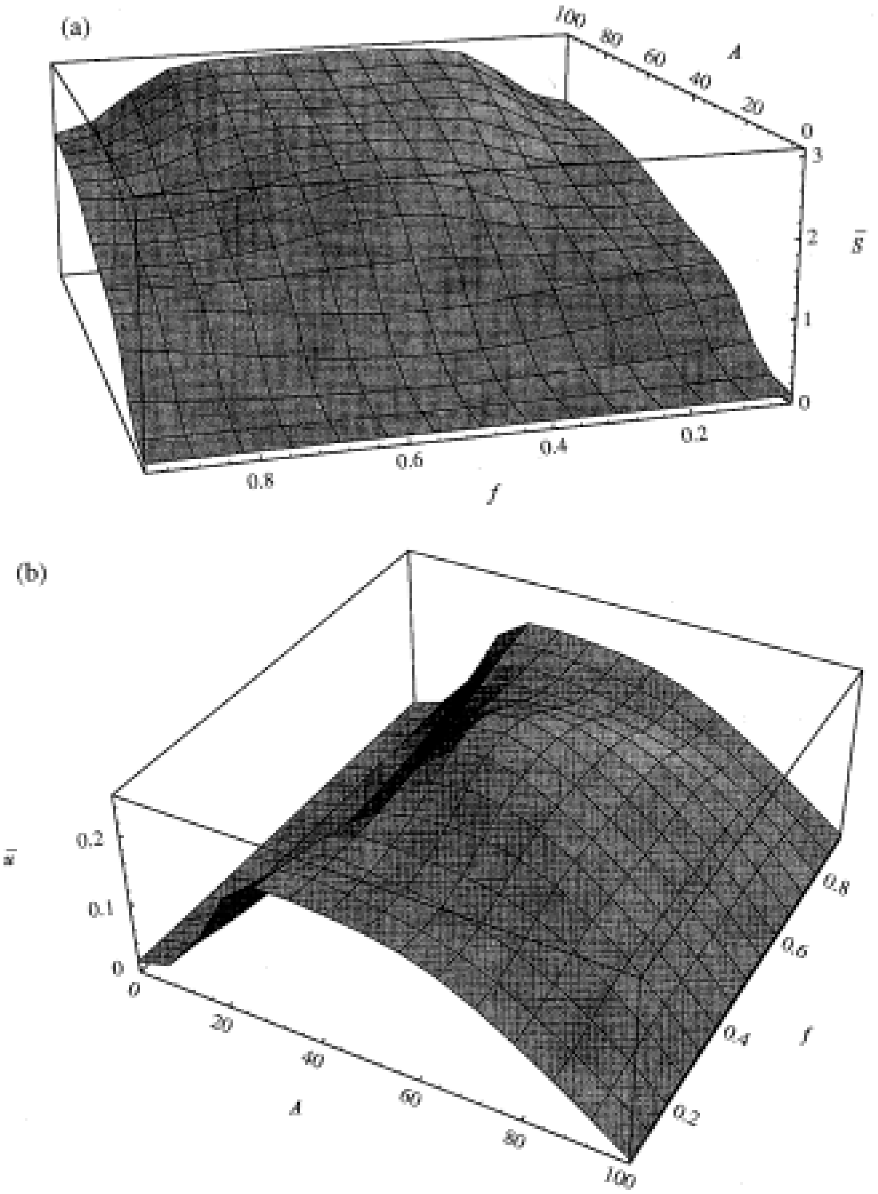

FIG. 3. Predicted relationship among total area conserved (A), proportion of area in forest (f), and (a) expected species richness ($\bar{s}$) based on source-sink model, four species having different habitat affinities ($[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$, where "source" (1) and "sink" (2) are either forested (f) or nonforested ($1 - f$) depending on species). (b) Expected utility ($\bar{u}$) of decisions represented by combinations of area conserved (A) and proportion of area forested (f) for above example; utility increases as species richness increases to a maximum of 4 [$u(s) = s/4$] but is discounted by required amount of area conserved [$u(A) = 1 - A/100$]; overall utility $u = u(s)$-$u(A)$.

ing hypotheses. It is then prudent to evaluate the sensitivity of decision outcomes to a range of relative beliefs (prior probabilities) in alternative hypotheses. For instance, a conservative decision might assume that persistence was less likely than suggested by the pure demographic model (Fig. 3a, b), even if no data were available to support that belief.

Finally, we acknowledge that the above models ignore relevant information about population and landscape dynamics. Our approach is not spatially explicit; thus, only the size and composition of the reserve, not the exact spatial arrangement of habitats within the reserve, will affect outcomes. Further, because we evaluated outcomes under an equilibrium model, the dynamic behavior of the species assemblages prior to equilibrium is unknown. However, the model captures essential species-specific scale dependencies, and is a useful first approximation to illustrate the relationship of spatially referenced data, and data uncertainties, to reserve design. More realistic models, including spatial explicitness, individual animal behavior, and dynamic habitats and animal populations (e.g., Dunning et al.

TABLE 1. Optimal reserve size (A^*) and utilities of decision (u) for landscapes with a priori fraction in forest (f), conditional on observed data (X), for simulated example involving four species in an artificial landscape.

f	L†	X‡	A^*	$\overline{u}(x)$ §	$\overline{u}$¶	EVPI‖
0.5	1	0	54.62	0.3127	0.3127	0
		1	54.62	0.3127		
	2.5	0	60.1351	0.2490	0.3163	0.0036
		1	48.4053	0.3836		
	5	0	63.877	0.2064	0.3267	0.0110
		1	43.2898	0.4409		
	10	0	67.3145	0.1689	0.3347	0.0221
		1	37.8867	0.5006		
	20	0	70.5183	0.1363	0.3491	0.0363
		1	32.2714	0.5618		
0.25	1	0	53.9200	0.2552	0.2552	0
		1	53.9200	0.2552		
	2.5	0	58.6673	0.2009	0.2615	0.006
		1	48.7748	0.3221		
	5	0	62.2298	0.1671	0.2740	0.0188
		1	44.2502	0.3810		
	10	0	65.7722	0.1381	0.2919	0.0367
		1	39.0835	0.4457		
	20	0	69.2160	0.1130	0.3137	0.0586
		1	33.3782	0.5145		
0.75	1	0	37.7219	0.2996	0.2996	0
		1	37.7219	0.2996		
	2.5	0	41.9980	0.2689	0.3038	0.0042
		1	33.6499	0.3388		
	5	0	45.2972	0.2486	0.3136	0.0133
		1	30.7631	0.3781		
	10	0	48.6118	0.2298	0.3296	0.0296
		1	27.9568	0.4293		
	20	0	51.9156	0.2119	0.3530	0.0534
		1	24.8760	0.4942		

† Likelihood ratio, $p(X=x|H_0)/p(X=x|H_a)$; see Appendix 2.

‡ Observed data, e.g., $X = 0$ is observed decline in average abundance for all four species, $X = 1$ is lack of observed decline.

§ Expected utility $\overline{u}(A, f \mid X)$ of the optimal decision (reserve area A), conditioned on the observation $X = 0$ or $X = 1$; optimization constrained to a priori fraction of reserve in forest (f).

¶ Expected utility, averaged across uncertain data outcomes 0.5 $\sum_{X=0}^{X=1}\overline{u}(A, f \mid X)$ see Eq. 11 and Appendix 2.

‖ Expected value of partial information, taken as the difference between expected utility of optimal decisions conditioned on data, and that unconditioned on data; EVPI = $\sum_{X=0}^{X=1}\overline{u}(A, f \mid X) - \overline{u}(A, f)$ (see Eq. 12, Appendix 2).

1992, McKelvey et al. 1993, Lamberson et al. 1994) will be needed to adequately represent the ultimate impact of management decisions.

RECOMMENDATIONS

Under certain circumstances, observed patterns of animal presence/absence or abundance, together with mapping of habitat (vegetation types), may be useful in conservation decision making. However, current methodologies and available data may be inadequate to produce optimal conservation decisions. For example, because of scale dependencies in habitat suitability-abundance relationships and persistence likelihoods, optimal decisions require further information about demographic processes and scaling relationships (e.g., habitat-specific λ and dispersal rates). Summary statistics (e.g., S) that combine presence/absence of species having disparate life histories are unlikely to be useful, may be misleading, and at a minimum are highly scale dependent.

As a first step toward improving existing methods, we suggest that species be grouped by life history attributes and spatial scaling relationships. The guild-indicator concept (e.g., Block et al. 1987), if used with caution, may be a useful starting point. Within a group (e.g., guild), effort should be focused on obtaining reliable, empirical estimates of parameters that scale an individual's relationship to the landscape. Published allometric relationships (e.g., Peters 1983) may be helpful as a first approximation, but deliberate sampling and experimentation will be needed for reliable parameter estimates. Finally, our approach, which emphasizes the impacts of local demography on species distribution and richness, might be effectively combined with approaches such as "target taxon analysis," which emphasizes the analysis of representative "information rich" taxa in reserve design (Kremen 1994).

Animal populations, and their habitats, are elements embedded in a hierarchy of processes operative at increasing spatiotemporal scales. Knowledge of a species' position in the hierarchy, and thus the appropriate map scale, are essential for effective conservation planning, including reserve identification, selection, and design. Multistage sampling (Thompson 1992, Schreuder et al. 1993), in which sampling and subsampling units are selected hierarchically, may be an efficient method to obtain reliable information from species distribution maps. Other approaches, such as the "coarse filter" approach of the Nature Conservancy (Noss 1987) or methods based on maximizing diversity of landscape features and taxonomic richness (Kirkpatrick 1983, Margules et al. 1988, Pressey and Nicholls 1989) Bedward et al. 1992, Belbin 1993) including GAP (Burley 1988, Scott et al. 1988, 1993) could be formalized as multistage, adaptive sampling (Thompson 1992), in which primary units initially are examined to determine whether secondary or tertiary units should be considered for more detailed sampling. However, the success of such an approach would be highly dependent on assumptions about transfer of information across scales, and the predictive reliability of habitat relationship models (e.g., Maurer 1986, Van Horne and Wiens 1991, Stoms et al. 1992). Deliberate sampling, and where possible experimentation, at multiple spatial scales is needed before such efforts can be used with any degree of predictive reliability.

Careful attention must be paid to whether the information gained from more intensive sampling will lead to marginally better conservation decisions. Not all data can or should be collected, but arbitrary decisions about data collection, made in response to conservation crises, can easily result in suboptimal management decisions. Decision theory forces a formal, a priori consideration of the goals of conservation planning: the selection of the best range of conservation actions possible in the face of uncertainty (Murphy and Noon 1991). Decision theory explicitly values data, whether from routine surveys and monitoring, or focused research, to the extent they contribute to decision-making. Finally, improvements in our understanding of and ability to predict in ecological systems, can and should be used interactively with management "experiments" to achieve conservation goals (Walters 1986, Johnson et al. 1993).

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APPENDIX 1

GENERAL SPATIAL GRADIENT MODEL FOR POPULATION DYNAMICS

Our model links occupancy of habitats to population and metapopulation phenomena, through simple assumptions about habitat selection and movement among habitats, and is similar in concept to Hanski and Gilpin (1991) and Wiens et al. (1993). For a given population, we assume that λ is largely determined by characteristics of the habitat, so that $\lambda(z)$ represents the relationship of expected finite rate of population growth to a vector z of habitat attributes, $z \in \boldsymbol{Z}$; z in turn is referenced to a mapped surface [i.e., $z(x, y)$]. We define "suitable" habitats sensu Pulliam (1988) as those having attributes such that net reproduction is greater than or equal to net mortality, so that on average $\lambda \geq 1$; conversely, in "unsuitable" habitats $\lambda < 1$. Attribute(s) z may be univariate (e.g., z_1 is amount of forest cover), but more generally z will be composed of many factors (e.g., canopy cover, tree density, proximity to edge, moisture, and so forth).

We assume that each species ($i = 1, \ldots, S$) within the assemblage potentially (1) has a unique demographic response to habitat gradients, i.e., the $\lambda_i[z(x, y)]$ response surfaces will differ, and (2) will respond uniquely to different habitat geometries (i.e., patterns) because of differing dispersal abilities. In turn, the pattern of distribution of a species' abundance, $N_i[z(x, y)]$, will be determined by both $\lambda_i[z(x, y)]$ and the rate and direction of movement of individuals across the landscape; in other words, the rest of the landscape "influences" $N_i[z(x, y)]$, and vice versa. In general, we can describe this influence function by weights $Q_i[u(x, y), v(x, y)]$ in a convolution

$$N_i'[\boldsymbol{z}(\boldsymbol{x},\boldsymbol{y})] = \int_z \int_{R(y)} \int_{R(x)} N_i[\boldsymbol{w}(\boldsymbol{u},\boldsymbol{v})] \cdot Q_i[\boldsymbol{z}(\boldsymbol{x},\boldsymbol{y}),\boldsymbol{w}(\boldsymbol{u},\boldsymbol{v})]\,du\,dv\,dw, \qquad (1.1)$$

where $N_i[z(x, y)]$, N_i' $[z(x, y)]$ are abundances at locations (x, y) having habitat attributes z at times t, $t + \Delta$, respectively, and $Q_i[z(x, y), w(u, v)]$ represents the influence, through birth, death, and dispersal, of locations in the landscape $\boldsymbol{R}$, including (x, y). Because most populations of interest are monitoring annually or less frequently, we make the additional assumption that the time units are 1 yr, incremented annually ($\Delta = 1$).

This model is spatially explicit; we next simplify the model under the assumption that $Q;$ depends only on habitat attributes z, not on their spatial location (x, y). We recognize the loss of realism in this model but believe it to be sufficiently realistic for our purposes; it clearly is more amenable to parameterization than a more complex, spatially explicit model (Conroy et al. 1995). Further, our essential points about differential dispersal among species, and the resulting impacts on community statistics, can be made without invoking spatial explicitness. The simplified model is

$$N_i'(\boldsymbol{z}) = \int_z N_i(\boldsymbol{w}) Q_i(\boldsymbol{z},\boldsymbol{w})\,dw, \qquad (1.2)$$

similar to the filter scaling function described by Allen and Starr (1982:20). For more generality, $O;(z, v)$ in Eq. 1.2 can include terms denoting interspecific interactions (e.g., competition) so that

$$N_i'(\boldsymbol{z}) = \int_z N_i(\boldsymbol{w}) \sum_{j=1}^{S} Q_{ij}(\boldsymbol{z},\boldsymbol{w})\,dw$$

and O_{ij} (u, v), $j \neq i$ includes interspecific effects on λ_i (a), for example through competition or predator-prey interactions. For simplicity we have ignored potential interspecific effects on modelled populations. We believe the inclusion of such effects will further complicate the transfer of information about population processes to summary statistics such as S. Other, more familiar models are special cases of this model. For example, it may often be realistic (as well as convenient) to treat habitat factors as constant at the scale of discrete patches, rather than as continuous gradients. Thus, if a population exists in a landscape $\boldsymbol{R}$ containing h habitat patches $\boldsymbol{R} = \boldsymbol{R}(1) \cup \boldsymbol{R}(2) \cup \boldsymbol{R}(3) \cup \ldots \cup \boldsymbol{R}(h)$, average growth $\mathrm{E}\{\lambda_i[\boldsymbol{R}(j)]\}$ may differ among patch types. Let II; [$\boldsymbol{R}(j)$, $\boldsymbol{R}(k)$] represent the probability of movement of individuals of species i from patch $\boldsymbol{R}(k)$ to patch $\boldsymbol{R}(j)$. Eq. 1.2 can be reformulated in terms of discrete habitats in a system of difference equations. The abundance of species i in habitat $\boldsymbol{R}(j)$ $j = 1, \ldots, h$ at $t + 1$ is given by the difference equation:

$$N_i'[\boldsymbol{R}(\boldsymbol{j})] = \sum_{m=1}^{h} N_i[\boldsymbol{R}(\boldsymbol{m})] Q_i[\boldsymbol{R}(\boldsymbol{j}),\boldsymbol{R}(\boldsymbol{m})] \qquad (1.3)$$

where $Q,[\boldsymbol{R}(j), \boldsymbol{R}(m)] = \lambda_i[\boldsymbol{R}(m)]\Pi_i[R(j), \boldsymbol{R}(m)]$, and the implicit order of events is growth (i.e., birth and death deter mining λ) first, followed by movement. To illustrate, if there are three habitats we have a system of difference equations:

$$N_i'[\boldsymbol{R}(\boldsymbol{j})] = \sum_{m=1}^{3} N_i[\boldsymbol{R}(\boldsymbol{m})] \lambda_i[\boldsymbol{R}(\boldsymbol{m})] \Pi_i[\boldsymbol{R}(\boldsymbol{j}),\boldsymbol{R}(\boldsymbol{m})],$$

$$j = 1, 2, 3$$

This is a patch-dynamic model (Levins 1969, Hanski and Gilpin 1991). As illustrated below, other models such as source–sink (Pulliam 1988) are special cases. From Pulliam (1988), abundance of species i at time $t + 1$ in the source habitat type (1) is

$$N_i'(1) = \begin{cases} \hat{N}_i(1), & N_i(1)\lambda_i(1) \geq \hat{N}_i(1) \\ N_i(1)\lambda_i(1), & N_i(1)\lambda_i(1) < \hat{N}_i(1) \end{cases} \qquad (1.4)$$

where $\lambda_i(1) \geq 1$, $0 \leq \lambda_i(2) < 1$, $\hat{N}_i(1)$ is the upper limit to abundance in the source habitats, and $N_i(1)\lambda_i(1) - \hat{N}_i(1)$ individuals disperse if $N_i(1)\lambda_i(1) \geq \hat{N}_i(1)$. In sink habitat (2), we have

$$N_i'(2) = \begin{cases} N_i(2)\lambda_i(2), & N_i(1)\lambda_i(1) < \hat{N}_i(1) \\ N_i(1)\lambda_i(1) - \hat{N}_i(1) + N_i(2)\lambda_i(2), & N_i(1)\lambda_i(1) \geq \hat{N}_i(1) \end{cases}. \qquad (1.5)$$

At equilibrium $N_i'(j) = N_i(j)$, $j = 1, 2$ and

$$\hat{N}_i(2) = \hat{N}_i(1)\frac{[\lambda_i(1) - 1]}{[1 - \lambda_i(2)]}. \qquad (1.6)$$

Total abundance in source is determined by its area; in sink, it is proportionally higher or lower according to $[\lambda_i(1) - 1]/[1 - \lambda_i(2)]$ (Pulliam 1988).

APPENDIX 2

SPECIES PERSISTENCE MODEL

Initially, we consider a model that perfectly predicts the probability of persistence for each species as a function of its abundance in the landscape; thus all uncertainty is inherently demographic. We then condition these probabilities on observed data, rendering them subject to uncertainty from statistical sampling, model errors, or both.

Let $\delta_i = 1$ represent the event that species i persists, with probability p_i. Conversely, $\delta_i = 0$ represents the event that species i fails to persist, with probability $(1 - p_i)$. We determined p$_i$ for the i = 1, four species with a logistic model

$$\ln\left(\frac{p_i}{1 - p_i}\right) = b_0 + b_1\hat{N}_i, \qquad (2.1)$$

where $\hat{N}_i$ are equilibrium abdundances predicted for each combination of species' life history and decision (A, f) by the source-sink model (Eq. 8). We arbitrarily selected values of $b_0 = -4.595$ and $b_1 = 0.0919$, to yield values of $p_i = 0.02$, 0.5, and 0.99 at $\hat{N}_i$ = 10, 50, and 100, respectively. The same logistic model and parameter values are used for all four species, giving rise to different p; depending on $\hat{N}_i$ and in turn on each species $\lambda_i(1)$, $\lambda_i(2)$ and the relative amounts of source or sink habitat in the reserve.

The pdf of S may be affected by uncertainty in information (e.g., estimates of N, λ, or model parameters), influencing the ability of this model to discriminate between persistence (δ_i = 1) and extinction ($\delta_i = 0$). Therefore, we condition p_i, and thus $p(S = s)$, on X, a vector of random variables (e.g., sample estimates of ($\lambda_i(j)$, $i = 1, 2$; $j = 1, \ldots, 4$, and coefficients in Eq. 2.1). In our simulations, we took X as binary, i.e., $X = 0$ or 1. For example, $X = 0$ might represent the outcome that average, estimated abundance from surveys of the four species has declined over a period of interest, whereas X = 1 represents no decline over the same period. The conditioning represents dependence of p_i on the uncertain relationship of sample data to predicted persistence. By Bayes' Theorem

$$p_{i|X=0} = P(\delta_i = 1 \mid X = 0) = \frac{p_i}{p_i + (1 - p_i)L_i}, \qquad (2.2)$$

where $L_i = p(X = 0|\delta_i = 0)/p(X = 0|\delta_i = 1)$ is the ratio of the likelihood under H_0: $\delta_i = 0$ to that under H_a: $\delta_i = 1$, and represents the contribution of data to discrimination between H_a and H_0. The conditional probability $p_{i|X} = 1$ for the case where the events $X = 0$ and $X = 1$ are mutually exclusive and exhaustive [i.e., $p(X = 0) + p(X = 1) = 1$] is given by Eq. 2.2 but with $1/L$ substituted for L. Values of $L = 1$ imply no contribution of the data, and Eq. 2.2 reduces to p_i unconditional on data. We considered a range of values of L = 1 to 20 (favoring H_0: $\delta_i = 0$ when $X = 0$), and causing $p_{i|X}$ to be less than that determined by Eq. 2.1. For example, if $\hat{N}_i$ = 100, $p_i = 0.990$ (Eq. 2.1), when $L = 10$, $p_{i|X=0} = 0.908$ Eq. 2.2).

The $p_{i|X=x}$ were then used to generate a phd for S, the number of persisting species. For example, $p(S = 1)$ is computed as the sum of the individual probabilities that species i but no others persists:

$$p(S = 1 \mid X = x) = \sum_{i=1}^{4}\left[p_{(i|X=x)}\prod_{\substack{m=1 \\ m\neq i}}^{4}\left(1 - p_{(m|X=x)}\right)\right]. \qquad (2.3)$$

Other values for $p(S = s|X = x)$ were similarly generated.