INTRODUCTION / INTRODUCTION

# Bayesian belief networks: applications in ecology and natural resource management[1]

Robert K. McCann, Bruce G. Marcot, and Rick Ellis

**Abstract:** In this introduction to the following series of papers on Bayesian belief networks (BBNs) we briefly summarize BBNs, review their application in ecology and natural resource management, and provide an overview of the papers in this section. We suggest that BBNs are useful tools for representing expert knowledge of an ecosystem, evaluating potential effects of alternative management decisions, and communicating with nonexperts about making natural resource management decisions. BBNs can be used effectively to represent uncertainty in understanding and variability in ecosystem response, and the influence of uncertainty and variability on costs and benefits assigned to model outcomes or decisions associated with natural resource management. BBN tools also lend themselves well to an adaptive-management framework by posing testable management hypotheses and incorporating new knowledge to evaluate existing management guidelines.

**Résumé :** Dans cette introduction à la série d'articles qui suivent sur les réseaux bayésiens d'appréciation (RBA), nous donnons un bref aperçu des RBA, révisons leur application en écologie et en gestion des ressources naturelles et présentons une vue d'ensemble des articles dans cette section. Nous croyons que les RBA sont des outils utiles pour représenter l'expertise existante au sujet d'un écosystème, évaluer les effets potentiels de décisions alternatives de gestion et communiquer aux profanes les enjeux liés aux décisions associées à la gestion des ressources naturelles. Les RBA peuvent être utilisés efficacement pour représenter la part d'incertitude dans notre compréhension et la variabilité dans la réponse des écosystèmes ainsi que l'influence de l'incertitude et de la variabilité sur les coûts et les bénéfices assignés aux résultats des modèles ou sur les décisions associées à la gestion des ressources naturelles. Les outils que constituent les RBA se prêtent bien également à un cadre de gestion adaptative en formulant des hypothèses de gestion qui peuvent être testées et en incorporant de nouvelles connaissances pour évaluer les directives actuelles concernant la gestion.

[Traduit par la Rédaction]

## Introduction

Bayesian belief networks (BBNs) are models that graphically and probabilistically represent correlative and causal relationships among variables (Cain 2001; Neopolitan 2003). In ecological modelling, BBNs are particularly useful for rapid scoping and intuitive presentation of ecological relationships. When applied to natural resource management (hereinafter resource management), BBNs can depict the influence of alternative management activities on key ecological predictor variables and thence on ecological and other response variables, and thereby help the manager choose the best course of action. In this paper we summarize concepts of BBNs, review their use in ecological modelling and resource management, and introduce the papers in this series.

BBNs have been used in ecological modelling to represent species–habitat relationships and population viability of terrestrial and aquatic vertebrates (Marcot 2007). For example, BBNs have been used to model responses of birds and mammals to habitat patterns (e.g., Wisdom et al. 2002; Rowland et al. 2003) and to model population viability of salmonids (Lee and Rieman 1997). In resource management, BBNs have been used in a broader decision-support framework (conceptual or computer-based tools that collectively facilitate the decision-making process; Cain 2001) to analyze effects on wildlife from land-planning alternatives by the USDA Forest Service and USDI Bureau of Land Management in their Interior Columbia Basin Ecosystem Management Project in the Pacific Northwest of the United States (Marcot et al. 2001; Raphael et al. 2001; Rieman et al. 2001). BBNs also have been used to predict and aid water-quality management (Reckhow 1999) and water-resource

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**R.K. McCann.**[2] P.O. Box 421, Mackenzie, BC V0J 2C0, Canada.
**B.G. Marcot.** USDA Forest Service, Suite 400, 620 SW Main Street, Portland, OR 97205, USA.
**R. Ellis.** R. Ellis & Associates Inc., 847 Sea Aira Heights, Victoria, BC V9E 2A2, Canada.

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[2]Corresponding author (e-mail: rmccann@interchange.ubc.ca).

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planning (Bromley et al. 2005), to aid fisheries management of Baltic cod (*Gadus morhua callarias* L.) (Kuikka et al. 1999), and to model meta-assessments of fish stocks (Hammond and Ellis 2002). Cain et al. (1999) emphasized the utility of BBNs to facilitate stakeholder participation in resource management planning and decision processes. This series of papers represents work completed by a team of Canadian and US ecological researchers and resource managers. In this series we introduce BBNs, provide guidelines for their development, and give examples of recent applications to address current issues in ecology and resource management in British Columbia.

Our objective in writing this series was to promote a broader understanding, awareness, and acceptance of BBNs as one of the tools that researchers and managers, committed to making more informed and disclosed decisions about resource management, should place in their toolbox, with appropriate caveats. BBNs are intuitive tools for (*i*) representing and combining empirical data with experts' understanding of ecological systems, (*ii*) graphically expressing complex relationships and problems in resource management, (*iii*) addressing, in a structured way, uncertainties that plague attempts to solve these problems, (*iv*) structuring and evaluating alternative decisions within a context of risk assessment that helps identify best decisions (Marcot 1998), and (*v*) fostering communication among ecologists, decision-makers, and stakeholders who may lack formal training in the underlying scientific disciplines (Cain 2001). Although BBNs do not replace field studies and experiments (Marcot et al. 2001), they can well complement other ecological modelling approaches such as simulation modelling and population-viability analysis (Lee and Rieman 1997; Steventon et al. 2006).

## Why Bayesian belief networks?

A BBN is a graphical network of nodes linked by probabilities (Fig. 1). Nodes can represent constants, discrete or continuous variables, and continuous functions, and how management decisions affect other variables. Nodes are comprised of states that are independent, mutually exclusive, and exhaustive propositions (Olson et al. 1990*b*; Cain 2001) about the values or conditions that the variable represented by the node can assume. Nodes are linked with arrows to represent direct correlations or causal influences (Olson et al. 1990*b*; Cain 2001). Nodes with no incoming arrows are input parent nodes; nodes with both incoming and outgoing arrows are summary child nodes; and nodes with no outgoing arrows are output child nodes. Underlying each node is a modeller-defined table that specifies the unconditional (prior) probability of each state for input nodes, or the conditional probability of each state for child nodes (nodes representing constants, functions, or decisions generally have no probability tables). The final "posterior probabilities" of states or values of the output nodes are calculated in the network using standard Bayesian learning statistics (Spiegelhalter et al. 1993). The computationally effective algorithms in commercial BBN modelling shells permit rapid updating of probabilities throughout the network as evidence becomes available by which to select the states of the input nodes. BBNs built from most such modelling shells are highly interactive.

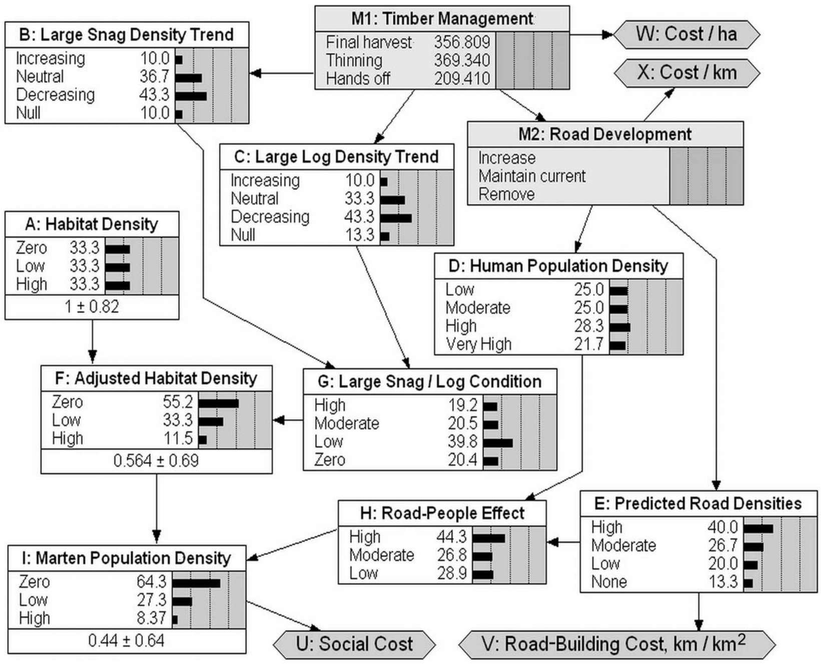
BBNs are somewhat similar to decision trees (e.g., VanderWerf et al. 2006) and other decision models that denote effects of alternative decision pathways or states of nature on probabilities of outcomes having expected utilities (values assigned to model outcomes that reflect socio-economic, political, legal, and management interests). However, BBNs have several distinct advantages. Principal among these are their graphical construction, which shows relationships among variables more clearly (Cain 2001) and facilitates the use of expert knowledge (Kuikka et al. 1999) and their use of Bayesian statistics to calculate probabilities of outcome states, whereas decision trees reveal more detail about chains of events initiated by decisions (Cain 2001) and use joint probability distributions. The Bayesian approach is far more flexible in that it can draw from both empirical data and expert judgment as a basis for the model structure and probability tables (Heckerman et al. 1994; Kuikka et al. 1999), account for prior knowledge and missing data, and use new data to update and refine the model structure and underlying probability tables, which other, more traditional modelling approaches such as decision-tree analysis generally cannot do.

The interactive and graphical representation of BBNs, and the ease with which they can be created and amended, permit more effective communication of cumulative effects and outcomes of alternative conditions and decisions than do more static models such as decision trees and other traditional statistical approaches like classification or regression trees. BBNs also are readily understood by nonmodellers and, if properly constructed, can reveal more underlying detail of how the system works than do fixed decision analyses (Cain 2001).

BBNs can be used for both data-rich and data-poor applications; however, in the latter case caution is warranted with BBNs (Marcot et al. 2006) as with other types of models (e.g., Beissinger and Westphal 1998). The use of expert judgment necessitates documenting, defending, and, where possible, validating the basis for the model structure and conditional probabilities. BBNs based mainly on expert experience should be used to generate testable hypotheses and should follow a rigorous procedure for developing, testing, and updating the model, such as that suggested by Marcot et al. (2006).

By representing different potential outcomes of management options with probabilities, managers can use BBNs to rank management options according to decisions that will most likely lead to desired outcomes. This can be done in BBNs by calculating expected values of the utility of alternative options shown in decision nodes (e.g., Nyberg et al. 2006), and by sensitivity analysis of part of or an entire BBN model. Most commercial BBN modelling shells (see Marcot et al. 2006; Nyberg et al. 2006) support sensitivity analysis, which allows examination of how robust a ranked set of management options is to varying parameter values within models or assumptions about the model structure (Peterman and Peters 1998) and can be useful in identifying key uncertainties and guiding decision-making under uncertainty. Some management options may be more robust to particular uncertainties or more effective at reducing the im-

**Fig. 1.** Example of a Bayesian belief network model predicting how decisions about timber management and road development can affect habitat quality for the American marten (*Martes americana* (Turton)) within a sub-basin in the interior western USA and how operational costs and social values associated with marten population densities can influence the timber-management decision. Input nodes A–E represent habitat conditions where node A is the density of marten mature-forest habitat in the sub-basin; nodes B–E are directly affected by timber-management and road-development decision nodes M1 and M2. Intermediate nodes F–H are calculated from underlying conditional-probability tables. Output node I shows the calculated posterior probabilities of marten population density. Utility nodes U–X represent various costs of management decisions and social values of marten population levels. Horizontal bars and values within nodes are probabilities of states of each variable; values in the decision nodes are expected values of costs, given the probability structure of the model and utility values; and values below nodes A, F, and I are expected values of habitat-quality or population indices (–1, 0, and 1 represent zero, low, and high densities, respectively) ± 1 SD (presuming a Gaussian error distribution). The basic model is based on Raphael et al. (2001), with added hypothetical management and utility nodes.




pacts of potential future uncertainties (e.g., environmental uncertainties estimated through simulation modelling) than others (Kuikka et al. 1999). Additionally, sensitivity analyses can be used to help build the model correctly (Marcot et al. 2006), aid in identifying restoration and research priorities (Nyberg et al. 2006), and help resolve conflicts about management objectives or beliefs about ecosystem function (Peterman and Peters 1998). Marcot et al. (2006) provide formulae and recommendations for sensitivity-analysis calculations and present some general insights into how BBN structure affects model sensitivity.

In addition to inferring the probabilities of alternative model outcomes for a given set of causal conditions or "states" of the key ecological predictor variables (i.e., forward propagation of conditional probabilities through the model structure), BBNs also can be used to infer the most likely set of causal conditions for a given outcome by solving the model's conditional probabilities backwards through the model structure. This is a most useful feature of BBNs, one that many other model structures such as decision trees cannot provide. This examination of likelihoods can be a useful approach to informing decision-makers of the combinations of variable states across the predictor variables that can be expected to produce the desired outcome. Marcot et al. (2006) further discuss probabilities and likelihoods in the context of BBNs.

## Models in ecological research and resource management

Refining our understanding, quantifying relationships, generating inferences about the relationships between ecological predictor variables and response variables, and forecasting potential effects of management actions are primary goals of ecological research and resource management (Marcot et al. 2006). Ecological models and related decision-support frameworks are simplifying abstractions of knowledge (Jones et al. 2002) that provide structure to what we know, and need to know, about a system of interest. Such abstractions are necessary to help define problems, convey ecological concepts and relationships (either known or assumed), characterize potential system responses to management perturbations, and evaluate alternative management policies.

We contend that models are particularly effective when they represent complexity, causality, uncertainty, and variability in a clear and intuitive fashion. Any model, however, will be founded on limiting assumptions. Models are not intended to be perfect descriptions of reality, and resultant predictions will always be imperfect (McCarthy et al. 2001). Nonetheless, models have contributed greatly to resource management when they have used and invoked further field research leading to new insights, model revisions, and more accurate predictions of the potential effects of management decisions. Such an approach to modelling fits well with the application of BBNs in adaptive management (Nyberg et al. 2006).

Most problems in resource management are characterized by scant data and uncertainty about how biological systems function and respond to specific human activities (Starfield and Bleloch 1986). This presents two challenges for resource managers: (1) how to make good, science-based management decisions; and (2) how to best acquire the data needed to improve understanding. These are also related problems in resource modelling. Uncertainty and the inherent complexity of ecological and resource management systems have been cited as the basis for legal challenges to the biological credibility of ecological models and associated resource-management decisions (Harrison et al. 1993; Noon and Murphy 1994; Taylor et al. 2000). We expand on the problems of complexity, causality, uncertainty, and variability in ecological modelling and decision-making, and suggest some desirable characteristics of tools — particularly BBNs — that are intended to address resource-management issues (Table 1).

**Complexity and causality**

Ecosystems are composed of heterogeneous, complex networks that exhibit nonlinear and transient behaviors (Green et al. 2005). Multiple interactions occur within ecosystems among plants and animals and are overlain by temporal, spatial, and abiotic (e.g., topographic, climatic) variation of species and system parameters (Olson et al. 1990*a*). Such complexity may require understanding of metapopulation and habitat patch dynamics, habitat connectivity, cumulative effects, feedback loops, and habitat affinities that are multiscalar and variable.

Ecosystem management is increasingly driven towards multiple goals, including lofty and at times conflicting expectations of sustainability of multiple resources over large areas and long time periods (Kangas and Kangas 2004). Management decisions that address value-laden resource descriptions such as biodiversity and ecosystem integrity defy easy analysis and quantification (Lämås and Eriksson 2003). They are better served by incorporating socio-economic, political, and cultural considerations (Cain et al. 1999; Cain 2001), by explicitly integrating the concerns of multiple stakeholders (Cain et al. 1999; Cain 2001; Kangas and Kangas 2004), and by reducing the value-laden descriptions to more objective and quantifiable parameters (Morrison and Marcot 1995). As management responds to the increasing and changing values and expectations placed on natural resources, resource-management systems themselves become more complex (Lämås and Eriksson 2003; Kangas and Kangas 2004).

Understanding and effectively managing complex ecological systems therefore require a multidisciplinary approach. A modelling approach such as that afforded by BBNs can represent the complexity of ecosystem and resource-management systems in hierarchical ways by decomposing or partitioning the problem into solvable steps, clearly representing value-laden concepts by empirical parameters, and combining knowledge from different disciplines and stakeholders (Cain et al. 1999).

**Uncertainty and variability**

Uncertainty is distinguished from variability in recognition of their differing ramifications for decision-making (Thompson 2002; Cullen and Small 2004). *Uncertainty* is a lack of information or knowledge (Thompson 2002; Kangas and Kangas 2004) and is a property of our limitations in observing or understanding a system (Finkel 1996). Difficulties in estimating system parameters arise from bias and sampling errors due to imperfect sampling techniques, and from measurement error. Limitations in obtaining sufficient information about a system's behavior prevent correct specification of causal relationships among system parameters and lead to incorrect specification of the underlying model (Finkel 1996). Uncertainty about parameter estimates and causal relationships often can be reduced with additional research (Finkel 1996; Thompson 2002).

*Variability* is a system property (Finkel 1996) and refers to naturally or anthropogenically induced variation in an ecological system over space and time: that is, the degree of lability, or susceptibility to change, in system parameters. Ecological processes vary and additional research cannot reduce true variability (Finkel 1996; Thompson 2002) but may lead to the degree and patterns of such variation in some parameters becoming well known.

Uncertainty and variability both are components of quantitative risk assessment but they invoke different treatment and interpretation in decision-making. Modelling uncertainty can involve eliciting expert judgment to determine probability distributions (Cleaves 1994; Cullen and Small 2004), whereas modelling variability may be addressed by theoretical or empirically derived frequency distributions (Cullen and Small 2004). Under uncertainty the true levels of risk associated with a decision are unknown (Cullen and Small 2004) because the expected outcome of the decision might not actually occur (Thompson 2002). Under variability an expected outcome might not be optimal for all individuals, geographic locations, or time frames (Thompson 2002; Cullen and Small 2004).

Resource managers may want to use a tool, such as BBNs, that can represent both uncertainty and variability in terms of probabilities of different potential outcomes or system responses, given initial conditions and human activities (Olson et al. 1990*a*, 1990*b*). Because of their probabilistic basis and their ability to explicitly represent and quantify the expected utility of alternative management decisions and strategies (decision sequences or combinations), BBNs lend themselves well to representing variability of the system and uncertainty of understanding, and their implications to possible management decisions (Kuikka et al. 1999). Compared to deterministic point estimate models, this accounting for uncertainty and variability in information may dramatically change managers' perceptions of both the current status and acceptable utilization rate of resources (Kuikka et al. 1999). Results derived from deterministic point estimate models or classical hypothesis testing may underestimate the attendant risks of a decision due to failure to consider all plausible parameter values and all plausible combinations thereof, or all plausible hypotheses, and the attendant uncertainties (Ludwig 1996; Kuikka et al. 1999). Bayesian approaches can be used to assess the relative plausibility of parameter values and hypotheses and weight them accordingly through ex-

**Table 1.** Useful characteristics of Bayesian belief network (BBN) models and caveats about their application in ecological modelling and resource management.

| Description of issue | Useful characteristics of BBNs | Caveats about using BBNs |
|---|---|---|
| **Complexity** | | |
| Requires a multidisciplinary approach to account for:<br>• multiple interactions among plants and animals<br>• temporal, spatial, and abiotic variation<br>• increasing and changing resource values<br>• socio-economic, political, and cultural considerations | Flexible use of information:<br>• diverse measurement scales (nominal, ordinal, continuous)<br>• diverse scientific disciplines<br>• diverse origins (empirical, expert-based, traditional knowledge from First Nations)<br>• can accommodate previous information<br>• case data can be used to update or test models<br><br>Rapid and flexible modelling environment:<br>• time- and cost-effective to build and apply<br>• models can be adapted to incorporate additional factors as required<br>• developed subcomponents of the models can often be applied to other problems<br>• are more amenable to updating than some competing knowledge representations | BBNs require a fully specified probabilistic model and often require elicitation of expert judgment<br>Nodes in the models should be empirically observable, quantifiable, or defensible<br>Care must be exercised to prevent unwieldy conditional probability tables<br>Approaches that use data to induce the model structure (i.e., nodes, states, and linkages) should be used sparingly to avoid creating unwieldy model structures<br>Feedback functions and temporal relationships are not possible or are poorly handled<br>Continuous variables must be discretized |
| **Uncertainty and variability** | | |
| Information is often insufficient to adequately define and predict ecosystem characteristics<br>Ecological processes vary naturally over space and time<br>Many ecosystem components interact in unpredictable ways, affecting outcomes of interest to management | Predicated on an established normative theorem that can explicitly represent uncertainty and variability<br>Appropriate for addressing both data-rich and data-poor problems<br>Can provide support for development of field experiments to reduce uncertainties in risk analysis and adaptive-management approaches | Usually do not explicitly represent bias or strict propagation of error<br>Models can be easily developed, entirely from expert judgment, with an unknown degree of bias and inaccuracy |

**Table 1** (*concluded*).

| Description of issue | Useful characteristics of BBNs | Caveats about using BBNs |
|---|---|---|
| **Acceptability and communication** | | |
| Models and policies must have "face validity" to policy makers and stakeholders<br>Models must be understandable to those who lack formal training in the underlying scientific disciplines | Can be presented to and understood by decision-makers and stakeholders:<br>• easily understood graphical representation<br>• are interactive and easily reveal how input conditions influence the probabilities of model outcomes<br>• protocols exist for testing, revision, and peer review<br>• support stakeholder input and promote acceptance and implementation of decision-support frameworks<br>Compared with mathematical models and other knowledge representations, they<br>• are more easily understood by those who did not build them<br>• serve better as a communication tool<br>• provide a repository of understanding for posterity | Modellers need to demonstrate causal relations<br>Modellers are required to fully consider how to present and explain the models to decision-makers and stakeholders<br>Potential explanatory variables or sources of uncertainty not included in the causal web should be identified and addressed |
| **Decision-making** | | |
| Decisions must be made in the face of complexity, uncertainty, and variability<br>Risk analysis and risk management are essential features of decision-making | Support a systematic approach to sensitivity analysis:<br>• permit identification of factors, or interactions between factors, that are most influential on model outcomes<br>• encourage risk analysis and risk management<br>• aid development of validation and effectiveness monitoring | Decision-makers must not assume that all relevant uncertainties regarding knowledge or objectives have been incorporated into the decision rules<br>BBNs should be incorporated into an adaptive-management process to aid decision-making rather than to dictate decisions |
| | Model outcomes can be examined for their most likely causes, which aids in understanding the model<br>Can be cast as decision networks that rapidly recalculate utilities, as alternative decisions or strategies are specified<br>Fit well with adaptive-management concepts | Model structure can influence the results of sensitivity testing and thus bias the apparent influence of some variables and will affect decisions and strategies |

plicit consideration of uncertain or subjective information, and can lead to a systematic approach to sensitivity analysis (Ludwig 1996).

### Acceptability and communication

Resource management is, at its heart, people management, and is mediated through revealing to decision-makers, the public, and others the consequences of competing management policies. The degree to which a proposed resource-use policy is acceptable to decision-makers and stakeholders lies, in part, in the validity of the underlying scientific evidence, consistency with existing social and cultural views, economics, and the degree to which the policy is understandable and commensurate with other existing, accepted policies (e.g., Carr et al. 1998; Butler and Koontz 2005). In modelling, "face validity" is used to determine if a model fits preconceived notions and makes sense (Gass 1977; Lacity and Janson 1994), and reflects its degree of acceptability. Models for guiding resource-use policy should have high face validity among experts and ultimate users, and therefore can help guide communication with nonexperts.

Most decision-makers, public interest groups, and legal professionals are not trained as ecologists or modellers and are unlikely to comprehend tests of null hypotheses, technical jargon (Ellison 1996), or complex representations of ecosystems (Boyce 1992). Thus, a modelling approach that provides a readily understandable representation of complex systems and human influences, without sacrificing desired levels of accuracy and validity, can be of vast help in communicating with nonspecialists. To this end, we have found that BBNs facilitate communication through their interactive nature and ability to demonstrate graphically how assumptions affect the probability of outcomes (Kuikka et al. 1999). Several papers in this series also describe the use of simplified "box and arrow" influence diagrams (Marcot et al. 2006; Nyberg et al. 2006; Walton and Meidinger 2006) that express expected causal relationships as the basis for representing or creating more complex BBN models (Zhang 1998); influence diagrams also have great value as a communication tool (Marcot 2006*b*) as well as providing the basis for alternative model structures, including BBNs.

### Decision-making

Resource management entails making difficult decisions in the face of interactions among complexity, uncertainty, and variability. Complexity makes understanding uncertain and communicating what we understand difficult; uncertainty about our understanding and inherent parameter variability make the results of decisions imprecise. We are not, however, absolved from making resource decisions (Beissinger and Westphal 1998; Peterman and Peters 1998). Classical hypothesis testing provides a poor basis for decision-making about resources because it does not reveal the probabilities and utilities of null and alternative hypotheses given the data, even though this information is what managers frequently want (Ellison 1996). Consequently, explicit treatment of uncertainty and variability through risk analysis (i.e., determining the probability of possible outcomes and their utilities; Marcot 1998) and risk management (i.e., articulating the manager's attitude to risk; Marcot 1998) is a component of effective decision-making, enhances the face validity of decisions and models used, and allows decision-makers to examine trade-offs between a desirable outcome and the chance (or risk) that a particular management decision may not lead to such an outcome (Cain 2001; Kangas and Kangas 2004).

The decision-making process can be supported by using Bayesian decision networks (BDNs; Nyberg et al. 2006), which are BBNs that incorporate nodes to represent potential management decisions and, optionally, utilities of outcomes. Other modelling approaches such as decision trees can explicitly show alternative decisions and utilities, but BDNs apparently are unique in that they instantly recalculate and clearly display probabilities of conditions and outcomes, and the resultant utility, as alternative decisions or strategies are specified. Comparing outcome values weighted by their respective probabilities among alternative management decisions is a representation of risk associated with the uncertainty, variability, and complexity surrounding potential management activities. BBNs also can contribute indirectly to sound decision-making by representing probabilities of ecological responses to natural events and management actions within larger decision-support frameworks. For example, dynamic landscape models can be used to generate inputs to BBNs that, in turn, predict outcomes of alternative simulations in meaningful ways that can aid a resource decision process, such as in the management of habitat for woodland caribou (*Rangifer tarandus caribou* (Gmelin); McNay et al. 2006).

### Shortcomings of and caveats about using BBN models

Notwithstanding tensions between "frequentists" and Bayesians (Dennis 1996), BBNs have, in addition to their strengths, specific weaknesses, and caveats are necessary regarding their use (Table 1). Construction of BBNs requires the specification of a full probability structure of variables and their relations (Olson et al. 1990*b*), which can be cumbersome to implement. For example, conditional probability tables (CPTs) of child nodes are usually derived from existing data sources, expert judgment, or a combination. Often data are scarce for particular configurations in the CPT and expert judgment must fill in the gaps. This can be a daunting task for rare events and when the number of probabilities to be estimated is large. CPTs can quickly become unwieldy (Marcot et al. 2006; Walton and Meidinger 2006) when they represent large numbers of states of multiple parent nodes and of the node being evaluated. Elicitation of expert judgment should follow structured approaches, particularly to address rare but important events and to minimize the potential for bias (Cleaves 1994). Marcot et al. (2006) and Marcot (2006*a*) provide guidelines on structuring BBNs to keep CPTs tractable and how to create CPTs using expert judgment.

Temporal dynamics are important considerations in ecology and resource management because biotic systems change over time. BBNs represent temporal dynamics poorly, however, through a cumbersome process of time expansion (Nyberg et al. 2006) that involves discretizing time-based variables, replicating the entire BBN structure for each instance of time, and establishing links between nodes in adjacent replicates of the BBN. For some applications, the temporal component can be handled outside the BBN, but this often requires substantial exchanges of data between models. In general, the difficulty of handling temporal dynamics highlights two additional drawbacks of BBNs: (1) the requirement to discretize continuous functions, which can result in lower precision of variable values, and (2) their inability to handle the feedback loops that are often important in ecology and other disciplines (Nyberg et al. 2006).

Although BBNs offer some advantages in addressing uncertainty and variability, they are still prone to many of the general limitations of other modelling approaches. In most applications it is unlikely that all sources of causality, uncertainty, and variability are incorporated in the model or enumerated without errors and inaccuracies. BDNs also are taxed by decision-rule uncertainty (Finkel 1990) that stems from difficulties in quantifying or comparing societal values and preferences. Poor enumeration or omission of relevant uncertainties, for example, results in overestimating system controllability and a too optimistic perception that some desired outcome will be attained (Kuikka et al. 1999).

BBNs, like other modelling approaches, should not dictate management decisions (Conroy 1999) but could aid decision-making as components of a larger process of management, research, and monitoring. The onus remains on the modeller to demonstrate causality and address potential explanatory variables not included in the model. Decision-makers should not assume that all relevant uncertainties (either informational or with respect to management objectives) and variability have been identified and included in the model. Marcot et al. (2006) and Nyberg et al. (2006) expand on several weaknesses of BBNs and caveats about their use in ecological and resource-management applications.

## Papers in this series

The remaining papers in this series on BBN applications in ecology and resource management provide readers with guidelines for their development and examples of recent applications of BBNs in these contexts. We briefly summarize the objectives of each paper here.

Approaches and insights concerning the correct building of BBNs are scattered widely throughout the literature. In “Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation”, Marcot et al. (2006) present practical procedures to guide the development, testing, and revising of BBNs and avoid spurious or unreliable models. They illustrate their approach with an example of an empirically based ecological BBN that predicts capture success for northern flying squirrels (*Glaucomys sabrinus* Shaw) as a function of the probability of squirrels’ presence due to habitat, and the probability of detection if they are present.

Applications of BBNs for resolving resource-management issues involving high-profile species are the focus of two papers. McNay et al. (2006) apply BBNs to aid in the evaluation of conservation-policy scenarios for woodland caribou seasonal ranges in “A Bayesian approach to evaluating habitat for woodland caribou in north-central British Columbia”. Following the procedures of Marcot et al. (2006), they develop BBNs to model seasonal ranges of woodland caribou and apply the BBNs to assess spatially explicit range conditions over four planning areas under optimal, current, and simulated future conditions that mimic a conservation-policy scenario and a natural-disturbance scenario. In this application BBNs help to articulate ecological understanding and threats to woodland caribou seasonal ranges, to focus decisions, and to support an assessment of attendant risks in the decision-making process.

In “A population-viability-based risk assessment of marbled murrelet nesting habitat policy in British Columbia”, Steventon et al. (2006) apply diffusion models implemented in a BBN framework to conduct population-viability analyses for the Marbled Murrelet (*Brachyramphus marmoratus* Gmelin). They use this approach to make regional and coastwide population-resilience assessments, considering policy inputs such as the amount and quality of nesting habitat, the number of subpopulations, and the time scale of the assessment. In addition to allowing explicit and flexible inclusion of uncertainty, the BBN approach permits rapid and interactive modifications of parameter value weightings (to explore sensitivity) and probability distributions (to express assumptions representing views of multiple decision-makers).

In Walton and Meidinger’s (2006) paper, “Capturing expert knowledge for ecosystem mapping using Bayesian networks”, BBNs are applied, apparently for the first time in British Columbia, as the knowledge base (i.e., a set of rules defining relationships between input variables and output predictions) for predictive ecosystem mapping. Large-scale ecosystem maps are fundamental tools for land managers responsible for assessing the impacts of resource-extraction activities such as forestry on other resource values (e.g., woodland caribou; McNay et al. 2006). Although map-accuracy results are similar to the prevailing belief-matrix approach to predictive mapping, the authors conclude that BBNs are easier to develop, interpret, and update.

In the final paper of this series, “Using Bayesian belief networks in adaptive management”, Nyberg et al. (2006) note that formal models are not always applied in adaptive-management programs and argue that many such programs would benefit from the use of the powerful and easily grasped modelling approach of BBNs. They outline the application of BBNs in the adaptive-management process and provide a supporting case example of a BBN applied to the adaptive management of forests and terrestrial lichens important as winter forage for woodland caribou. Important benefits of a BBN in this context are the promotion of a shared understanding of the system and the fomenting of rigorous consideration of alternative resource-management policies.

## Conclusion

BBNs are effective tools in structuring and focusing ecological research. They can be applied in two main ways to guide ecological research. The first way is to evaluate understanding of the overall functioning of the ecosystem portrayed. Research can focus on the “arrows” of the BBN and address the functional relationships of the ecosystem, or on the “rules” used to construct the conditional probabilities for a node and address the mechanisms that describe the interaction of factors in determining the values of resulting response variables. Research and BBN modelling can address questions as to what ecological processes are involved, which ones are most important in influencing outcomes, how they interact, and how predictor variables contribute to ecological processes.

The second use of BBNs in research is to evaluate the values of the response nodes. Research can focus on field evaluations that test the model and can provide empirical information that is quantitative, useful, and focused on a key ecological variable. BBNs can aid such research by identifying variables that have the greatest influence on outcomes but are understood the least, and by supporting the structuring and designing of adaptive-management trials to test responses to management decisions.

Most applications of BBNs for resource-management purposes should be placed within a framework that supports learning from what we do, links management to science, and promotes continual improvement in management protocols. We recognize seven steps in the development of such a framework: (1) the need for a decision is acknowledged (Olson et al. 1990*a*); (2) the problem is clearly articulated by engaging the stakeholders; (3) a "causal-web" understanding of the system (the "model") is built; (4) potential future consequences of each decision are listed, probabilities are assigned, and values (utilities) of each identified outcome are calculated (risk analysis); (5) the decision-maker ("manager") articulates their decision criteria and risk attitude (risk management); (6) the decision-maker makes the appropriate decision (Olson et al. 1990*a*); and (7) the researcher conducts supportive field experiments and monitors clearly established indicators to provide baseline information, ensures that activities are in compliance with the decision, determines the effectiveness or success of the decision with respect to desired future conditions, and validates the assumed causality under which the decision was derived. In essence, these steps define an adaptive-management program (Nyberg et al. 2006) with the proviso that field experiments and monitoring result in iterative refinement of steps 2 through 7. BBNs can play increasingly helpful roles within an adaptive-management framework such as causal-web models to aid understanding of ecosystem response (step 3) within larger modelling environments that support decision-making and resource management, and as decision networks (steps 4–6) that clearly display the anticipated effects of alternative management decisions and strategies.

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