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Habitat Relations

Using Bayesian Networks to Incorporate Uncertainty in Habitat Suitability Index Models

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ABSTRACT Habitat suitability index (HSI) models rarely characterize the uncertainty associated with their estimates of habitat quality despite the fact that uncertainty can have important management implications. The purpose of this paper was to explore the use of Bayesian belief networks (BBNs) for representing and propagating 3 types of uncertainty in HSI models—uncertainty in the suitability index relationships, the parameters of the HSI equation, and measurement of habitat variables (i.e., model inputs). I constructed a BBN–HSI model, based on an existing HSI model, using Netica™ software. I parameterized the BBN's conditional probability tables via Monte Carlo methods, and developed a discretization scheme that met specifications for numerical error. I applied the model to both real and dummy sites in order to demonstrate the utility of the BBN–HSI model for 1) determining whether sites with different habitat types had statistically significant differences in HSI, and 2) making decisions based on rules that reflect different attitudes toward risk—maximum expected value, maximin, and maximax. I also examined effects of uncertainty in the habitat variables on the model's output. Some sites with different habitat types had different values for E[HSI], the expected value of HSI, but habitat suitability was not significantly different based on the overlap of 90% confidence intervals for E[HSI]. The different decision rules resulted in different rankings of sites, and hence, different decisions based on risk. As measurement uncertainty in habitat variables increased, sites with significantly different ($\alpha = 0.1$) E[HSI] became statistically more similar. Incorporating uncertainty in HSI models enables explicit consideration of risk and more robust habitat management decisions. © 2012 The Wildlife Society.

KEY WORDS Bayesian network, habitat modeling, habitat suitability index, HSI, risk.

Uncertainty is inherent to every management decision affecting wildlife and their habitats. Uncertainty is pervasive because ecosystems are wickedly complex (Ludwig 2001) and they exhibit irreducible natural variability at multiple spatial and temporal scales. Natural resource managers who ignore uncertainty may adopt overly optimistic or pessimistic beliefs; leading to decisions that ultimately result in environmental degradation or forgone economic opportunities (Ludwig et al. 1993, Reckhow 1994). Managers who approach decisions with resolute certainty may fail to anticipate problems or recognize potential risks. In contrast, dealing with uncertainty enables managers to plan for contingencies and minimize potential losses (Morgan and Henrion 1990:2). Management decisions should be well informed about the uncertainty of consequent outcomes, and the risk of undesirable outcomes should be evaluated and dealt with appropriately (Murphy and Noon 1991, Burgman et al. 2005).

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Scientists should characterize uncertainties associated with information they provide managers. In fact, Morgan and Henrion (1990:44) believe scientists have a professional and ethical responsibility to do so. Despite repeated calls to characterize uncertainty and incorporate it into management decisions (Hilborn 1987, Murphy and Noon 1991, McCarthy and Burgman 1995, Harwood and Stokes 2003, Steel et al. 2009), it is still not a universal practice. This failing is especially prevalent in the construction and use of habitat suitability index (HSI) models.

The concepts and methodology for HSI models were developed over 30 years ago (U.S. Fish and Wildlife Service [USFWS] 1980, 1981). Habitat suitability index models are based on the assumption that habitat quality can be described through an index. The index ranges from 0 to 1, with 0 being non-habitat and 1 being optimal habitat. Habitat quality is described in terms of carrying capacity (USFWS 1980), where optimal habitat has maximal carrying capacity and a site's HSI value is the ratio of the site's carrying capacity to maximal carrying capacity (USFWS 1981). The inputs to an HSI model are measurable habitat variables. Suitability index (SI) relationships, which also range from 0 to 1, relate each habitat variable to habitat quality. Suitability indices are typically constructed through expert knowledge informed by a review of the scientific literature. The SI relationships usually take the form of piece-wise linear functions represented graphically, as opposed to analytical formulations, but the HSI methodology places no constraints on SI relationships and more complex functions are also used (e.g., Spies et al. 2007). Suitability indices are mathematically combined via the HSI equation. The equation is typically a weighted arithmetic or geometric mean of the SIs, although minimum, maximum, and logical functions are occasionally employed. Parameter values (i.e., weights) and the equation's structure are invariably based on expert knowledge, again, informed by the scientific literature.

Habitat suitability index models are regularly employed for assessing the effects of forest management (Marzluff et al. 2002, Spies et al. 2007) and environmental mitigation requirements (Duberstein et al. 2007, Ashley and Muse 2008). Hence, the reliability of HSI models and the nature of their outputs affect decisions with real consequences for wildlife habitats (Brooks 1997, Roloff and Kernohan 1999). Well over 150 HSI models for fish and wildlife species were published before 1990 (Terrell and Carpenter 1997), and many others have been developed since then (e.g., McComb et al. 2002, Dussault et al. 2006, Kroll and Haufler 2006, Burnett et al. 2007, Spies et al. 2007). All the aforementioned models have a major shortcoming in common—they do not characterize the uncertainty associated with their HSI estimates.

An HSI model has 4 main sources of uncertainty: 1) SI relationships, 2) parameters of the HSI equation, 3) structure of the HSI equation, and 4) habitat variables. The first 3 stem from the lack of knowledge (epistemic uncertainty) about a species' autecology and the natural variability (aleatory uncertainty) in a species' demographic response to habitat conditions. The fourth is the result of measurement uncertainty. Van Horne and Wiens (1991) were the first to suggest that SI relationships could be structured to account for uncertainty. They proposed an approach whereby uncertainty would be represented in 3 dimensions via a triangular distribution defined by piece-wise linear relationships: the upper and lower limits and a central tendency. Burgman et al. (2001) implemented this idea with triangular fuzzy numbers, which are typically used to deal with conceptual vagueness (Regan et al. 2002) and in Burgman et al. (2001), fuzzy numbers quantified expert opinion about "agreement" between a particular value of a habitat variable and "the concept of suitable habitat." The result is not a probability distribution over the domain of SI values, but rather possibility levels for suitable habitat.

Uncertainty has been incorporated into HSI models in other ways as well. Johnson and Gillingham (2004) used Monte Carlo methods to incorporate uncertainty in the 4 factors of an HSI equation. Uncertainty was represented as either a triangular or uniform probability distribution, with the center and limits of each distribution based on expert opinion. The model's output was a probability distribution of HSI values. Larson et al. (2004) incorporated uncertainty into their SI relationships with 3 different sets of relationships that yielded 3 separate HSI values—upper, lower, and best estimates, and Ray and Burgman (2006) dealt with uncertainty in the parameters and structure of their model by constructing 22 equally plausible models and bounding the "range of subjective uncertainty" by the HSI values at the upper and lower extremes. Neither of these approaches generated a probability distribution for HSI values, which is problematic because extreme values could have extremely small probabilities of being the true HSI value. Bender et al. (1996) dealt with uncertainty of habitat variables (i.e., model inputs) through Monte Carlo and bootstrapping methods. Using empirically derived estimates of habitat variables, they generated 90% confidence intervals for the mean HSIs of 6 different habitat types. If confidence intervals of different habitat types did not overlap, then they concluded that the mean HSIs of those habitat types were significantly different.

Although various approaches have been explored for incorporating uncertainty in HSI models, most have addressed only 1 source of uncertainty; only Ray and Burgman (2006) dealt with more than 1 source. Furthermore, several of these approaches did not produce a probability distribution over HSI values, and therefore, could not generate particular types of information useful for management decisions: expected value of HSI, the probability of extreme HSI values, and whether differences in HSI values between sites or between habitat types were significantly different.

Perhaps a practical modeling framework that facilitates the representation and propagation of uncertainty would encourage HSI models that provide a fuller and more useful characterization of uncertainty. One such modeling framework is Bayesian belief networks (BBNs). Bayesian belief networks are a type of probabilistic graphical model (Jensen and Nielsen 2007), which have proven utility for ecological modeling (Marcot et al. 2006, Uusitalo 2007), and have been used for numerous assessments of wildlife habitats (e.g., Raphael et al. 2001, Lee and Irwin 2005, McNay et al. 2006, Smith et al. 2007).

Bayesian belief networks possess 3 useful features for building HSI models that incorporate uncertainty. First, all variables in a BBN are represented as random variables (i.e., as probability distributions). Second, BBNs enable uncertainty to be explicitly incorporated into each functional relationship of an HSI model. These uncertainties propagate through the network and are expressed at the model output as a random variable. And third, the graphical nature of BBNs enables straightforward translation of an HSI model to a BBN through a computer-user interface typical of software applications such as Netica™ (Norsys Software Corp., Vancouver, British Columbia) or Hugin Expert™ (Hugin Expert A/S, Aalborg, Denmark).

BBNs may be a practical modeling framework for representing and propagating uncertainty in HSI models. The purpose of this paper is to explore the use of BBNs for the implementation of HSI models. My objectives are to 1) explain the translation of an HSI model to a BBN–HSI model, 2) explain how to incorporate HSI model uncertainties into a BBN, and 3) demonstrate how the output of a BBN–HSI model can be used to make more informed management decisions. The scope of my exploration is confined to 3 of the 4 types of uncertainty: SI relationships, HSI equation parameters, and measurement of habitat variables.

METHODS

The methods consist of 2 stages: 1) construction of a BBN–HSI model and 2) a demonstration of the model's utility for representing and propagating uncertainty in HSI models.

Construction of a BBN–HSI Model

The initial steps of constructing a BBN–HSI model are the same as an ordinary HSI model: 1) selecting habitat variables (i.e., model inputs), 2) constructing SI relationships for each habitat variable, and 3) formulating an equation that combines SIs into the HSI (USFWS 1981). Additional steps necessary to construct a BBN–HSI are: 4) quantifying uncertainty in each SI relationship, 5) assembling the network, 6) discretizing input variables, 7) discretizing intermediate and output variables, 8) quantifying uncertainty in parameters of the HSI equation, and 9) parameterizing the BBN.

For steps 1 through 4, I used an existing HSI model that quantified uncertainty in its SI relationships (Burgman et al. 2001). This model, for the Florida scrub-jay (*Aphelocoma coerulescens*), is described by the following equations:

$$\mathrm{SI}_{1a} = G_{1a}(\text{percent shrub canopy comprised of scrub oaks}) \quad (1)$$

$$\mathrm{SI}_{1b} = G_{1b}(\text{distance from scrub oak ridge}) \quad (2)$$

$$\mathrm{SI}_{2a} = G_{2a}(\text{percent of cover comprised of sand or herbs}) \quad (3)$$

$$\mathrm{SI}_{2b} = G_{2b}(\text{distance to ruderal area}) \quad (4)$$

$$\mathrm{SI}_{3a} = G_{3a}(\text{percentage of pine canopy cover}) \quad (5)$$

$$\mathrm{SI}_{3b} = G_{3b}(\text{distance to forest}) \quad (6)$$

$$\mathrm{SI}_{4a} = G_{4a}(\text{mean height of oak scrub}) \quad (7)$$

$$\mathrm{SI}_{4b} = G_{4b}(\text{mean height of palmetto scrub}) \quad (8)$$

$$\mathrm{SI}_1 = \max(\mathrm{SI}_{1a},\ \mathrm{SI}_{1b}) \quad (9)$$

$$\mathrm{SI}_2 = \max(\mathrm{SI}_{2a},\ \mathrm{SI}_{2b}) \quad (10)$$

$$\mathrm{SI}_3 = \min(\mathrm{SI}_{3a},\ \mathrm{SI}_{3b}) \quad (11)$$

$$\mathrm{SI}_4 = \mathrm{SI}_{4a} \text{ if scrub oak cover} > 30\%, \quad \text{else} \quad \mathrm{SI}_4 = \mathrm{SI}_{4b} \quad (12)$$

$$\mathrm{HSI} = (\mathrm{SI}_1^{w_1}\mathrm{SI}_2^{w_2}\mathrm{SI}_3^{w_3}\mathrm{SI}_4^{w_4})^{1/(w_1+w_2+w_3+w_4)} \quad (13)$$

where each G_z is a graphical function depicting the relationship between a suitability index and a habitat variable; z denotes 1a, 1b, 2a, 2b, 3a, 3b, 4a, 4a, or 4b; and w_1, w_2, w_3, and w_4 are parameters that determine the relative influence of SI_1, SI_2, SI_3, and SI_4, respectively, in the calculation of HSI. The ecological basis for the HSI model is explained in Breininger (1992) and Breininger et al. (1998).

The model of Burgman et al. (2001) represents expert uncertainty in each SI relationship, equations 1–8, by means of 3 piece-wise linear functions corresponding to the best guess, lower bound and upper bound of a triangular fuzzy number (Fig. 1). I assumed that these graphical representations of uncertainty corresponded to the mode, lower bound, and upper bound of a triangular probability distribution (sensu Van Horne and Wiens 1991). In effect, each SI_z is a random variable described by a probability distribution and the shape of that distribution is determined by G_z and the value of the habitat variable.

Equation 13 is a weighted geometric mean. The model of Burgman et al. (2001) and Breininger et al. (1998) used an unweighted geometric mean, which is equivalent to $w_1 = w_2 = w_3 = w_4 = 1$. The assertion that SI_1, SI_2, SI_3, and SI_4 are equally influential was an expert judgment, and like the expert judgments made to construct the graphical SI relationships, there certainly was uncertainty associated with that judgment. However, Burgman et al. (2001) did not incorporate this parameter uncertainty in their model. I modeled uncertainty in w_1, w_2, w_3, and w_4 by treating them as random variables described by probability distributions (explained below).

I assembled the network, step 5, with Netica™ (version 4.08). This software provides all the functionality needed to construct and run BBN models. A BBN consists of nodes and links. Variables are represented as nodes. Nodes can be inputs to the model, outputs of the model, or intermediate variables. A link between nodes indicates a cause-and-effect relationship, and hence, is always unidirectional. No link between nodes implies no cause-and-effect relationship exists and is equivalent to statistical independence. At the beginning of a link is a parent node and at the end of a link is a child node. Every child node holds the probabilistic relationship between its output and its parent nodes. The relationship is stored as a conditional probability table (CPT) with each row corresponding to a unique combination of the parent's states and each column corresponding to the child's output states. Nodes and links are well suited for representing HSI models, which can be decomposed into modular components and do not possess feedback loops.

All variables in a BBN must be either categorical or binned, and therefore, continuous variables must be discretized. Discretization partitions the domain of a continuous random variable into a finite number of intervals (or states). The resulting discrete random variable assumes the intervals' center values: $x_1, x_2, x_3, \ldots, x_N$. Discretization results in numerical errors, and if too coarse will cause linear relationships to behave nonlinearly. These problems can be avoided through finer discretization, but with a practical limitation—computer memory and computational burdens increase exponentially with N. Therefore, the number of states should

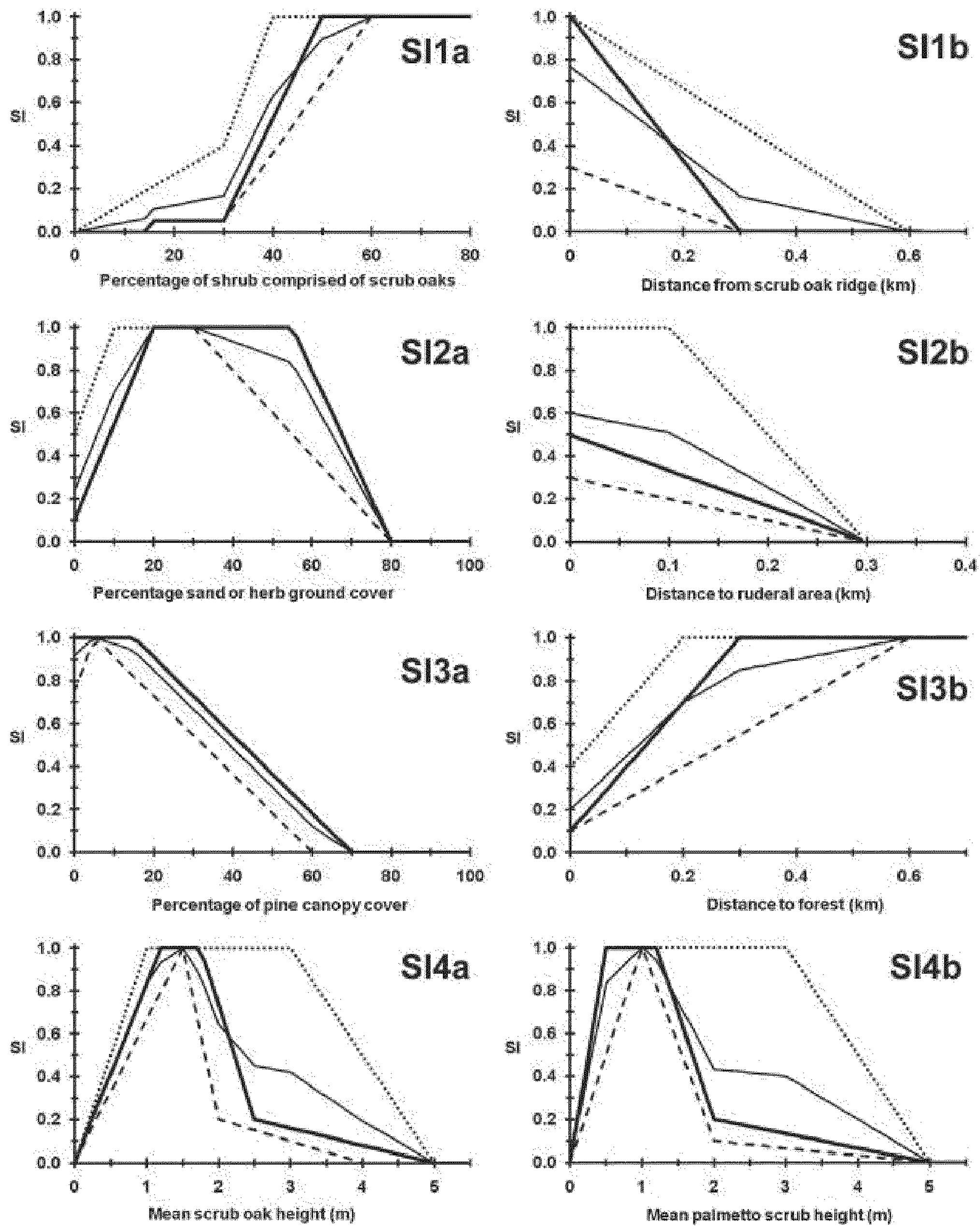

Figure 1. Suitability index (SI) relationships based on Burgman et al. (2001). Dotted, dashed, and thick solids lines represent the upper limit, lower limit, and mode, respectively, of a triangular probability distribution located in a third dimension perpendicular to the page. Thin solid line is the expected value of SI calculated from the triangular distribution.

be the smallest number that provides a satisfactory approximation of the continuous random variable.

I translated the equations of the HSI model into a BBN (Fig. 2). Equations 1–12 imply no dependent relationships among SI_z, SI_1, SI_2, SI_3, and SI_4 and this is represented by the absence of links between these nodes. Equation 13 specifies that HSI is dependent on SI_1, SI_2, SI_3, and SI_4, and consequently, links connect these SI nodes to the HSI node (i.e., the model's output node). Each G_z function was represented by 2 nodes: 1 to discretize and represent uncertainty in the habitat variable and 1 to represent the graphical SI relationship. The outputs for SI_1, SI_2, SI_3, and SI_4 are from nodes that select from a pair of SI relationships (e.g., SI_{1a} or SI_{1b}). The max and min nodes are functions that operate on the probability distributions of random variables. I implemented the if-then operation, equation 12, as a binary deterministic node that assumed 1 value for scrub oak cover $>30\%$ and another value for scrub oak cover $\leq 30\%$. I used the output of this if-then node to select between SI_{4a} and SI_{4b}.

The main reasons for implementing an HSI model with a BBN are to represent and propagate uncertainty (Fig. 3). Uncertainty is represented through discrete random variables and CPTs. Uncertainty can be propagated through the network in either forwards or backwards directions. Backwards propagation, also known as diagnostic reasoning

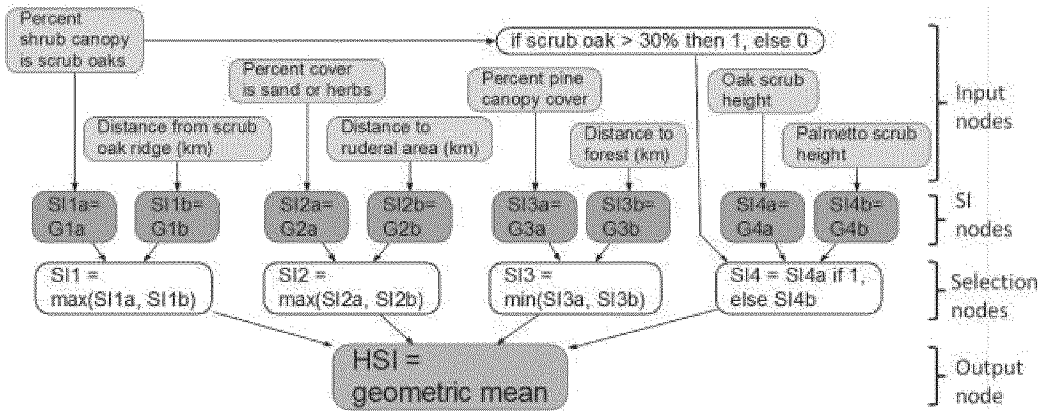

Figure 2. Bayesian belief network that implements the habitat suitability index model of Burgman et al. (2001). Input nodes discretize the habitat variables. SI nodes (SI_{1a}, SI_{1b}, SI_{2a}, . . .) contain conditional probability tables (CPTs) for the suitability index (SI) relationships. Selection nodes select 1 SI from each pair (via minimum, maximum and if-then functions) and pass it on to the HSI node. The HSI node contains a CPT for the weighted geometric mean of the 4 parent nodes.

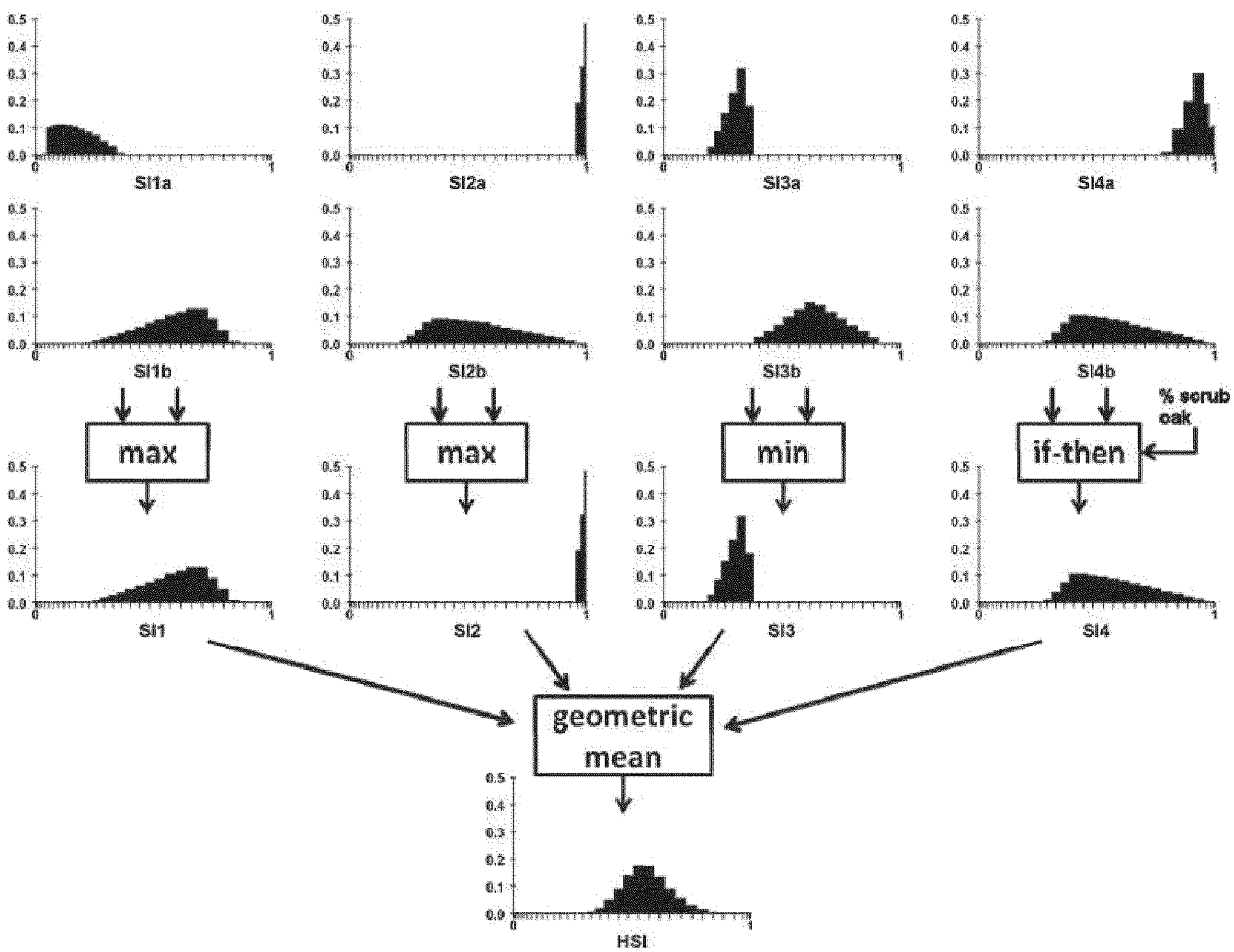

Figure 3. Example of uncertainty propagating through a Bayesian belief network–habitat suitability index (HSI) model. The shape of the probability mass functions (PMFs) for the suitability index (SI) variables SI_{1a}, SI_{1b}, SI_{2a}, SI_{2b}, SI_{3a}, SI_{3b}, SI_{4a}, and SI_{4b} (SI_z) are based on the habitat variable values input into the 8 graphical functions G_z. Selection nodes operate on pairs of SI_z (e.g., SI_{1a} and SI_{1b}). The selection nodes' outputs are passed to a node that calculates a weighted geometric mean, and the result is a PMF for HSI. Boxes represent nodes in the Bayesian belief network model. Arrows represent links between nodes. Note the 36 unequal discretization intervals on the SI-axes.

(Kjaerulff and Madsen 2008:18) relies on Bayes Rule and enables inference of causes from effect. Forward propagation, also known as causal reasoning, relies on the marginalization of joint probabilities and is the direction of propagation in the BBN–HSI. The output of a node is related to the inputs through the fundamental rule of probability (Kjaerulff and Madsen 2008:50). For instance, the relationship between the HSI node and its parent nodes is:

$$P(\mathrm{HSI},\ \mathrm{SI}_1,\ \mathrm{SI}_2,\ \mathrm{SI}_3,\ \mathrm{SI}_4) = P(\mathrm{HSI}|\mathrm{SI}_1,\ \mathrm{SI}_2,\ \mathrm{SI}_3,\ \mathrm{SI}_4)P(\mathrm{SI}_1,\ \mathrm{SI}_2,\ \mathrm{SI}_3,\ \mathrm{SI}_4) \quad (14)$$

where $P(A,\ B)$ is the joint probability, or conjunction, of random variables A and B, and $P(A \mid B)$ is the conditional probability of A given B. SI_1, SI_2, SI_3, and SI_4 are independent variables, therefore:

$$P(\mathrm{HSI},\ \mathrm{SI}_1,\ \mathrm{SI}_2,\ \mathrm{SI}_3,\ \mathrm{SI}_4) = P(\mathrm{HSI}|\mathrm{SI}_1,\ \mathrm{SI}_2,\ \mathrm{SI}_3,\ \mathrm{SI}_4)\ P(\mathrm{SI}_1)\ P(\mathrm{SI}_2)\ P(\mathrm{SI}_3)\ P(\mathrm{SI}_4) \quad (15)$$

In equation 15, the first factor is given by the node's CPT and the subsequent factors are the probability distributions of the random variables SI_1, SI_2, SI_3, and SI_4. The marginalization of the joint probability is done through the rule of total probability (Kjaerulff and Madsen 2008:41):

$$P(\mathrm{HSI} = x_\mathrm{m}) = \sum_{i=1}^{N}\sum_{j=1}^{N}\sum_{k=1}^{N}\sum_{l=1}^{N} P(\mathrm{HSI} = x_\mathrm{m}|\mathrm{SI}_1 = x_i,\ \mathrm{SI}_2 = x_j,\ \mathrm{SI}_3 = x_k,\ \mathrm{SI}_4 = x_l)$$
$$P(\mathrm{SI}_1 = x_i)P(\mathrm{SI}_2 = x_j)\ P(\mathrm{SI}_3 = x_k)\ P(\mathrm{SI}_4 = x_l) \quad \forall m \in 1,2,3,\ldots,N \quad (16)$$

where x_m is one state of the child node's N output states and x_i, x_j, x_k, and x_l, are states of the parent nodes. Equation 16 is repeated for the N states of the child node and the result is a discrete probability mass function (PMF) at the output of the HSI node.

Discretization of the input variables, step 6, was based on measurement precision. I inferred the measurement precision for each variable from Breininger (1992:18), and set the discretization to meet or exceed measurement precision (Table 1). For instance, measurements by Breininger (1992) of percent shrub layer comprised of scrub oak were to the nearest 1%, and hence, the discretized states of this habitat variable were 0, 1, 2, ..., 59, and $\geq$60. At 60%, the SI relationship for percent shrub layer comprised of scrub oak, SI_{1a}, reaches a constant value of 1 (Fig. 1).

Discretizing the intermediate and output variables, step 7, entailed an iterative trial-and-error process of searching for a discretization scheme with the smallest number of states that met specifications for acceptable numerical error (see Appendix, available online at www.onlinelibrary.wiley.com). A discretization scheme that met my error specifications had 36 unequal intervals (Table 2). I applied it to the SI relationship nodes, the selection nodes, and the output node.

In step 8, I represented uncertainty in the parameters of the HSI equation—w_1, w_2, w_3, and w_4—by treating them as random variables. For all 4 parameters, I chose the probability distribution that requires the fewest assumptions—the uniform distribution. Relative to other unimodal, closed-domain distributions, it has the largest variance over a given domain (i.e., represents the greatest uncertainty). I centered the distribution on 1 to comport with the parameter values in Burgman et al. (2001), and set its lower and upper bounds to 0 and 2, respectively. The uncertainty in w_1, w_2, w_3, and w_4 represented by these uniform distributions reflects my uncertainty and is unlikely to reflect the uncertainty of biologists with expert knowledge on Florida scrub jay habitats.

Parameterizing the CPTs, step 9, employed 3 different techniques for the 3 different types of nodes containing CPTs–SI relationships, selection functions, and the HSI node. For the SI relationships, each row of the CPT corresponded to a discrete state of the input variable and each column was 1 of the 36 unequal discretization intervals. The probabilities in each row correspond to the PMF created when a vertical slice is taken through the SI graph (Fig. 4). The CPTs for the SI relationships ranged in size from 2,196 to 4,356 cells. I generated them in Excel® (version 2007,

Table 1. Habitat variables and pairings of suitability index (SI) relationships (Burgman et al. 2001), and characteristics of input nodes for a Bayesian belief network–habitat suitability index model (Fig. 2). Sub-headings a and b refer to separate SI relationships (e.g., SI_{1a} and SI_{1b}). Within the varying domain, the slope of the SI relationship varies. Above the varying domain, the slope equals 0 and SI values equal 0 or 1. The discretization interval is applied over the varying domain and the last discretization interval in each node is an inequality that covers values above the varying domain. Square brackets denote inclusive endpoints of the domain.

	S_1		S_2		S_3		S_4	
	a	b	a	b	a	b	a	b
Variable name	% Shrub canopy is scrub oaks	Distance from scrub oak ridge	% Cover is sand or herb	Distance to ruderal area	% Pine canopy cover	Distance to forest	Mean oak scrub height	Mean palmetto scrub height
Units	%	km	%	km	%	km	m	m
Varying domain of input node	[0,60]	[0,0.6]	[0,80]	[0,0.3]	[0,70]	[0,0.6]	[0,5]	[0,5]
Complete domain of input node	[0,100]	[0,∞]	[0,100]	[0,∞]	[0,100]	[0,∞]	[0,∞]	[0,∞]
Discretization interval of input node	1	0.005	1	0.005	1	0.005	0.05	0.05
No. of intervals in input node	61	121	81	61	71	121	101	101
Selection function	Max		Max		Min		If scrub oak cover >30%, then S_{4a}, else S_{4b}	

Table 2. Discretization scheme for suitability index (SI) relationship nodes, the selection nodes, and the output node. In Netica™, the lower limit of each interval is inclusive and the upper limit is exclusive.

Interval	Lower limit	Upper limit	Width	Center (x_n)
1	0	0.00000001	0.00000001	0.000000005
2	0.00000001	0.0005	0.00049999	0.000250005
3	0.0005	0.0051	0.0046	0.0028
4	0.0051	0.0127	0.0076	0.0089
5	0.0127	0.023	0.0103	0.01785
6	0.023	0.0357	0.0127	0.02935
7	0.0357	0.0508	0.0151	0.04325
8	0.0508	0.068	0.0172	0.0594
9	0.068	0.0873	0.0193	0.07765
10	0.0873	0.1087	0.0214	0.098
11	0.1087	0.132	0.0233	0.12035
12	0.132	0.1572	0.0252	0.1446
13	0.1572	0.1843	0.0271	0.17075
14	0.1843	0.2132	0.0289	0.19875
15	0.2132	0.2438	0.0306	0.2285
16	0.2438	0.2763	0.0325	0.26005
17	0.2763	0.3104	0.0341	0.29335
18	0.3104	0.3463	0.0359	0.32835
19	0.3463	0.3838	0.0375	0.36505
20	0.3838	0.4229	0.0391	0.40335
21	0.4229	0.4637	0.0408	0.4433
22	0.4637	0.5061	0.0424	0.4849
23	0.5061	0.55	0.0439	0.52805
24	0.55	0.595	0.045	0.5725
25	0.595	0.64	0.045	0.6175
26	0.64	0.685	0.045	0.6625
27	0.685	0.73	0.045	0.7075
28	0.73	0.775	0.045	0.7525
29	0.775	0.82	0.045	0.7975
30	0.82	0.865	0.045	0.8425
31	0.865	0.91	0.045	0.8875
32	0.91	0.955	0.045	0.9325
33	0.955	0.9775	0.0225	0.96625
34	0.9775	0.98875	0.01125	0.983125
35	0.98875	0.99999999	0.01124999	0.994374995
36	0.99999999	1	0.00000001	0.999999995

Microsoft Corp., Redmond, WA) with a script written in Visual Basic.

I built deterministic CPTs for the selection functions for the max and min nodes using Netica's facility for building CPTs from equations. Each selection node contained a table consisting of 1 column and 1,296 rows (36^2).

The HSI node has 4 parent nodes with 36 states each, which results in a CPT with 1,679,616 rows. Each row contains 36 conditional probabilities, which I calculated through a Monte Carlo simulation (Law and Kelton 2000) as follows. First, I randomly generated 40,000 sets of the parameters w_1, w_2, w_3, and w_4 from the probability distributions described in step 8. Second, for each row of the CPT, I used the random parameter values and that row's unique combination of parent node states in equation 13 to calculate 40,000 HSI values. And third, I applied the 36 discretization intervals to the 40,000 HSI values to generate a PMF for that row. I implemented the Monte Carlo simulation with R statistical software (R Development Core Team 2005).

Model Demonstration

I demonstrated the BBN–HSI model's utility for representing and propagating uncertainty in 3 ways. First, I showed how the model can be used to test a null hypothesis: E[HSI] of site A $=$ E[HSI] of site B, where E[HSI] is the expected value of HSI. This was done by comparing the 2-tailed 90% confidence intervals of HSI for sites A and B. If the confidence intervals do not overlap, then the sites are significantly different at the $\alpha = 10\%$ level (Schenker and Gentleman 2001). In other words, the probability of the model producing a Type I error (rejecting the null hypothesis when it is true) is less than 10%. With respect to Type I error, this test is conservative; if the intervals overlap, the null hypothesis is accepted even though the sites may be significantly different (Schenker and Gentleman 2001). The source of variation in a site's HSI values is expert uncertainty. Therefore, significant, in this context, means that the expert is confident that E[HSI]s for site A and site B are different. I compared 13 real sites for which vegetation data were provided in Breininger (1992:18); each site supported a different habitat type. Data for distance from scrub oak ridge, distance to ruderal area, and distance to forest were not provided, and so the values for these habitat variables were set such that the selection functions selected SI_{1a}, SI_{2a}, and SI_{3a}.

Second, I demonstrated how the model's probabilistic output could be used for management decisions. A realistic

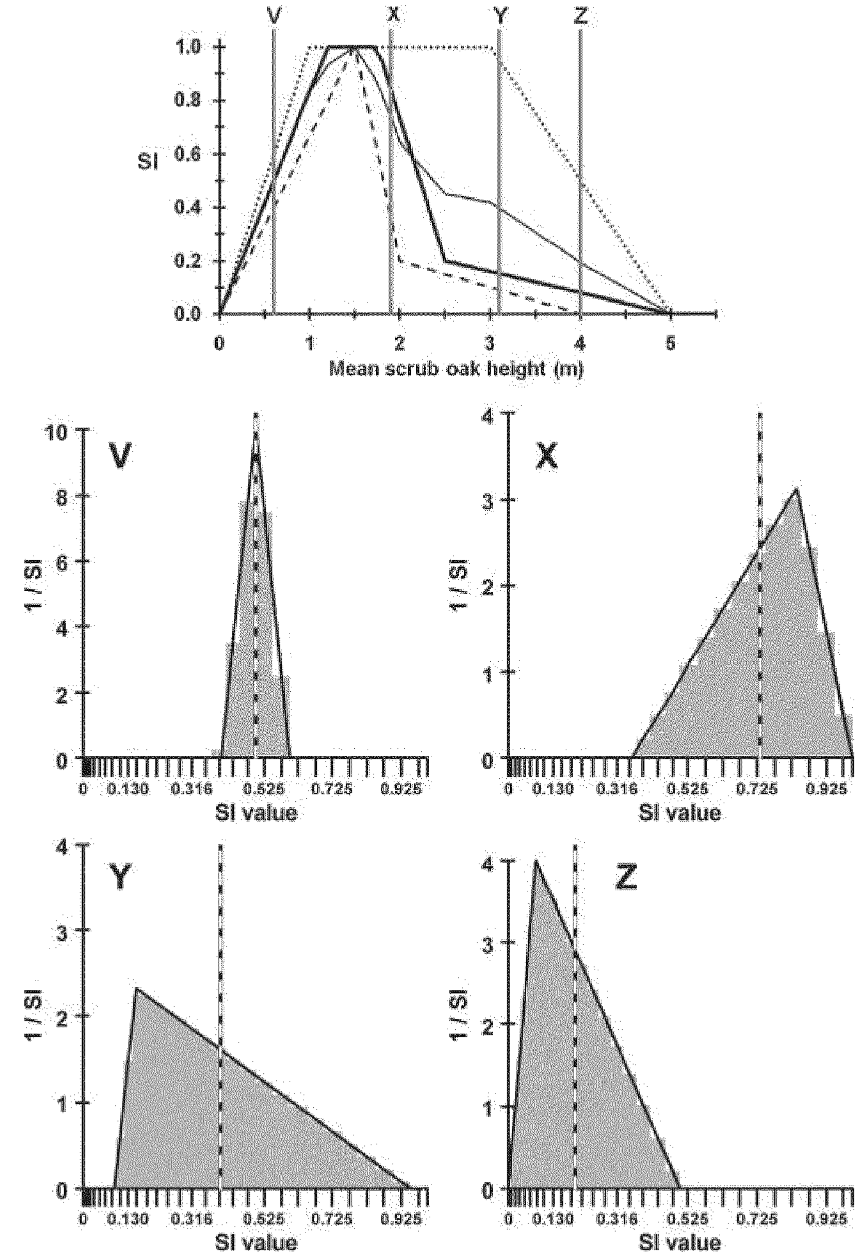

Figure 4. The suitability index (SI) relationship for mean scrub oak height (relationship SI_{4a}; top frame) from Burgman et al. (2001), and the continuous triangular distribution (black line) and discrete probability mass function (PMF; gray shading) corresponding to mean scrub oak height equal to 0.6 m (*V*), 1.9 m (*X*), 3.1 m (*Y*), and 4.0 m (*Z*). Each PMF becomes a row in the conditional probability table of node SI_{4a}. Vertical black and white dashed lines represent the expected values of continuous distributions and the PMFs. Note the 36 unequal discretization intervals on the SI-axes.

management scenario is the evaluation and selection of sites to serve as mitigation for habitats to be destroyed by impending commercial development. Managers may want to determine which available sites have the highest quality habitat or have habitat quality equal to or greater than the site to be destroyed. I applied 3 decision rules: maximin, maximax, and maximum expected value (Bunn 1984:17–19). The maximin rule guards against the worst-case scenario. A risk-averse manager seeking to select sites with high habitat suitability should select the site with largest of the worst-case HSI values. In an extremely skewed probability distribution the worst-case HSI value could have a minuscule probability ($\sim 10^{-6}$). Therefore, maximin decisions based on simply the lowest possible HSI value would be overly pessimistic. Hence, I defined the plausible worst HSI for a site as the lowest value with cumulative probability greater than 5%. The maximax rule selects the site with the largest of best-case HSI values. It is risk-seeking, and therefore, not recommended for natural resource management; however, evaluating the maximax rule provides a fuller understanding of all site options. The plausible best HSI for a site was defined as the lowest value with a cumulative probability greater than 95%. The expected value rule chooses the site with the largest expected value; it is risk neutral. I applied the decision rules to a set of dummy sites reflecting plausible values for the habitat variables.

The first 2 demonstrations ignored uncertainty in the measurement of habitat variables. The third demonstration incorporated measurement uncertainty of habitat variables, and examined its affect on the model output and consequent decisions based on that output. Uncertainty in model inputs refers to the statistical variance of each habitat variable that results from taking measurements at multiple plots within a site. Because of spatial heterogeneity of habitat conditions within a site, a habitat variable is not a single value, but a variety of values described by a mean and standard deviation and can be represented as a probability distribution. To explore the affects of uncertainty in the model inputs, for each habitat variable I created probability distributions with coefficients of variation equal to 5%, 10%, 20%, 40%, and 60%. A larger coefficient of variation corresponded to greater spatial heterogeneity. The probability distributions were approximately symmetric, unimodal beta distributions, and the expected values of the probability distributions for each habitat variable remained constant. I completed these steps for each of the 13 real sites.

RESULTS

Each type of uncertainty that I examined (SI relationships, HSI equation parameters, and measurement of habitat variables) contributed additional uncertainty to the PMF of HSI. In the scrub jay example, for the mesic disturbed habitat type and the unburned pine habitat type, the widths of the 90% confidence intervals for the BBN–HSI models with uncertainty in only the SI relationships were 46% less than the confidence interval widths for the models with uncertainty in the both SI relationships and the parameters w_1, w_2, w_3, and w_4 (Fig. 5). In addition, the widths were 83% less than the confidence interval widths for the models with uncertainty in the SI relationships, the parameters w_1, w_2, w_3, and w_4, and the 8 habitat variables. Clearly, neglecting 1 or more sources of uncertainty could result in a mischaracterization of overall uncertainty.

The BBN–HSI model can be used to determine whether HSI of separate sites or different habitat types are significantly different (Fig. 6). The 13 sites from Breininger (1992:18) exhibited a range of E[HSI] from 0.29 to 0.91. The site with the slash pine-oak habitat type had E[HSI] equal to 0.84. A deterministic HSI model would indicate that the slash pine-oak site had higher habitat suitability than 10 other sites with different habitat types. However, overlap of the 90% confidence intervals indicates that the slash pine-oak site is significantly different than only 6 of those other sites: palmetto scrub, pine savanna, pine woodland, unburned pine, shrubby pine forest, and grassy pine forest. In other words, a manager can be confident that the slash pine-oak site is higher quality than these 6 other sites because, according to the expert uncertainty represented in the BBN–HSI, the probability of Type I error is less than 10%. Likewise, the unburned pine site had smaller E[HSI] than 10 sites; however, only 4 of those sites are significantly different than the unburned pine site. For the other 6 sites, the overlap of confidence intervals indicated that these sites could have the same E[HSI] as the unburned pine site. A manager desiring a site with higher habitat suitability than the unburned pine site should select from the 4 sites that are significantly different.

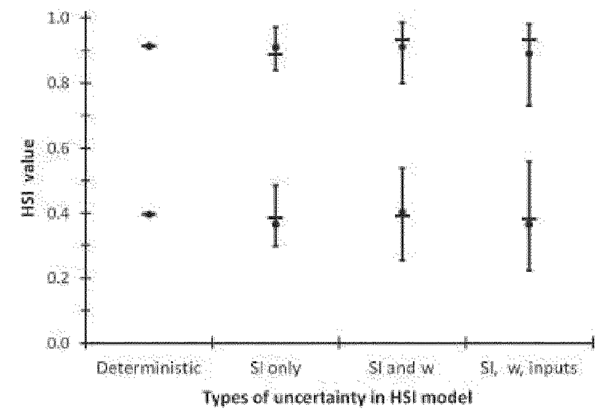

Figure 5. Contributions of different types of uncertainty to overall uncertainty at model output for 2 different habitat types. Vertical bars are the 90% confidence interval of E[HSI], the expected value of the habitat suitability index (HSI), determined from the discrete probability mass function. Filled circles are E[HSI] and short horizontal bars are modes. I present uncertainty contributions from the suitability index (SI) relationship nodes, SI_z, the parameters w_1, w_2, w_3, and w_4 (w) in the weighted geometric mean, and the input variables. Mean coefficient of variation for simulated inputs was 10%, and mean values for simulated inputs were from Breininger (1992). Upper site is mesic disturbed habitat type and the lower site is unburned pine habitat type. Deterministic outputs were calculated with certain inputs and the expected values of the suitability index relationships and weight parameters.

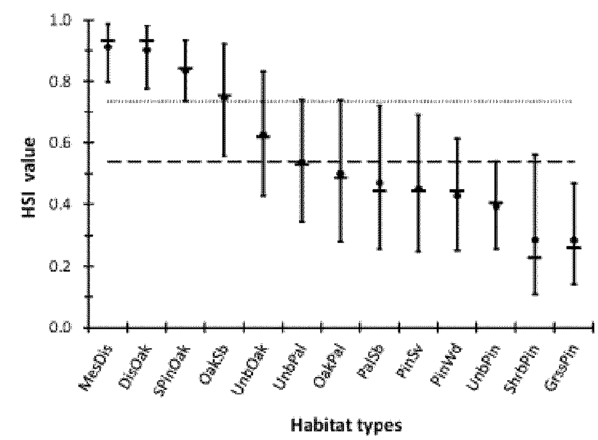

Figure 6. Demonstration of how a Bayesian belief network–habitat suitability index (HSI) model can be used to determine whether habitat suitabilities of sites are significantly different using data on Florida scrub jay habitat from Breininger (1992). Vertical bars are the 90% confidence interval of E[HSI], the expected value of HSI, determined from the discrete probability mass function. Filled circles are E[HSI] and short horizontal bars are modes. Dotted line marks the lower limit of the 90% confidence interval for slash pine-oak (SPinOak) habitat type. All habitat types with confidence intervals completely below this line are significantly different from the SPinOak type at the $\alpha = 10\%$ level. Dashed line marks the upper limit of the 90% confidence interval for the unburned pine (UnbPin) habitat type. All habitat types with confidence intervals completely above this line are significantly different from the UnbPin type. Other habitat types include mesic disturbed (MesDis), disturbed oak (DisOak), oak scrub (OakSb), unburned oak (UnbOak), unburned palmetto (UnbPal), oak-palmetto (OakPal), palmetto scrub (PalSb), pine savanna (PinSv), pine woodland (PinWd), shrubby pine forest (ShrbPin), and grassy pine forest (GrssPin).

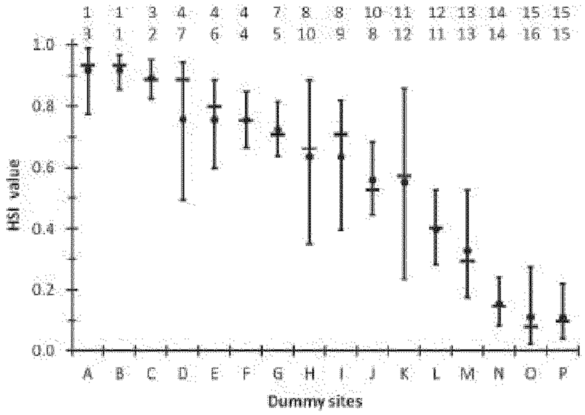

Figure 7. Hypothetical data demonstrating different decision rules that can be employed with a Bayesian belief network–habitat suitability index (HSI) model: maximum expected value and maximin. Filled circles are E[HSI], the expected value of HSI, and short horizontal bars are modes of the discrete probability mass function. Vertical bars are 90% confidence intervals, and the upper and lower limits of each interval correspond to the plausible best and plausible worst HSI values, respectively. Numbers are ranking of each site based on maximum expected value (top) and maximin (bottom).

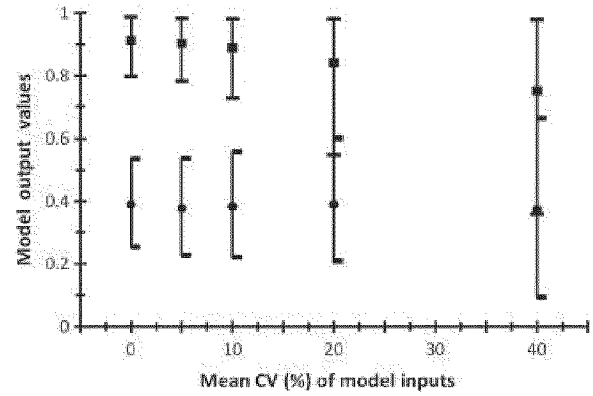

Figure 8. Effects of uncertainty in input variables on model output. As uncertainty in input variables increases, expressed as mean coefficient of variation (CV) of the 8 input variables, uncertainty at model output also increases. Sites with low habitat heterogeneity (CV = 5% and 10%) are significantly different. Two sites with greater habitat heterogeneity (CV = 20%) are not significantly different. Filled circles and squares are E[HSI], the expected value of HSI. Vertical bars are 90% confidence intervals. The upper site is mesic disturbed habitat type and the lower site is unburned pine habitat type.

Analysis of dummy sites shows why knowledge of uncertainty is essential for sound management decisions (Fig. 7). Suppose site E is to be destroyed by impending commercial development and either site D or site F can be protected as mitigation. A deterministic HSI model would indicate that habitat suitability at the 3 sites is equivalent, so all other considerations being equal, managers would be indifferent toward site D or site F. The BBN–HSI model enables a manager to assess the risk of worst-case scenarios and make risk-averse decisions by applying a maximin decision rule. The plausible worst HSI for site D is much lower than the plausible worst HSI of site F. Therefore, the risk-averse manager should select site F for mitigation. Furthermore, managers selecting site F as mitigation for the loss of site E could feel confident that adequate mitigation will be obtained because the plausible worst HSI of F is greater than that of E.

Different decision rules lead to different determinations of the best site. If site K or site L were offered as mitigation for destruction of site M, then site K is much better under a maximum expected value rule but site L is better under a maximin rule. Hence, the risk-neutral manger would select site K and the risk-averse manager site L. If one assumes a best-case scenario, then site K would be better under a maximax decision rule.

Incorporating uncertainty in input variables changes the PMF at the model output. In the scrub jay example, a mesic disturbed habitat site and an unburned pine habitat site are significantly different when the habitat conditions at both sites are completely homogeneous (mean CV = 0) or when within-site habitat heterogeneity is low (mean CV = 5% and 10%; Fig. 8). Two sites are unlikely to be significantly different for greater levels of habitat heterogeneity (mean CV = 20%). A deterministic HSI model cannot make use of the variance estimates obtained by sampling habitat variables. Hence, 2 sites with high levels of habitat heterogeneity (mean CV = 40%) would be thought to have different habitat suitability when in fact they may not. This could lead to poor decisions regarding the management of these sites.

DISCUSSION

The methods demonstrated in this paper can be applied to any HSI model for representing and propagating uncertainty. The structure of the scrub jay HSI model (Burgman et al. 2001) used to demonstrate these methods is representative of most HSI models, and the variety of mathematical operations in the scrub jay model (minimum, maximum, if-then, and the geometric mean) shows the versatility of the BBN modeling framework.

The BBN–HSI model outputs could all be generated through Monte Carlo simulation. In fact, CPTs in the scrub jay HSI–BBN model are simply tabular approximations of Monte Carlo simulations. The BBN–HSI trades the substantial computer memory required to implement it for convenience and accessibility. A BBN–HSI model is accessible to nearly all practitioners and managers. Specialized expertise is needed to construct a BBN–HSI model—in particular, the elicitation of expert knowledge and the parameterization of large CPTs. However, once the model is constructed, Netica™ or comparable software serve as user-friendly interfaces that are highly portable. Entering values for habitat variables is a simple point-and-click operation or batches of sites can be processed through input files.

I demonstrated 2 potential uses of the probabilistic output of a BBN–HSI—testing for significant differences in E[HSI] between sites and understanding the risk of worst-case habitat suitability—but there are others uses as well. For instance, managers who want to protect high sites could identify those sites most likely to be high quality sites. This could be accomplished by calculating the cumulative probability that a site's HSI value is greater than some high suitability threshold, say HSI > 0.8. Managers might also want to know which sites among a set of sites are most likely to have similar habitat suitability. The probability that 2 sites have equivalent HSI values can be estimated by the overlap of their PMFs.

This demonstration neglected 1 major form of uncertainty in HSI models—the structure of the HSI equation. This uncertainty could be incorporated in the model by expanding the Monte Carlo method used to generate the CPT of the HSI output node. Experts could construct plausible HSI equations and assign a subjective probability to each. These probabilities would reflect the expert's degree of belief that an equation is the 1 that most accurately estimates habitat suitability. The probabilities would be used to calculate a weighted arithmetic mean of the HSI values generated by each of the plausible HSI models within each iteration of the simulation process.

The proper interpretation of the model's probabilistic output is a Bayesian interpretation. That is, the probabilities represent an expert's degree of belief that a particular value is the true HSI value of a site. An expert's belief is an amalgam of direct knowledge (i.e., observations or measurements in the field) and indirect knowledge (e.g., the literature and interactions with other experts). Direct knowledge and indirect knowledge conflate both irreducible aleatory and reducible epistemic uncertainties. As the ideal expert gains knowledge, the uncertainty of his or her beliefs will converge toward purely aleatory uncertainty. In the real expert, cognitive and motivational biases affect his or her interpretation of their accumulated knowledge (Cleaves 1994) and no such convergence may occur. Hence, when using expert-based models, we should remember this caveat: such models do not represent ecological relationships; the best we can hope for is a model that accurately represents the knowledge of the experts (Garthwaite et al. 2005).

Despite their obvious shortcomings, models based on expert knowledge are often the only practical alternative when assessments of habitat quality are needed. This situation is expected to continue for the foreseeable future. Expert-based models should characterize an expert's uncertainty about his or her knowledge. I presented a modeling framework with which to incorporate expert uncertainty in HSI models, however, I avoided the more difficult task of eliciting expert uncertainty. Such avoidance is apparently endemic to natural resource management; serious attention to elicitation of expert uncertainty has received scant attention in the natural resource management literature (although see Choy et al. 2009). In contrast, engineering has recognized the importance of rigorous elicitation methods and developed a substantial body of research (e.g., Merkenhofer 1987, Kenny and von Winterfeldt 1991, Chhibber et al. 1992). Improving the reliability of expert-based models ultimately depends on enforcing more demanding standards for the elicitation of expert knowledge and uncertainty. Developing and testing such standards should be an active area of research.

MANAGEMENT IMPLICATIONS

When an outcome is uncertain and a possible outcome imposes a cost, then there is risk. The precautionary principle of natural resource management mandates a risk-averse approach to management (Gullet 1997). Therefore, managers need to be aware of risks, and for them to be fully informed, scientists must provide estimates of uncertainty. Habitat suitability index models are still used to assess the effects of forest management and environmental mitigation requirements, and yet, nearly all HSI models fail to incorporate uncertainty in their HSI estimates. Lacking information on uncertainty, managers will be unaware of the risk incurred with some management options, and make decisions that inadvertently cause the loss or degradation of wildlife habitats. Model uncertainty is often misinterpreted as lack of knowledge, however, models that report uncertainty, such as a BBN–HSI, provide information on not only the most likely outcome but also on all other possible outcomes (Steel et al. 2009). Understanding the likelihood of the full range of possible outcomes enriches a manager's understanding, thereby leading to more robust management decisions. This paper demonstrates 1 method for incorporating uncertainty in HSI models.

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