



Review

# Choice and development of decision support tools for the sustainable management of deer–forest systems

Jean-Pierre Tremblay<sup>a,b,c,\*</sup>, Alison Hester<sup>c,d</sup>, Jim Mcleod<sup>c</sup>, Jean Huot<sup>a,b</sup>

<sup>a</sup>Département de Biologie, Chaire de Recherche Industrielle CRSNG-Produits forestiers Anticosti,

Université Laval, Pavillon Alexandre-Vachon, Qué., Canada G1K 7P4

<sup>b</sup>Centre d'études nordiques, Université Laval, Qué., Canada G1K 7P4

<sup>c</sup>The Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

<sup>d</sup>Northern Studies Centre, Aberdeen AB24 3UU, UK

Received 19 August 2003; received in revised form 19 October 2003; accepted 17 November 2003

## Abstract

Situations where a natural resource is both an asset, as well as a threat, to the integrity of ecosystem function and biodiversity are difficult to manage sustainably. One such situation happens when native deer populations, which are managed for sport are overexploiting forests to a point where they severely compromise natural forest regeneration. Managers facing those situations need support from the scientific community to analyse and synthesise information on deer–forest relationships and thus help to predict the potential outcomes of different management options for both the deer and the forests. Research scientists are increasingly expected to provide expertise and support into the decision-making process. One way to achieve this is to develop decision support tools (DSTs) based upon sound, scientific understanding of the deer–forest systems. Our objective is to explore a range of approaches that have been used for the development of DSTs for deer–forest management and to propose criteria for selecting a specific approach or combination of approaches for specific situations. DST and research-oriented models were catalogued according to two modelling paradigms: bottom-up models, which simulate systems through inductive inference, by scaling up from fundamental processes to the inherent behaviour of the system—the best known applications are forest gap and individual-based models; and top-down models which proceed by deductive, rule-based inference—they include expert systems, qualitative simulation models, frame-based models, Markovian process models and Bayesian networks. Uncertainty assessment in both modelling paradigms is discussed. The analysis is put in the context of two very different examples of deer–forest systems currently requiring DST development to guide their management: (1) the upland red/roe deer—fragmented temperate/boreal forest system of Scotland; and (2) the white-tailed deer—eastern boreal forest system of Anticosti Island, Québec, Canada. We conclude that a top-down approach with explicit uncertainty assessment should be aimed for, as a deliverable product to the end-users, keeping in mind that simulation models from the bottom-up family may be required to gain insights about the underlying mechanisms.

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**Keywords:** Plant–herbivore interactions; Boreal forest; Deer browsing; Ecological modelling; Decision support tools; Uncertainty

\* Corresponding author. Present address: Département de Biologie, Chaire de Recherche Industrielle CRSNG-Produits forestiers Anticosti, Université Laval, Pavillon Alexandre-Vachon, Qué., Canada G1K 7P4. Tel.: +1-418-656-2131x8152; fax: +1-418-656-2043.

E-mail address: [jean-pierre.tremblay@bio.ulaval.ca](mailto:jean-pierre.tremblay@bio.ulaval.ca) (J.-P. Tremblay).

## 1. Introduction

Decision-making in conservation and natural resource management is a bold enterprise. Stakeholders entrusted with the responsibility for sustainable management of the natural heritage need to integrate complex ecological processes, social, cultural and political values, as well as economic feasibility. The more complicated the management system and the greater the volume of information to be considered, the more difficult it is for managers to assimilate and interpret the essential information, which increases the likelihood of poor decisions being made (Cain, 2001). In fact, people have a tendency to believe that the accuracy of their forecasts increases with more information; such an illusion of knowledge is an obstacle to good management (Montier, 2002). Situations where a natural resource is a major asset as well as a threat for ecosystem integrity are especially difficult to manage. One such situation occurs when wild deer populations managed for hunting are overexploiting forests to a point where they severely compromise natural regeneration (Gill, 1992a; Hobbs, 1996); this type of situation forms the focus of this paper. It is well known that selective browsing by deer can reduce the establishment of preferred tree species and alter forest successional patterns (Miller et al., 1982; Gill, 1992b; Alverson and Waller, 1997; Stromayer and Warren, 1997; Potvin et al., 2003). Deer can also induce major changes in forest understorey plant communities (Putman et al., 1989; Hester et al., 1991; Waller and Alverson, 1997; Augustine and Frelich, 1998; Rooney, 2001). Furthermore, impacts of heavy browsing on other animal species have also been reported (Putman et al., 1989; de Calesta, 1994). Therefore, heavy herbivore impacts in forest areas can present problems not only for wood production, but also in relation to wider resource management, conservation and biodiversity issues, both nationally and internationally (e.g. Council of European Communities, 1992; Beaumont et al., 1994; UK Department of the Environment, 1994; Waller and Alverson, 1997; Canadian Council of Forest Ministers, 1998; Danell et al., 1998; Humphrey et al., 1998).

In recent years, deer–forest conservation issues in boreal and temperate forests of Europe and North America have shifted from a primary focus on habitat management to increase carrying capacity for deer and restrictive hunting regulations, towards a focus on

reduction of deer impacts on ecosystems and the concept of sustainable deer populations (Humphrey et al., 1998; Hester et al., 2000a). Accordingly, natural resource managers are increasingly asked to take more complex decisions that integrate multiple and interacting information, to show transparency in their decision process and to evaluate trade-offs publicly (Bunnell and Boyland, 2003). Managers facing those situations need support from the scientific community to analyse and synthesise information and help to predict the potential outcomes of management options on ecosystem sustainability. One way to provide such support is to develop decision support tools (DSTs), which are defined here as computer-based systems that provide information by means of forecasting models and access to databases, for example geographical information systems or climatic databases, in order to support a decision-maker in complex and un-/semi-structured management issues (Klein and Methlie, 1990; Turban, 1995). Unstructured decision-making refers to unclear and complex problems for which there is no standard solution. In the context of deer–forest systems, decision-making generally requires prediction of future states of the forest and deer populations according to multiple parameters. Thus, DSTs related to deer–forest systems need to provide managers with scientifically sound forecasts integrating deer population dynamics and forest development parameters under different deer and forest management schemes. Moreover, DSTs could be used to underpin further interactions between management and science as a basis for the development of adaptive management strategies (Walters and Holling, 1990).

Applied research scientists facing the challenge of integrating available knowledge into a deer–forest DST are confronted with a host of different models and techniques (Bunnell and Boyland, 2003). The objective of this paper is thus to explore a range of approaches that have been used to date for the development of DSTs for deer–forest management. As implied by the previous definition of a DST, much emphasis is put on the inference engine of a DST and less to the user-interface and report management sub-systems. We have chosen to include research-oriented models in our analysis since they are often found at the core of DSTs as quantitative predictive tools. From the analysis of those models and a selection of relevant DSTs, we propose criteria that could be used to select a specific approach

or a combination of approaches for the development of DSTs for deer-temperate/boreal forest systems, according to the knowledge-base available. We have selected, as examples, two very different deer-forest systems both currently requiring DST development to guide their management: (1) the upland red deer (*Cervus elaphus*)/roe deer (*Capreolus capreolus*)—fragmented temperate/boreal forest system in Scotland; and (2) the white-tailed deer (*Odocoileus virginianus*)—eastern boreal forest system of Anti-costi Island, Québec, Canada. The former represents a system with currently very little natural forest (<4%; Mackenzie, 1999; Gilbert, 2001) associated with heavy browsing by large herbivores (primarily red and roe deer, together with domestic sheep; Birks, 1988; Mitchell, 1990; Beaumont et al., 1994; Hester and Miller, 1995) and little regeneration; the second is a heavily forested system but with regeneration problems for the tree species preferred by deer (Côté et al., in press; Potvin et al., 2003).

## 2. Methods

Existing DSTs and research-oriented models of deer-forest system dynamics are reviewed and catalogued below according to two development paradigms: bottom-up and top-down. The former seeks to simulate systems through inductive inference, i.e. scaling up from fundamental processes (such as plant physiology, animal energetics, etc.) to the inherent behaviour of the whole system (Gordon, 2000). Included in this group are individual-, agent- and process-based models. The complexity of deer-forest systems requires translation from reality and simplification of natural mechanisms through statistical modelling and mathematical formulation (Botkin et al., 1972; Bugmann, 2001; Bunnell and Boyland, 2003). Forest gap models are built according to the bottom-up paradigm. The top-down paradigm of DST development proceeds by deductive, rule-based inference. It models the system using hypotheses, e.g. expert knowledge, and rules to reach conclusions about its state (Tester et al., 1997; Cain, 2001). Expert systems and their variants are examples of top-down DSTs. The two paradigms are not mutually exclusive; some DSTs may use both approaches at different levels, thus the categorisation used here is based on the dominant approach used for any specific tool.

Considering the objective mentioned earlier, we did not try to review all existing tools but rather to get an overview of the main existing DSTs and predictive models based on the two main development paradigms. Preference was given to DSTs and models related to deer-forest systems. DSTs associated with other plant-herbivore systems were also considered when the approach they used was lacking in the deer-forest interactions literature. Considering the lack of empirical knowledge available to describe the multiple processes of deer-forest systems, particular focus was placed on approaches that allow decision-makers to account and deal with uncertainty in order to reduce the illusion of control over the outcome of uncontrollable events (Montier, 2002). Information about DST/model structure, input and output was generally obtained directly from scientific literature. In some cases, authors were contacted and asked for a compiled version of their models so that further details could be extracted.

## 3. Bottom-up modelling of deer-forest interactions

### 3.1. Forest gap models

Most models of deer-forest interactions in the bottom-up category belong to the forest gap model of the JABOWA/FORREST family (Botkin et al., 1972; Shugart and West, 1977; Table 1). Those models simulate the recruitment, establishment, growth and mortality of individual trees in a gap, usually the size of a fallen tree, through mathematical or statistical rules based on species-specific natural life history traits. Changes in a gap environment, induced by the plant themselves (e.g. shading) or by a disturbance, shape the succession pattern in line with the relative competitive abilities of the plants. Light is the main limiting resource for individual trees in a gap. The overall forest dynamics are simulated as the sum of discrete gap dynamics. Forest gap models have been extensively used to simulate forest community development under different disturbance regimes. One of the early gap models includes a simple rule to simulate disturbance caused by selective browsing by deer (FORET; Shugart and West, 1977). The rule randomly allocates a higher susceptibility to browsing in some

Table 1

Level of mechanistic representation of the plant and animal processes included in the main sub-models of bottom-up deer forest models (0: not simulated, 1: simple empirical/knowledge-based rules or stochastic functions, 2: combination of empirical functions and mechanistic equations, 3: highly mechanistic). Included sub-models are those that are considered to be of primary importance in the simulation of deer–forest interactions based on Price et al. (2001) and Weisberg et al. (in press)

	Forest gap					Gap/system flow SAVANNA <sup>f</sup>	Individual foraging EASE <sup>g</sup>
	FORET <sup>a</sup>	FORECE <sup>b</sup>	ZELIG <sup>c</sup>	FORGRA <sup>d</sup>	FORSPACE <sup>e</sup>		
<b>Plant model</b>							
<b>Tree layer</b>							
Growth	2	2	2	3	3	3	0
Mortality	1	1	1	2	3 <sup>h</sup>	3 <sup>h</sup>	0
<b>Shrub layer</b>							
Sapling growth	0 <sup>i</sup>	–	0 <sup>i</sup>	0 <sup>i</sup>	3	3	1
Mortality	1	–	0	0	2 <sup>j</sup>	3	1
<b>Herb layer</b>							
Seedling growth	0	1 <sup>k</sup>	2	3	3	3	0
Seedling mortality	0	1	2	3	3	3	0
Seedling establishment <sup>l</sup>	1	1	1	3 <sup>m</sup>	3	3	0
Herbs/grass dynamics	0	0	0	2	3	3	0
<b>Herbivore model</b>							
Energetics, body weight	1	0	0	0	2	3	3
Foraging, distribution	0	0	1	0	1 <sup>n</sup>	3	3
Diet selection, intake	1 <sup>o</sup>	1	1	2	2 <sup>o</sup>	2 <sup>p</sup>	2
Population dynamics	0	0	0	0 <sup>q</sup>	2	3	3
Cervid species <sup>r</sup>	Ov	Cc, Ce	Ov	Cc, Ce	Cc, Ce	Ce	Aa, Ov
Non-cervid herbivores	Small mammals	Rr		Bt, Eq	Bt, Eq		

Included sub-models are those that are considered to be of primary importance in the simulation of deer–forest interactions based on Price et al. (2001) and Weisberg et al. (2003). Forest gap models reviewed illustrate a gradient of bottom-up deer–forest models.

<sup>a</sup> Shugart and West (1977).

<sup>b</sup> Kienast et al. (1999).

<sup>c</sup> Urban et al. (1991) as adapted by Seagle and Liang (2001).

<sup>d</sup> Jorritsma et al. (1999).

<sup>e</sup> Kramer et al. (2001, 2003).

<sup>f</sup> Weisberg and Coughenour (2003), balance nutrient cycling model.

<sup>g</sup> Moen et al. (1997, 1998).

<sup>h</sup> Simulates decomposition of organic matter and inclusion in the litter layer.

<sup>i</sup> Saplings are considered as trees from the moment they are recruited into the population at a fixed DBH  $\geq 0.5$ –2.5 cm.

<sup>j</sup> Species-specific trampling mortality rate in the shrub layer.

<sup>k</sup> Seedlings and saplings between 0.1 and 1.30 m are considered susceptible to browsing and grouped into one layer.

<sup>l</sup> Establishment includes seed fall, germination, and initial growth and survival.

<sup>m</sup> Seedlings initially described as a cohort, individuals are added to a plot when height or age of a cohort exceeds a critical value.

<sup>n</sup> Selection of a plot depends on digestibility of the plant in the plot, herbivores are assumed to have perfect knowledge of the area and eat until the depletion of metabolic energy before moving to a lower quality plot.

<sup>o</sup> A true or false state rule through which herbivores (deer and small mammals) reduce sapling recruitment of browse-sensitive species.

<sup>p</sup> Only one tree species (*P. tremuloides*) is included in this model and it is assumed to represent  $\sim 7\%$  of elk diet in winter.

<sup>q</sup> *A. alces* (Aa), *Bos taurus* (Bt), *C. capreolus* (Cc), *C. elaphus* (Ce), *Equus callabus* (Eq), *O. virginianus* (Ov), and *Rupicapra rupicapra* (Rr).

<sup>r</sup> Static deer density for each simulation scenario.

years, resulting in failure of the preferred tree species to establish. Although FORET has been influential in the field of forest gap modelling, few gap models have carried on with the selective browsing/disturbance rule

or tried to improve it (but see Weisberg et al., in press for a review).

Gap models included in Table 1 seek to quantify the impacts of deer grazing/browsing on forest

development FORGRA (Jorritsma et al., 1999); FORSPACE (Kramer et al., 2001, 2003); ZELIG (Urban et al., 1991) as adapted by Seagle and Liang (2001) and FORECE (Kienast et al., 1999). FORET (Shugart and West, 1977) is included as a comparative reference. EASE (Moen et al., 1997, 1998) and SAVANNA (Coughenour, 2001; Weisberg and Coughenour, 2003) are non-gap deer–forest models and will be discussed later. These models illustrate a gradient of complexity in their representation of the effects of deer herbivory. Models of the JABOWA/FORET type are limited in their representation of disturbance caused by deer herbivory since they do not explicitly simulate the life history stages that are affected by direct and indirect impacts of deer. Saplings spontaneously enter those models at a mean DBH size varying between 0.5 cm (Botkin et al., 1972) and 2.5 cm (Shugart and West, 1977), the number of recruits being modulated by environmental filters (light availability, sum degree-days, soil moisture content, etc.; Bugmann, 2001). In Table 1, the plant model section reveals that most gap models concentrate on tree stages and, to a lesser extent, sapling stages. Earlier life stages are generally not considered because of: (1) the high stochasticity and lack of knowledge of growth and mortality rates of seedlings and saplings; and (2) the computational demand of handling thousands of small individuals that are generally doomed to die (Bugmann, 2001). FORECE uses site-specific deer grazing intensity data on tree seedlings and saplings between 0.1 and 1.3 m as well as species-specific empirical height and diameter growth functions to simulate the effects of deer on seedling growth and mortality. In ZELIG, photosynthetic curves are used to estimate seedling (>0.1 m) and sapling growth in relation to light availability in the understorey; empirical data from marked seedlings were used to construct seedling mortality algorithms. FORGRA and FORSPACE introduce higher explicit simulation of growth mechanisms during the seedling and sapling life stages. Seedling growth is related to species-specific growth rate, leaf area index and light availability at the forest floor. Allocation algorithms partition newly formed biomass among organs for seedlings as well as trees and saplings. Mortality of seedlings depends on competition for light and space and on the presence of herbivores. Saplings are recruited when a seedling cohort reaches a threshold value. Weisberg et al.

(2001) are developing a mechanistic model of browsing effects on sapling growth coupled to the forest gap model FORCLIM (Bugmann, 1996).

Apart from direct effects on small tree growth and mortality, deer browsing can indirectly influence seedling establishment through local environmental changes. The removal of plant biomass is in some situations followed by a reduction of local soil resource depletion rates (water, nutrients, etc.) that can foster growth of invasive or browse-resistant species (Huntly, 1991). Selective foraging can also give rise to an apparent competitive gain in browse-tolerant species (Crawley, 1997b), facilitating their invasion of disturbed gaps. Invasive species can further reduce the availability of suitable germination beds through allelopathic effects (Crawley, 1997a) or change to the physical environment (reduced temperature and moisture, depth of the litter; Lieffers and Macdonald, 1993). On the other hand, large herbivores can in some instances aid germination by creating bare soil patches (Hester et al., 2000b). Selective foraging by moose (*Alces alces*) on hardwoods and avoidance of conifers has been shown to alter community composition and structure, which in turn can affect nutrient cycles and productivity (Pastor et al., 1993). When not accounted for, such positive feedbacks can significantly change forecasts about the evolution of a system. In the gap models shown in Table 1, only FORGRA and FORSPACE include a sub-model of herbs, grass and shrub dynamics in the understorey. This allows for a more realistic simulation of forage selection and intake and competition between seedlings and herbs, grasses and shrubs. In FORGRA, the cover of herbs and shrub layer is used as a proxy for germination bed suitability. FORSPACE explicitly simulates the turnover of plant parts (dead trees, foliage, branches, stalks of herbs, roots and seeds) and their inclusion in the litter layer.

A complete simulation of the regeneration process should include seed production, dispersal and germination as well as seedling initial establishment and survival up to their recruitment in the sapling stage. Price et al. (2001) reviewed existing forest gap models with regard to their ability to represent regeneration processes, in particular in relation to herbivore impacts.

Table 1 also demonstrates the fact that few gap models actually provide a complete integration of plant–herbivore interactions including feedbacks of

intake on herbivore populations. The herbivore model of FORSPACE integrates a mechanistic population dynamics sub-model. According to the input from the energetics sub-model, itself being modulated by food intake and food digestibility, FORSPACE determines the annual proportion of pregnant females, number of births and mortality due to starvation and ageing in a given population. Individuals of the next population are then allowed to forage and their food intake is fed into the plant population model.

### 3.2. Other process-based models

The SAVANNA model is composed of highly mechanistic hydrologic, plant biomass production, plant population dynamics, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, ungulate population dynamics and wolf predation sub-models (Coughenour, 2001). It differs from previously reviewed forest gap models by the inclusion of the water cycle as a driving variable in gaps in combination with light (both link to monthly weather data). Since it has been developed to simulate grassland, shrubland, savanna and forested ecosystems, SAVANNA includes strong representation of the relationships between the herbaceous layer, tree layer and tree establishment. It can be used to simulate multi-species plant communities, but it is designed to simulate interactions among plant functional groups such as sun-adapted herbs, shade-tolerant herbs, shrubs, deciduous trees and evergreen trees. Weisberg and Coughenour (2003) used SAVANNA to estimate levels of elk (*C. elaphus nelsoni*) numbers that would be compatible with long-term, significant aspen regeneration (*Populus tremuloides*). It should be noted that SAVANNA is the only bottom-up model reviewed that includes the predation trophic level.

EASE (Moen et al., 1998) tackles the simulation of plant–herbivore interactions from the animal point of view. An animal model simulates the energetics of ruminants in a virtual, spatially explicit environment (Moen et al., 1997). The animal model is linked to a plant-growth model and to a population model for long-term simulations. The animal model determines the energy requirements of individual animals based on their body condition. The foraging and food intake process is described using rules to determine when an animal decides to stop feeding in a location

and where to move while feeding. Following food intake, EASE simulates digestion and allocates metabolism energy to different vital functions of the animal. Conversely, the plant-growth model is based on generic plant-growth relations that modulate the availability of browse based on the level of browse intake. Moose population dynamics are simulated using an age-structured model where survival and natality rates are adjusted annually based on body mass changes of a reference cow moose. Food availability and distribution is simulated in a habitat model.

### 3.3. Relevance of bottom-up modelling for the Scottish and Anticosti deer–forest systems

Bottom-up models are synthesis and predictive tools primarily used to acquire scientific understanding of the interactions between components of a system in conditions where other techniques may be constrained by time or where direct experiments may be inappropriate. Their forecasting capacity makes them suitable as decision support tools in themselves, if: (1) they maintain strong connections to the real world; (2) they include management activities as driving variables (Weisberg et al., in press); (3) the data required to run the model are relatively easy to gather (e.g. local climate, deer population, vegetation composition and biomass); and (4) if they account for uncertainty of the model outcomes.

Integrated bottom-up deer–forest models should include a seedling/sapling growth model component as an intermediary between forest and deer population models, since deer mainly impact upon these life history stages of trees (Weisberg et al., in press). The dynamics of the shrub/grass layer should also be simulated, since plants from this layer are a source of food for herbivores and interact with tree regeneration through competition and/or modification of germination beds (Piggott, 1983; Cornett et al., 1998; Jorritsma et al., 1999; Saunders and Puettmann, 1999; Bell et al., 2000). FORSPACE and SAVANNA include most of the previously stated requirements, but both models require parameterisation for different soil types, tree and herbivore species and include detailed simulation of specific components that may not be relevant to management objectives in all areas.

The complexity of bottom-up models may make them difficult to master and, therefore, may put off the decision-makers from using them directly. For example, a DST designed to assist the management of red deer on the open hill in Scotland (HillDeer) has been found to be difficult to use by novices or occasional users (I. Hope, pers. comm.). Although the main outputs of the model (vegetation and population dynamics over the course of the simulation) were designed to be easily interpreted by end-users, it has also been found that the underlying reasons for the changes in vegetation or population are not generally obvious and some skill in ecology is required to properly interpret the more detailed outputs of the model and translate that interpretation into useful changes in management activities. This experience and the recognition that, in general, the uptake of DSTs by managers of agri-ecosystems has been low (McCown et al., 2002) has led to a rethinking of the best way of implementing DSTs. One approach is to provide consultancy services to the end-user community whereby experts ‘drive’ the tool rather than expecting the decision-makers to run the DST directly themselves. This approach removes the need for specific training and expertise for the end-user, as well as the overhead of developing user-friendly interfaces, while allowing the addition of ‘expert’ interpretation of the results and the ability to set them in the required management context.

Knowledge gained using research-oriented models developed from the bottom-up paradigm can also be used to devise simpler predictive tools that grasp the key processes driving the dynamics of a system. For example, in relation to one of the case studies selected here (Augustine et al., 1998) and (Stromayer and Warren, 1997) suggest that one key process in the system is the existence of non-linear relationships between white-tailed deer and forest vegetation states; the conversion of balsam fir (*Abies balsamea*) forest to pure white spruce stands due to white-tailed deer browsing (Potvin et al., 2003) could lead to the existence of multiple equilibriums in this system (Scheffer et al., 2001). In such an example, a bottom-up, conceptual state-and-transition model could be usefully developed for management purposes (Westoby et al., 1989). However, scientific understanding of this system is not sound enough to conclude about the presence of more than one equilibrium. A controlled grazing experiment has been

implemented to examine whether there are thresholds of herbivory, sensu (Hester et al., 2000a), which shift the system between potential alternate stable states in the relationships between deer and forest regeneration. A bottom-up simulation approach could be used to widen the extent of the results to alternative deer densities and larger time and spatial scales, keeping in mind that simulation too far outside the range of the experiments will greatly increase uncertainty of the simulation results. At this stage, a parsimonious model, for example using a state-and-transition model built into a top-down approach as described below, could be developed as a deliverable DST.

#### 4. Top-down modelling of deer–forest interactions

##### 4.1. Top-down models

Top-down models usually emphasise the proximate management objectives using qualitative or semi-quantitative analysis and forecasting techniques (Starfield, 1997). Most of them share the basic requirement that variables must take ordinal rather than continuous values. It means that the system can only be described as having discrete successional stages, vegetation layer/functional groups or age/sex classes. Transition rules, either expressed as probabilities or expert knowledge, link the states so that the model can infer the status of the ecosystem at a later time. Those requirements are met in the state-and-transition conceptual model proposed by Westoby et al. (1989).

Plant et al. (1999) developed a qualitative simulation model establishing a relationship between the rules of a rule-based expert system and the transition rules of a state-and-transition model. Although not specifically addressing deer–forest systems in temperate/boreal forests, this model is reported here because of its potential applications in such systems. The method makes use of an expert system, a computer program that forms logical chains of transition rules, linked to discrete geographic units included in a GIS (e.g. forest stands). Each time step of the simulation is a successive execution of: (1) an a-spatial stage; and (2) a spatial stage. The a-spatial stage determines the future value of the system attributes of each geographic unit using the transition rules built into the

expert system algorithm. Those new attributes are stored in GIS layers (shapefiles). The spatial stage uses the power of the GIS to compute spatial interactions between units; for example, distance to the nearest unit with high cover of shrub may be calculated so that the probability of invasion by shrubs might be higher in the next time step. Each iteration uses the logical inference engine of the expert system to integrate the spatial information with the transition rules, generating a predicted landscape at a later time.

Starfield et al. (1993) developed an alternative modelling approach also rooted in the state-and-transition concept and expert system technology, in conjunction with the artificial intelligence concept of a frame to simulate ecological systems. Tester et al. (1997) used this so-called frame-based modelling strategy to examine the effect of weather, fire and deer population density on the management of a white pine (*Pinus strobus*) ecosystem. Tester et al.'s model is based on the principle that vegetation states can be explained using probabilistic rules, which respond to the model driving variable for disturbance and environmental conditions (Rupp et al., 2002). Each frame is an independent sub-model representing a vegetation state. The temporal dynamics of the system are partitioned in such a way that at any time in a simulation, only one frame is operational for a specific unit (stand, cell). Each frame calculates and monitors factors and processes that could cause a switch to another state. Quantitative and qualitative data are both used in the simulation, as well as probabilistic rules. Transition rules establish the occurrence of a switch to another state, deactivate the current sub-model and activate the sub-model corresponding to the new state initialised according to previous conditions and disturbance. Spatial variables can be introduced into the model using data from a GIS (Rupp et al., 2002).

State-and-transition can also be modelled numerically using Markov (Scanlan, 1994) and semi-Markov process models (Moore, 1990). Markovian models are stochastic mathematical models used to predict the future development of a successional sequence. Transition probabilities from one state to another are built into a matrix, which can be solved analytically or through simulation to predict equilibrium composition and steady-state probabilities. Estimation of transition probabilities can be a tedious task, especially when there are a lot of alternative states in the model (transi-

tion number = state number<sup>2</sup>). It is usually done using empirical data, chronosequences of vegetation surveys, published data (including expert knowledge) or process-based simulation model outputs.

Usher (1981) criticised the basic assumptions of Markov models which imply that: (1) transition probabilities between states are constant over time; and (2) transition probabilities depend on the preceding states only, independently from previous ones. This may not hold true in many situations that prevail in nature; transition probabilities may change according to stochastic events, management actions or wider environmental change, such as global warming, while the states of the system are most probably influenced by previous successional stages. Scanlan (1994) reported applications that make use of multiple transition matrices corresponding to alternative weather periods or grazing management options, in order to bypass the violation of the first assumption. In the context of a dynamic simulation of a deer–forest system, this technique could be used to choose a specific probability matrix of vegetation changes, given the status of the deer population. Moore (1990) used a semi-Markov process to override the time independence assumption at the price of more complex mathematics. This also provides an analytical solution for backward inference, i.e. knowing the preferred final state of the system, the model can run backwards to infer the management decision that optimises the probabilities of reaching this state. This approach is commonly used in ecology.

Bayesian networks (BN) is a third approach drawn from decision analysis theory and related to expert systems that explicitly quantify uncertainty using probabilistic, rather than logical, inference (Charniak, 1991). In BN, key variables representing the system, each with discrete states, are built into a network using links suggestive of causal relationships. Each variable is associated with a conditional probability table containing the probability that a variable will be in a specific state given the states of those variables that affect it directly (parent variables sensu Cain, 2001). As with Markovian models, the information needed to fill the conditional probability table may come from empirical or published data, be elicited from expert knowledge or predicted from bottom-up model outputs (Peterman and Peters, 1998; Cain, 2001). When the conditional probability tables are built from empirical data, each event or record is used to adjust

the probabilities of reaching the event state given the status of its parent variables. In fact, the network is using a learning algorithm to increase the level of confidence in the value of the conditional probability tables in a way related to experience. Accordingly, probability tables built from a large number of events leads to more precise predictions and the addition of new information does not produce much change. When using expert knowledge, learning can be simulated as a large number of events to raise the level of confidence of the conditional probability table for which experts have higher belief. Probabilistic inference is the process of finding a posterior probability distribution, given a prior distribution, a network and some data. The prior probability distribution reflects knowledge or beliefs about the transition probabilities from one state to another before the study is conducted, while the data modify this distribution to produce the posterior distribution, i.e. the probabilities of outcomes of the different potential states that a

variable may take, according to the network structure (Bergerud and Reed, 1998).

The BN approach appears to have good potential for use in deer–forest DST’s, primarily because it includes: (1) a capacity to update its prior distribution as new information is obtained, in a process similar to human learning (Bergerud and Reed, 1998); (2) a diagrammatic representation that facilitates the understanding of the system and the uncertainty in the predictions (Fig. 1; Cain, 2001); (3) a common-sense interpretation of statistical conclusions (in the form of a given likelihood that a variable will be in a specific state given previous information); and (4) explicit assessment of uncertainties and its projection in time. However, BNs appear to be limited in their ability to model dynamic ecological systems in time and space. Simple BNs do not allow feedback loops among variables, particularly from the response variable (e.g. forest state) back to predictor variables (e.g. deer density; Marcot et al., 2001). However, it is possible to

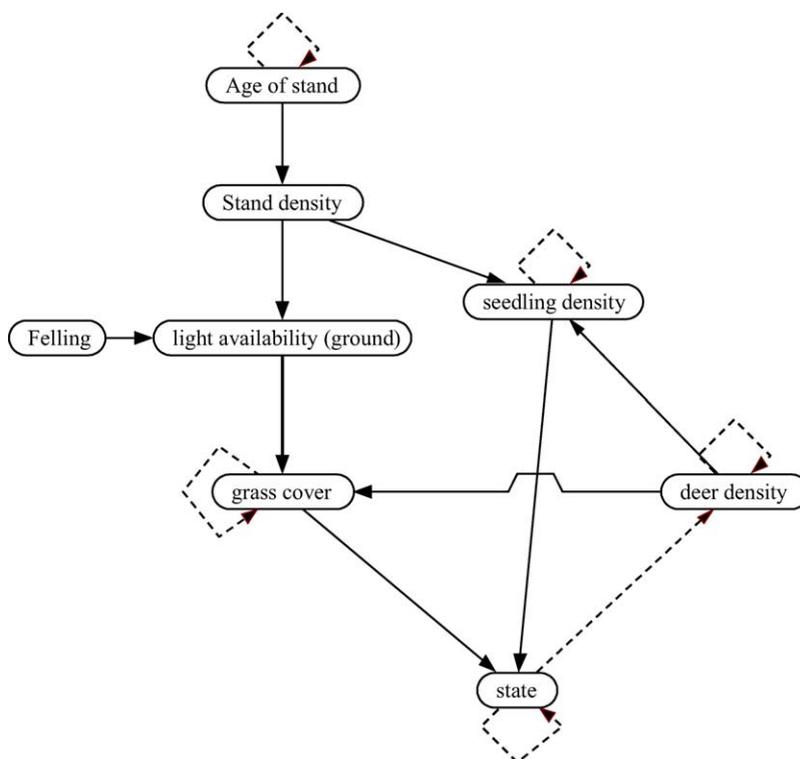


Fig. 1. Directed acyclic diagram of a partial Bayesian network before the execution of probabilistic inference. The network represents a simple deer–forest system (see text for description). Dotted line arcs represents feedback loops. Some relationships have been omitted (e.g. a feedback loop between felling and the following year stand density and age of stand) for the sake of clarity of the run version of the networks (see Fig. 3).

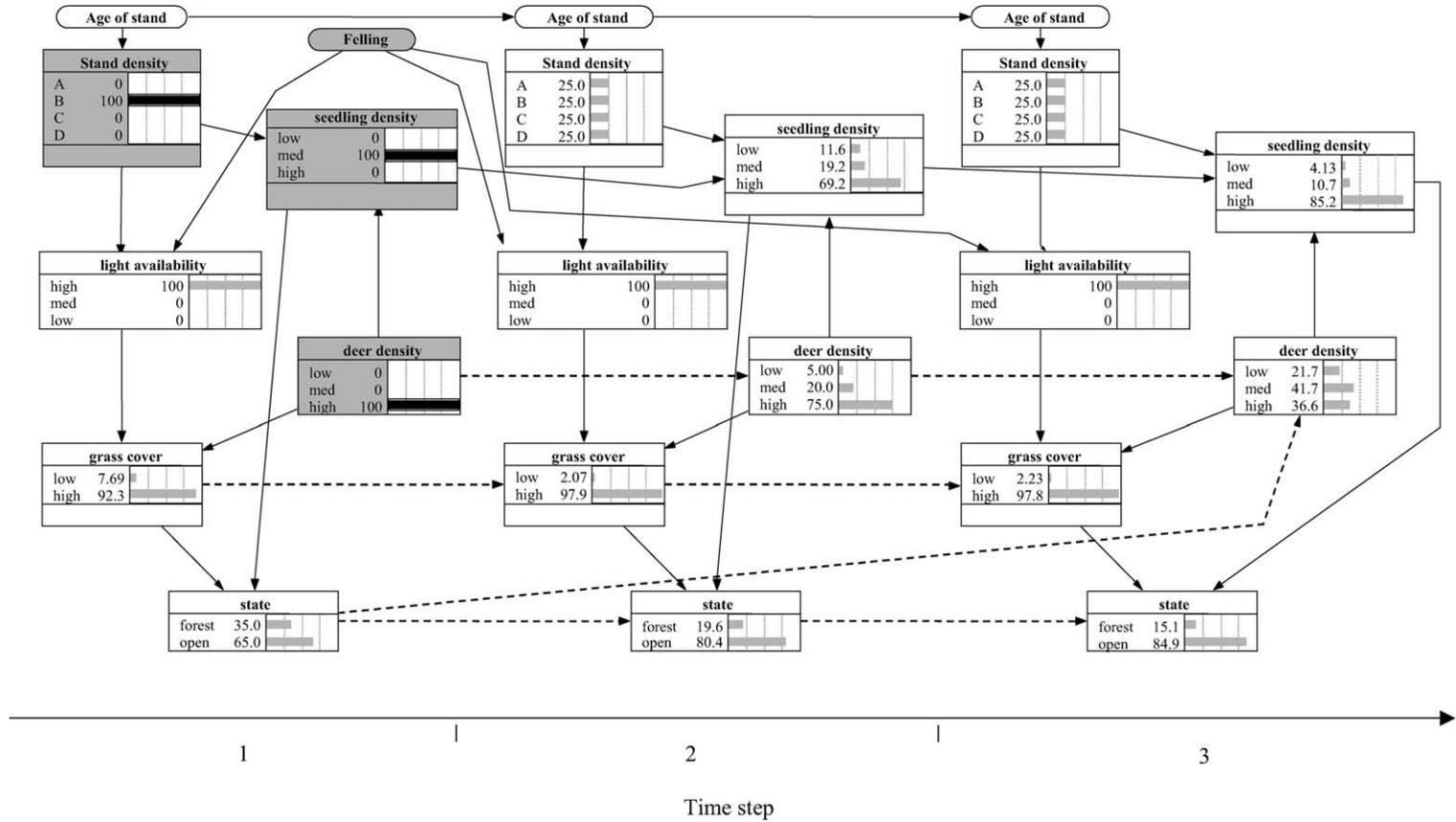


Fig. 2. A 3-year time-expanded version of the Bayesian network shown in Fig. 2. Numbers and bars in nodes are posterior distributions calculated using probabilistic inference based on their conditional probability table (fictive prior probability tables). Highlighted nodes denote variables for which the actual state is known or simulated. Dotted line arcs represent feedback loops.

build feedback loops by expanding the network in time, at the price of a less concise BN (Cain, 2001), as illustrated in Fig. 2. The main limitation of BNs is related to the large amount of data required when conditional probabilities are based on empirical data, although simulated learning could be used to reduce this problem (Cain, 2001).

#### 4.2. Potential applications of top-down modelling for an example deer–forest system

A striking observation that arises from the selected top-down modelling approaches is the absence of integration between vegetation and animal population dynamics. Grazing is simulated as a constant or user-controlled parameter. Habitat suitability models could be used as a proxy for animal abundance and BNs provide a promising framework for the development of such models (Marcot et al., 2001). BNs are explored further below in the context of an example deer–forest system. Fig. 1 illustrates a simple general Bayesian network relating the state of a system to forest stand characteristics affecting the availability of light to the grass/shrub layer, different management scenarios and deer population densities. The diagram includes feedback loops showing that the previous state of the system influences the current one, itself exerting a feedback on the deer population. Causal links show direct impacts of deer on seedling regeneration and indirect impacts on grass cover, through modification of competitive relationships between plants (of course the deer will also graze the grass—a direct effect). Grass cover is also influenced by light availability to the grass/shrub layer and by a positive feedback loop simulating invasive species. An expanded version of the network (Fig. 2) shows that a 2-year time lag between habitat state and deer has been built in the network. Predictive inferences using fictive conditional probability tables without any learning were performed using Netica (NORSYS, Vancouver, CA). This simple BN suggests that, conditional to the stand density being ‘B’ (61–80% canopy cover), seedling density medium, deer density high and the forest stand being felled, there is a 84.9% posterior probability that the system will be in an open state after 3 years, while there are 21.7, 41.7 and 36.6% probabilities that deer densities will be low, medium or high, respectively. This exercise gives an example of the potential of a

BN, although the development of a complete network would necessitate the specification of conditional probability tables using existing data and knowledge, and validation of the network prediction with independent data (Marcot et al., 2001).

For complex systems, as in a large scale, multiple species and habitats model of the Scottish uplands example, the modular design of frame-based models would provide a framework for continuous development as more knowledge and information becomes available. Thus the frame-based models could be used for general specification of the system and identification of key links in the system requiring targeted research funding. This would also allow for a direct feedback with end-users early in the development and promote a continuous improvement process. Combination of frame-based modelling and BN could thus be a powerful approach, but the feasibility of such a link remains to be explored.

To gain reliable knowledge, top-down models should be integrated into an active adaptive management framework (Walters and Holling, 1990; Starfield, 1997). In such a framework, management decisions are implemented as experiments built to test alternative hypotheses expressed as models with different assumptions. For the Anticosti Island white-tailed deer–boreal forest system example, three different hypotheses about the equilibrium of the system can be proposed in relation to: (1) monotonic negative linear relationships between deer density and system state (one stable state); (2) non-monotonic linear relationships (one stable state); and (3) non-linear relationships (multiple stable states; Scheffer et al., 2001). Monitoring could then be seen as a form of hypothesis-testing that feeds the iterative hypothetico-deductive scientific cycle.

## 5. Uncertainty assessment in DSTs

Uncertainty assessment is the process of describing, in quantitative terms, the quality and reliability of information and thus the degree of belief in a given outcome. Most reviewed models (including bottom-up models, qualitative simulation and frame-based models) incorporate stochasticity in their output through the use of random number generators or sampling from a distribution function. This allows some kind of

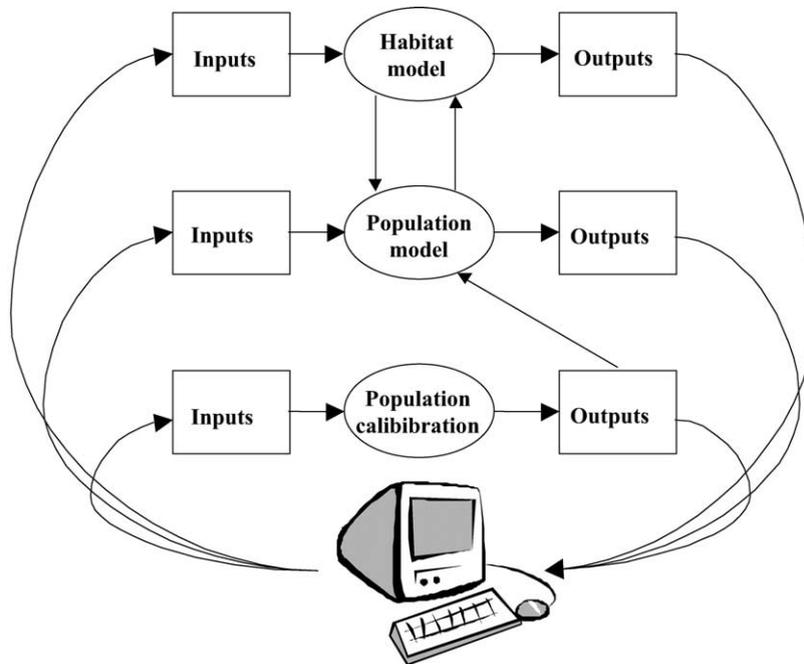


Fig. 3. Structure of the decision support tool HillDeer showing relationships between models. Each model can be run independently from one another but, when combined, the models dynamically exchange data. The population model can be calibrated using data from local deer populations (cull and count data, larder weights, age structure of the population, area).

uncertainty assessment by generating variation in output using multiple runs of the model (Monte Carlo simulation), but there is still uncertainty in the inputs which is not always addressed. A Bayesian framework is used to assess uncertainty in the input data for the population dynamics module of HillDeer (Buckland et al., 1998; Partridge et al., 1998). The overall DST consists of two main components, a habitat and a population model, sharing information between each other (Fig. 3). The habitat model describes the interactions between vegetation and the main large herbivores present (red deer, sheep and rabbits). The population model is built in a Bayesian inference framework to account for uncertainty about the population dynamics of the deer population. It integrates prior information about demographic parameters and age structure, obtained from count and cull data from the target population (Trenkel et al., 2000; Trenkel, 2001). The posterior distribution is simulated sequentially for a large number of slightly different parameter sets (2000 by default) and improbable sets are replaced each year in which there is a count available to test against the modelled parameter set (which

assumes that the counts are accurate—another cause of uncertainty). It should be noted that only the uncertainty in deer population levels and structures is accounted for in HillDeer. Similarly, uncertainty assessment in Markovian models implies the resolution of multiple matrices with slight differences in transition probability values.

Nevertheless, uncertainty considerations prompt for caution when developing a model in the context of a DST. Aggregation of complex fine-grain estimates across broad spatial extents or long time horizons over which management decisions apply may lead to high levels of uncertainty (Moir and Mowrer, 1995). In such cases, overconfidence in model outputs may misguide the decision process it was made to support. Bayesian networks may offer a useful framework for explicit uncertainty assessment in input data and in time.

## 6. Conclusions

Criteria for the choice of modelling strategy as a forecasting component of a DST need to be anchored

to the objective of taking efficient and quality decisions for the best possible management of natural resources (Starfield, 1997). Cleaves (1995) proposes that a good decision should: (1) accurately describe the problem; (2) use available information; (3) distinguish between reality, myths, values and uncertainties; (4) describe the consequences of alternative solutions; and (5) lead to choices that are consistent with multiple interacting values.

The level of detail that needs to be incorporated into a model, whatever the development paradigm, depends on the level of complexity of the system and on the available data. Bugmann (2001) suggests that a useful bottom-up model of forest dynamics must employ a combination of statistical and mechanistic approaches. Statistical models usually give a better fit to the data but they need extensive site-specific data for their parameterisation (see description of the population dynamic module of HillDeer above) and cannot deal with situations where dramatic changes occur. Mechanistic models are more general and require less experimental data for their construction, but it can be difficult to track the interactions of multiple processes and to account for multiple sources of uncertainty. The complexity of a model, be it built according to the bottom-up or top-down paradigm, should range from similar to slightly over-designed (the Parsimony Principle) in comparison with the input data that the end-users are expected to feed into it (Tester et al., 1997; Mowrer, 2000). As an example, there is no need for a detailed description of biogeochemical processes involved in forest succession dynamics if the managers of the deer–forest system do not have access to data on soil carbon and nutrients pools of the landscape; implicit embedding of those processes into global functional parameters might better serve the goal of the DST in such a case. The time and spatial scale of the model should also be relevant to the decision objective, i.e. in the case studies presented here, to deer ecology and to forest growth. It means that a DST should address management at a range of scales related to deer population dynamics, seasonal habitat use, spatial pattern of harvesting by hunters, tree regeneration strategies and disturbance regimes. Scaling to relevant space and time should ideally account for increasing uncertainty. As for time, only BN seems to allow such a projection of uncertainty, since time-expanded net-

works accumulate uncertainty from parent nodes at previous time steps, reducing the predictive power of the network as time passes. Other sources of uncertainty may be assessed using multiple BN with different basic assumptions, in terms of causal links or conditional probability tables, to account for different hypotheses. Kangas and Kangas (in press) concluded that the most important point is that uncertainty is not ignored, but that it is accounted for in decision-making one way or another and that decision-makers are aware of it.

Models used in DSTs should explicitly include management actions (Tester et al., 1997; Weisberg et al., in press). Since management objectives may change rapidly following new findings or catastrophic events, models should be easy to modify or to parameterise to represent new management scenarios. In the context of deer–forest systems, they need to predict threshold population sizes for regeneration of various tree species according to different deer and forest management requirements. Accordingly, the complex relationships between deer density and the state of different forest systems must be better understood to be able to do this (Humphrey et al., 1998; Hester et al., 2000a).

From a management perspective, decision-makers may not be immediately concerned about the mechanistic explanation of a system dynamic (Bunnell and Boyland, 2003). That is not to say that mechanistic knowledge is not significant to the decision-making process, but rather that decisions can perhaps be taken on qualitative and semi-quantitative information (e.g. information on forest stands state/species composition or deer density classes rather than species-specific volume of timber or deer counts). In our view, both bottom-up and top-down approaches are necessary for the improvement of natural resource management, as are inductive and deductive reasoning in the scientific thinking process. They should be examined as complementary tools which can be used independently or in combination, depending on the objective and available knowledge-base. We propose that a pragmatic approach with explicit uncertainty assessment, following the top-down paradigm, should be aimed at as a deliverable product to the end-users, keeping in mind that bottom-up simulation may be required to gain insights about the underlying mechanisms (which is often the only way for the scientist to improve their

understanding of the system and thus their end-users product). Moreover, the full power of both modelling approaches as tools to gain reliable knowledge, as well as decision support tools, relies on their use in an active adaptive management framework (Bunnell and Boyland, 2003).

## Acknowledgements

The authors would like to thank Iain Gordon for discussions and comments on a previous version of the manuscript. I.T.M. Jorritsma and A.M. Starfield kindly shared a compiled version of their model. JPT was supported by a postgraduate scholarship provided by Natural Science and Engineering Research Council of Canada and the Fonds de Recherche sur la Nature et les Technologies du Québec. Most of this work was carried out during a remote training program for JPT at the Macaulay Institute, supported by the Fonds de Recherche sur la Nature et les Technologies du Québec, in the context of his Ph.D. research program.

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