Research Report

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Standardized occupancy maps for selected wildlife in Central British Columbia

R. Scott McNay[1], Glenn Sutherland[2], and Donald G. Morgan[3]

Abstract

Habitat occupancy models were developed for 10 vertebrate species that we expected would demonstrate a gradient of response to extensive losses of lodgepole pine (*Pinus contorta*) and other linked habitat alterations resulting from the mountain pine beetle (*Dendroctonus ponderosae*) infestation and gradual changes in regional climate. A process-based Bayesian Belief Network approach was used to develop interlinked species models focussed at two levels of land management: (1) the forest stand level including changes in forest overstorey and understorey species composition, within-stand structures, canopy closure, and amounts of standing and fallen deadwood; and (2) the landscape level including changes in size of habitat patches, seral stage composition, and proximity to roads. We also considered indirect influences of broad ecological changes including alteration of some key species interactions (e.g., displacement from preferred habitat and [or] increased risk of mortality). We used results of this modelling to provide preliminary predictions of species occupancy in a large area of British Columbia designated by the Nature Conservancy of Canada as their Central Interior ecoregion. This work demonstrates an approach to building species occupancy models capable of representing the effects of large-scale disturbances on habitat supply at both the stand and landscape levels of habitat management. The resultant occupancy maps are also useful when integrated into various strategic planning initiatives including species recovery, silvicultural investments, and long-term conservation planning.

KEYWORDS: *Central Interior Ecoregion; climate change;* Dendroctonus ponderosae*; habitat supply modelling; lodgepole pine; mountain pine beetle;* Pinus contorta*; species occupancy.*

Contact Information

1 Forest / Wildlife Ecologist, Wildlife Infometrics Inc., PO Box 308, Mackenzie, BC V0J 2C0. Email: scott.mcnay@wildlifeinfometrics.com

2 Cortex Consultants Inc., Suite 2a–1218 Langley Street, Victoria, BC V8W 1W2. Email: gsutherland@cortex.ca

3 Ecosystem Protection and Sustainability Branch, B.C. Ministry of Environment, Bag 5000, Smithers, BC V0J 2N0. Email: Don.Morgan@gov.bc.ca

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Introduction

Even though infrequent but large-scale insect outbreaks are a natural phenomenon, the recent infestation of mountain pine beetle (*Dendroctonus ponderosae*) in British Columbia will undoubtedly have widespread and significant effects on wildlife (Bunnell et al. 2004) at a time when other ecological stressors (e.g., changes in climate regimes) are also occurring. With over 35% of the area of the Nature Conservancy of Canada's Central Interior ecoregion dominated by lodgepole pine (*Pinus contorta*), this infestation and its effect on wildlife ought to be a key factor in planning the conservation of biodiversity in the region. Chan-McLeod and Bunnell (2004) estimated that 195 vertebrate species may be affected by the outbreak and (or) the associated management intended to control or mitigate the beetle-mediated effects. Beetle-induced mortality of trees and the resultant timber-salvaging activities cause widespread changes in forest overstorey, understorey, and deadwood composition and structure (Eng et al. 2006) and therefore the ecological and physical characteristics of habitats available to wildlife. Wildlife also are experiencing chronic alterations of local and regional ecology attributed to changes in global climate (Pojar 2010; e.g., snowpack depths, timing of snowmelt in spring, availability of standing water in summer). Together, the mountain pine beetle and climate change are establishing unprecedented dynamics in the temporal supply and spatial locations of habitat elements where many wildlife species seek critical life requisites such as resources for foraging and reproduction. Potential long-term consequences for wildlife populations could include

- degradation of remaining habitat below the quality and configurations needed to sustain populations;
- altered community structure through shifts in ranges of other species, causing potential food-web shifts and altered predator prey interactions; and
- changes in dispersal opportunities resulting in altered gene flows and potential failures to access or re-occupy parts of species ranges (Pojar 2010).

These anticipated and widespread effects will challenge resource managers throughout British Columbia and elsewhere but especially in the Central Interior where beetle-induced tree mortality has had both intensive and extensive impacts on landscapes, stand structures, and ecological functions (see Eng et al. 2006).

Our overall goal was to develop habitat occupancy models for several vertebrate species on which to base studies of the potential effects on wildlife resulting from the broad changes in habitat characteristics expected from climate change-mediated disturbances as exemplified by the mountain pine beetle outbreak.

Strategic and widespread changes in natural resource use policy may be needed as a result of these fundamental ecological changes; however, what is the range of potential management interventions and how should policy change? Should the way in which we plan for the conservation of biodiversity be amended? Assessing consequences of large-scale ecological changes on biodiversity is a multi-faceted problem, requiring consideration of factors determining vulnerability, sensitivity, and adaptive capacity within and among species and ecological communities (Dawson et al. 2011). Importantly, we need to determine which species, habitats, and ecosystems will be most vulnerable, exactly what aspects of their ecological and evolutionary biology determine this vulnerability, and what we can do about managing this vulnerability and minimizing the realized impacts on biodiversity (Williams et al. 2008).

In this study, our overall goal was to develop habitat occupancy models for several vertebrate species on which to base studies of the potential effects on wildlife resulting from the broad changes in habitat characteristics expected from climate change-mediated disturbances as exemplified by the mountain pine beetle outbreak. Estimating the likely habitat occupancy by wildlife species over the foreseeable future (e.g., 10–80 years) could lead to more informed management decisions. Such decisions include the choice of methods used to recover populations of species at risk, the mitigation of beetle infestation impacts through silviculture investments, the establishment of robust conservation designs, and the assessment of the cumulative effects of ecological dynamics and resource development. The work fits well with the objectives of Central Interior Ecoregional Assessment led by Nature Conservancy of Canada and its partner organizations (Iachetti 2008; Nature Conservancy of Canada 2010). We worked with the assessment project team to ensure our species occupancy models would aid their conservation planning efforts in this region as well as elsewhere.

Specifically, our objectives were threefold:

1. to identify the key ecological linkages between habitat attributes affected by the mountain pine beetle and the life requisites needed by a broad range of vertebrate species of management concern;
2. to develop a common ecological process-based modelling framework for projecting habitat occupancy by these species in response to expected changes in habitat supply; and
3. to compare current and future occupancy patterns for these species, an indicator of potential biodiversity shifts, to inform regional strategic management planning.

In this research report, we focus on the first two of these objectives.

Study area

The Nature Conservancy of Canada's Central Interior ecoregion is a geographically distinct assemblage of natural communities extending over 25.7 million ha in the Sub-Boreal Interior and Central Interior ecoprovinces of British Columbia. The region consists largely of interior plateaus (Chilcotin, Nechako, and McGregor) that integrate with the mountain ranges of the Chilcotin, Bulkley, Tahtsa, Hart, Omineca, and Skeena areas. Major rivers are those of the Skeena, Dean, Nass, and the headwaters of the Fraser. Within the rain shadow of the Coast Mountains, the area generally has cold winters and hot summers typical of continental climates. About 35% of the forested land base consists of lodgepole pine stands, a tree species subject to frequent natural disturbances and the primary host for the recent outbreak of the mountain pine beetle. About 10% of the ecoregion is within protected areas and parks—Ts'yl-os, Itcha Ilgachuz, Entiako, Big Creek, and Tweedsmuir.

Methods

Choice of target species

We used recent scientific literature sources to compile a list of 32 species considered as most likely affected by the mountain pine beetle infestation in the province. We then scored each of the listed species using criteria that would reveal relative ranks of priority for including the species in our modelling. The criteria used were species conservation status, spatial distribution, habitat use, key ecosystem function, stakeholder interest, and perceived beetle-based threat to the species habitat needs (McNay et al. 2008). The list of candidate species was discussed with the Conservancy to ensure consistency between the species selected for habitat modelling and the subset of species selected by their Terrestrial Animals and Freshwater teams for the Central Interior assessment. Many of the criteria we used were similar to those used by the Nature Conservancy of Canada (e.g., for terrestrial animal species, see Horn 2011:54–71; for freshwater species, see Howard and Carver 2011:72–87).

The species conservation status was determined by its rank with the Council on the Status of Endangered Wildlife in Canada and the British Columbia Conservation Data Centre. Spatial distribution was defined as a coarse resolution (e.g., 1:250 000 scale) binary ("yes" or "no") status condition of overlap between the species and the beetle outbreak area and included areas forecast to become infested by the mountain pine beetle in the future. Habitat use was also defined as a coarse resolution binary statement of the species' requirement for forested areas dominated by lodgepole pine. The key ecosystem function designation is based on Bruce Marcot's definition of the general type of relationship between a species and its environment (Marcot and Vander Heyden 2001; see also ***http://www.spiritone.com:80/~brucem/kef1.htm***). Stakeholder interest was defined as a coarse resolution binary statement of the species having been previously noted as a management concern by stakeholders. The perception of beetle-based threats to the species was a general criterion under which we reviewed the nature of the potential threats from an outbreak. We ranked the 32 species by scoring each criterion with an overall weight and then scored each stratum under the criterion as a percentage of that weight.

Choice of the modelling approach

The focus of our work was to develop a tool that would assist the management decision-making process rather than as a tool for predicting ecological consequences (Bunnell 1989). Further, we considered that our application involved significant uncertainty in projected habitat patterns and that many ecological relationships related to the effects of habitat alterations of this magnitude were not presently well documented. It was primarily for these reasons that we chose to base the modelling on a functionally explicit (i.e., mechanistic), deductive, Bayesian platform (i.e., Bayesian Belief Networks, or BBNs) that operated on spatial data from a time series of simulated landscape changes. In general, BBNs consist of nodes and linkages, where nodes represent environmental correlates, disturbance factors, population factors, and species response indicators and states (see Marcot et al. 2006 for more detailed descriptions of terms and components of BBNs). Note that a primarily deductive modelling approach, such as we used here, is usually process based. The approach uses theory and conceptual ideas to define locations that are used by wildlife based on the relationship of environmental variables present at a site and the known (or assumed) life requisites of a species.

All nodes (factors) in a BBN are linked by probabilities, and the likelihood of each outcome is calculated as weighted posterior probabilities based on the modelled influence of all the antecedent (input) factors. Input nodes (e.g., the topographic and environmental prediction variables) contain marginal ("prior") probabilities of their states determined from existing conditions, intermediate nodes (e.g., describing attributes of each species' habitat) contain tables of conditional probabilities based on empirical studies and (or) expert judgement, and output nodes (species occurrence probabilities) are calculated as posterior probabilities.

We selected this approach on the basis of the following methodological considerations.

- **Algorithm structure:** Although correlative models could have sufficed for our purpose, we chose to construct models representing mechanistic ecological functions to provide a basis for subsequently asking questions about the potential effects of the beetle outbreak, the implications of climate change, and the inherent ecological interactions brought on by these two dynamic forces.
- **Ecological complexity:** We considered retention of ecological complexity to be important and therefore the availability of model reduction routines (i.e., sensitivity analyses) to also be important.
- **Treatment of time:** We designed the model platform to support the use of disturbance simulators as an enabling foundation for forecasting comparative scenarios of beetle attack, climate change, and management.
- **Spatial and temporal resolution:** We chose a grid size spatial resolution of 1 ha more or less arbitrarily. We varied the temporal resolution through the simulated scenarios—initial time steps were annual, whereas the time step was expanded to decadal later in the forecasts when less resolution was necessary.
- **Type of reasoning used:** We considered that deductive models would best suit our needs because our goals were focussed on existing researches, and thus supported explanations for particular environmental interactions.
- **Statistical foundation:** Bayesian methods were selected because: (1) they can offer practical guidance in situations where the hypotheses are not based solely on mechanistic or statistical models (e.g., physical properties of systems); and (2) the probabilities can be used in a relative sense (i.e., the relative evidence that alternative hypotheses are supported by the observations).
- **Outputs:** Most models produce an output that is related to (or can be interpreted as representing) the suitability of a site to meet the needs of a species. Suitability is typically a static picture presented for a specific time step. Evaluating the capability of a site involves the assessment of the potential for providing life requisites irrespective of limitations on the supply of resources. In other words, it is a depiction of habitat quality under optimal conditions that is independent of time or other non-site functional elements (i.e., displacement or mortality). Although we did model capability, our modelling goal was mostly focussed on characterizing the changing suitability of sites at varying time steps, as this is a relevant indicator for assessing effects on biodiversity.
- **Type of result:** Models can be either deterministic or stochastic in nature (and frequently the same model can be operated in either mode). Given uncertainties associated with the beetle outbreak, we believe spatial resultants obtained from a stochastic model better facilitate investigations of potential ecological outcomes resulting from this outbreak.

Species occupancy and the supply of life requisites

The modelling procedures largely followed those used by the Conservancy's internal project.[1] Software used to implement the modelling included ArcMap® (Environmental Systems Research Institute, Redlands, Calif.), Netica™ (Norsys Software Corp., Vancouver, B.C.), and MS Access® (Microsoft Corp., Redmond, Wash.). Data inputs (and their sources) used to characterize condition of habitat are displayed in Table 1.

[1] Sutherland, G. and R.S. McNay. 2008. Predicting species occurrences in response to large-scale disturbances. B.C. Ministry of Forests and Range, Victoria, B.C. Internal report.

TABLE 1. A list of data inputs used in Bayesian Belief Networks to model the potential effects of mountain pine beetle and climate change on selected wildlife in central British Columbia

Data input	Description	Data source[a]
Stand age for leading species	Projected age of the stand at each time step	TSR
Stand height for leading species	Projected height of the stand at each time step	TSR
Species type for leading/ secondary species	Species code for tree species	VRI
Species composition for leading/ secondary species	Percentage of each species in each stand	VRI
Disturbance history	Year and type of last disturbance	VRI, TSR, BCMPB
Inventory type group	Tree species composition	VRI
Site index	Measure of tree height at 50 years of age	VRI
Site class 5 m	Calculated from site index values	VRI
Non-forest descriptor	Indicates a forest polygon is potentially productive for supporting commercial forests	VRI
Non-productive code	Coded value identifying non-productive areas	VRI
Non-productive descriptor	Descriptor of non-productive areas	VRI
Cumulative kill %	Cumulative mortality of pine 2009–2026	BCMPB
Mountain pine beetle—age since death	Calculated age of pine since death	VRI, BCMPB
Number of large trees	Number of trees > 25 cm dbh	SS
Number of small trees	Number of trees 11–25 cm dbh	SS
Number of tiny trees	Number of trees < 10 cm dbh	SS
Remnant ages	Age for a part of the stand not killed by mountain pine beetle	TSR, VRI, BCMPB
Aspect	Aspect of a slope in degrees	DEM
Slope	Landscape slope in degrees	DEM
Elevation	Elevation in metres above sea level	DEM
Topographic curvature	Upward or downward curvature of landscape	DEM
Solar radiation	Summer and winter solar radiation inputs as influenced by topography, latitude, and date	DEM
Moisture regime	Moisture regime	PEM
Roughness	Terrain ruggedness	DEM
Ice and bare areas	Non-vegetated surfaces	BTM
Proximity to First Nations	Proximity to First Nations communities	BTM
Proximity to human	Proximity to other human communities	BTM
Winter precipitation	Precipitation sum December–February	PRISM
FHV	Fisher Habitat Value	WHR
BBHV	Black Bear Habitat Value	WHR
LHV	Lynx Habitat Value	WHR
WHV	Wolverine Habitat Value	WHR
Biogeoclimatic variant	Biogeoclimatic variant classification	BEC
PTR	Proximity to roads	TSR, QR
SiteMC_S1	Biogeoclimatic site class	TEM/PEM

[a] TSR refers to Timber Supply Review data (*http://www.for.gov.bc.ca/hts/tsr.htm*); VRI refers to British Columbia Vegetation Resources Inventory program (*http://www.for.gov.bc.ca/hts/vri/*); BCMPB refers to data from the annual aerial overview survey of forested land affected by the mountain pine beetle (*http://www.for.gov.bc.ca/hfp/health/overview/overview.htm*); SS refers to a data set of stand structure built for the Quesnel Timber Supply area (*http://www.tesera.com/index.php/forest-resource-planning-projects/100-quesnel-forest-inventory-imputation-of-stand-structure-attributes*); DEM refers to a digital elevation model from the British Columbia Terrain Resource Information Management program (*http://archive.ilmb.gov.bc.ca/crgb/products/*); PEM refers to predictive ecosystem mapping (*http://www.env.gov.bc.ca/ecology/tem/*); BTM refers the Baseline Thematic Mapping program (*http://archive.ilmb.gov.bc.ca/crgb/products/*); PRISM refers to Oregon State University's PRISM Group precipitation modelling (*http://www.prism.oregonstate.edu/*); WHR refers to Wildlife Habitat Ratings (*http://www.env.gov.bc.ca/wildlife/whr/*); QR refers to a spatial layer of roads within the Quesnel Timber Supply Area (data received from the Quesnel Mitigation Committee); BEC refers to a spatial coverage of the biogeoclimatic ecosystem classification system for British Columbia (*http://www.for.gov.bc.ca/hre/becweb/*).

We applied the BBNs to two management scenarios:

1. a Timber Supply Review simulation (B.C. Ministry of Forests and Range 2010) that included salvage of beetle-killed timber; and
2. a hypothetical landscape free of human influence but subject to disturbance by natural wildfire events.

We created this latter hypothetical situation by removing all human constructs from our model inputs (e.g., roads, communities, mines, etc.). Then, using the Spatially Explicit Landscape Event Simulator (Fall and Fall 2001), we aged the landscape by 400 years allowing only fires to disturb the landscape. This generated a random, mixed-age snapshot of the study area, where all evidence of forest harvest had been removed through growth and wildfire. As this simulator is a stochastic spatial model, the results of a natural disturbance simulation are never the same twice. Therefore, to allow for a statistical assessment of the stochastic properties, we ran five replicates of the natural disturbance scenario to create a hypothetical range of natural disturbance results.

Application of the BBN models occurred in a specific chronological order according to the need for spatial analyses or use of output in subsequent BBNs (e.g., outputs from one or more species models [important prey species] were required as inputs to other species' models [predators]). Accordingly, a sequence of six model runs, which were based on the chronological order of BBNs, was required to complete the analysis. The resultant of these BBN applications was then used to produce small- and large-scale habitat maps by first classifying the expected occupancy value in ArcMap. These same classes were used with SAS® (Statistical Analysis System, Cary, N.C.) to summarize the amount of area in each class for each species in each modelled scenario. The data summary was exported to MS Excel® (Microsoft Corp., Redmond, Wash.), in which graphs were made to reveal the percent change in habitat for each species through time using current conditions (as of 2009) as the basis to determine relative changes. We also calculated the mean and standard deviation of the amount of area that occurred in each habitat class for each species across the five simulations of natural disturbance using a standard normal statistical approach available in SAS.

Results

Choice of species

Four wildlife species—grizzly (*Ursus arctos*), caribou (*Rangifer tarandus*), wolverine (*Gulo gulo*), and fisher (*Martes pennanti*)—were ranked as highest priority for modelling by our methods (Table 2). Although these particular species range widely throughout the province and hence overlap with the beetle-affected area, their particular life-history characteristics flag them as sensitive species and therefore they were expected to respond negatively to increased fragmentation brought on by management responses to the beetle outbreak. Six other vertebrate species were ranked highly as research and mapping priorities and were expected to range widely in their response to the beetle infestation and climate change: Spruce Grouse (*Falcipennis canadensis*), marten (*Martes americana*), Lewis's Woodpecker (*Melanerpes lewis*), red squirrel (*Tamiasciurus hudsonicus*), badger (*Taxidea taxus*), and ermine (*Mustela erminea*).

Species occupancy

The probability of occurrence[2] for any particular species of wildlife can be conceptually generalized as the accumulation of life requisites that are regulated by the state of environmental attributes governing their availability (Figure 1). For example, caribou are known to require forage, cover from thermal extremes (in theory at least), minimal risk of mortality, and minimal energetic cost while optimizing, or at least satisfying, all life requisites. A unique environmental attribute that apparently reduces risk of mortality for caribou in predator-regulated situations is a landscape condition that includes large, contiguous tracts of range.

Large amounts of habitat allow caribou to occur at low density and this rareness is considered to limit interaction with predators (Bergerud 1992). Provided that the environmental attributes that affect life requisites are favourable, forage on a site is considered useful to caribou and, in conditions of low potential for mortality, caribou have an opportunity to remain healthy and to proliferate. This general conceptual model can be used to help identify stressors that cause changes in influential environmental attributes and particularly in those that may limit (i.e., imply a "threshold") and [or] regulate (i.e., imply a "systemic feedback") caribou populations.

[2] "Occurrence" is defined by Master et al. (2009) as an area of land and [or] water in which a species or ecosystem is (or was) present. In this case, our intention is to describe the probability of making such an observation.

TABLE 2. A ranking of priority for modelling habitat supply among species anticipated to be adversely affected by the mountain pine beetle outbreak in British Columbia. Note: The codes 1, 2, 3, and 0 are defined under the footnotes explaining each criterion: 10 000 replaces a 0 for calculation purposes.

		Status		Stakeholder[a]					Threat[b]										
Rank	Species	CDC[c]	COSEWIC[d]	MOE[e]	NCC[f]	Distribution[g]	Key ecosystem function[h]	Habitat pine[i]	Large trees	Dead trees	Coarse woody debris	Shrubs	Canopy	Deciduous	Continuity	Roads	Wetlands	UWR/WHA[j]
	Scores[k]	13	4	3	3	5	15	17	3	6	6	2	6	3	3	4	3	4
1	Fisher	1	0	1	1	7	3	2	1	1	1	1	1	1	1	1	0	0
2	Grizzly	2	3	1	1	9	3	2	0	2	1	1	2	0	1	1	2	1
3	Caribou	2	2	1	1	5	1	1	1	0	0	1	1	0	1	1	0	1
4	Wolverine	2	3	1	1	7	3	2	2	2	1	2	2	2	1	1	0	0
5	Spruce Grouse	3	0	1	0	9	2	1	2	0	2	1	1	0	0	0	0	0
6	Marten	3	0	1	1	9	2	2	2	0	2	0	1	2	1	0	0	0
7	Lewis's Woodpecker	1	3	0	0	1	2	2	2	1	2	1	1	2	0	0	0	0
8	Red squirrel	3	0	1	0	9	2	2	2	1	2	0	2	0	2	0	0	0
9	Badger	1	1	0	1	1	2	2	0	0	0	0	0	0	1	1	0	0
10	Ermine	3	0	1	0	9	2	2	2	2	2	0	0	0	2	0	0	0
11	Mule deer	3	0	0	1	8	2	2	2	0	0	2	1	0	0	0	0	1
12	Clark's Nutcracker	3	0	0	1	3	1	1	2	0	0	0	2	0	0	0	0	0
13	Canada lynx	3	0	0	1	5	2	1	0	0	2	0	0	0	0	0	0	0
14	Ruffed Grouse	3	0	1	0	9	2	2	0	0	2	2	0	0	0	0	0	0
15	Barrow's Goldeneye	3	0	0	1	9	2	2	0	0	0	0	0	0	0	0	1	0
16	Lesser Scaup	3	0	0	1	9	2	2	0	0	0	0	0	0	0	0	1	0
17	Red fox	3	0	1	0	9	2	2	0	0	2	0	0	0	0	0	0	0
18	Long-tailed weasel	3	0	1	0	5	2	2	2	2	2	0	0	0	2	0	2	0
19	Northern Goshawk	3	0	0	1	9	2	2	2	0	0	0	0	0	0	0	0	0
20	Great Blue Heron	2	3	0	1	2	2	2	2	0	0	0	0	0	2	0	1	0
21	Bighorn sheep	2	0	0	1	1	2	2	0	0	0	0	0	0	2	2	0	1
22	Bobcat	3	0	1	0	5	2	2	2	0	2	0	2	0	2	0	0	0
23	Least weasel	3	0	1	0	7	2	2	2	0	2	0	0	0	2	0	0	0
24	White-tailed deer	3	0	0	0	3	2	2	2	0	0	2	1	0	0	0	0	1
25	Elk	3	0	0	0	3	2	2	2	0	0	2	1	0	0	0	0	1
26	Peregrine Falcon	1	2	0	0	1	2	2	0	0	0	0	0	0	0	0	0	0
27	Mountain goat	3	0	0	1	6	2	2	0	0	0	0	0	0	0	2	0	1
28	Sandhill Crane	2	0	0	1	1	2	2	0	0	0	0	0	0	0	0	1	0
29	Moose	3	0	0	0	8	2	2	0	0	0	0	0	0	0	0	2	1
30	Thinhorn sheep	3	0	0	1	1	2	2	0	0	0	0	0	0	0	0	0	1
31	Sharp-tailed Grouse	2	0	0	0	2	2	2	0	0	0	2	0	0	1	0	2	0
32	Townsend's big-eared bat	2	0	0	0	2	1	2	0	0	0	0	0	0	0	0	2	0

[a] Species of concern listed by that stakeholder = 1, not listed = 0
[b] Highly dependent on component = 1, lower dependence on component = 2, component not needed = 0
[c] CDC (Conservation Data Centre) designation: red-listed = 1, blue-listed = 2, yellow-listed = 3
[d] COSEWIC (Council on the Status of Endangered Wildlife in Canada) designation: endangered = 1, threatened = 2, special concern = 3, not at risk = 0
[e] MOE (Ministry of Environment) designation: losers = 1, unaffected or winners = 0
[f] NCC (Nature Conservancy of Canada) designation: high priority = 1, moderate priority = 2, low priority = 3, no priority = 0
[g] Distribution is represented by a number between 1 and 10; the higher the number, the wider its distribution throughout the province.
[h] Represents number of Key Ecological Function categories: high = 3, medium = 2, low = 1
[i] Dependent on pine = 1, less dependent = 2
[j] Classified as requiring Ungulate Winter Range (UWR) or Wildlife Habitat Area (WHA) = 1, not classified as requiring UWR or WHA = 0.
[k] Weight of each criterion

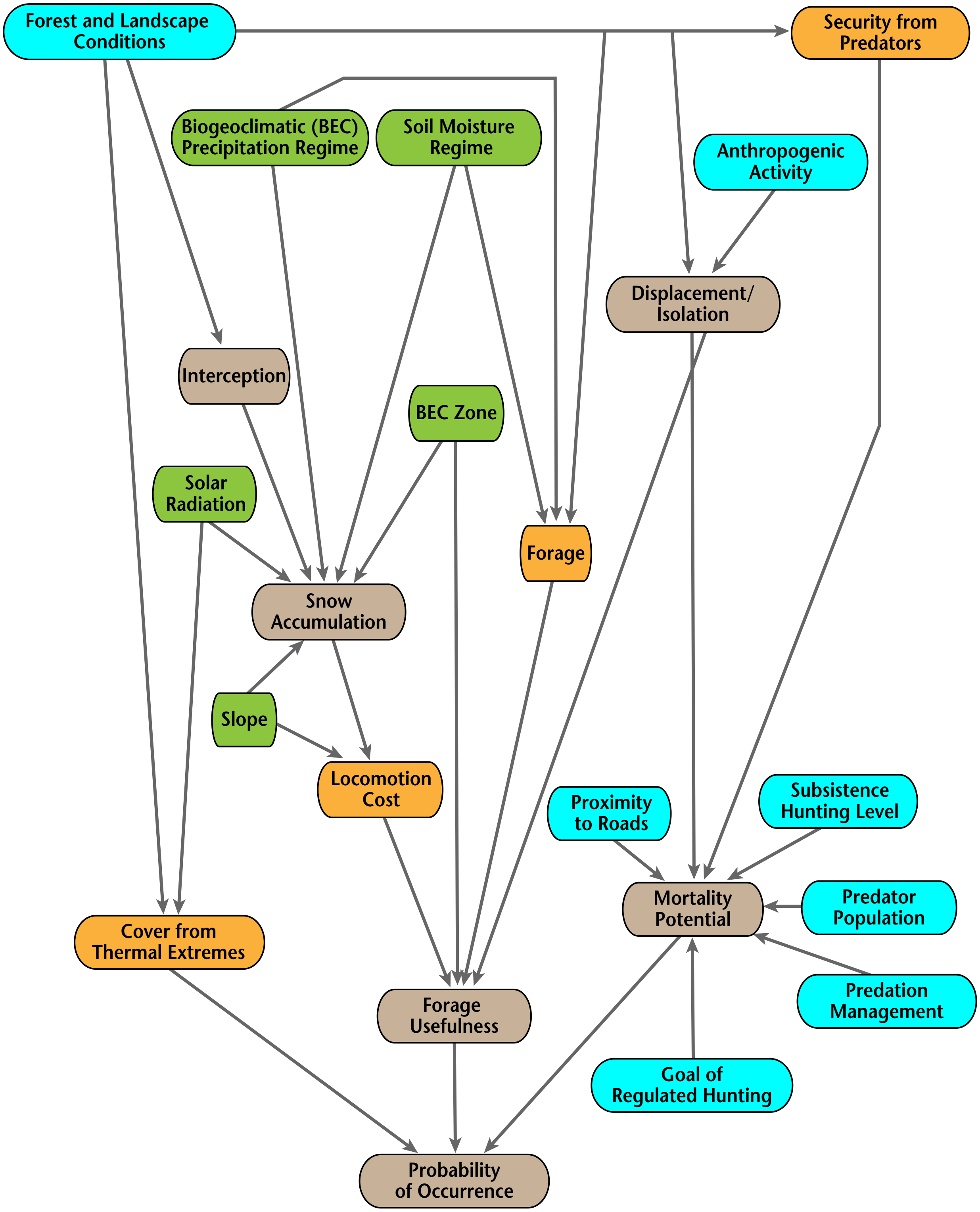

FIGURE 1. A general conceptual model of the probability of occurrence for a particular species of wildlife based on life requisites (orange nodes) and the ecological factors that affect them. Ecological factors can be distinguished as manageable (blue nodes) or not (green nodes).

For example, stressors that affect environmental attributes (e.g., forest conditions, predator populations, proximity to roads, or our ability to manage hunting levels and predators) will all affect the probability of caribou occurrence. By affecting these environmental attributes, the stressors affect forage (directly), the energetic cost of locomotion (indirectly through interception of snow), thermal conditions (directly), and mortality potential (both directly and indirectly). Other abiotic environmental attributes (e.g., slope, solar radiation, soil moisture regime, and broad biogeoclimatic conditions) also play an interactive role in determining the outcome of caribou occupancy. Until the relatively recent shifts in global climate regimes, these latter attributes were considered relatively "enduring" (Pojar 2010), unmanageable (Stevenson and Hatler 1988),[3] and free from the influence of stressors; however, this is no longer the case, at least for attributes strongly related to climate.

The conceptual model illustrated in Figure 1 demonstrates the resulting standard foundation for occupancy modelling that allowed us to populate BBNs for each of the 10 selected species. A partial depiction of our BBN for fisher is provided as an example (Figure 2). The probability of occupancy (expressed in our model as carrying capacity) was determined from the conditions in the environment (blue nodes in Figure 2) that determine usefulness or availability of primary and secondary prey and potential for mortality. Other life requisites in the model (i.e., quality of thermal/resting cover, denning habitat quality, and competition from marten) were determined in a similar fashion from other environmental factors in the extended network. Some input nodes, which we refer to as "management levers" (*sensu* Holling [editor] 1978), represented environmental correlates that are responsive to resource management policies (orange nodes in Figure 2), either directly (e.g., mortality rates attributed to hunting) or mediated through unmanaged or managed disturbance (e.g., access by trappers and [or] hunters using roads). These levers could be adjusted on the basis of input states from scenario simulations to estimate the variable effects of management on each species.

Disturbance effects from mountain pine beetle

We considered that the most likely effects of beetle-induced tree mortality on terrestrial species would operate through changes in habitat structure and distribution at two resolutions:

1. finer-resolution (within-stand) changes in overstorey and understorey species composition, within-stand structures, canopy closure, and amounts of standing and fallen deadwood; and
2. coarser-resolution (among stands) changes in size of habitat patches suitable for meeting different life requisites, changes in seral stage composition, and proximity to roads (and other sources of disturbance).

These changes at both resolutions occur as a consequence of the loss of trees in pine-dominated stands and as a result of salvage harvesting and potential follow-on disturbances (e.g., fires) that may occur in the wake of the beetle outbreak. In addition, more indirect effects may occur such as the potential for displacements from key areas (e.g., denning sites, seasonal ranges) related to disturbance or competition from other species, or the increased probabilities of mortality related to increased predator access to habitats, increased predator numbers, or increased mortality from contact with humans.

To evaluate the impacts of mountain pine beetle on habitat suitability for species at the resolution of individual stands, we required information on leading and secondary tree species of forest stands (blue nodes in Figure 3). These data allowed us to estimate the relative proportion of each stand that would potentially be affected by mountain pine beetle. The relative proportion of the stand attacked and the time since beetle attack (pink nodes in Figure 3) were then used to amend and update regular forest inventories with anticipated post-beetle conditions for various forest variables (e.g., crown closure, crown volume, stand age, density of standing dead wood, volume of fallen dead wood). Once these structural attributes of forests were determined for a given map pixel, the model inputs were used in individual species models to influence the state of key life requisites (forage quality, availability, quality of security and thermal cover, availability of sites for reproduction) for individual species. In the model for fisher, for example, the mountain pine beetle was considered to eventually affect the supply of such habitat requisites as interception of snow by forest canopies, forest structural stage, fisher denning habitat quality, and fisher thermal/resting cover (green nodes in Figure 3).

[3] Bentham, P. 2005. Caribou "state of the science" backgrounder. Canadian Association of Petroleum Producers. Calgary, Alta. Unpublished report.

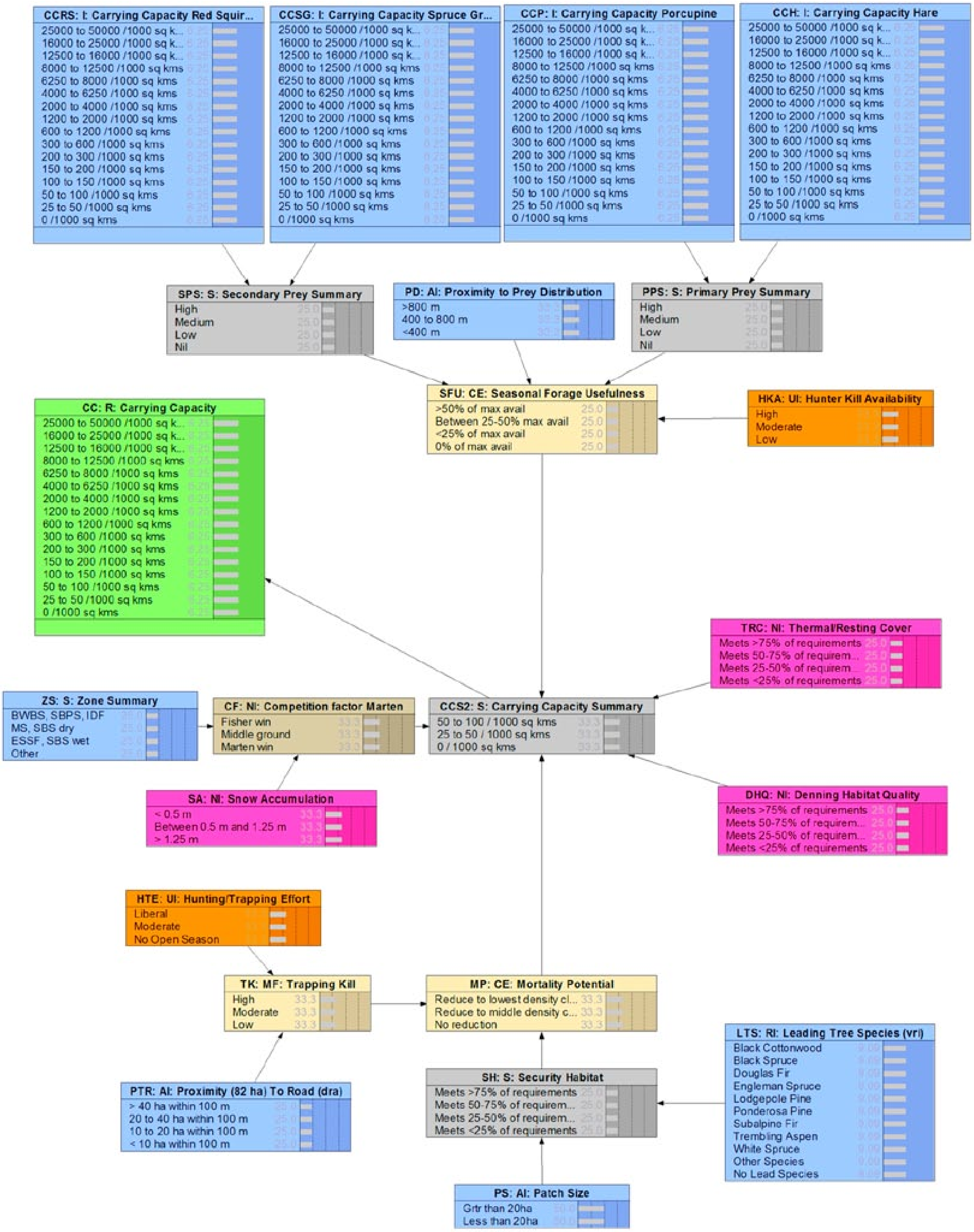

FIGURE 2. A Bayesian Belief Network (BBN) representing the effect of key environmental factors (blue nodes), management levers (orange nodes), and the availability of other life requisites (obtained from other BBNs) in determining the probability of occurrence (characterized here as carrying capacity) for fisher (*Martes pennanti*).

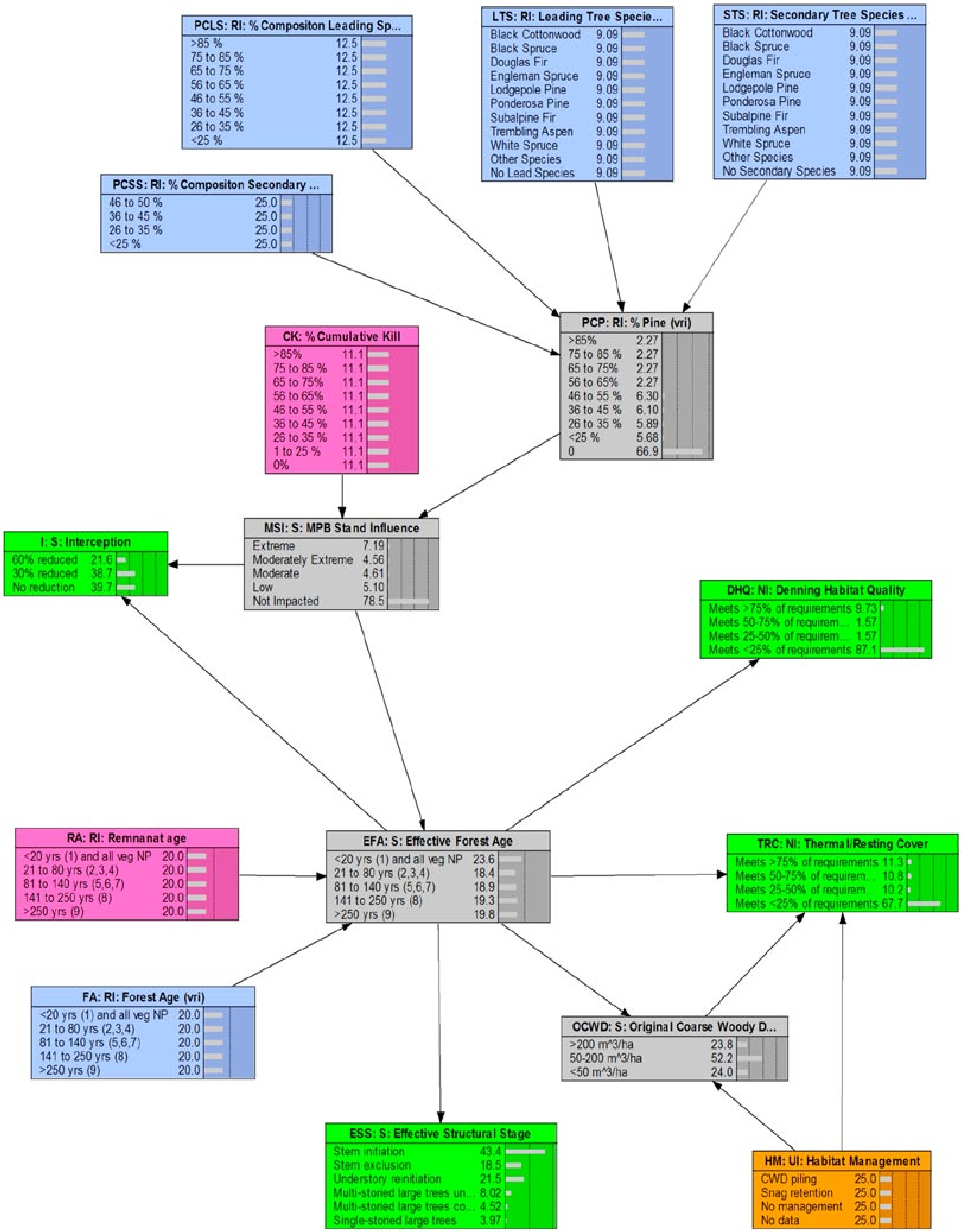

FIGURE 3. A Bayesian Belief Network representing the effect of forest stand factors (blue nodes) and other factors associated with an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*; pink nodes) on other factors deemed important in determining quality of habitat for fisher (*Martes pennanti*).

The supply of life requisites

We successfully estimated the spatial probability of occurrence for 10 vertebrate species for the study area through the iterative implementation of the steps described above; that is, the assembly of geographic information system and species data (ArcMap), the simulated spatial projections of landscape dynamics and management policies, the species habitat evaluations (Netica BBNs), and the generation of maps (SAS and ArcMap). Because of the size (over 40 million ha) and the 1-ha resolution of the land base data for the whole study area, we simulated occurrence probabilities for each species by subarea (33 subareas in total). Resultant probability-of-occurrence maps for the entire study region were formed by making composites of the sub-areas.

In the example resultant for fisher (Figure 4), the total of low-, moderate-, and high-valued habitats was about 48% of the test area under current environmental conditions. Most of the high-valued habitat for this species, a relatively small portion of the total, was located in narrow strips along major rivers and other relatively hygric terrain positions. The total amount of fisher habitat decreased by about 29% through the simulated timber supply scenario (Figure 4c), likely attributed to a decrease in the amount of low-valued habitat, which dominated the habitat totals. The amount of high-value habitat increased by more than 10% after 2014 but decreased below current amounts by 2029 (Figure 4c). At the end of the simulation, there was 208 203 ha less habitat than would be expected on average under a natural disturbance scenario (Figure 4d). The total amount of habitat for fisher was already well below the lower bounds of natural disturbance, even at the start of the simulation.

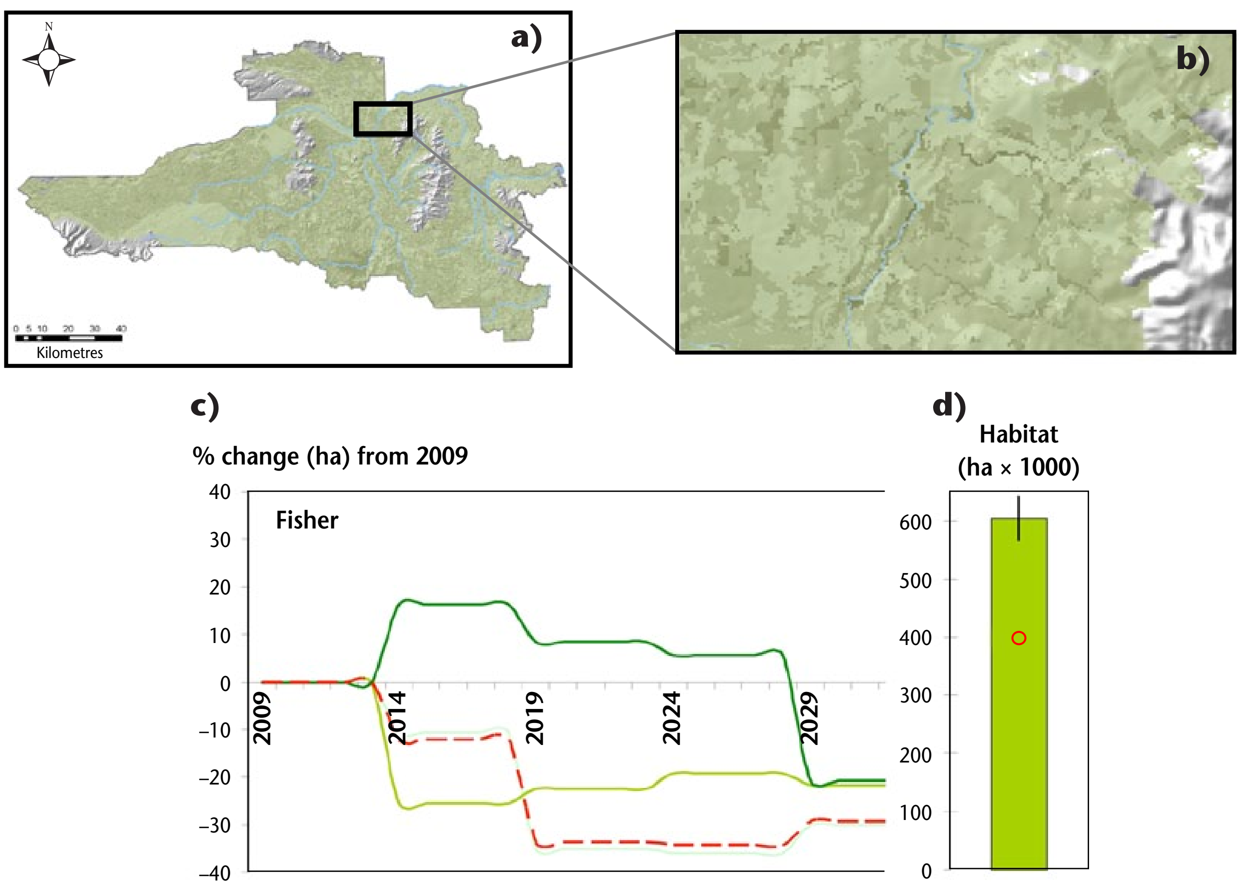

FIGURE 4. Modelled habitat supply for fisher in the western portion of the Quesnel Timber Supply Area (TSA) of central interior British Columbia (a), showing increasing probability of occupancy (b) in deeper shades of green. Relative percent change in probability of occupancy (c) from current time (2009) is shown for three classes of habitat (high – dark green, moderate – medium green, and low – light green) and the sum of all classes (red dashed); all forecasted to 2029 based on a scenario of timber harvest. The total (histogram), expected range (standard deviation bar), and amount in 2029 (red circle) of all three habitat classes under assumed conditions of natural disturbance is shown in (d).

Discussion

Effects on selected species

Our highest priority species (grizzly, caribou, wolverine, and fisher) correspond to those most likely affected by the habitat fragmentation resulting from post-outbreak silviculture. Traditionally, conservation of habitat for these species is mandated through legislated designated management areas; however, the long-term integrity of this policy has become uncertain because of the mountain pine beetle outbreak and associated management. For example, caribou depend on terrestrial lichen sites to provide a major component of their seasonal diets and these sites are often found within forests dominated by lodgepole pine. Lichen (and caribou) response to the changes brought on by beetle-killed pine stands is currently unknown (Whittaker and Wiensczyk 2007), yet hundreds of thousands of hectares of habitat will be affected, much of this within legally designated Ungulate Winter Ranges. Grizzly bear is found throughout much of British Columbia but its range is decreasing and is now extirpated from south-central and southern regions of the province (Bunnell et al. 2004). Even though the grizzly may draw some benefits from the beetle outbreak, eventual loss of habitat components such as coarse woody debris, increased habitat fragmentation, and increased access by humans will undoubtedly have detrimental effects on this species (Bunnell et al. 2004). Although the wolverine is rare, this species occurs throughout much of the province, depending largely on carrion as food. Wolverine therefore require the presence of other carnivores as well as the associated prey species (Bunnell et al. 2004). Increased access by humans and other effects of the beetle outbreak are a threat leading to potential loss of prey as well as increased wolverine mortality related to hunting and trapping (Bunnell et al. 2004).

The fisher is also rare and occurs at low densities in central and northeast British Columbia (Bunnell et al. 2004). This species is found in forested landscapes with a preference for structural complexity and habitat components such as large trees, gaps in the canopy, understorey, dead and dying trees, and coarse woody debris; its movement around broad landscapes appears correlated with canopy closures of at least 30% (Bunnell et al. 2004). Loss of these components and habitat fragmentation related to the beetle outbreak will negatively affect this species (Bunnell et al. 2004). In our study region, our results show this loss will likely be significantly exacerbated by standard management, and well above any effects resulting from natural disturbance patterns. Determining the extent to which other sources of landscape alteration (i.e., those related to climate change and disturbances due to changes in warmer annual temperatures and shifts in precipitation patterns) will affect habitat suitability for this and other species remains a challenging modelling task (Kurz et al. 2008).

Choice of modelling approach

One of our main objectives was to develop and test a platform for linking broad-scale spatial and temporal changes in projected future habitat conditions with estimated likelihoods of future occupancy by species of management or conservation interest. We found that the most suitable algorithm structure to meet our overall objective was process-based and deductive rather than correlative in orientation. Alternative, more inductive approaches to modelling (e.g., empirical or niche-based models) depend on detailed observations to make general expressions of habitat use by a species. Derivation of these models is mostly correlative because modellers evaluate habitats on the basis of a combination of environmental factors present at locations either used (or assumed not to be used) by animals (Hebblewhite and Merrill 2008). This approach is an important source of evidence supporting predicted responses to climate changes, both past and present (Dawson et al. 2011). It is also scientifically attractive because it is closely linked to well-developed frameworks of experimental design and robust hierarchical statistical methods that can be used to extract patterns of animal use. Nevertheless, inferences based solely on inductive approaches may lead to proposed management solutions that are less able to align effectively with novel situations and are potentially weaker at making informative comparisons among alterative management options.

We argue that our choice of modelling approach, which combines mechanistic BBN submodels with spatially explicit habitat supply models, offers some significant advantages for this type of broad-scale, multi-species analysis for strategic conservation purposes. First, and most importantly, these models enable key ecological processes that link habitat attributes associated with changes resulting from beetle and climate change effects to be represented in a common hierarchy of spatial scales, which is easily adapted across species. The necessary level of ecological complexity sought (i.e., functional resolution) is not only influenced by the particular modelling goals of the study but also by the availability of data or information, the amount of available resources (e.g., time, computer capability), and sophistication of the model platform. For our purpose, *explanation* of these potential interactions was more important than the ability to *predict* them. Bunnell (1989) used this characteristic of purpose to distinguish between the interests of the scientific community and those of the resource management community. Although these two goals are related and somewhat inseparable, our use of simulation modelling was clearly a research investigation to improve understanding and strategic direction and not necessarily an attempt to construct an operational management tool. In this context, our models are necessarily more complex. In particular, we needed the ability to model future beetle attack and post-attack management and to simulate the ecological results of these disturbances into the future. This activity is similar to Peterson et al.'s (2003) view of scenario planning. Second, we represented ecological processes in a common probabilistic framework, enabling more explicit representation of uncertainty (e.g., stochastic effects, or incomplete knowledge of model relationships). Third, the models allowed interspecific interactions to be taken into account. The power of this approach to capture a large number of ecological interactions, which in turn determine the probabilities of species occupancy via a relatively concise set of model structures, requires that the flow of information through the submodels must be very carefully structured.

Two general statistical foundations available for modelling are:

1. *frequentism*, in which prediction is the probability of observing a specific outcome based on frequency of data observed; and
2. *Bayesian*, in which prediction is the probability of observing a specific hypothesis based on the data observed.

The frequentist approach asks, "How likely are these observations, given a hypothesis (an "expectation")?" The Bayesian approach asks, "How likely is the hypothesis, given these observations?" Although a more thorough discussion of the differences between these approaches is available elsewhere (e.g., see Berger [1985] for a more theoretical treatment; and Clark [2005] for some implications for ecologists), we offer that frequentist methods emphasize the "hypothesis under investigation" and therefore work best when the hypotheses are based on well-understood properties of systems. By comparison, Bayesian methods emphasize the strength of the relationship between observations and one or more hypotheses, and a probability is interpreted as the likelihood that a given hypothesis could have given rise to the set of observations. The practical differences between these two approaches are subtle, but we propose two ideas that relate to the goals of this study.

We suggest that our modelling approach offered the extended benefit of resulting in formal and explicit hypotheses that could be evaluated and tested through more traditional statistical methods and inductive approaches as data for them becomes available. Bayesian modelling in ecology is not new (McCann et al. 2006) and has proven useful in other resource management issues particularly when empirical approaches (i.e., solution characterization) were intractable (Reckhow 1999; Marcot and Vander Heyden 2001; Peterson and Evans 2003; Rowland et al. 2003; Poirazidis et al. 2004; McNay et al. 2006). Results in Bayesian modelling are characterized by measurable uncertainty allowing for risk assessments and other forms of decision analysis. The approach is therefore consistent with at least some properties of formal decision making (Berger 1985; Peterman and Peters 1998) and advances a problem-solving technique to support critical decisions about species recovery, the effects of the mountain pine beetle outbreak on other elements, and planning for conservation of biodiversity. In the context of cross-scale (i.e., from organism to ecosystem) changes that are directly or indirectly attributable to climate change (Parmesan et al. 2000; Raffa et al. 2008), the Bayesian approach is a tractable way to make climate-informed management and conservation decisions at landscape scales (Millar et al. 2007), at least until climate–plant–animal relationships become better quantified. Integration of multiple approaches and perspectives is critically needed to make efficient use of information about which species and habitats in which places are likely most at risk from large-scale changes and disturbances (Dawson et al. 2011).

Known platforms for modelling species distributions and (or) quality of range vary widely in their application and are referenced somewhat indiscriminately in the literature. Some platforms include element distribution models,[4] habitat supply models (Jones et al. 2002), resource selection functions (Manley et al. 2002), habitat suitability indices (Verner et al. 1986), and wildlife

[4] Beauvais, G.P., D.A. Keinath, P. Hernandez, L. Master, and R. Thurston. 2006. Element distribution modeling: A primer. Version 2.0. NatureServe Element Distribution Modeling Workshop. Unpublished report.

habitat ratings (B.C. Ministry of Environment 1999). Although these platforms differ, the user goals and objectives and the types of results obtained are similar in many ways (e.g., to produce maps of wildlife range). No one "ideal" platform or approach yet defines species distribution modelling. Deductive, Bayesian approaches to modelling habitat for individual species provide a flexible foundation on which to project the potential implications of broad ecological change on the spatial and temporal dynamics of habitat supply. Individual models can be linked to form integrated solutions or disassembled for more focussed investigations. Input data representing environmental conditions are not restricted to specific formats but can come from various data sources, even those forecasted from forest estate models or other landscape simulators. The models essentially represent explicit hypotheses about ecological interactions and can therefore act as transparent research statements and a logical basis for setting priorities for focussed data collection.

Our work to apply these models in the context of management and conservation planning, such as the Nature Conservancy of Canada's Central Interior Ecoregional Assessment, has only begun. Our intention in this study has been to ensure that, by working collaboratively with interested parties in the planning and development stages of the project, we have created products that are optimally useful for broad practical application. Following the integration of "multiple lines of evidence" approaches to conservation planning suggested by Dawson et al. (2011), we offer three suggestions for circumstances in which these models and their successors may be useful as information to managers about the relative urgency and type of conservation actions that may be necessary. First, the models can be used to help identify the most adaptable and (or) least sensitive species, or those with minimal exposure to projected habitat changes. These species may only need minimal interventions combined with low-intensity monitoring. Second, where species' exposure and sensitivity to habitat changes increases, more strategic options are required, such as designating new protected areas supported by fine-scale habitat management activities that support the species ability to adapt to change. Third, for some sensitive species, active habitat management strategies (e.g., maintenance of specific habitats or species interactions) may alleviate the potential for increasing likelihoods for population decline. Among the benefits of effective, strategic-level conservation planning, cumulative effects assessments and silviculture-investment initiatives

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could derive from the resultant habitat maps. By identifying and potentially adopting actions early enough, managers can avoid a deferred "extinction debt" trap (Kuusaari et al. 2009) that would then require further investments and more costly management interventions in the future; however, we clearly recognize that further assessment and validation of this and related modelling approaches is needed before these products can be applied at operational levels.

Currently, a plethora of proposed ways exist to derive expressions of habitat value for wildlife, depending on the data available and the questions asked. For example, many previous studies have recognized differences in habitat selection among spatial scales (e.g., Gustine et al. 2006; Mayor et al. 2007) and, thus, the analytical approach must be selected based on the appropriate spatial scale (or scales) for answering the ecological or management question. Adequate samples of animal movement data (e.g., from individual animals or groups of animals; Hebblewhite and Merrill 2008; Koper and Manseau 2009), sufficient to develop predictive models across the scales needed to address many management and conservations issues, are lacking for most of the species we selected. This work has shown that strategic initiatives could benefit from a standardized deductive approach such that results can be compared among large areas within political jurisdictions.

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Test Your Knowledge . . .

Standardized occupancy maps for selected wildlife in Central British Columbia

How well can you recall some of the main messages in the preceding Research Report?
Test your knowledge by answering the following questions. Answers are at the bottom of the page.

1. Give one reason why a deductive Bayesian modelling approach is well suited to making predictions about future range values for wildlife?
   A) A Bayesian statistical foundation is probabilistic and emphasizes the strength of the relationship between observations and one or more hypotheses, and hence is appropriate for uncertain future conditions
   B) A deductive approach is mechanistic and therefore emphasizes the functional relationships between species and their environment and therefore is more suited (than inductive modelling) to help explain changes in habitat occupancy
   C) All of the above
   D) None of the above

2. Name three wildlife species that were determined the most likely to be affected by broad ecological changes brought on by the mountain pine beetle outbreak in British Columbia?
   A) Grizzly bear, caribou, wolverine
   B) Fisher, wolverine, caribou
   C) Mule deer, otter, wolf
   D) A and B

3. What are the common "management levers" that can influence the quality of range for wildlife?
   A) Forest and landscape conditions, anthropogenic activity levels, road placement, predator populations, and hunting levels
   B) Forage quality, availability, quality of security cover
   C) Road placement, predator populations, and hunting levels
   D) A and C

ANSWERS

1. C 2. D 3. D