

Bayesian networks for habitat suitability modeling: a potential tool for conservation planning with scarce resources

NARUEMON TANTIPISANUH,^{1,3} GEORGE A. GALE,¹ AND CARMEL POLLINO²

¹*Conservation Ecology Program, School of Bioresources and Technology, King Mongkut's University of Technology Thonburi, Bangkok 10150 Thailand*

²*CSIRO Land and Water, Canberra, Australian Capital Territory 2601 Australia*

Abstract. Bayesian networks (BN) have been increasingly used for habitat suitability modeling of threatened species due to their potential to construct robust models with limited survey data. However, previous applications of this approach have only occurred in countries where human and budget resources are highly available, but the highest concentrations of threatened vertebrates globally are located in the tropics where resources are much more limited. We assessed the effectiveness of Bayesian networks in generating habitat suitability models in Thailand, a biodiversity-rich country where the knowledge base is typically sparse for a wide range of threatened species. The Bayesian network approach was used to generate habitat suitability maps for 52 threatened vertebrate species in Thailand, using a range of evidence types, from relatively well-documented species with good local knowledge to poorly documented species, with few local experts. Published information and expert knowledge were used to define habitat requirements. Focal species were categorized into 22 groups based on known habitat preferences, and then habitat suitability models were constructed with outcomes represented spatially. Models had a consistent structure with three major components: potential habitat, known range, and threat level. Model classification sensitivity was tested using presence-only field data for 21 species. Habitat models for 12 species were relatively sensitive (>70% congruency between observed and predicted locations), three were moderately congruent, and six were poor. Classification sensitivity tended to be high for bird models and moderate for mammals, whereas sensitivity for reptiles was low, presumably reflecting the relatively poor knowledge base for reptiles in the region. Bayesian network models show significant potential for biodiversity-rich regions with scarce resources, although they require further refinement and testing. It is possible that one detailed ecological study is sufficient to develop a model with reasonable sensitivity, but BN models for species groups with no quantitative data continue to be problematic.

Key words: *Bayesian network models; Chitra; conservation planning; habitat suitability mapping; hairy-nosed otter; Lutra sumatrana; protected areas; striped narrow-headed softshell turtle; Thailand; threatened vertebrate species.*

INTRODUCTION

Protected areas are used worldwide to conserve biodiversity by managing threats within their boundaries (Bruner et al. 2001, Andam et al. 2008). However, protected areas are often biased, favoring selected habitats, leaving many communities and species unprotected. To increase representation of protected area systems, comprehensive information about species occurrence is needed. This information can be retrieved from habitat suitability maps, indicating areas of different probabilities of occurrence. Several methods have been developed to produce habitat suitability models (Guisan and Zimmermann 2000, Elith et al. 2006). All have been applied for producing habitat suitability models for a broad range of species (e.g.,

Wilting et al. 2010, Jennings and Veron 2011, Jenks et al. 2012). However, many of these methods require extensive survey data to obtain meaningful results. This is a major limitation, especially in countries with limited resources for data collection. This problem is exacerbated by the rarity of threatened species, such that survey data are often scarce, even when resources are available.

One method that can be used to create habitat suitability maps with limited data is Bayesian networks, BN (Noon et al. 2008). BN models are graphical models showing probabilistic relationships between variables (Heckerman 1996). The models have a graphical structure and are often constructed to support decision making (Cain 2001). This method can incorporate various sources of knowledge including survey data, expert opinion, and information from literature reviews (Uusitalo 2007), and can be used for generating habitat suitability maps where data sets are small or incomplete (Myllymaki et al. 2002). BN models have been applied

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³ E-mail: ttpisanu@gmail.com

previously to predict habitat suitability for several species including amphibians and mammals (e.g., Smith et al. 2007a, Wilson et al. 2008). Smith et al. (2007a) used such models to generate habitat suitability maps of an endangered mammal, given alternative management scenarios. Wilson et al. (2008) used a combination of statistical and BN methods to predict occurrence of four amphibian species in streams with incomplete habitat information.

Although the effectiveness of BN in habitat modeling has now been demonstrated in several studies (Marcot et al. 2001, Raphael et al. 2001, Smith et al. 2007a, Wilson et al. 2008, Chen and Pollino 2012), all were conducted in countries where a number of experts familiar with the focal species, as well as budgets for conducting surveys, are available. However, globally threatened vertebrates are concentrated in tropical countries (Myers et al. 2000, Grenyer et al. 2006), where resources devoted to biodiversity management are scarce, resulting in very limited knowledge for most threatened species (e.g., Rowley et al. 2010, Tantipisanuh and Gale 2013). Therefore, it is critical to test BN models under conditions typically found in many tropical countries.

Thailand signed the Convention on Biological Diversity in 1992, and has set up broad goals and strategies for wildlife conservation, including an extensive network of protected areas. However, budgets and human resources devoted to scientific management or conducting surveys of threatened species within these areas are particularly limited: approximately US\$5 million in 2013. This represents ~2% of the total budget of the Department of National Parks, Wildlife and Plant Conservation, the primary agency responsible for wildlife management (Chula Unisearch 2013). Given the encroachment of development across Thailand, especially in habitats outside the current protected area system, the suitability of remaining habitat is declining. A number of threatened species in the country are still underrepresented in protected areas, and the availability of information regarding habitat use varies greatly among species (Tantipisanuh and Gale 2013).

This paper assesses the effectiveness of BN methods in generating habitat suitability models, using Thailand as a case study. Here our aim was to identify areas of potentially suitable habitat for target species. The BNs were used to create habitat suitability maps for several terrestrial vertebrates, including amphibians, reptiles, birds, and mammals, at a landscape level. The outputs were evaluated using field survey data. BN models for two species and maps of suitability probability of four species from four vertebrate taxa are presented in detail.

METHODS

Background to Bayesian networks

Model structure.—BN models are directed acyclic graphs consisting of two elements: “nodes” and “arcs” (Cain 2001); see Appendix A. Nodes are elements

representing variables in the system that can be either discrete or continuous. Arcs are arrows representing causal relationships between nodes. Arcs originate from the “cause” node (referred to as a “parent node”) and terminate at the “effect” node (“child node”). Each node has at least two “states” representing values, or a range of values, that a node can possess. These values can be defined qualitatively or quantitatively.

Model probability.—BNs have two forms of probability: marginal (unconditional) and conditional probabilities (Pollino et al. 2007). Parentless nodes are described by marginal probabilities (e.g., “distance to river” and “human activity” nodes in Appendix A), which can be obtained by populating GIS layers in the BN model. A conditional probability is the probability of the state of each child node, given the states of its parent variables (Cain 2001). The conditional probability is recorded as a table (conditional probability table or CPT) within each child node.

Model probabilities are defined during model parameterization. The probabilities in the CPT can be defined using several approaches, e.g., data from field surveys, values obtained from equations, or expert opinion (Woodberry et al. 2004). All approaches indicated here can be used separately or in combination to derive conditional probabilities (Pollino et al. 2007). Bayesian algorithms allow opinions from experts to provide an initial estimate of marginal and conditional probabilities. Model probability can be updated subsequently to better fit the data, when additional data become available, using various methods, e.g., expectation maximization algorithms, learning gradient analysis, and probability fading (Dempster et al. 1977, Bauer et al. 1995, Marcot et al. 2006).

Spatial data can also be interfaced with models such that marginal probabilities of parentless nodes can be derived from spatial data (e.g., Smith et al. 2007a). The probability of the outcome node from a BN model can then be visualized as a map using GIS software (e.g., Raphael et al. 2001, Smith et al. 2007a, Chen and Pollino 2012).

Model evaluation.—Several aspects of BN models can be evaluated (Marcot et al. 2006, Pollino et al. 2007). Accuracy of model predictions can be assessed by comparing the predicted node state with actual survey data. Model structure can be evaluated by asking experts to review whether model structures reasonably represent a particular environment or whether a model’s behavior is consistent with their current understanding of a system (Marcot et al. 2006). Model sensitivity analysis is used to measure sensitivity of changes in probability of child nodes when parent nodes and the CPT are changed (Pollino et al. 2007). Output from the analysis can identify sensitive nodes for the node of interest by ranking nodes according to their relative importance to the node of interest.

Description of study area

Thailand includes two biogeographical subregions: Indochinese and Sundaic. The land area is 513 115 km², with elevations ranging from sea level to 2565 m. Thailand is usually classified into six geographical regions: North, Northeast, West, Central, East, and South (Peninsula); see the map of Thailand in Appendix B. The North and West are mainly mountainous, divided by four major rivers that drain into the Central region of marshy alluvial plains, extending to the Gulf of Thailand; the Northeast is an upland plateau, typically with dry, poor soils; the South (Peninsula) has a mountain spine extending along the west as a backbone of this region (Lekagul and Round 1991). Main natural habitats include terrestrial forest (deciduous, evergreen, pine, swamp), mangrove forest, and freshwater wetlands. The climate is influenced by tropical monsoons, resulting in distinct wet and dry seasons. Most of Thailand has rain from May to October, and a dry climate from November to April. The Peninsula and the extreme southeastern provinces also receive more rain from the northeast monsoon, during November and January (Lekagul and Round 1991).

From 1980 to 2009, land use in Thailand underwent significant changes. Land Development Department (LDD) data indicate urban areas dramatically increased (from 0.5% to 4.7%), along with agricultural areas and water sources (e.g., reservoirs) (from 46% to 53% and from 0.8% to 2.7%, respectively), while forest areas were reduced from 42% to 35% of total area (data available online).⁴ These changes have threatened the survival of several species. Their potential habitats have been reduced both in size (from urban expansion and deforestation) and quality (forest fragmentation and water pollution) (Pattananavibool and Dearden 2002, Cheevaporn and Menasveta 2003), while animals themselves have been illegally hunted and traded for several reasons (e.g., food, traditional Chinese medicine, pets) (Shepherd and Nijman 2008, Oswell 2010), resulting in reductions in both species richness and abundance.

As of 2010, there were 426 protected areas in Thailand: 58 wildlife sanctuaries, 123 national parks, 113 forest parks, 60 non-hunting areas, 16 botanical gardens, and 56 arboreta. These areas cover 103 810 km² of Thailand (~20%). However, coverage of protected areas is skewed toward higher elevations, and most of these are located inside a limited subset of forest types (Tantipisanuh and Gale 2013).

Previously, we have identified 229 terrestrial vertebrate species that are globally near-threatened or threatened and also underrepresented by Thailand's protected area system (Tantipisanuh and Gale 2013). From this list, we chose species that are heavily and moderately underrepresented, and selected 52 of these to focus on for modeling (see the list of species in Appendix

C). Habitat utilizations of these focal species were reviewed, and focal species that use similar habitat types and have similar distribution ranges were classified into common habitat groupings for each of the four vertebrate classes, resulting in 22 groupings (see Appendix D). One habitat suitability model was constructed for each group.

Spatial layers and model development

We used ArcGIS 9.3 (ESRI 2008) to prepare spatial layers: six forest types (evergreen, mixed deciduous, dry dipterocarp, peat swamp, mangrove, secondary), salt flat, sandbar, beach, grassland, wetland/marsh/swamp, reservoir, lake/pool/pond, stream/river, paddy field, agriculture, aquaculture, elevation, slope, and human footprint index (HFI). Habitat spatial layers were derived from a land use map produced in 2000, provided by the Department of National Parks, Wildlife and Plant Conservation (DNP) and the land use map prepared in 2008/2009 provided by LDD. Elevation data were downloaded from the Earth Remote Sensing Data Analysis Center (available online).⁵ HFI was developed by the Socioeconomic Data and Applications Center of Columbia University (WCS and CIESIN 2005; data available online).⁶

Bayesian network models were developed using the methods of Smith et al. (2007a). Habitat models were created using Netica software version 4.02 (Norsys, Vancouver, British Columbia, Canada). Model development followed four steps: (1) literature review, (2) model development, (3) model evaluation, and (4) visualization of outcomes (see the process diagram in Appendix E).

Step 1: Literature review.—Habitat utilization (habitat categories), distribution range by region and elevational use, and known threats to each focal species were reviewed using local peer-reviewed journals (e.g., *Journal of Wildlife in Thailand*, *Natural History Journal of Chulalongkorn University*), international literature, field guides, IUCN Red List data (available online),⁷ and BirdLife International data (available online).⁸ Literature was reviewed from 90 sources. The number of sources used for each species varied from 2–3 sources per species for amphibians, 3–11 (median = 6 sources) for reptiles, 3–12 (median = 6) for birds, and 8–16 (median = 11) for mammals. Amphibians and reptiles were the least studied; consequently, models developed for these were the simplest.

Step 2: Model development.—

1. *Model structure.*—Habitat suitability models were composed of three components: potential habitat, known range, and threat level (Fig. 1), with outcomes

⁵ <http://www.jspacesystems.or.jp/ersdac/GDEM/E/>

⁶ <http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic>

⁷ <http://www.iucnredlist.org/>

⁸ <http://www.birdlife.org/datazone/home>

⁴ <http://www.ddd.go.th/Ldd/>

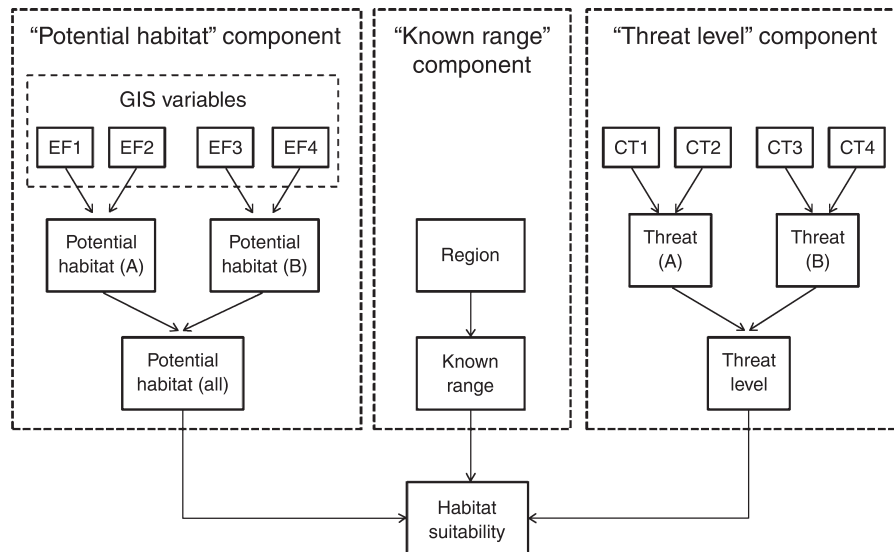


FIG. 1. Conceptual structure of our habitat suitability models. The models consist of three main components: potential habitat, known range (optional) and threat level. EF represents environmental factors, which include habitat types and elevation ranges where species are currently (or used to be) distributed or have a high probability of occurring. Environmental factors are grouped into each potential habitat group (here, A or B) according to their characteristics. All potential habitat groups are combined into one potential habitat (all). Region is the region of Thailand where species were distributed, are currently distributed, or have a high chance of being distributed. CT is the cause of the threat that may negatively impact target species survival. Threat causes are linked with each threat group (here, A or B) resulting from these causes. All threats are combined to determine the threat level.

of these merged to determine habitat suitability. Habitat suitability is a relatively common metric for habitat modeling (e.g., Brotons et al. 2004, Catullo et al. 2008) and was chosen here due to the relatively scant knowledge of the focal species in which more informative data such as abundance, reproductive success, or survival was almost always unavailable. All nodes mentioned in this publication are described in Appendix F. The rationale for the structure of the Bayesian network was that firstly, we restricted the range of the suitable habitat based on the species' known geographical ranges. Then within this known range, we identified from the literature potential habitats that species were likely to utilize or have a chance to utilize. Then within these potential habitats, we identified the level of suitability based on an anthropogenic threat level index (i.e., human footprint index, HFI).

For the "Potential habitat" component, habitat types and elevation ranges (referred to here as environmental factors) that focal species have used historically, or have potential to occur in currently, were included. These habitat types were grouped into four main categories: forest, non-forest, human-dominated, and freshwater. All categories were then linked to form the "Potential habitat (all)" node (see Fig. 2). Environmental factors included in the models of each focal species are listed in Appendix D.

For the "Known range" component, the known distribution range of a species was considered. The node was connected with the "Regional" node used as a surrogate for landscape context (e.g., climate, geology).

However, this component was optional. If information about species distribution range was unavailable, this component was omitted.

For "Threat level," known threats across species were identified from the literature. In total, five threats were identified (habitat loss/degradation, hunting/poaching, accidental killing, food depletion, and interspecific competition). Spatial data were not available at the local/site scale, so we used "human footprint index" (HFI) as a surrogate for threats. HFI is an evaluation of human influence on the land surface based on human population density, land transformation, human access, and electrical power infrastructure (Sanderson et al. 2002). HFI ranges from 0 to 100, with higher scores indicating greater human influence.

1. *Model probabilities.*—For each species, probability of habitat being suitable was parameterized based on information obtained from the literature and expert opinion. Probabilities were assigned as follows.

Initially, probabilities were set according to information from literature. Where it was known that a species uses a habitat (Y, yes), probability of suitability was set to 100%; where the species is likely to use a habitat (P, possibly), the probability of suitability was 70%; and where habitat was known to be unsuitable (N, no), the probability was 0%.

Probabilities derived using the literature were then adjusted based on expert review. Experts were asked via a questionnaire to determine if a given habitat was suitable, likely, or unsuitable for a given species. Expert input was combined with literature information, and

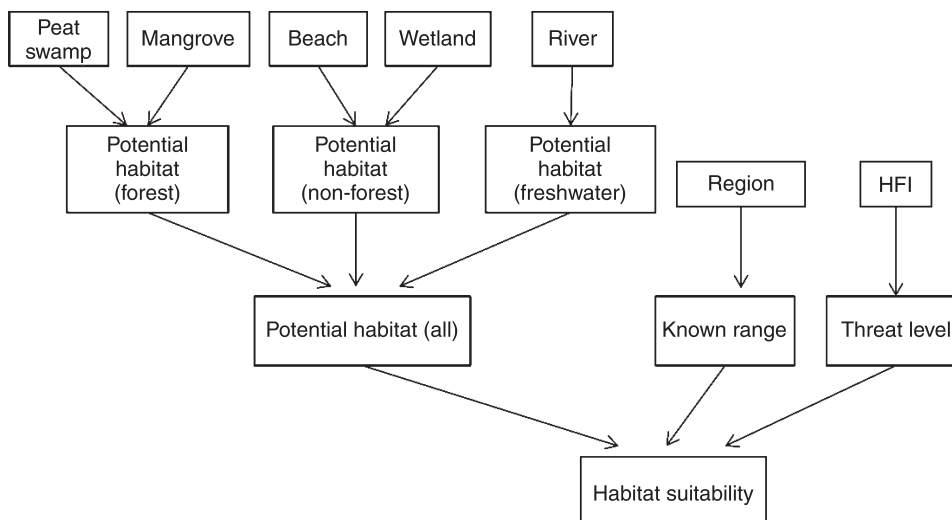


FIG. 2. Bayesian Network model structure of habitat suitability for the hairy-nosed otter (*Lutra sumatrana*). HFI is the human footprint index (following Sanderson et al. 2002).

weighted by the number of experts requesting that change. The adjusted probability was calculated following Eq. 1:

$$\text{Adjusted probability} = \text{prior probability} + \frac{\sum \Delta}{n(\text{experts})} \quad (1)$$

where the prior probability is the probability obtained from the literature review, Δ is the value added when the state of suitability changed based on each expert's opinion, and $n(\text{experts})$ is the total number of experts reviewing particular species. When the state of suitability changed in a positive direction (from N to P/Y or from P to Y), Δ was +40%. If change occurred in the opposite direction, Δ was -40%.

For "Threat level," this component was described using "HFI." Threat level was considered low when HFI was less than 35%, medium when between 35 and 70%, and high when HFI was >70%. Choice of these thresholds is arbitrary, but can be adjusted when new information becomes available.

The "Habitat suitability" node is a combination of "potential habitat," "known range," and "threat level" components. The CPT (conditional probability table) of this node is shown in Appendix G. The probability is used to describe the likelihood of being in each of the states. Final probability was visualized as an output to GIS.

Step 3: Model evaluation.—Model evaluation was conducted by expert review, an accuracy assessment using actual field data, and sensitivity analysis.

For the expert review, 15 experts were asked to review model structures and nodes (see numbers of experts for each species in Table 1). Model structure and the CPTs were revised based on this expert opinion, as described previously. Additional literature was also identified by experts. Experts sometimes added information about

habitat types or elevational ranges that was not published in the literature. All of their opinions pointed the same direction (i.e., there was no disagreement among observers in these cases).

For model accuracy, because only presence data were available, only one form of classification accuracy, "sensitivity," could be measured, whereas "specificity" could not be evaluated (Fielding and Bell 1997). Species presence data were obtained from three sources: data owners (S. Nimnuan, S. Thong-aree, and P. D. Round), local publications (*Journal of Wildlife in Thailand* and *Natural History Journal of Chulalongkorn University*), and published species maps (manually digitized). In total, there were 980 data points representing presence locations for 40 species. For some species there were fewer than 10 data points available for assessment, which we deemed too few for model evaluation. Therefore, only 21 species from 10 models were assessed for accuracy.

Model classification sensitivity was assessed by comparing the spatial overlap between predicted grid cells that had probabilities of suitability greater than 70% with field observation points. We used chi-square tests to compare our observed classification sensitivity with an expected random distribution of suitable habitat from our model based on the number of observed field points and the total number of suitable pixels generated for the entire country. For example, if species A was observed at 100 locations, and our model estimated that 10% of Thailand was expected to be suitable habitat, then we would expect at random 10 of the 100 observed locations would fall into "suitable" habitat by chance. We then compared the percentage of this expected distribution (in this example, 10%) with the number of observed pixels classified as suitable by our model.

TABLE 1. Bayesian network model classification sensitivity for 21 focal species in three model groups (R, two reptiles; B, 15 birds; and M, four mammals) sorted from lowest to highest model accuracies.

Model group	Species	Total points	Points with $p \geq 70\%$	Classification sensitivity (%)	P , not random	Most sensitive factors	References	Experts
M02	banded langur	15	0	0	1	potential forest	10	2
R02	big-headed turtle	44	0	0	1	N/A	10	1
R01	striped narrow-headed softshell turtle	10	3	30	0.2105	sandbar	6	1
B08	Chinese Egret	43	14	33	<0.001	region	6	5
M01	smooth-coated otter	40	14	35	<0.001	potential elevation	16	2
M01	small-clawed otter	45	18	40	<0.001	lake close to forest edge	12	2
B06	Spot-billed Pelican	44	24	55	0.0302	wetland, beach	7	5
B06	Painted Stork	54	33	61	0.0018	wetland, beach, salt flat	11	5
B08	Asian Dowitcher	91	63	69	<0.001	estuary	10	6
M01	hairy-nosed otter	11	8	73	<0.001	region	9	2
B08	Great Knot	25	23	92	<0.001	region	8	6
B08	Spotted Greenshank	96	90	94	<0.001	coastal wetland	10	7
B05	Asian Golden Weaver	23	22	96	<0.001	wetland	5	6
B08	Black-tailed Godwit	47	45	96	<0.001	potential elevation	12	6
B10	Spoon-billed Sandpiper	29	28	97	<0.001	N/A	10	6
B08	Eurasian Curlew	75	73	97	<0.001	region	11	6
B03	Hume's Pheasant	39	38	97	<0.001	N/A	9	9
B08	Oriental Darter	40	39	98	<0.001	HFI	5	6
B06	Greater Spotted Eagle	12	12	100	<0.001	potential freshwater	8	7
B04	Yellow-breasted Bunting	22	22	100	<0.001	potential elevation	5	8
B08	Black-headed Ibis	43	43	100	<0.001	potential elevation	8	5

Notes: "Total points" represents the number of confirmed locations used to assess the classification sensitivity for each species. Points with $p \geq 70\%$ are those assessed by the model as having at least 70% probability of being suitable habitat. " P , not random" indicates P values from chi-square tests comparing our observed classification sensitivity with an expected random distribution of suitable habitat based on the number of observed field points and the total number of suitable pixels generated by each model for the entire country. The "most sensitive factors" are factors most sensitive for a given species model, as obtained from sensitivity analysis. "References" indicates the number of publications reviewed to produce the Bayesian network models. "Experts" is the number of researchers/specialists who reviewed the Bayesian network models.

To assess the relative effects of different input variables on model outputs, sensitivity analyses were performed to identify the "sensitive" node of each model. This was done using the "Sensitivity to Findings" function in Netica. This function calculates entropy reduction for discrete/categorical nodes and variance reduction for continuous nodes (Korb and Nicholson 2004). The higher the reduction, the greater the relative importance of the particular node toward the node of interest. If sensitivity of the model indicated unexpected behavior (e.g., the node that was assumed to be very important was less sensitive than another node assumed to be of limited importance), the model was revised (back to step 2).

Step 4: Visualization.—We adopted methods from Smith et al. (2007a) to produce suitable habitat maps. A map composed of 25-ha square grid cells covering Thailand was overlaid with habitat layers to extract the values of environmental factors represented in BN models. The attribute table of the grid layer was used to create a "case file" (set of observations showing parentless node variables) which was used as input data for processing all BN models. The "Process Cases" function in Netica was used to obtain the probability of habitat suitability for each grid cell. The outputs were

joined back to the attribute table of the grid layer and mapped.

We categorized habitat suitability results from the models into three categories: low, medium, and high suitability. Areas with probability of suitability lower than 35% were assigned as less suitable, between 35% and 70% were assigned as medium, and more than 70% were assigned as highly suitable.

RESULTS

Based on different levels of knowledge available for a given species, BN models obtained here were classified into two types: (1) complicated models for species with a good knowledge base, and (2) simple models for species with a poor knowledge base. Among the 21 species for which models were evaluated, we found that 12 species had relatively high classification sensitivity (>70% of observation points correctly classified), three birds had moderate sensitivity (50–70% correct), one reptile, one bird, and two mammals had low sensitivity (30–50%), and for two species (one reptile and one mammal), none of the observation points was correctly classified (Table 1). Of the 21 species, 18 had classifications significantly different than expected by random chance ($P < 0.05$) (Table 1).

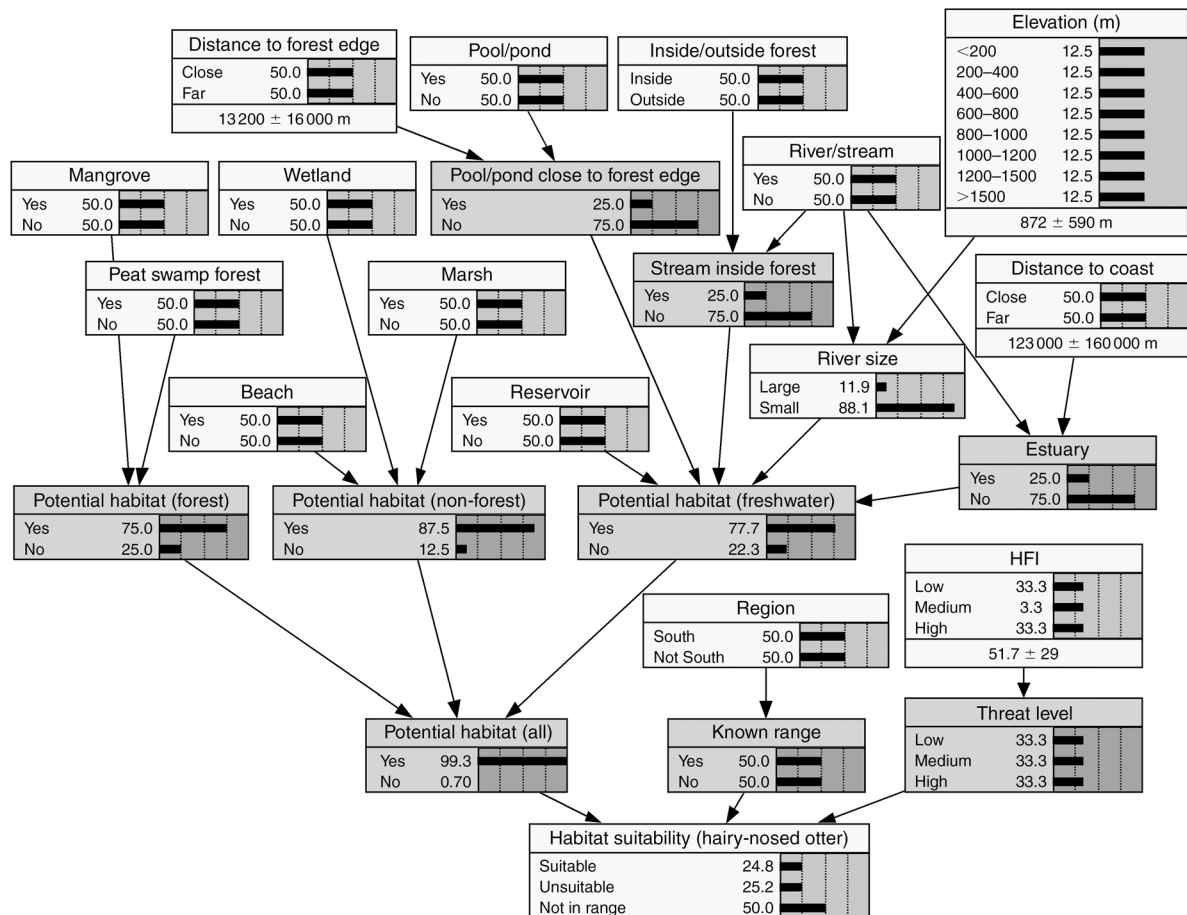


FIG. 3. The revised model structure for hairy-nosed otter (*Lutra sumatrana*) showing model states; the bar graphs represent the probabilities (as percentages) of being in a given state. Panels that are entirely gray-shaded are the nodes where states are defined as deterministic. For elevation, distance to forest edge, distance to coast, and HFI, the values at the bottom of the panels are means with 95% confidence intervals.

Habitat suitability models of two focal species, the endangered hairy-nosed otter (*Lutra sumatrana*) and the critically endangered striped narrow-headed softshell turtle (*Chitra chitra*), will be shown in detail as examples of models with high and low knowledge bases, respectively.

Example 1, Hairy-nosed otter

Step 1: Literature review.—In total, nine publications were reviewed, including both national and international publications highlighting results of surveys in Thailand and other neighboring countries. From the review, this species utilizes several habitat types, both forest and non-forest. These otters are found in melaleuca forest, peat swamp forest, and mangrove forest, and also found along the Andaman coast and rivers, wetlands, and freshwater swamps; but not in paddy fields (Thongaree et al. 1999, Kanchanasaka 2001, Kanchanasaka et al. 2003, Nabhitabhata and Chan-ard 2005, Kanchanasaka 2008). Their distribution range is limited to just southern

Thailand (Kanchanasaka et al. 2003). Threats to hairy-nosed otter include deforestation, habitat alteration, hunting for trade, and conflict with humans (Kanchanasaka et al. 2003, Francis 2008).

Step 2: Model development.—The first draft of the BN model was built based on information obtained from the literature. The structure of the model is shown in Fig. 2. Prior probabilities in the CPT of the potential habitat nodes (an aggregate of habitat types) were defined as being 100%. These were modified, where relevant, using expert opinion.

Step 3: Model evaluation.—The resulting model obtained from the second step was sent to two experts: one from Thailand and another from the IUCN Otter Specialist Group. Both experts recommended more literature to be reviewed, and suggested other experts. After reviewing more literature, the model structure was adjusted by including additional habitat variables to the freshwater habitat (Fig. 3).



PLATE 1. (Top) Spoon-billed Sandpiper (*Eurynorrhynchus pygmeus*) at the Khok Kham district, Samut Sakhorn province, Thailand, on the morning of 19 January 2013. The bird was feeding in a dry salt pan, walking toward the photographer. (Bottom) Spoon-billed Sandpiper engaging in a brief territorial dispute with a Red-necked Stint (*Calidris ruficollis*). Photo credits: Khemthong Tonsakulrungruang.

In total, 11 survey points manually digitized from published maps (Kanchanasaka 2008) were used to evaluate model classification sensitivity. Among these, eight points fell within grid cells with a suitable probability greater than 70%, which translated into 73% classification sensitivity. The moderately good sensitivity of our hairy-nosed otter model was probably due to two primary reasons. First, the knowledge base to support building the model was relatively extensive because otters, in general, are well studied compared to many other threatened species (Tantipisanuh and Gale 2013). Second, and probably most important, the hairy-nosed otter appears to be highly restricted in its range in

Thailand to relatively obvious geographic features, unlike the more wide-ranging generalist otters. For example, our model of small-clawed otter (*Aonyx cinerea*), was comparatively weak, with <40% sensitivity (Segurado and Araujo 2004, Evangelista et al. 2008).

From the sensitivity analysis of the input variables, “region” was the variable that had the most influence on habitat suitability (Table 1).

Step 4: Visualization.—The habitat suitability map is shown in Fig. 4a. Areas with high probability of suitability comprise ~1% of the area of Thailand (5873 km²).

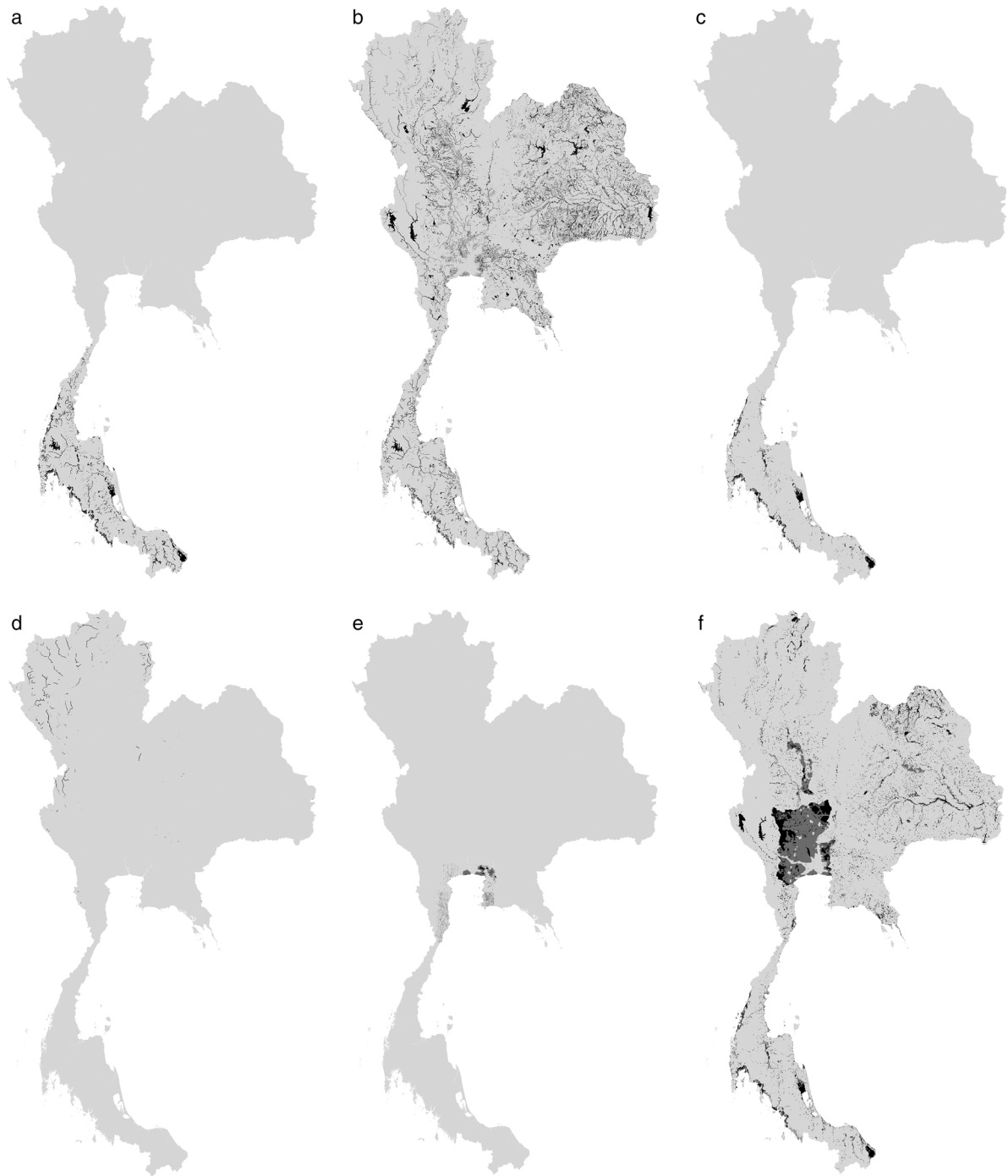


FIG. 4. Habitat suitability maps across Thailand for six vertebrate species: (a) hairy-nosed otter (*Lutra sumatrana*), (b) striped narrow-headed softshell turtle (*Chitra chitra*), (c) peat swamp frog (*Limnonectes malesianus*), (d) big-headed turtle (*Platysternon megacephalum*), (e) Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*), and (f) fishing cat (*Prionailurus viverrinus*). Light gray areas indicate low probability of suitability. Dark gray areas have medium probability of suitability, and areas in black have high probability of suitability.

Example II, Striped narrow-headed softshell turtle

Step 1: Literature review.—Only six publications (three textbooks and three national publications) were available for review. From the literature review, this

turtle prefers large rivers, reservoirs, and adjacent sandbanks (Thirakhupt and van Dijk 1994, Cox et al. 1998, Kitimasak and Thirakhupt 2002, Kitimasak et al. 2005). Threats include habitat destruction (reservoir/

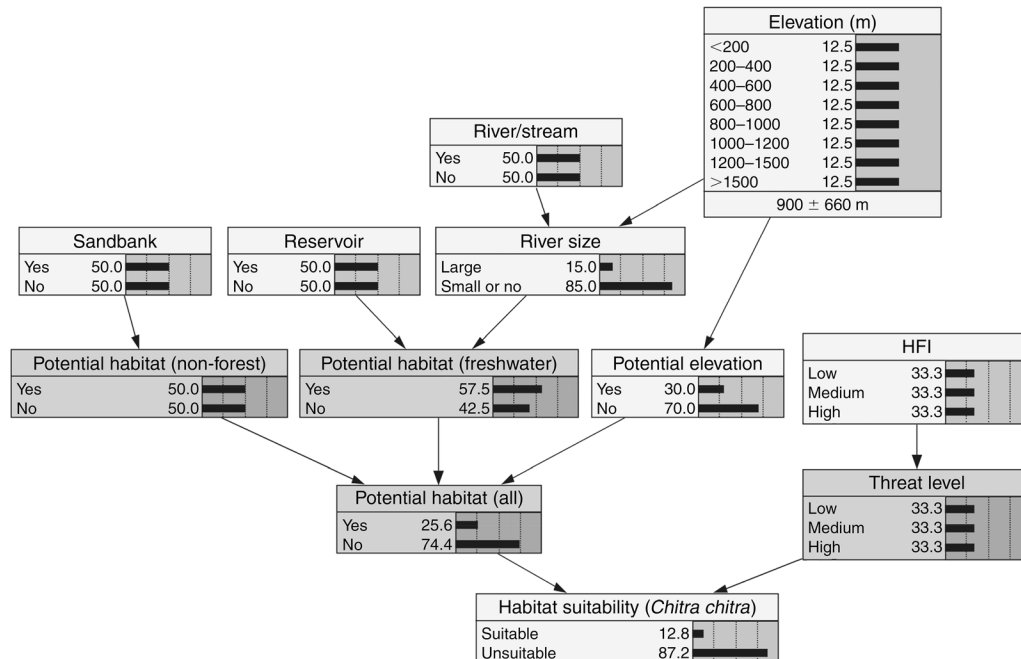


FIG. 5. The revised model structure for striped narrow-headed softshell turtle (*Chitra chitra*) showing model states; the bars represent the probabilities (as percentages) of being in a given state. Panels that are entirely gray-shaded panels are the nodes where states are defined as deterministic.

dam construction, sand mining, water pollution), and hunting for food/trade.

Step 2: Model development.—The first draft of the BN model is shown in Appendix H. The prior probabilities in the CPT of the potential habitat nodes were set at 100%. These were modified, where relevant, using expert opinion. Relative to the previous example, the model's structure is simple, reflecting the limited knowledge base.

Step 3: Model evaluation.—The model was evaluated by one expert. The expert extended habitat use to reservoirs and limited the elevation to just lowland areas. A specific elevational range (lowland) was added to the model, and the probability that reservoirs were suitable habitat was changed to 60%, according to the calculations described previously (Fig. 5).

In total, 10 survey points from three publications (Thirakhupt and van Dijk 1994, Kitimasak and Thirakhupt 2002, Kitimasak et al. 2005) were used to evaluate model classification sensitivity. Only three points fell within the grids with suitable probability >70%, resulting in an estimate of 30% classification sensitivity. The rest fell within the grids classified as unsuitable habitat. The habitats of these grids were evergreen forest, dry dipterocarp forest, wetland, grassland, and agriculture. Part of the reason for this low sensitivity is that five survey points were from locations where the turtles were reported, rather than from field locations, i.e., from markets and collector's homes. Although all were in close proximity to where they were

actually collected, some were probably sufficiently distant to cause classification errors.

From the sensitivity analysis, "HFI" was the variable that had the most influence on habitat suitability, suggesting that potential habitat was mostly limited by threats (Table 1).

Step 4: Visualization.—The habitat suitability map is shown in Fig. 4b. Land cover with a high probability of suitability for this turtle covered ~4% of Thailand (21 972 km²).

Overview of outcomes across taxa

Amphibians.—Only two amphibians were included in this study. BN models of both species were simple, with fewer than five environmental variables, reflecting the scarcity of information. No survey data were available for either species; therefore, model classification sensitivity could not be evaluated. The probability map of habitat suitability for the peat swamp frog (*Limnonectes malesianus*) is presented in Fig. 4c. This frog is a peninsular species, where suitable habitat is confined to only a few sites in southern Thailand. Its area of high probability of suitability is less than 0.6% of the country area (2642 km²).

For reptiles, 12 species were included in this study separated into six groups. BN models ranged from simple (3–4 nodes) to complicated (>10 nodes). We had survey data to evaluate model classification sensitivity for just two species (striped narrow-headed softshell turtle and big-headed turtle *Platysternon megacephalum*); both are simple models. The model classification

sensitivities for both species were low (30% and 0%, respectively). The habitat probability map for the big-headed turtle is presented in Fig. 4d. The area with high probability of suitability is less than 0.3% of the area of Thailand (1180 km²) for this turtle.

For the birds, 33 species were included, separated into 10 groups. Available information for these taxa was extensive, although there was little information for Manchurian Reed Warbler (*Acrocephalus tangorum*) and Mekong Wagtail (*Motacilla samveasnae*). Survey data were available for 15 bird species. Model classification sensitivity was high for 11 species (>90%), whereas models of three species had moderate sensitivity (50–70%) and one had low (33%). The habitat suitability map for the critically endangered Spoon-billed Sandpiper (*Eurynorhynchus pygmeus*, see Plate 1) is presented as an example (Fig. 4e). The area for this species with high probability of suitability is less than 0.1% of the country area (312 km²). Model sensitivity for this bird species is 97%.

Six species of mammals were included, separated into four groups (wetland species, otters; wetland species, small cats; forest species; and grassland species). Similar to the birds, most of the BN mammal models were relatively complicated, except that for hog deer (*Axis porcinus*). Survey data were available for assessing model classification sensitivity for most species, except for hog deer and fishing cat (*Prionailurus viverrinus*). Classification sensitivity of the hairy-nosed otter model was moderate (73%), whereas models of the other two otter species had low sensitivity (35–40%). The banded langur (*Presbytis femoralis*) model had 0% sensitivity. Habitat suitability for the fishing cat is presented (Fig. 4f). The area with high probability of suitability was estimated at 4% of the country area (20 746 km²).

DISCUSSION

This study demonstrates that BN models can produce habitat suitability maps with acceptable classification sensitivity using relatively small amounts of data. However, BNs performed poorly for species lacking information of sufficient depth. Although it is difficult to quantify how much information is needed to be considered “adequate,” we found that publications that are specific to particular species or a group of species (e.g., Gale and Thongaree 2006, Sankamethawee et al. 2008, Cutter and Cutter 2009) provide comprehensive information for modeling. Field identification guides that aggregate information about species typically provided us little useful information (e.g., Nabhitabhata and Chan-ard 2005, Das 2010). Data provided by these guides were typically redundant, providing essentially the same information. Therefore, although there were several sources available to be reviewed for a particular species, information for habitat modeling was generally inadequate. In contrast, if the literature covered various aspects of ecology and explained in some detail the

habitat use of a particular species, the information was more valuable.

Assessment of model accuracy was limited by a lack of dedicated, standardized surveys with both presence and absence data (e.g., camera-trap data). We therefore were unable to evaluate whether the models were over-predicting suitable habitat (i.e., false positive rate) (Fielding and Bell 1997). This study used 10 field observations as a minimum size for model evaluation; currently, however, there are no quantitative guidelines to determine such minimums and we presume that 10 represents an absolute minimum for such evaluations. In addition, for the field data that were available, there was probably some observation bias with the relatively well-known species (e.g., rare shore birds), such that observers were likely to frequent well-publicized locations where they had high chance of observing target species instead of systematically searching available suitable habitat. Observation bias was probably less for most other species, which required more directed surveys (e.g., otters), because information on where to observe these species regularly was not available or these species were simply less predictable.

Model classification sensitivity tests were limited to 21 species. The remaining 31 species could not be evaluated because even presence data were insufficient. Where assessments were possible, predictive errors of models were probably due to multiple sources. Information about utilized habitats was incomplete (due to insufficient survey effort and a lack of systematic record keeping); consequently, some models could not correctly predict significant portions of a target species' range (Fielding and Bell 1997, Barry and Elith 2006). This occurred with our target amphibians, reptiles, and even a few mammals. Lack of experts to review models was another cause of prediction error. We suspect that this deficiency of data and resources is widespread in biodiversity-rich countries.

Another limitation is scale. Different species have different scales at which they can be mapped (Guisan and Thuiller 2005). Modeling habitats for birds and large mammals on a landscape scale provided acceptable results, but habitat for amphibians, reptiles, and small mammals tended to be over-predicted. Therefore, we suggest producing habitat models for these groups at a smaller scale, using microenvironmental variables (e.g., Marcot et al. 2001). Errors may also be related to quality of land use maps, with resolutions and accuracies of available maps being unknown (Tantipisanuh and Gale 2013). We suspect that this was a problem for the few bird species with low-to-moderate model accuracies, despite relatively extensive knowledge of their habitat preferences.

The final limitation is that known locations of some species fell within areas with high threat levels. Consequently, although these areas might be potential habitat, models predicted these as unsuitable. Survey detections of species in areas with high threat levels could result

from several factors including the following: (1) HFI exaggerated threat levels; (2) species themselves tolerated threats (Isaac and Cowlshaw 2004); (3) species were present but declining, or were present in the past when surveys were conducted, but are now locally extinct.

The classification sensitivities of the BN models in this study ranged from 0% to 100% (mean = 69.7%, $n = 21$), suggesting that our BN models still require further development and refinement. In particular, model refinement is urgently needed for the amphibians and the reptiles because the quality of the current models is still questionable, while model classification sensitivity of birds was relatively high. We found that one-on-one discussion with experts was particularly useful for improving models of species with particularly sparse data. The models would also benefit from input from additional experts, both local and international, and need to be reviewed and revised when new survey data become available (Marcot et al. 2006, Uusitalo 2007). Furthermore, BNs have been applied in the context of adaptive management (Nyberg et al. 2006, Smith et al. 2007b, Henriksen and Barlebo 2008), and would in principle be appropriate for our models. Outcomes from previous operational management policies could be used to improve BN models, reducing uncertainty and better representing system relationships. Such revised models could then be used for future management decisions.

Where accuracies of BN models are high, predicted habitat suitability maps could be helpful for conservation planning by identifying potential areas for future surveys and conservation management for selected species groups. Gap analyses could be performed to identify gaps in protected area coverage, evaluate their representation, and then select additional areas to increase the overall representation of protected areas (Margules and Pressey 2000). Even maps from BN models where accuracies are still questionable, although currently less useful for conservation planning, may be useful in identifying potential habitat and guiding future surveys.

To understand potential conservation hotspots (e.g., the inner gulf of Thailand, where >25 species in this study were predicted to occur), habitat suitability maps could be integrated to identify areas that are suitable for several species simultaneously (Myers et al. 2000). This would improve the effectiveness of conservation management and reduce costs from the redundancy of conducting species by species management. Alternatively, conservation management might focus on umbrella species of several ecosystems (e.g., otter species for wetland, mangrove, and coastal habitats) to minimize the number of species that need to be managed, while still protecting large numbers of species (Roberge and Angelstam 2004).

Species habitat modeling hereafter also may need to focus on impacts of climate change that might alter species distribution ranges (Harrison et al. 2006), as these models will mostly be used for conservation

planning for the future. Integrating impacts from climate change may also improve the correspondence between model predictions and altered species distribution ranges.

Although not part of this study, BNs can also be applied as a support tool for management decisions. In particular, BN models are ideal for illustrating a conceptual understanding of system relationships for communicating with a range of stakeholders (Cain 2001, McCann et al. 2006, Nyberg et al. 2006). Such models can easily simulate potential outcomes of different management policies probabilistically, providing information to managers and stakeholders to support decision-making (Ames et al. 2005, McCann et al. 2006, Henriksen et al. 2007).

This study demonstrates the potential of BNs in producing models not only for developed countries with relatively extensive resources, but also in biodiversity-rich countries where resources are much more limited. Although accuracies of BN models still depend on several factors related to the adequacy of available data and human resources as we have discussed, a small increase in the number of quantitative surveys of target species is likely to significantly improve BN model performance.

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SUPPLEMENTAL MATERIAL

Appendix A

An example of a Bayesian network ([Ecological Archives A024-201-A1](#)).

Appendix B

Map of Thailand showing its six geographic regions and two biogeographical subregions ([Ecological Archives A024-201-A2](#)).

Appendix C

List of threatened species included in this study ([Ecological Archives A024-201-A3](#)).

Appendix D

Environmental factors included in the Bayesian network models of 22 focal species groups and description of each focal group ([Ecological Archives A024-201-A4](#)).

Appendix E

Process diagram illustrating Bayesian network model development ([Ecological Archives A024-201-A5](#)).

Appendix F

List and description of Bayesian network nodes used in this publication ([Ecological Archives A024-201-A6](#)).

Appendix G

The conditional probability table of the “habitat suitability” node ([Ecological Archives A024-201-A7](#)).

Appendix H

Bayesian network model structure of habitat suitability for *Chitra* ([Ecological Archives A024-201-A8](#)).