HABITAT MODELING FOR BIODIVERSITY CONSERVATION

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ABSTRACT—Habitat models address only 1 component of biodiversity but can be useful in addressing and managing single or multiple species and ecosystem functions, for projecting disturbance regimes, and in supporting decisions. I review categories and examples of habitat models, their utility for biodiversity conservation, and their roles in making conservation decisions. I suggest the use of influence diagrams in structuring causal webs and structural equation modeling to quantify relations, as a general framework for building models of habitat from which a known degree of inference can be made to biodiversity variables.

Key words: biodiversity conservation, habitat modeling, indicators, surrogates, multi-species, influence diagrams, structural equation modeling

In the United States, federal land management agencies that are focally charged with managing species' habitats often are faced with a dilemma of also providing for biodiversity. Biodiversity has many definitions and variables (for example, DeLong 1996; Callicott and others 1999) although it is generally defined as the diversity of multiple levels of biological organization at multiple scales of space and time. Noss (1990) defined it as an array of compositional, structural, and functional variables at biological organizational levels ranging across genes, population and species, and communities and ecosystems (Table 1). In this paper, I address how modeling of habitat can serve to inform and guide management of the fuller suite of biodiversity variables. My objectives are to review how habitat modeling can be structured to represent biodiversity, to quantify the degree to which habitat alone can serve as a surrogate or estimator of biodiversity variables, and to suggest a generalized modeling framework from which many different kinds of models can be developed to address multiple variables of biodiversity.

MODELS AS ESTIMATORS

A model can be used as an estimator of some parameter. In the context of this paper, a model can use some measurable habitat surrogate or indicator from which inference is made to some biodiversity variable, for example, habitat quality serving as a surrogate or an estimator of the presence or abundance of some species. Studies suggest that some habitat attributes can predict some biodiversity variables but the degree of predictability varies by the type of statistics used and the variables in question.

For example, Schtickzelle and others (2005) used surrogate data from a healthy metapopulation of a fritillary butterfly to analyze viability of an endangered metapopulation of the same species. They used this tactic to circumvent the need for high quality data from the endangered metapopulation which would otherwise be required to parameterize population viability models. This approach carried the assumptions that the dynamics of the healthy metapopulation can represent those of the endangered one and that threats to the latter were external to population dynamics.

In another example, Barve and others (2005) used surrogate data on human settlements, livestock, roads, and other habitat features to evaluate threats to a wildlife sanctuary in southern India. They validated their model by finding a positive correlation between their threat index levels and anthropogenic disturbance activities and a negative correlation between threat index levels and tree species richness, which in turn represented integrity of the wildlife sanctuary ecosystem. However, there was no direct measure of ecosystem integrity beyond tree species richness, so the assumed link between this variable and other ecosystem variables remains untested.

TABLE 1.   Components of biodiversity with some example measurable variables (after Noss 1991). Note that only the community-ecosystem structural variables are what are typically regarded as ''habitat'' variables.

Level of biological organization	Composition	Structure	Function
Gene or genome	Allelic diversity Rare alleles	Effective population size Heterozygosity	Inbreeding depression Gene flow
Population or species	Abundance Biomass	Dispersion, range Population structure	Vital rates Metapopulation trends Phenology
Community or ecosystem	Functional groups Rare communities	Vegetation structure Physical features	Key ecological functions Nutrient cycling

Oliver and others (2004) reported that types and variety of land classes served as surrogates to biodiversity, principally the spatial configuration of biological assemblages, for conservation planning. To test this relation, they studied vascular plants, invertebrates, and microbiota in 4 land classes varying in degree of size and isolation in Australia. They found that type of land class correlated with, and thus served as a surrogate for, unique biota even though many individual species may not have been uniquely associated with each land system. This meant that types of land classes could be used as surrogates to general species assemblage composition but not individual species. Also, degree of isolation of the land classes did not account for a significant amount of the variation observed in the species assemblages, and thus additional, explicit modeling of any isolation effects would need to be further pursued.

Other uses of surrogates, successful to varying degrees, include representing endangered species (Burton 2003), identifying optimal bioreserve networks (Rothley 2002), using landscape variables as ecological indicators of forest fragmentation effects (Lindenmayer and others 2002), using topography, soil, and hydrology to represent bird and dung beetle assemblages (Wessels and others 1999), and using vascular plants to represent fungal species richness in reserve design (Chiarucci and others 2005). Wilsey and others (2005), however, found that plant species richness incompletely represented grassland biodiversity.

The lesson from these examples is that the degree to which surrogate variables represent various aspects of biodiversity varies depending on the context and specific variables used. Thus, instead of searching for 1 surrogate to represent biodiversity, it may be more appropriate to develop a general modeling approach to depict and evaluate efficacy of using habitat or other variables to represent biodiversity. Here, I suggest generalized methods for developing testable habitat models to represent and predict biodiversity variables.

Influence Diagrams Depict Relations

One broad approach to developing habitat models to represent biodiversity variables may entail use of influence diagrams. At their simplest, these are pictures of boxes and arrows showing relations among variables (Fig. 1; Varis 1997) or more complex representations of directly measured variables, latent or unobserved variables, various correlation or causal relations, and unexplained variation (Fig. 2). An example of a latent variable is ''habitat quality'' which may be represented by a habitat suitability index (the HSI nodes in Fig. 2) calculated from observable habitat attributes.

Using influence diagrams is an efficient and useful way to depict current understanding and expert judgment of the relations between habitat variables and various dimensions of biodiversity. Influence diagrams can be developed from an individual's expertise, from rigorously querying a panel of experts, from synthesizing literature, or from a combination of these approaches. The advantages of using influence diagrams are that they are relatively easy to construct and to understand, they can represent a wide variety of variables and relationships, and unlike most statistical models they do not depend on having a large body of empirical data. However, they should be thought of as only the 1st step in developing more quantitative and testable models.

Although not always called such, influence diagrams are widely used in ecological and other modeling (for example, Jensen and Jensen 1996; Zhu and others 1998). A simple influence
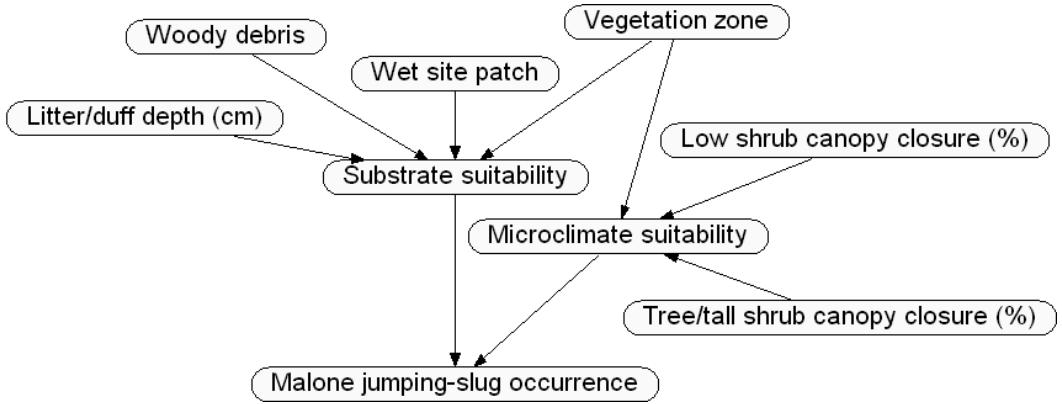
FIGURE 1.   A simple influence diagram depicting habitat suitability for a terrestrial mollusk, the Malone jumping-slug (*Hemphillia malonei*), in the US Pacific Northwest.
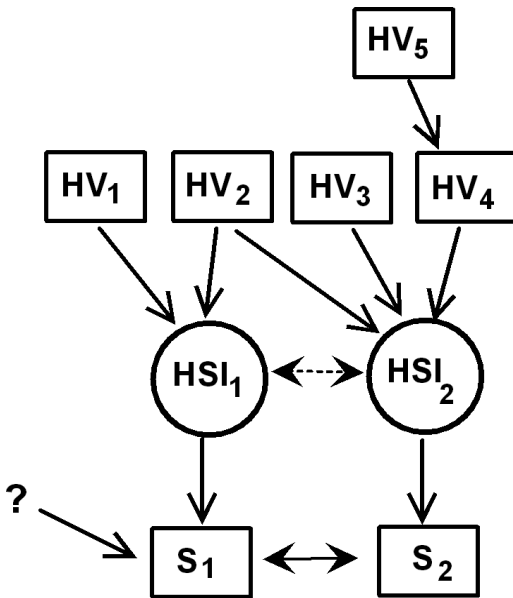

FIGURE 2.   Correlates and causes represented in a hypothetical species influence diagram. HV = habitat variable, HSI = habitat suitability index value derived from habitat variables, S = species presence or abundance, ? = unobserved influence. Boxes represent observed or directly measured variables, circles represent latent (unobserved) factors or constructs, single-headed arrows indicate causal relationships between variables and constructs, double-headed arrows indicate associations between variables or constructs with no attribution of causation, and arrows not originating in a variable represent residual unexplained variances due to unmeasured factors, chance variation, or both.

diagram might depict inference made from some habitat surrogate variable to some biodiversity variable, for example key environmental and habitat correlates of a species of interest. At best, it would depict proximate causal factors, showing a ''causal web'' of influences (for example, Shipley 2002; Fabricius and De'ath 2004).

An influence diagram then can be expanded or embellished into many other model forms which can help depict and explain the degree to which habitat variables can serve as surrogates to biodiversity variables, and which can be explicitly tested for their accuracy of prediction. Some examples follow.

Expanding Influence Diagrams Into Other Model Forms

Partitioning the Variance.—An influence diagram can serve as a picture of the statistical relations between predictor (habitat) variables and response (biodiversity) variables. The question of how well habitat can represent biodiversity can be restated as the degree to which the variability in some biodiversity variable is indexed or estimated by habitat variables. This can be represented in standard ANOVA fashion by partitioning variance of the response variable into among-groups (or treatment) sources and residual (or error) sources. The residual sources are essentially a statement of the degree to which variation in the biodiversity variable is not explained by the habitat variable(s). This is the unexplained variation shown in the influence diagram (Fig. 2). The complement of

this describes the degree to which management of the habitat variables can reasonably be expected to influence the biodiversity variable of interest.

Also, surrogate habitat variables can be viewed broadly as statistical estimators of the biodiversity variable(s). Statistical estimators have particular characteristics, namely precision, accuracy, bias, and consistency, in how well they can serve as surrogates or indicators for the response variables they index. Partitioning the variance can help explain and quantify some of these characteristics such as precision, but additional statistical analyses such as goodness-of-fit tests would be useful to determine other characteristics.

Also important is evaluating rates of Type I and Type II errors by controlling for confidence and power of statistical predictions of biodiversity variable(s) from habitat surrogates. Methods for controlling and evaluating such errors are beyond the scope of this paper and useful reviews are available elsewhere (Steidl and others 1997; Di Stefano 2001; Verhoeven and others 2005).

Partial Correlation Analysis.—Another way to describe the degree of predictability in statistical models is to calculate the standardized partial correlation between the habitat variable(s) and the biodiversity variable of interest. Partial correlation tells the degree of relation between the variables given influence from other sources, not all of which may be known. Standardizing the values makes it possible to directly compare relative effects among the variables. Many multivariate statistical modeling forms can be used for partial correlation analysis, such as traditional multiple linear (or logistic) regression. As an example, King and others (2005) used partial correlation analysis to describe the relative influence of various land-cover classes in predicting stream nitrogen and macroinvertebrate assemblages. A partial correlation model by itself, however, does not distinguish between causal and noncausal relationships between variables as used in an influence diagram (Fig. 2). Causality must be determined by other means, such as from corroborative studies or direct experimental manipulative studies (Marcot 1998).

Path Regression Analysis.—One particularly useful tool to depict partial correlation is path regression (Shipley 2002). A path regression
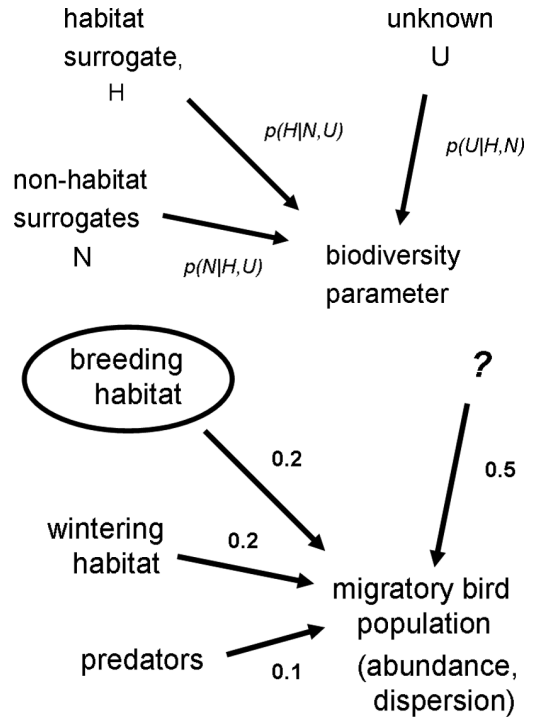

FIGURE 3.   Path regression models. Top: A generalized path regression model explaining variation in some biodiversity variable from a habitat variable (H), non-habitat variables (N), and unknown influences (U). Labels on the lines represent individual influences or conditional probabilities (p). Bottom: A simple hypothetical path regression model of abundance of some migratory bird species.

model looks like an influence diagram with the arrows labeled according to their partial correlation (or conditional probability as may be used in a belief network, discussed below) (Fig. 3 top). For example, a simple influence diagram might depict the effect of breeding habitat, wintering habitat, predators, and unknown sources, on the abundance or dispersion of some migratory bird population (Fig. 3 bottom). The local manager may wish to know the degree to which managing for breeding habitat alone would provide for the population, and this would be depicted by the partial correlation between breeding habitat and the population variable.

In this hypothetical example (Fig. 3 bottom), path regression analysis may suggest that only 20% of the variation in a migratory bird population can be affected by conserving or re-
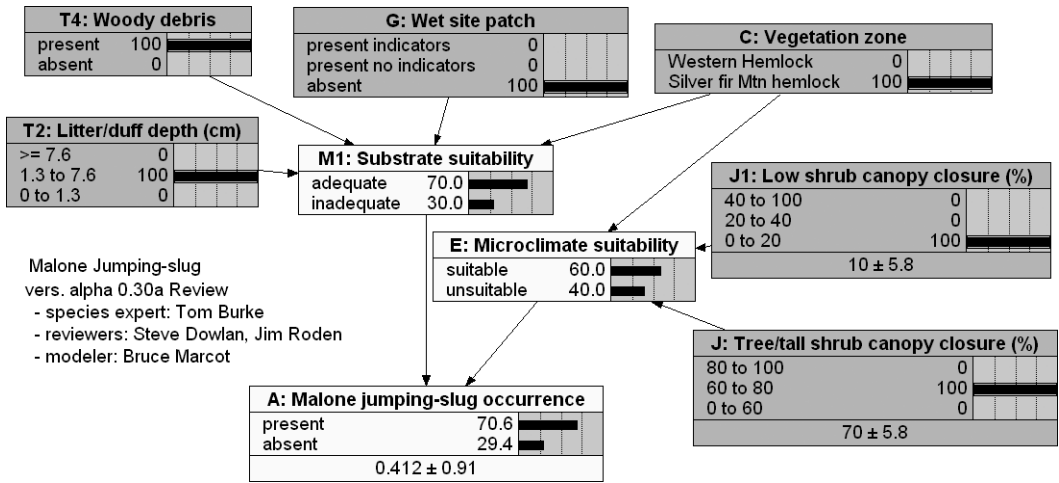
FIGURE 4.   A Bayesian belief network model of Malone's jumping-slug based on the influence diagram shown in Fig. 1. This figure illustrates running the model for a specific location within the silver fir–mountain hemlock zone with a moderate litter–duff layer, presence of woody debris, absence of wet site patches, open canopy closure of low shrubs, and moderate canopy closure of trees and tall shrubs. Values by the solid bars are probabilities; for example, the model predicts an approximately 71% probability that this site has slugs present. Numbers below boxes A, J, and J1 are mean and standard deviation (assuming a Gaussian error distribution), where values in box A are scaled from −1 for absence to +1 for presence (thus, 0.412 denotes moderate evidence of slug presence). This model was developed, peer-reviewed, and refined from species expert experience, but was not further validated in the field.

storing local breeding habitat alone, and the remainder of the variation is influenced by other known and unknown factors. This does not mean that local breeding habitat is inconsequential; it may be a critical causal link to the persistence of the bird's population. But such an analysis can inform managers as to what outcomes they should realistically expect from a local habitat management program.

In fact, one can expect that only approximately 20 to 50% of the variation in the presence and abundance of most wildlife populations is accounted for by measurable habitat variables; large unexplained residual variances are common in ecological models, such as pollination models (Mitchell 2001). This means that at least half, often substantially more, of the variation is influenced by factors other than local measurable habitat variables. Habitat is still essential, but may not completely account for a desired population outcome.

Process Simulation Modeling.—Influence diagrams also can serve as the basis for process simulation models. Simulation models are typically time-dynamic based and often use some form of difference equations to represent incremental changes in values of variables. An example is Hudson's (1995) process model of the demand and output of commercially exploited wildlife. Hudson used the STELLA modeling shell which provides time-dynamic estimates of model variables such as population size, habitat extent, kill rates, and product values.

Other examples of process simulation modeling are commonly found as part of population viability analyses. Examples include spatially explicit, individual-based population simulation models (Schumaker 1992; Schiegg and others 2005), models of patch occupancy and metapopulation dynamics (Moilanen 2004), and models of dispersal (Higgins and others 2001).

Bayesian Belief Network Modeling.—Influence diagrams can become the basis for Bayesian belief network (BBN) models (Marcot and others 2001). BBNs depict probabilistic relations among causal variables and use Bayesian statistics to calculate probabilities of outcome states such as population presence, given conditions of input variables such as habitat conditions (Fig. 4). BBNs are based on unconditional or prior probabilities of input variables

TABLE 2. A conditional probability table of microclimate suitability in the Malone jumping-slug model (node E in Fig. 4). Probability values under the columns Suitable and Unsuitable were derived from expert judgment and experience and from an initial set of known site data.

| Predictor variables of microclimate suitability | | | Microclimate suitability (node E) | |
Tree or tall shrub canopy closure (%) (node J)	Vegetation zone (node C)	Low shrub canopy closure (%) (node J1)	Suitable	Unsuitable
80 to 100	Western hemlock	40 to 100	100	0
80 to 100	Western hemlock	20 to 40	80	20
80 to 100	Western hemlock	0 to 20	70	30
80 to 100	Silver fir-mountain hemlock	40 to 100	100	0
80 to 100	Silver fir-mountain hemlock	20 to 40	90	10
80 to 100	Silver fir-mountain hemlock	0 to 20	80	20
60 to 80	Western hemlock	40 to 100	100	0
60 to 80	Western hemlock	20 to 40	70	30
60 to 80	Western hemlock	0 to 20	50	50
60 to 80	Silver fir-mountain hemlock	40 to 100	100	0
60 to 80	Silver fir-mountain hemlock	20 to 40	80	20
60 to 80	Silver fir-mountain hemlock	0 to 20	60	40
0 to 60	Western hemlock	40 to 100	40	60
0 to 60	Western hemlock	20 to 40	20	80
0 to 60	Western hemlock	0 to 20	0	100
60 to 60	Silver fir-mountain hemlock	40 to 100	50	50
0 to 60	Silver fir-mountain hemlock	20 to 40	30	70
0 to 60	Silver fir-mountain hemlock	0 to 20	0	100

(for example, box T2 in Fig. 4), conditional probabilities of intermediate variables (latent constructs in influence diagrams, such as boxes E and M1 in Fig. 4), and posterior probabilities of output or response variables (box A in Fig. 4). Prior and conditional probabilities (for example, Table 2) are typically assigned by expert judgment, literature review, empirical data, or some combination, and posterior probabilities are calculated using Bayesian learning statistical methods. BBNs also can explicitly include management and utility nodes that depict alternative activities and values (costs or benefits) of different outcomes, respectively.

Structural Equation Modeling.—A generalized approach to embellishing an influence diagram for modeling biodiversity from habitat factors may use structural equation modeling (SEM; Pugesek and others 2003), sometimes also called causal modeling. SEM is not a particular model structure per se but rather a way to construct and formalize relationships among variables. It is more useful with observational rather than experimental data and is a generalization of many statistical techniques commonly found in the habitat modeling literature, including regression, discriminant analysis, canonical correlation, factor analysis, and others. As a general approach, SEM can be used to address ill-conditioned problems that lack neat analytic solutions, such as modeling habitat to predict biodiversity variables. Iriondo and others (2003) provided a good discussion of SEM and demonstrated its use to model causal relationships in threatened plant populations. SEM statistical methods are covered well in recent texts (Shipley 2002; Kline 2004; Schumacker and Lomax 2004).

SEM is structured by differentiating among direct causal relationships, indirect causal relationships, spurious relationships, and association without causation (Fig. 2). The 1st step in SEM is to create the model structure as an influence diagram of variable relations, such as depicting a species (or other biodiversity variable) as a causal function of habitat variables, not forgetting to depict the unexplained variance. The next step is to expand the latent variables into their components (Bollen 1989), such as expanding "habitat" into discrete, measurable variables of vegetation structure and topographic condition (for example, Pugesek and Tomer 1996; Fig. 2). Then, estimates of regression weights are computed for each variable relation, for example, the degree to which each habitat variable component affects the species of interest; regression weights can be derived using partial correlation analysis or Bayesian

conditional probabilities (discussed above). Next, measurement errors of each component variable are estimated. This step is seldom done in more traditional process or analytic modeling but is a vital part of SEM and can usefully depict the amount of uncertainty in the habitat-biodiversity relations represented in the model. Measurement error and uncontrolled variation are the inescapable hallmark of observational studies, such as retrospective studies (for example, Montes and others 2005) and time- or location-based comparison studies (Benedetti-Cecchi 2001; Bro and others 2004).

The final SEM model is a depiction of specific variable relations, the strength of their relations, and the degree of uncertainty of those variables and their relations. The aim of SEM is to test the hypothesized underlying causal relations among variables by analyzing their covariance structure. This is done by using goodness-of-fit tests to evaluate the congruence between the variance-covariance matrix derived from observational data to that suggested by the hypothetical causal structure (the predicted moment matrix). Many methods of estimation in SEM can be used for this final analysis step. They typically include maximum likelihood estimation (MLE) with multivariate normal data and a large sample size (about 200+ observations); weighted least squares (WLS; also called asymptotically distribution free) methods with continuous but nonnormal data; and polychoric correlation analysis with ordinal variables, which computes correlation between unobserved normal variables and then uses WLS. A number of software packages are available specifically for SEM including LISREL, EQS, AMOS, and CALIS (Iriondo and others 2003), and some general statistical packages such as SYSTAT have procedures for doing SEM.

Information-theoretic Modeling.—Another class of modeling is based on information theory (Anderson and others 2000; Burnham and Anderson 2002). These models depict relations and predictions as likelihoods. Information-theoretic models have become somewhat popular recently in the wake of some authors deemphasizing the value of traditional statistical testing of null hypotheses (Guthery and others 2001). They suggest that likelihood analysis in information-theoretic models can at least partially replace null hypothesis testing (Anderson and others 2000) and that structuring our

understanding as reliable knowledge has priority over letting statistical tools dictate how we test and understand ecological relations. This philosophy fits well with use of influence diagrams and their quantitative cousins, which force us to 1st frame the research hypothesis and causal relations among variables before determining the statistical hypotheses and significance of relationships among variables.

Anderson and others (2001) and Anderson and Burnham (2002) offered caveats on avoiding spurious findings and misuse of information-theoretic models in wildlife studies, including suggestions on avoiding problems of analytic methods and on framing the basic question. Properly framing the initial influence diagram to correctly represent potential surrogates and various relationships among variables (Fig. 2) could go a long way to avoiding such pitfalls and creating more useful models.

Other Modeling Approaches.—A host of other modeling approaches can tier from the influence diagram framework including Markov chain, transition matrix, and loop analysis or graph theory models to depict ecological succession, vegetation growth and development, ecosystem disturbance, and community structure and ecosystem process. Specific models of these types are many and include VDDT (Barrett 2001; ESSA 2005), SITES (Andelman and others 1999), SELES (Fall undated), MARXAN (Ball and Possingham 2000), ECOSIM and ECOPATH (Pauly and others 2000), BioMapper (Hirzel and others 2002), and PATH (Schumaker 1992). Influence diagrams also can serve as the basis for more traditional species-habitat relationships models including habitat suitability index, habitat effectiveness, and habitat evaluation procedures models (for example, Roloff and Kernohan 2000).

DISCUSSION

Limitations of Habitat Models

Habitat models address only a few biodiversity variables directly (namely, structural aspects of communities and ecosystems, Table 1), but can indirectly serve as surrogates to other biodiversity variables to varying degrees. Although habitat of species and organisms is necessary for biodiversity conservation, habitat alone usually is incomplete. Habitat models therefore will never fully serve as perfect esti-

mators of all biodiversity variables, regardless of the type of model used. Depending on their management objectives and information needs, managers may wish to engage other specific models to more directly estimate selected facets of biodiversity. There is only so much that habitat models can tell you about such biodiversity variables as genomes, ecological functions of species, viability of metapopulations, and ecosystem processes.

A risk-analysis approach to biodiversity conservation can entail estimating the extent to which habitat alone will provide for a specified array of biodiversity variables. This will inform the manager as to the degree to which habitat conservation or restoration will provide for biodiversity; that is, it will provide a realistic expectation of successful biodiversity conservation given management activities focused on habitat. One might also heed the discussion by Failing and Gregory (1999) of common mistakes made in designing biodiversity indicators for guiding forest management policy; their advice can help correctly structure influence diagrams from the beginning such as by attending to indicators that management can influence, identifying appropriate response variables, and using tightly-linked estimator variables. Lindenmayer and others (2000) provided a useful discussion of selecting appropriate indicators for sustainable forest management, offered caveats against use of some taxon- and species-based indicators, and suggested using and testing structure-based biodiversity indicators of vegetation stand complexity, connectivity, and heterogeneity.

Some Practical Guidelines

Influence diagrams, especially when depicting causal webs, are 1 of the more useful and robust ways to begin such an indicator or surrogate modeling exercise. Influence diagrams can become the basis for many specific model forms and for quantifying relations among variables, especially habitat surrogates for biodiversity variables. Some practical guidelines for constructing useful influence diagrams are as follows.

First, the modeler should clearly define the objectives of the model, including its intended audience, use, and geographic area. Objectives should include clearly listing the variable(s) of biodiversity intended to be represented in the model, and the environmental or habitat variables that could be used in the model as surrogates or predictors.

Second, the modeler should take stock of existing knowledge regarding the biodiversity variables in the geographic area of interest or in similar ecological situations. This can include literature review, compiling data sets, and querying experts.

The modeler is then in a position to compile this information into 1 or more representations of relations among variables, that is, to build an influence diagram of causal relations between habitat and biodiversity variables. Building the influence diagram can be done with the informal aid of individual domain experts or more formally in expert panels. The resulting influence diagram then constitutes a representation of current knowledge.

Next, the influence diagrams can be used as the basis for quantitatively modeling variable relations, as with Bayesian belief networks and information-theoretic approaches. They can also serve as a basis from which to prioritize field studies to determine degree of association among variables, as with partial correlation and path regression models. Such models can be further calibrated and validated by testing and updating the model structure and incorporating data on new variable relations.

Finally, results can be conveyed to managers in terms of the degree to which specific habitat variables, and management activities affecting those variables, can be expected to influence desired biodiversity outcomes. Uncertainties in model predictions should be made clear and be part of any risk analysis.

The future of habitat modeling for biodiversity also could explore a formal approach using structural equation and information-theoretic modeling. This would explicitly quantify relations between habitat variables and biodiversity variables, and especially the uncertainties and measurement errors associated with variables and their relations, although it is still the onus of the modeler to demonstrate causation among variable relations. Any such modeling approach should have as its goal a means of informing resource managers the degree to which providing habitat alone will suffice to ensure the full array of biodiversity variables, which is likely to be far less than expected or assumed.

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