Final Report to the Muskwa-Kechika Trust Fund:

Uncertainty and Sensitivity in Habitat Suitability Models

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OVERVIEW

Since we began this work with Muskwa-Kechika seed funding in 2000, there have been several changes in the way in which wildlife suitability models are developed in British Columbia. On the positive side, there is now some recognition among those that develop the modeling tools, that consideration needs to be given to understanding the effects of variation in expert opinion, and assumptions, on the predictions of the models. In addition, there is now a much more flexible framework in which to build different assumptions about habitat-species interactions on model predictions. Concurrently, however, the thrust to simultaneously develop models that rank wildlife habitat for vast expanses of British Columbia, in particular various management zones of the Muskwa-Kechika MA, has meant basing models on less-exact PEM maps and in further automation of the mapping process. We still do not have a method to explore the effects of proposed landscape-level perturbations on spatially explicit wildlife-suitability models.

Expert opinion is frequently used to aid decision making. When species are difficult or expensive to monitor, experts' knowledge often serves as the foundation for habitat suitability models and maps produced from these models. Across British Columbia, expert-based habitat suitability models currently help guide resource planning and development. Despite the long history and wide-spread use of expert-based models, there has been little recognition or assessment of uncertainty in predictions. Between 1 December 2003 and 30 June 2004, we developed a test model for caribou using the spatial data from the Graham/Halfway PEM and the caribou Habitat Ratings model. We used this model to investigate the spatially explicit implications of acknowledging uncertainty in these wildlife habitat rating (WHR) models. Our model allowed us to examine variation for all parameters in a WHR model. We used simulations to identify the most sensitive parameters in the WHR model, the precision of ratings for a number of ecosystem units, and variation in the total area of high-quality habitats due to uncertainty in expert opinion. The greatest uncertainty in habitat ratings resulted from simulations conducted using a uniform distribution (high uncertainty) and a standard deviation calculated from the range of possible scores for the model attributes. For most ecological units, the mean score, following 1000 simulations, varied considerably from the reported value. When applied across the study area, assumed variation in expert opinion resulted in dramatic decreases in the geographic area of high- (-85%) and moderately high-quality habitats (-68%). The majority of habitat polygons could vary by up to one class (85%) with smaller percentages varying by up to two classes (9%) or retaining their original rank (7%). Results from our current simulations suggest that even simple expert-based predictive models can be sensitive to variation in opinion. The magnitude of uncertainty that is tolerable to decision making, however, will vary depending on the application of the model, which contains more details on our analyses.

Decisions makers continue to need tools to aid in landscape-level planning. Therefore, they must not only be aware of the shortcomings of the tools that they are currently using, but they must also understand the strengths and weaknesses of alternative approaches. As part of this report we explore some of the strengths and weakness of alternative methodologies for understanding the important of landscapes to wildlife species. We believe that it is important that multiple approaches continue to be explored – a process that continues to be limited by government requirements that all contracted habitat mapping use a prescribed system that many government biologists choose not to use (see Gillingham 2001).

This document is a final report for our Muskwa-Kechika Management Trust funded project. It primarily focuses on a summary of our work on the mapping of sensitivity of wildlife habitat ratings models (Johnson and Gillingham 2004), but also explores issues of error and uncertainty with other approaches to mapping wildlife-habitat use[1].

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[1] Johnson, C,J., and Gillingham, M.P. Sensitivity of predictive species distribution models to imprecise data and model design. *In Review*.

Johnson, C,J., and Gillingham, M.P. Predictive accuracy and interpretation of mapped species distribution models. *In Review*.

BACKGROUND

Due to the limited resources available for widespread, intensive population inventories, and the time frame imposed by the pre-tenure planning process, management decisions within the Muskwa-Kechika pre-tenure planning areas will continue to rely heavily on the concept of wildlife habitat suitability and preclude the use of other more detailed approaches such as resource selection functions (e.g., Boyce et al. 2001; Manly et al. 2002), and other forms of logistic regression (e.g., Massolo and Meriggi 1998) to discern between suitable and unsuitable habitats for specific species. The planning process will continue to be informed by species-specific research (e.g., Parker 2003), but development decisions at the landscape level are progressing much faster than species-specific research can continue to inform.

In using a habitat modeling approach for pre-tenure planning, however, participants in the pre-tenure planning process should be aware of the accuracy, reliability and sensitivity of current wildlife suitability approaches and models and how the specific models used in the Muskwa Kechika differ from those used in other parts of British Columbia (Resources Inventory Committee (RIC) 1999) and throughout North America. Since the early 1980's a variety of habitat-based models have been developed for use in large-scale landscape planning. The impetus for building these models was the need to develop tools for examining potential impacts of habitat manipulations on specific wildlife species – tools that did not necessarily require accurate population-based models for individual species. In these original models (United States Fish and Wildlife Service [USFWS] 1980), habitat units were used to compare the relative value of different areas at a point in time and the relative value of the same area at future points in time (USFWS 1980). Many of these models have been adapted for use in a variety of habitat types through the United States and Canada (e.g., American marten (*Martes americana*): Allen 1982; Takats et al. 1999). This approach has also been applied to a wide range of vertebrate species including species of fish and birds (Cade and Sousa 1985; Conway and Martin 1993) in addition to mammals (Gabler et al. 2000; Zeigenfuss et al. 2000; Boroski et al. 1996; Thomasma et al. 1991).

Quantitative habitat models and predictive distribution maps are now important tools for the conservation and management of animals and plants (Guisan and Zimmerman 2000; Pearce and Ferrier 2001; Raxworthy et al. 2003). The wide-spread application of these models is a function of the availability of geographic information system (GIS) data and the ready availability of computationally intensive numerical techniques. In many instances, however, decision making is often guided by expert opinion.

In its simplest form, a habitat suitability index (HSI) is an equation of an additive, multiplicative or logical form with coefficients representing the relative value of environmental features. Typically, coefficients are scaled between 0 and 1 and are estimated using best available knowledge as surveyed from experts or published literature. Depending on the definition of habitat suitability, model predictions can represent environmental carrying capacity, reflected by population density, biomass per unit area or more simply patch occupancy (e.g., Schroeder and Vangilder 1997; Oldham et al. 2000; Loukmas and Halbrook 2001). In conjunction with a GIS and data representing the spatial distribution of model inputs, HSI equations can be used to generate maps of ranked habitat units (e.g., Li et al. 2002; Store and Jokimaki 2003).

A model that poorly reflects perceived or actual conditions, however, will not only fail as an evaluation or guidance tool, but may result in misplaced resources or harmful conservation and management actions (Loiselle et al. 2003). HSI models, as an example, are ubiquitous in the management and conservation arenas yet they are infrequently validated and the criteria and approaches for validation may be questioned (Roloff and Kernohan 1999). Because expert-based approaches are typically a response to no or poor-quality data it is not surprising that HSI models are infrequently validated following conception.

An alternative to validation is uncertainty (UA) and sensitivity analyses (SA). Uncertainty analysis and sensitivity analysis allow the user to quantify the range and distribution of predictions and identify data, model structure or parameters that require improvement (Crosetto et al. 2000). Failing to quantify and understand the variation in model predictions due to uncertainty can lead to assumptions about data accuracy and output that are not valid and ultimately impact management practices and decisions (Regan et al. 2002). Variation in expert opinion, however, is often difficult to quantify. A variation of the Delphi technique is often used (e.g., Crance 1987) in which experts are polled on a series of questions; the responses are tabulated, analyzed and fed back to the experts and then the experts reanswer the questions in light of the information in the aggregate responses. This approach could seemingly be employed to also to quantify the variation on the 'value' by various users and experts alike. In order to be able to examine model sensitivity to assumptions, however, the sources of error in a model must be made explicit.

In our work, we used Monte Carlo simulations to assess the degree of uncertainty and identify sensitive parameters for habitat classifications and associated maps generated from expert opinion. We applied simulation-based uncertainty and sensitivity analyses to wildlife habitat ratings mapped for a 2400-km^2 area of British Columbia currently subject to pre-tenure planning. We focused on quantifying the magnitude and sources of uncertainty for ratings of one species during one season. Simulation results revealed the most sensitive parameters in the ratings model, the precision of wildlife habitat ratings for a number of ecosystem units, and variation in the total area of high-quality habitats due to uncertainty in expert opinion. As a tool to aid decision making, we generated a map of uncertainty in wildlife habitat ratings.

Ecosystem mapping and wildlife habitat ratings

Across B.C., ecosystem mapping (EM) is the most current source of ecological and habitat information for resource development planning. Maps portray large-scale (1:20,000-1:50,000) ecological units developed within a hierarchical framework of climate, topography, vegetation, and soil attributes (PEM Data Committee 2000). For each ecosystem mapping area, project proponents identify important wildlife species and biologists, often under contract, develop relative habitat ratings for ecosystem units according to expert opinion, limited field investigations, and existing literature describing habitat relationships. Ratings tables are then used to assign and summarize index scores for the model attributes that identify ecosystem mapping ecological units. Scores range from 0 to1 and serve as a relative index of an attributes contribution to the value of an ecosystem unit as seasonal habitat for a particular species; when combined, scores serve as an overall Resource Suitability Index (RSI). Resource Suitability Indices are similar to HSI except the former accommodates a greater range of potential environmental attributes. There have, however, been few efforts to determine the degree of uncertainty in ecosystem unit designations or wildlife habitat ratings.

There is no standard for combining index scores; however, a linear multiplicative model is common. As the final step in the habitat rating process, index scores are classified for mapping purposes; typically, a six-, four-, or two-class scheme is used. Ecosystem mapping polygons potentially represent three ecological units where the percent area of each unit is specified as a decile. When mapping habitat rating classes, one can choose to represent the average score, the highest score irrespective of decile, or the score that occupies the greatest percentage of the polygon.

Uncertainty and sensitivity analysis

Typically, uncertainty analysis is conducted as a simulation, where one runs a model multiple times and recalculates the predicted outcome for each systematic perturbation of the input variables. Input can vary in many ways, but is usually sampled from a distribution of values with known properties. Following the simulation, the variation in outcomes indicates the level of uncertainty in model predictions one might expect given a known or assumed distribution of scores for the input data. Uncertainty analyses allow us to consider all sources of uncertainty simultaneously and determine if the model and input data reliably support the decision process. Sensitivity analysis works in the opposite direction, revealing model components or data with the greatest influence on the variation in predictions. A range of statistical techniques (e.g., linear regression, correlation analyses, sensitivity indices, etc.) are available for performing sensitivity analysis (Saltelli et al. 2000). Although uncertainty analysis is more prominent in the field of GIS-based modeling, uncertainty analysis and sensitivity analysis are complementary approaches that provide support for model predictions and highlight areas where assumptions need to be addressed and source data improved or augmented (Crosetto and Tarantola 2001).

MODELING APPROACH

Ecological mapping and associated wildlife habitat ratings assisted a planning process designed to minimize the impacts of oil and gas exploration on 11 regionally and provincially significant wildlife species (EBA Engineering 2002a). The ecosystem mapping project was conducted between February 2000 and March 2002 for four geographically distinct planning areas that covered approximately 1.2 million ha of the Muskwa-Kechika Management Area (MKMA; EBA Engineering 2002a). Ecosystem units range in elevation from 420 m across valley bottoms to a maximum elevation of 2840 m across alpine areas. A wide variety of forested, wetland, nonforested, and alpine vegetation communities are found across the study area (EBA Engineering 2002a). For mapping and wildlife habitat ratings purposes, the Biogeoclimatic Ecosystem Classification (BEC) system was used to hierarchically stratify vegetation associations according to progressively finer scales of climate, soils, and site conditions (Meidinger and Pojar 1991). Four BEC zones, the coarsest unit of ecological stratification, occurred across the planning area. In our work we focused our analyses on the ratings for woodland caribou (*Rangifer tarandus caribou*) habitat during the spring season.

Uncertainty and sensitivity analyses

We used a Monte Carlo simulation to perform uncertainty analysis and sensitivity analysis for wildlife habitat ratings from a sample of ecological units found across the MKMA ecosystem mapping. We selected three units representing low, mid, and high RSI scores for each of the four BEC zones found across the study area. Attributes defining that model included BEC, site series, structural stage, and site modifier (EBA Consulting 2002b; Equation 1). In a hierarchical fashion, BEC represents a multi-ecosystem-unit description of climate, site and soil conditions; site series describes climax vegetation for a particular ecosystem unit; structural stage represents the successional stage of the ecosystem unit; and site modifier describes atypical occurrences of the site series with respect to variation in topography, moisture, soil, and soil characteristics (PEM Data Committee 2000).

$$\mathbf{RSI_{caribou/spring} = BEC \times Site\ Series \times Structural\ Stage \times Site\ Modifier} \qquad \text{(Equation 1)}$$

Perturbations introduced during a Monte Carlo uncertainty analysis should represent the range of reasonable assumptions about the nature of uncertainty expected from the model or source data. Those assumptions are explicitly defined by a statistical probability distribution from which the source data are sampled. The analyst must choose the appropriate distribution and define parameters such as the mean and standard deviation that shape the distribution. For this project, only a single score was reported for each attribute in a ratings table. The wildlife habitat rating process did not allow an evaluation or provide an estimate of divergence in expert opinion. Therefore, we could not empirically define the distribution of index scores or the variance in scores. As an estimate, we used the index score reported for each ecological unit to define the hypothetical mean value of the distribution of scores. To cover the possible range of opinions from which index scores may have occurred, we performed the uncertainty analysis using two probability distributions and three different calculations of variation in ratings.

For each of the 12 ecological units subjected to uncertainty analysis, we sampled scores for the Monte Carlo simulations from a triangular and uniform distribution. A triangular distribution is defined by a minimum, mid, and maximum value with sampled index scores having a higher probability of selection as they approach the mid score. The uniform distribution is defined by the minimum and maximum extent with all scores between those two points having an equal probability of being sampled. The parameters for each distribution were taken from the reported data. The midpoint for the triangular distribution was the reported score and the extents of both distributions were calculated as ±1 standard deviation from the midpoint. Standard deviations were calculated in one of three ways for each RSI model attribute: from the range of scores contained within a ratings table; from the ratings for the attribute across all ecological units; and from the ratings for the attribute across ecological units found within each of the four BEC zones. In the latter case, the value of the standard deviation was specific to BEC zone, whereas in the former two cases the standard deviation was calculated from and applied across all zones. Johnson and Gillingham (2004) report on the details of the approaches to quantifying and exploring uncertainty and sensitivity in wildlife habitat ratings.

We also constructed a simulation program (Visual Basic) to produce analyses of the change in the area and ranking of habitats resulting from uncertainty in estimates. The first component of this model allowed us to rigorously check all polygon estimates against those supplied by the actual caribou model (EBA Consulting 2002b; Figure 1). The model then enabled us to run sensitivity analyses on a range of options for model calculations (Figure 2). For each of the 4736 polygons found across the most southern planning area, the Visual Basic

Figure 1. Screen capture of the query interface of our Visual Basic model for woodland caribou in spring, which enabled us to check our simulation model against the model developed for the pre-tenure planning process.

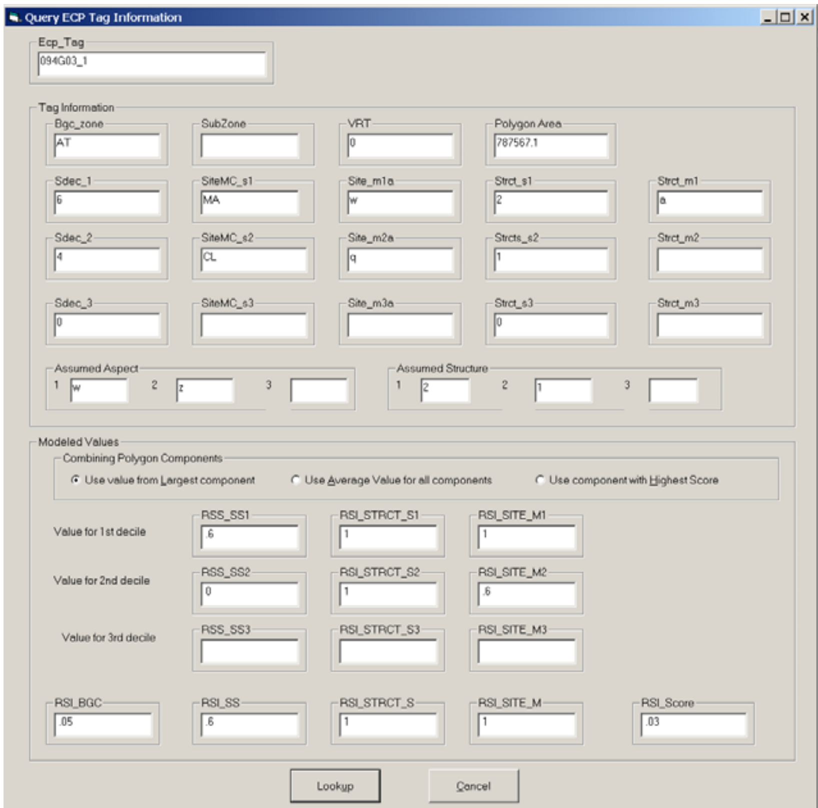
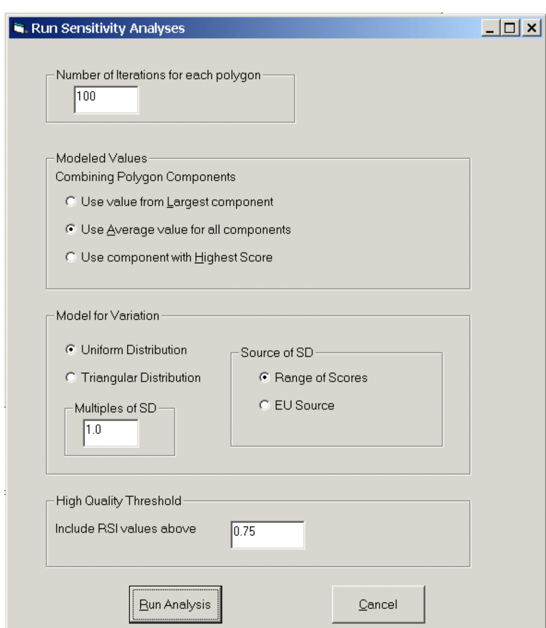


Figure 2. Screen capture of the simulation interface of our Visual Basic model for woodland caribou in spring, which enabled us to simulate methods of combining polygon components, to specify types of variation, and to set thresholds for high-quality habitat.



program simulated 100 RSI scores and estimated the variation in area of moderate- and high-quality habitat across model runs and the potential range of ratings for each polygon (mean ±1 standard deviation). Area of habitats and ratings overlap was considered in the context of a six-class wildlife habitat ratings scheme. For simulation parameters, we looked to the first set of uncertainty analysis and used the combination of distribution and standard deviation that generated the smallest and largest levels of uncertainty. Because ecosystem mapping polygons potentially represent three ecological units, we performed the uncertainty analysis considering the average and the largest RSI score as well as the decile with the greatest area.

RESULTS

Mean RSI scores summarized from 1000 Monte Carlo simulations for 12 sample ecological units demonstrated considerable divergence from the expert scores (Figure 3). In general, uncertainty was greatest for simulations conducted using a uniform distribution and a standard deviation defined by the range of possible scores for the model attribute. Alternatively, we observed the smallest variance for simulations conducted with a triangular distribution and a standard deviation defined by the observed scores within each BEC zone. The initial expert's attribute score influenced the magnitude of uncertainty and the mean simulated score. Typically, ecological units with scores near 1 were consistently biased toward 0 (Figure 3).

The introduction of uncertainty in expert opinion led to variation in the ranking and geographic area of polygons falling within one of the six habitat classes. Across all permutations, a uniform distribution with a RSI defined by the largest decile resulted in the greatest uncertainty in polygon rating. Using a six-class rating system, the mean RSI score ±1 standard deviation indicated that 4007 polygons could vary by one wildlife habitat rating class and 407 polygons could vary by two classes (Table 1). Results were less extreme for the triangular distribution where 1877 polygons varied by one rating class.

The method of incorporating RSI scores across deciles did not have a large influence on variation in the total amount of high- and moderately high-quality habitats (Table 2; Figure 4A). In contrast, the introduction of uncertainty in expert opinion resulted in dramatic changes in the percentage area of class 1 and 2 habitats. Relative to the area of habitats calculated using the unperturbed model, we observed an 85 and 68% reduction in high- and moderately high-quality habitats after introducing uniformly distributed uncertainty averaged across deciles (Table 2;

Figure 3. Uncertainty in estimates of resource suitability indices (●) for three ecological units found within the Alpine Tundra, Spruce Willow Birch, Boreal White and Black Spruce, and Engelmann Spruce Subalpine Fir Biogeoclimatic Ecosystem Classification Zones. A Monte Carlo simulation was used to estimate uncertainty given a triangular (▲) and uniform (■) distribution of estimates and variances calculated from the range of possible scores for the model attribute (□), observed scores across all BEC zones (■), and observed scores within each zone (■).

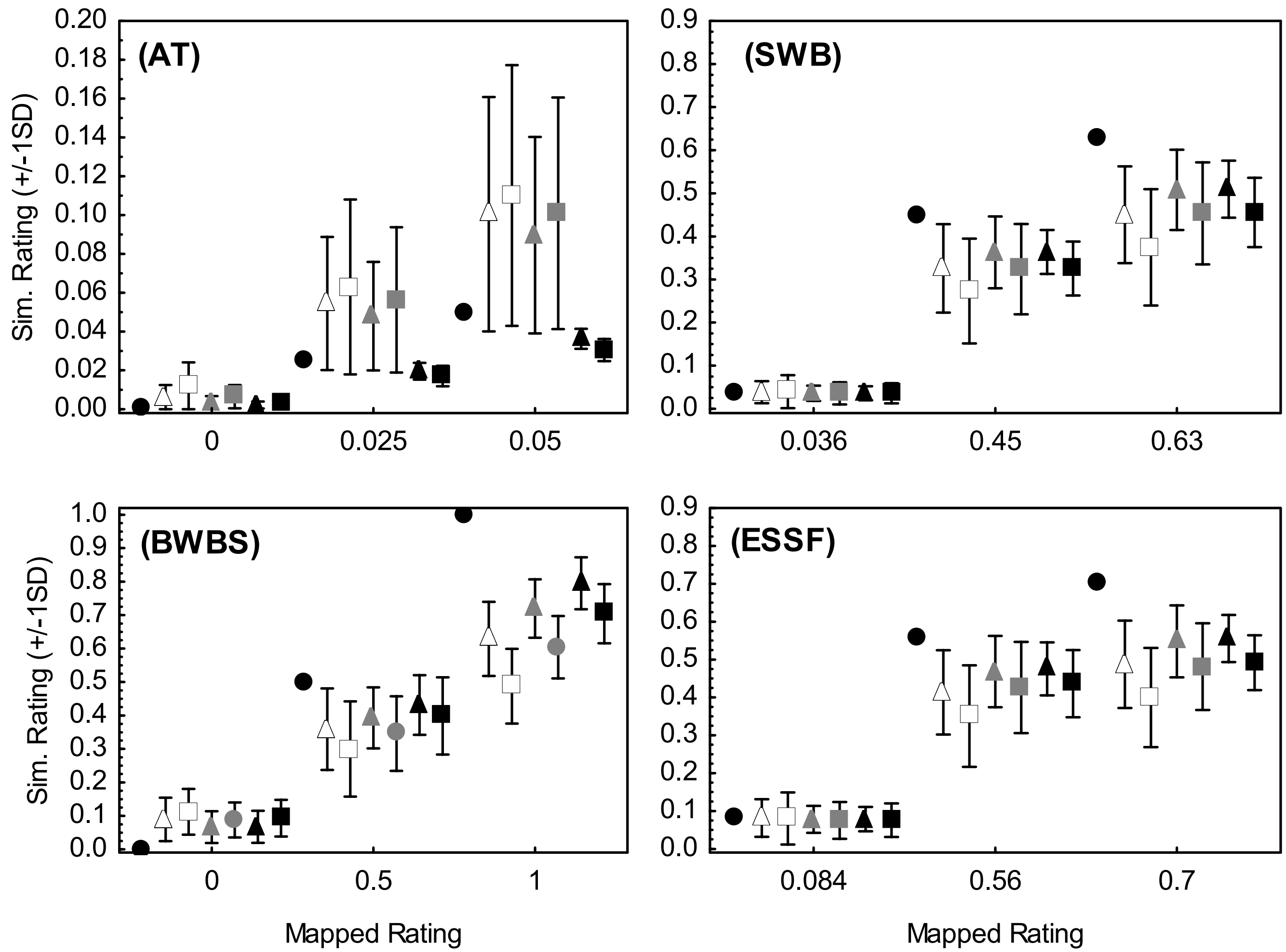


Table 1. Number of habitat polygons with a sufficient level of uncertainty to fall within one or more adjacent rating classes. Uncertainty in expert opinion was represented by two distributions (Uniform, Triangular) and three methods for combing polygon deciles: the weighted average RSI score across deciles, the score from the largest decile, and the highest score from among the three deciles. For each polygon we used the mean RSI score ±1 standard deviation to determine overlap with adjacent rating classes.

Class Overlap	**Average RSI Score**		**Largest Decile**		**Largest RSI Score**	
	Uni Dist	Tri Dist	Uni Dist	Tri Dist	Uni Dist	Tri Dist
0	559	3040	322	2859	330	2929
1	3873	1696	4007	1877	4009	1807
2	304	0	407	0	397	0

Table 2. Variation in area (km^2) of high- and moderately high-quality habitat due to simulated uncertainty in expert opinion. Uncertainty was represented with uniform (Uni) and triangular (Tri) distributions and three methods for combining polygon deciles: the weighted average RSI score across deciles (Average), the score from the largest decile (Largest), and the highest score from among the three deciles (Highest).

Polygon scores calculated by combining deciles according to:	Area	SD Area	Minimum Area	Maximum Area	% Change
Average Score					
No Uncertainty	39.3	–	–	–	–
Uniform Distribution	5.8	2.6	1.0	12.1	-85.2
Triangular Distribution	32.6	4.0	22.8	44.2	-16.9
Largest Decile					
No Uncertainty	37.2	–	–	–	–
Uniform Distribution	7.8	3.0	2.2	19.5	-78.9
Triangular Distribution	33.7	4.3	24.3	42.2	-9.4
Highest Score					
No Uncertainty	45.3	–	–	–	–
Uniform Distribution	8.8	3.1	2.9	19.1	-80.6
Triangular Distribution	40.9	5.2	29.1	53.5	-9.7

Figure 4. Wildlife habitat ratings for the most southern planning unit of the Muskwa-Kechika Management Area, northeastern British Columbia (A) and simulated variation in ratings given uncertainty in expert opinion (B). Maps were constructed using the largest decile for each habitat polygon and simulated scores were draw from a uniform distribution with a standard deviation defined by the range of possible scores for each model attribute.

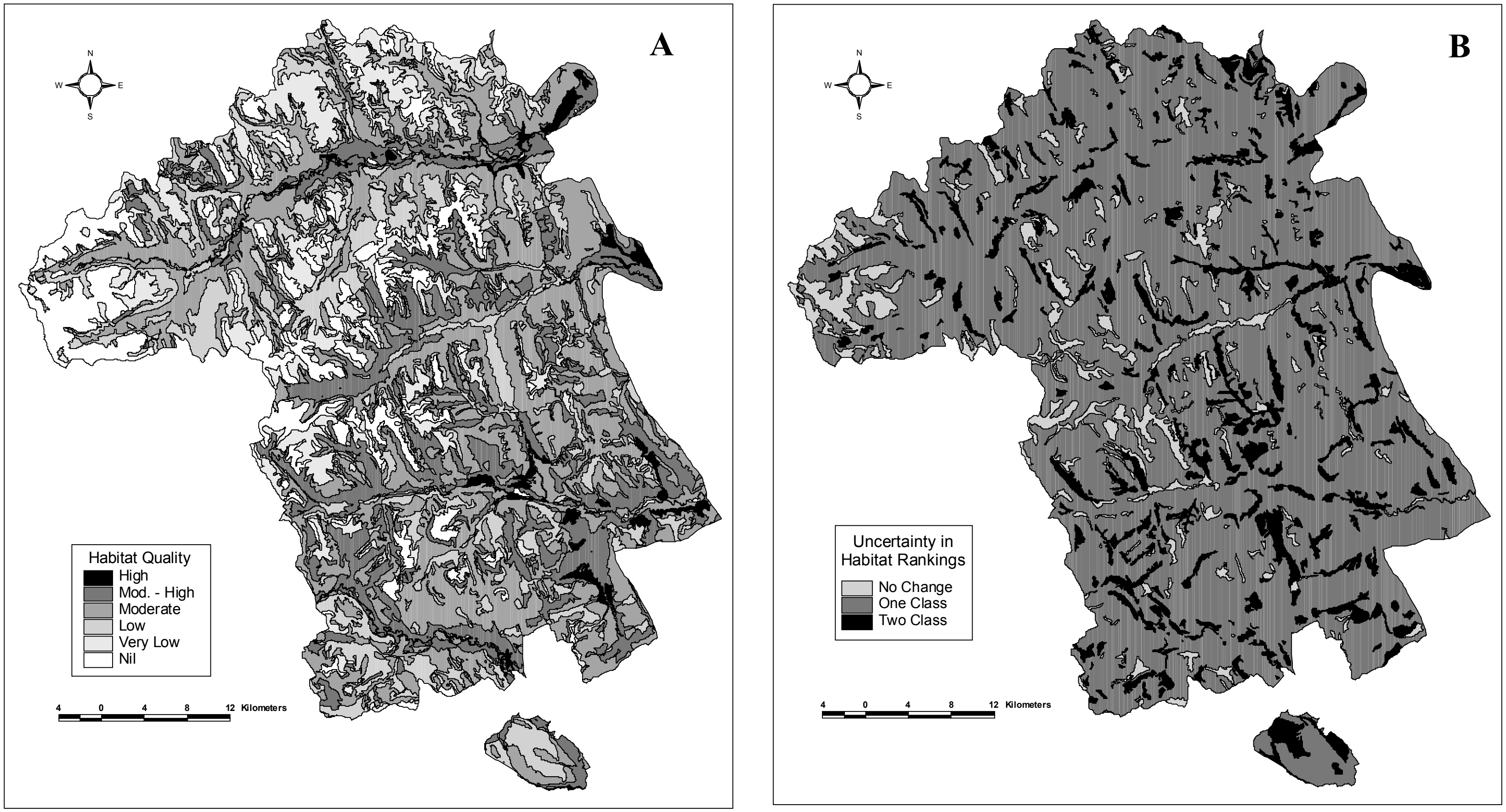


Figure 4B). Results were less extreme following application of the triangular distribution: area of class 1 and 2 habitats differed by 17 and 32%, respectively, when compared to the RSI habitat ratings for the published model (Table 2).

DISCUSSION

Wildlife Habitat Ratings Models

Expert opinion is an important source of information for conservation and resource management decision making. In contrast to the inferences from specific empirically-based research studies, experts can provide a synthesis perspective drawing on their own observations and those presented as published data. Costs of monitoring wide-ranging or rare species also can be time consuming and prohibitively expensive (Johnson et al. 2002). In some cases, we have only the knowledge from experts to guide conservation and management initiatives (Pearce et al. 2001). Furthermore, conservation biology is a crisis discipline. Initiatives designed to halt the decline, extirpation or extinction of a species often cannot wait for the development, funding, implementation, and conclusion of empirically-based research or monitoring studies.

The lack of uncertainty analysis and sensitivity analysis for expert-based models may partially be a function of how expert opinion is solicited. Inherent within a Monte Carlo or other simulation approach is an estimate of variability in model parameters, in this case, stemming from differences in expert opinion. If only one expert is consulted or a process is used that builds consensus among experts without recording differences, we must assume the shape and type of probability distribution. For our analyses, only point estimates were reported for each model parameter for each ecological unit. Lack of measured variation forced us to assume a range of plausible distributions. Uncertainty and sensitivity analysis are more realistic and defensible when simulated values are drawn from distributions defined by a sample of repeated observation. In most cases, however, it is unlikely that enough experts would be available for identifying the frequency distribution of opinions on any one question. Nonparametric bootstrapping is an alternative to Monte Carlo simulations where statistical parameters are difficult to identify (Efron and Tibshirani 1993). Researchers have championed the iterative and interactive modified Delphi approach as an approach for soliciting and defining levels of agreement between experts (Uhmann et al. 2001, Hess and King 2002). We are uncertain, however, if divergence in opinion should be considered after the first or last round of expert consultation.

In situations where uncertainty in expert opinion cannot be quantified we encourage researchers to test a range of possible uncertainties. Repeating analyses for a full range of plausible distributions reveals the sensitivity of the uncertainty analysis to underlying statistical parameters. For each ecological unit, we calculated the standard deviation in index scores three ways and applied that parameter to two statistical distributions. Our choice of methods was a function of the available data. We assumed that the variance in expert opinion and thus uncertainty increased with the range of possible scores for each attribute and the diversity of ecological units across BEC zones. Selection of distribution was largely arbitrary; however, our guiding criterion was distributions constrained to generate values between 0 and 1. A triangular distribution is more conservative and assumes that expert opinion is centred on the reported score. Alternatively, a uniform distribution assumes that we have no assurances that the reported rating is correct and that scores from multiple experts could range freely within the bounds set for the index score.

In the case of ecosystem mapping wildlife habitat ratings, we question the metrics against which RSI index scores are assigned. Past HSI projects have developed functional relationships between model variables and the life-history of the focal species (e.g., Prosser and Brooks 1998, Uhman et al. 2001). Shrub height, for example, might be included as a model component because it provides security cover or nesting habitat. Biogeoclimatic ecosystem classification, site series, structural stage, and site modifier may be useful for identifying plant associations, but they only serve as vague proxies for factors that dictate the distribution and population dynamics of caribou. Published habitat studies can guide with the identification of ecologically relevant RSI variables.

Results of our work suggest that variation in expert opinion can have dramatic effects on model predictions and ultimately conservation and management actions. Assuming that variation in expert opinion was uniformly distributed, we recorded a maximum 85% reduction in the area of high-quality habitat. Differences were less extreme using the triangular distribution, but still notable. Uncertainty and sensitivity analysis are rarely applied to habitat suitability models; however, in agreement with our findings Bender et al. (1996) reported high uncertainty and overlapping confidence intervals for an HSI of forest types occupied by gray squirrel (*Sciurus carolinensis*). They assumed static HSI values and instead considered uncertainty in ecological inputs. A logical extension of their simulations would have been a sensitivity analysis to identify input parameters with the strongest impact on model uncertainty. Such post hoc analyses are essential for model and data improvement. For our ecosystem unit analyses, BEC and site series were the most influential parameters. Collapsing the number of BEC and site series classes, would reduce variation in index scores and model uncertainty.

Study-wide uncertainty analysis suggest that in the absence of uncertainty, experts consistently over estimated the area of high-quality habitats (Table 2). Apparent bias is an artifact of the truncated range of possible scores, 0 – 1, and the multiplicative model. A low value for any one of the four constituent variables (BEC, site series, structural stage, site modifier) dictates the final RSI and a maximum value of 1 prevents the inclusion of a compensatory score. Given the extreme sensitivity of the final RSI to just one low score, results suggest that wildlife habitat ratings for high-quality habitats are potentially underrepresented. Furthermore, the probability of misclassification will increase with model complexity (i.e., the number of variables). Combining scores with a geometric mean would reduce the overall influence of a single low value, but continue to render a polygon unsuitable if an ecological condition necessary for animal occupancy was not satisfied.

Uncertainty in RSI scores revealed that following a six-class rating system most habitat polygons could degrade or improve in ranking by one class. Regardless of distribution or method of combining decile, relatively few habitat polygons maintained their initial ranking following the inclusion of uncertainty. Magnitude of development impact and conservation objectives for the focal species will determine the significance of a one- or two-class change in ranking.

Alternative Approaches

The success of model-based planning will be best informed by several approaches using as much area-specific data as are available. Models that predict species distribution are an important tool for understanding ecological processes and patterns and for guiding the conservation and management of plants and animals (Raxworthy et al. 2003). Once an effective model is identified, results provide a measure of the importance of ecological variables that correlate with species distribution and in some cases abundance (Boyce and McDonald 1999, Treves et al. 2004). Because model results can be applied to digital spatial data to produce maps representing the likelihood of species occurrence (Carroll et al. 2001), they are useful tools to inform resource planning. The absolute or relative likelihood of occurrence then serves as a metric to rank habitats for conservation initiatives such as habitat restoration, enhancement or protection (Johnson et al. 2004).

Numerous approaches are available for predicting and mapping species occurrence and important habitats. Quantitative techniques range from the suite of generalized linear models to rule-based methods (Guisan and Zimmermann 2000). Although there are many types of distribution models, most are dependent on two sources of data: an unbiased and precise sample of species locations and an accurate sampling or maps of environmental data that correlate with species distribution. Depending on the species, ecologically plausible variables could represent vegetation, soil parameters, topography, human disturbance, and inter-specific interactions (Manly et al. 2002).

Arbitrary decisions during the modeling process, and error and bias in requisite data, can reduce predictive power or lead to incorrect inferences and maps of species distribution and important habitats (Elith et al. 2002). A model that poorly reflects actual species-environment relationships will not enlighten our understanding of ecological processes and patterns and might result in misplaced resources or harmful conservation and management actions (Loiselle et al. 2003). Although modelers and practitioners often are aware of potential sources of error, bias, and variation during model construction and use, sources of uncertainty have largely been ignored on the grounds that appropriate evaluation techniques do not exist (Openshaw 1989). This is an incorrect assumption. In the case of species distribution models, researchers have evaluated and discussed the predictive performance of a number of models (Pearce and Ferrier 2000, Manel et al. 2001, Boyce et al. 2002, Loiselle et al. 2003); the sensitivity, uncertainty, and efficacy of expert-based approaches (Pearce et al. 2001, Clevenger et al. 2002, Dettki et al. 2003, Johnson and Gillingham 2004); model performance relative to factors of scale, natural variation, and model design (Karl et al. 2000, Gutzwiller and Barrow 2001, Seoane et al. 2004); and the influences of error and bias in geographic information system (GIS) data (Stoms et al. 1992, Frair et al. 2004, Gu and Swihart 2004). Although we have witnessed a recent surge in the use and evaluation of species distribution models and requisite data, we are unaware of any work that provides a comprehensive comparison of the relative sensitivity of model predictions to multiple sources of bias and error and alteration in model design.

We performed a sensitivity analysis for one type of species distribution model, a resource selection function (RSF), that is formulated using logistic regression (Manly et al. 2002) and is widely use for mapping habitat selection by vertebrates. Using these sensitivity analyses we can make several broad recommendations[1]. First, the interpretations of RSF species distribution models can be confounded by error and bias in the dependent and independent variables and differences in model design. Conclusions are most sensitive to the strict interpretation of coefficients when compared to prediction success and categorical maps of habitat quality. Second, assuming that inherent error and bias in our data had a linear effect on coefficient values, we suggest that species location error should be of concern when it approaches 200 m, efforts should be undertaken to rectify sampling bias when it exceeds a total location loss across all habitats of 35%, and thematic misclassification in maps may affect model outcomes following a 10% reduction of area for highly selected types. Recommendations are slightly more liberal if model results are used to map and rank habitats, but interactions between the various sensitivity factors could lead to much more severe impacts on the conclusions of such studies. Uncertainty inherent to model selection, non-representative sampling of study subjects, and positional error in resource maps are other factors that could further threaten the precision and accuracy of predictions.

We could find few examples of species distribution studies reporting the sensitivity of model data and uncertainty around predictions (but, see Stoms et al. 1992, Buckland and Elston 1993, Lindenmayer et al. 1995, Loiselle et al. 2003, Johnson et al. 2004). Although less onerous, most researchers also fail to evaluate and report anticipated or measured error and bias in species locations and maps or the implications of model choice. Our results confirm the recommendations of others: researchers should evaluate and report the data from which models are constructed, rectify the most sensitive sources, and conclude with an uncertainty analysis to determine the range of potential results (Burgman et al. 2001, Elith et al. 2002, Regan et al. 2002). Sensitivity and uncertainty analyses are essential if models are to

[1] Details of this work, can be found in Johnson, C,J., and Gillingham, M.P. Sensitivity of predictive species distribution models to imprecise data and model design. *In Review*.

enlighten our understanding of ecological processes and patterns or to provide useful guidance for management and conservation decision making.

How well do habitat suitability index models perform compared to other methods of mapping habitat value? In a final set of comparisons[1], we used empirical data for woodland caribou to examine four species-distribution models: a qualitative habitat suitability index (like those used in the MK pre-tenure planning process), a quantitative resource selection function, Mahalanobis distance model (a multivariate dissimilarity statistic), and an ecological niche model. Relative to the three quantitative models, the habitat suitability index was a poor predictor of caribou distribution during early winter (the season that we evaluated). Specifically, the model was ineffective at identifying high-quality (class 1) habitats. We assume that the poor correspondence with the validation data was a function of the bench marking procedure designed to rank habitats across the study area in relation to the best woodland caribou habitat in the province (Madrone Consultants, 1999a). Such an approach allows planners and managers to assess the value of habitats among individual mapping projects, but it fails to recognize the relative significance of habitats within populations. By contrast, the quantitative approaches that we explored were specific to the data used to build the models and may generalize poorly to other populations, time periods, or portions of a study area where animal locations are unavailable (Hobbs and Hanley, 1990; Knick and Rotenberry, 1998; Johnson et al. 2004).

CONCLUSIONS

There is evidence to suggest that, at some scales of management, expert-based habitat models are inferior to those developed using empirical data and statistical approaches (Pearce et al. 2001). Although debate around the relative value of each system continues, formalized expert opinion will remain an important information source for some conservation and management problems (Johnson et al. 2004). Our emphasis was not the comparison of empirical and expert-based models. Regardless of how coefficients are generated, model evaluation should be an integral component of the process. Evaluation may include validation relative to some criteria, such as successful prediction, but would benefit greatly from uncertainty analysis and sensitivity analysis (Fielding and Bell 1997). Even where models are considered accurate, uncertainty

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[1] For details see: Johnson, C,J., and Gillingham, M.P. Predictive accuracy and interpretation of mapped species distribution models. *In Review*.

analysis and sensitivity analysis can reveal situations under which prediction may be unreliable, aid with the identification and visualization of quantitative bounds for potential model outcomes, and identify flaws in model structure or areas of improvement for input data. Framing results of modeling exercises in the context of uncertainty analysis and sensitivity analysis is crucial to understanding the reliability of wildlife habitat models. These analyses, however, can only be done theoretically without some basis for the variability surrounding the opinions of the experts used to develop the models. Therefore, we suggest that all model parameters estimated by experts should be accompanied by an estimate of error associated with these individual predictions. Ideally this would be based on canvassing multiple experts for each parameter, but at the very least should consist of a single expert identifying the error likely associated with each prediction.

RECOMMENDATIONS

Based on our work we offer the following recommendations:

1. Tremendous effort has gone into the BEC, whether based on TEM or PEM information – we need to make the most of those data, but we also need to recognize their limitations with respect to understanding vertebrate distributions. Models based on just vegetation maps lack mechanistic relationships and should be treated with extreme caution when they are used to make spatially explicit predictions of habitat use.
2. No landscape is static, particularly one under industrial development. WHR models are static and, therefore, need to be continually updated. Ideally, managers need these types of models to help *interactively* plan disturbances/perturbations. For example, if a road is build into a drainage then the value of the habitat for a species changes. Future efforts should be focused towards using these models as interactive, scenario-planning tools, rather than to make landscape-level decisions on models that do not include planned and cumulative effects.
3. There is no perfect model, but our confidence increases when different approaches lead us to the same conclusions. The current requirement that all contracted wildlife habitat rating models in BC must follow a single standard stifles this approach.

Moreover, the 'required' process is not adequate nor does it adequately capture, or portray, the uncertainty upon which they are based in the final products. Parallel and alternative approaches need to continue to be developed and approaches need to be thoroughly evaluated (including peer-reviewed) before they become standards on which long-term land-management decisions are based.

4. A model should only be applied and evaluated if it has ecological relevance, the requisite data are available and reliable, and neither the data nor model violates statistical or ecological assumptions (Austin, 2002). Once these criteria have been satisfied and the model constructed, numerous techniques are available for measuring the accuracy of predictions (Fielding and Bell, 1997; Manel et al. 2001) – this latter step must be taken to gain any confidence in the predictions of the model.
5. Sensitivity and uncertainty analyses are a second level of investigation that can reveal the range of possible predictions and guide the improvement of model performance (Elith et al. 2002). Numerous models might need to be employed before satisfactory results are achieved.
6. Regardless of whether the model is based on qualitative or quantitative information, individuals developing the models must include information about the range of uncertainty surrounding every model input. Without such information the consequences of the uncertainty cannot be evaluated relative to the model predictions.

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