
Utility of Dynamic-Landscape Metapopulation Models for Sustainable Forest Management

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Abstract: We evaluated the utility of combining metapopulation models with landscape-level forest-dynamics models to assess the sustainability of forest management practices. We used the Brown Creeper (*Certhia americana*) in the boreal forests of northern Ontario as a case study. We selected the Brown Creeper as a potential indicator of sustainability because it is relatively common in the region but is dependent on snags and old trees for nesting and foraging; hence, it may be sensitive to timber harvesting. For the modeling we used RAMAS Landscape, a software package that integrates RAMAS GIS, population-modeling software, and LANDIS, forest-dynamics modeling software. Predictions about the future floristic composition and structure of the landscape under a variety of management and natural disturbance scenarios were derived using LANDIS. We modeled eight alternative forest management scenarios, ranging in intensity from no timber harvesting and a natural fire regime to intensive timber harvesting with salvage logging after fire. We predicted the response of the Brown Creeper metapopulation over a 160-year period and used future population size and expected minimum population size to compare the sustainability of the various management scenarios. The modeling methods were easy to apply and model predictions were sensitive to the differences among management scenarios, indicating that these methods may be useful for assessing and ranking the sustainability of forest management options. Primary concerns about the method are the practical difficulties associated with incorporating fire stochasticity in prediction uncertainty and the number of model assumptions that must be made and tested with sensitivity analysis. We wrote new software to help quantify the contribution of landscape stochasticity to model prediction uncertainty.

Key Words: Brown Creeper, landscape ecology, population model, population viability analysis, succession model

Utilización de Modelos Metapoblacionales en Paisajes Dinámicos para el Manejo Sustentable de Bosques

Resumen: Evaluamos la conveniencia de combinar modelos metapoblacionales con modelos de dinámica de bosques a nivel de paisaje para estimar la sustentabilidad de las prácticas de manejo de bosques. Como estudio de caso utilizamos a *Certhia americana* en bosques boreales del norte de Ontario. Seleccionamos a *Certhia americana* como un indicador potencial de sustentabilidad porque es relativamente común en la región pero depende de tocones y de árboles viejos para anidar y forrajear; por ello puede ser sensible a la cosecha de madera. Para el modelo utilizamos RAMAS Landscape, un paquete de software que integra a RAMAS GIS (software para modelar poblaciones) y a LANDIS (software para modelar la dinámica de bosques). Utilizando LANDIS derivamos predicciones de la composición y estructura florística del paisaje bajo una variedad de escenarios de manejo y perturbaciones naturales. Modelamos ocho escenarios alternativos de manejo de bosques, que variaron en intensidad desde la no cosecha de madera y un régimen natural de fuego hasta la cosecha intensiva de madera con corte de árboles después de incendios. Predijimos la respuesta de la

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metapoblación de *Certhia americana* en un período de 160 años y utilizamos el tamaño poblacional futuro y el tamaño poblacional mínimo esperado para comparar la sustentabilidad de los diferentes escenarios de manejo. Los métodos de modelación fueron aplicados fácilmente, y las predicciones de los modelos fueron sensibles a las diferencias entre los escenarios de manejo, lo que indica que estos métodos pueden ser útiles para evaluar y clasificar la sustentabilidad de las opciones de manejo de bosques. Las principales preocupaciones acerca del método incluyen las dificultades prácticas asociadas con la incorporación de la estocasticidad del fuego en la incertidumbre de los pronósticos y el número de suposiciones que se deben hacer y probar mediante análisis de sensibilidad. Desarrollamos nuevo software para ayudar a cuantificar la contribución de la estocasticidad del paisaje a la incertidumbre en las predicciones del modelo.

Palabras Clave: análisis de viabilidad poblacional, *Certhia americana*, ecología de paisaje, modelos de sucesión, modelo poblacional

Introduction

Assessing the sustainability of forest management is a complex task (Aplet et al. 1993). Monitoring biological indicators of sustainability has been proposed as a strategy to demonstrate the effects of environmental change on species, communities, and ecosystems (Noss 1990; Meffe & Carroll 1994; Montréal Process 2000). Indicators are often associated with long-term and broad-scale monitoring to assess population trends and inform management in an adaptive manner (Walters & Holling 1990; Johnson 1999). Few examples exist, however, in which systematic monitoring of biological indicators has provided timely input into the forest management process, and there is increasing evidence that long-term monitoring alone cannot provide useful information to address forest management concerns (Temple & Wiens 1989; Mulder et al. 1999; Venier & Pearce 2004).

Recently there has been increasing emphasis on modeling available habitat for bioindicators (Thompson et al. 2003). Bioindicators are defined here as species thought to be sensitive to, and therefore to serve as an early warning of, environmental change (sensu Lindenmayer et al. 2000). Modeling habitat availability for bioindicators does not explicitly consider environmental and demographic stochasticity or the spatial attributes of bioindicator species' biology such as dispersal and Allee effects. Consequently habitat modeling methods alone may not capture the potential landscape-scale effects of forest management activities on habitat composition and configuration, or temporal fluctuations in habitat occupancy that affect population persistence (Andren 1994; Schmiegelow et al. 1997).

Metapopulation models facilitate the comparison of management scenarios to some reference condition (e.g., a natural disturbance scenario) in terms of relative population declines (or increases) across the range of scales at which indicator species operate. A predicted decline in an indicator relative to a reference condition infers an impact attributable to a management scenario. Choosing indicators that are sensitive to ecosystem stressors predicted to arise from management activities permits

inferences about the impact of management on individual species and ecosystem integrity. Examples of ecosystem stressors that may arise from timber management include (1) a landscape-level reduction in the availability of denning and nesting sites resulting from the truncation of older forest tree cohorts, the removal of snags, and broad-scale changes in tree species composition and (2) an overall reduction in the availability of suitably moist microhabitats because of increased numbers of canopy openings. Impacts on ecosystem integrity would be inferred if the ecosystem were unable to support the abundance of bioindicators characteristic of its reference state. We propose that modeling the response of bioindicators to the ecosystem stressors brought about by management may be a coherent method for evaluating the sustainability of ecosystem management options. Metapopulation models also provide a framework for synthesizing knowledge and informing future research priorities by identifying factors that most affect populations (Possingham et al. 1993).

For evaluating management scenarios, metapopulation models require predictions of change in vegetation composition and structure resulting from alternative scenarios (Holt et al. 1995). Dynamic-landscape models incorporate deterministic and stochastic disturbances such as timber harvesting, fire, and succession. The program RAMAS Landscape (Akçakaya et al. 2003) links LANDIS 3.7 (He et al. 1996), a dynamic-landscape model, and RAMAS GIS 4, a metapopulation software package (Akçakaya & Root 2002).

Our objective was to explore the utility of dynamic-landscape metapopulation (DLMP) models as a tool for predicting the effect of alternative management scenarios on an indicator species. To evaluate this approach we developed a case study of the Brown Creeper (*Certhia americana*) in an actively managed, boreal landscape in north-central Ontario, Canada. We constructed a DLMP model in RAMAS Landscape and used it to evaluate and rank the sustainability of eight forest management scenarios in terms of their impact on the landscape-level abundance of the Brown Creeper over 160 years (two timber harvesting rotations based on current rotation lengths).

The utility of the modeling method was assessed in terms of practicality (how easily the method is applied), generality (how easily the method might be applied to other species), sensitivity (how well the method discerns between alternative forest management scenarios), and realism (how well the method captures the complexity and subtlety of the problem).

Methods

Study Area

Our research area (170,000 ha) in north-central Ontario (85° 47'N, 48° 31'W) includes an area actively managed for timber production for the past 35 years and the north-east corner of Pukaskwa National Park. The dominant tree species in the study area are jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* Mill.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamifera* [L.] Mill.), and white birch (*Betula papyrifera* Marsh.), with lesser amounts of white spruce (*Picea glauca* [Moench] A. Voss), eastern white cedar (*Thuja occidentalis* L.), and tamarack (*Larix laricina* Koch).

Modeling Approach

Two separate modules comprise RAMAS Landscape: RAMAS GIS, which simulates a species' metapopulation dynamics over time, and LANDIS, which simulates forest change by modeling tree species composition in 10-year age classes. The LANDIS module models succession based on interactions among species life-history attributes, site conditions, disturbance regimes, and management, all of which are set by the user. Life-history characteristics of tree species include longevity, age at sexual maturity, shade and fire tolerance, and seed dispersal distance. Site conditions are encapsulated by land types, which can be derived from climatic, physiographic, and edaphic properties. The model incorporates natural processes (fire, windthrow, succession, and seed dispersal) and anthropogenic processes such as timber harvesting and prescribed burning. It allows silvicultural treatments such as thinning, selection harvesting, gap harvesting, and clearcutting to be modeled. The RAMAS Landscape program is composed of several components that implement various stages of DLMP modeling (see p. 2 in Akçakaya et al. 2003).

We describe the implementation of the Brown Creeper DLMP model in four general steps: (1) building a habitat model, (2) developing a model of population dynamics, (3) linking these models in a metapopulation model, and (4) building a forest-dynamics model and linking it to the metapopulation model to evaluate management options.

Step 1. Building a Habitat Model for the Brown Creeper

The Brown Creeper, a tree-trunk-foraging insectivorous bird, occurs in coniferous forests throughout the Northern Hemisphere, nesting in hammock-like nests behind loosened flaps of bark on dead or dying trees (Hejl et al. 2002). They are dependent on large trees of particular species for foraging and nesting and are associated with a closed canopy and snags (Raphael & White 1984; Mariani & Manuwal 1990; Adams & Morrison 1993). Previous creeper habitat suitability models for the Brown Creeper included conifer stand height, degree of canopy closure, and proportion of spruce and fir in the canopy (Banks et al. 1999). Timber harvesting truncates older tree cohorts and reduces the number of snags (McRae et al. 2001; Thompson et al. 2003). Consequently, retention of mature forest between logged stands is probably necessary to maintain this species (Imbeau et al. 1999).

We combined observational data, expert knowledge, and information from a literature review to develop a mathematical model describing the relationship between Brown Creeper occupancy and environmental variables such as forest composition, topography, and climate. Brown Creeper occupancy (presence/absence) data, obtained over 2 years in the study area, was used to explore Brown Creeper habitat relationships using logistic regression analysis (McCullagh & Nelder 1989). Details about the data and data collection methods are described elsewhere (www.glf.cfs.nrcan.gc.ca/landscape/pukbirds_e.html). We explored relationships between Brown Creeper occupancy and environmental variables such as stand height, stand maximum age, tree species composition, mean annual temperature, mean annual rainfall, and topographic roughness. Environmental variables were restricted to those for which mapped data exist so that the model could be used to predict the locations of suitable habitat across the whole study area.

Regression analyses strongly supported a positive relationship between Brown Creeper occupancy and stand age ($p < 0.05$), explaining approximately 15% of the variation in observation data. Expert opinion and prior studies supported the exclusion of pure stands of jack pine and black spruce from suitable habitat; otherwise, habitat quality was assumed to be a function of forest age according to

$$\text{Pr(occupancy)} = \frac{\exp(-2.788 + 0.05 \cdot \text{age})}{[1 + \exp(-2.788 + 0.05 \cdot \text{age})]}, \quad (1)$$

where age is the age of the dominant stand strata. We used the model to predict the probability of Brown Creeper occupancy across the study region based on raster maps (grid cell size = 1 ha) of forest tree species composition and age from forest resource inventory maps dated 1970 (Gillis & Leckie 1993), representing a before-harvest distribution of habitat for the species. Areas of pure jack

pine and black spruce were excluded from the predicted distribution of suitable habitat.

Step 2. Developing a Population Model for the Brown Creeper

In northern Ontario, Brown Creepers are migratory, moving south during the winter months (McLaren & McLaren 1981). We assumed immigration into the study area equaled emigration on the basis that populations in North America are thought to be stable (Hejl et al. 2002).

The Brown Creeper is assumed to be monogamous (Hejl et al. 2002). Pairs produce one brood of four to seven eggs per year, breeding in the first year (Hejl et al. 2002), although clutch size may be reduced in the first year of breeding (L.V., personal observation). Brown Creepers are territorial during the breeding season (Hejl et al. 2002), with territory sizes ranging from 2.3 to 6.4 ha (Davis 1978).

We constructed a stage-structured population model in RAMAS GIS (Akçakaya & Root 2002). The stage matrix was based on available information about survival, fecundity, and the probabilities of transition from each stage to the next (Table 1). No accurate estimates were available for the survival rate of each stage. Hence parameters were based on the maximum age recorded (4 years and 7 months; Klimkiewicz et al. 1983) and the estimated annual survival rate for the Eurasian Tree-Creeper (*Certhia familiaris*) (44%; Peach et al. 1995). The stage matrix had a finite rate of increase of 1.11.

$$\begin{bmatrix} 0 & 1.65 & 2.3 & 2.3 & 2.3 \\ 0.4 & 0 & 0 & 0 & 0 \\ 0 & 0.44 & 0 & 0 & 0 \\ 0 & 0 & 0.44 & 0 & 0 \\ 0 & 0 & 0 & 0.44 & 0 \end{bmatrix}$$

Both sexes were modeled because the assumption of monogamy implies that the availability of either males or females may limit population growth. There was no information about the standard deviations of most parameters. We made plausible estimates and tested their influence on model predictions with sensitivity analysis.

All individuals from all stages contributed to density dependence because resource consumption was thought to be approximately even across all stages of the Brown Creeper's life cycle. Contest competition was selected because of the territorial nature of the species, implying that density dependence operates according to the Beverton-Holt equation (Akçakaya & Root 2002). The maximum population growth rate (R_{max}) required for modeling density dependence under contest competition was set at 1.5 on the basis of observed upper limits of clutch size and reproductive success that would be expected in the absence of density dependence (Hejl et al. 2002). For the Brown Creeper model, density dependence was set to affect only fecundity because nesting sites and reproductive success are assumed to be the most limiting factors. We incorporated demographic and environmental stochasticity in the model. Environmental stochasticity was assumed to be log-normally distributed and incorporated the variation in vital rates and carrying capacity (SD = 10% of the mean) arising from random environmental processes. The RAMAS Metapop files and a file explaining the model parameterization are available online along with all RAMAS Landscape files and instructions for running the Brown Creeper DLMP (www.botany.unimelb.edu.au/envisci/brendan/browncreeper.htm).

Step 3. Linking Habitat and Population Models

The RAMAS GIS program employs a patch-recognition algorithm (Akçakaya et al. 1995) that identifies discrete patches of connected habitat from the habitat suitability map developed in step 1. Patches are treated as discrete populations. In the Brown Creeper model, patches were considered discrete if they were separated by a distance of 200 m, based on an estimate of the species' largest expected within-home-range movement. We set a habitat suitability threshold of 0.25 on the basis that it was the lowest predicted habitat value that intersected with an observation of presence during recent surveys in the region (L.V. et al., unpublished data).

Carrying capacity (K) and initial number of individuals in each patch were estimated as a function of patch

Table 1. Data sources for survival, fecundity, and transition rates used in each stage of the Brown Creeper model.

Stage	Description	Survival and fecundity	Transition
Fledgling	<1 year old	40% survival (Peach et al. 1995) with 10% SD; survivorship lower than other stages because of high predation rate (Peach et al. 1995)	all surviving individuals move to adult 1
Adult 1	1 year old	44% survival (Peach et al. 1995) with 10% SD; 3.3 fledglings produced each year	all surviving individuals move to adult 2
Adult 2	2 years old	44% survival (Peach et al. 1995) with 10% SD; 4.6 fledglings produced each year (calculations based on Davis 1978 from Hejl et al. 2002)	all surviving individuals move to adult 3
Adult 3	3 years old	44% survival (Peach et al. 1995) with 10% SD; 4.6 fledglings produced each year (calculations based on Davis 1978 from Hejl et al. 2002)	all surviving individuals move to adult 4
Adult 4	4+ years old	10% survival (at least some birds probably survive beyond maximum recorded age); 4.6 fledglings produced each year (calculations based on Davis 1978 from Hejl et al. 2002)	maximum recorded life span is 4 years 7 months (Klimkiewicz et al. 1983)

habitat quality. A simple linear relationship between K and habitat suitability (predicted probability of occupancy) could be used because Brown Creepers are thought to exist at densities ranging between 0.2 and 1 bird/ha (Apfelbaum & Haney 1977). During model simulations, K is sampled from a distribution with mean equal to the estimated K and SD set by the user. In the absence of relevant data about fluctuations in K , we specified an SD of 10% of the mean and tested the importance of this assumption with sensitivity analysis. The initial abundance of each patch was set to K because there were no grounds for assuming that the species was recovering from a period of low habitat occupancy.

The probability of dispersal between the edges of any two patches depended on the separation distance of the patches according to the function

$$M_{ij} = 0.3^* \exp(-D_{ij}^{0.8}/4), \quad (2)$$

where M_{ij} and D_{ij} are the probability of dispersal and distance between patches i and j , respectively. The maximum dispersal distance was set at 5 km ($D_{\max} = 50$). The dispersal function plays an important role in metapopulation models because it determines how quickly empty or partially occupied patches can be colonized by immigrants from other populations (Akçakaya 2000). Our dispersal function was based on expert observation (L.V.,

unpublished data), and the sensitivity of the model to this parameterization was tested (see Table 2).

Spatially structured populations tend to experience spatial autocorrelation in fluctuations of vital rates because the environmental influences on vital rates are themselves spatially structured (Akçakaya & Root 2002). This spatial autocorrelation was modeled with the function

$$C_{ij} = \exp(-D_{ij}/20). \quad (3)$$

Little information was available for specifying the autocorrelation function, although the sensitivity of the model to alternative assumptions about the form of autocorrelation was tested.

Step 4. Linking a Forest-Dynamics Model to the Metapopulation Model

We used the LANDIS model to generate predictions about the future structural and floristic composition of the forest under a variety of management scenarios.

FOREST COMPOSITION AND SUCCESSIONAL DYNAMICS

Succession dynamics of the seven dominant tree species were modeled. Estimates of life-history parameters, including longevity, seeding distance, age at sexual maturity,

Table 2. Sensitivity analysis for the Brown Creeper model based on three population repetitions on each of 50 landscapes for each parameter change.

Simulations	N_{160}^a		MP^b		S^c
	mean	SE (mean)	mean	SE (mean)	
Base (no timber harvesting, natural fire)	71438	1587	34131	491	
Low vital rates (lower bound of recorded fecundities and survivorships: Hejl et al. 2002)	69788	1944	29108	380	-15
High vital rates (upper bound of recorded fecundities and survivorships: Hejl et al. 2002)	74605	1745	37799	582	11
Low SD in vital rates (-20%)	72197	1631	34818	466	2
High SD in vital rates (+20%)	70531	1894	33461	503	-2
Low K (-20%)	59081	1194	28441	348	-17
High K (+20%)	85038	2229	39092	582	15
Low SD of K (-20%)	69684	1754	33724	458	-1
High SD of K (+20%)	74497	1950	34311	541	1
High maximum growth rate ($R_{\max} = 1.6$, based on highest recorded vital rates)	71802	1681	34888	525	1
Low maximum growth rate ($R_{\max} = 1.2$, based on lowest recorded vital rates)	65392	1742	29689	592	-13
Density dependence affects survival	67697	2394	9311	214	-73
Density dependence affects all vital rates	46321	3860	1305	169	-96
High dispersal ($M_{ij} = 0.3 \exp(-D_{ij}^{0.8}/8)$, $D_{\max} = 100$)	70148	1823	32652	450	-4
Stochasticity log normal uncorrelated	72864	1846	34803	398	2
Stochasticity normal correlated	72726	1773	34919	459	2
Stochasticity normal uncorrelated	74374	1870	36780	471	8
Mating system monogamous	71320	1836	32979	429	-3
Demographic stochasticity excluded	70864	1766	33508	535	-2

^aPopulation at end of simulation (after 160 years).

^bMinimum population size.

^cSensitivity of this parameter change, as determined by Eq. 4.

shade tolerance, and fire tolerance, were available for each species (Farrar 1995). Initial species composition and age-class distribution were specified according to historical inventory data and were imported to the LANDIS module as raster maps.

FIRE

To simulate fire we estimated mean fire-return intervals and fire size distributions. In the boreal forest of Ontario the natural fire cycle is thought to be between 80 and 200 years, although modern fire suppression efforts may have increased the cycle to between 400 and 2000 years (Rowe & Scotter 1973). Average fire return times were estimated at 110 years for forest dominated by jack pine and 325 years for mixed-species forests in the study region (M. Flannigan & T. Lynham, personal communication). We assumed that intensity of fire increases linearly with time since last fire for 200 years. A fire size distribution for the region was developed on the basis of fire-history data collected between 1921 and 1999 for the study region (M. Flannigan, unpublished data). The data closely fitted an exponential distribution, matching the assumption of the LANDIS module (Akçakaya et al. 2003). The observed distribution of fire sizes results from a mixture of modern fire suppression methods in the late 1900s and less efficient fire suppression strategies in the early 1900s. The mean fire size was estimated to be approximately 2000 ha.

We modeled a second fire scenario assuming that continued fire suppression results in an increase in average fire return times and distribution of long-run fire size. The mean fire-return interval for the second scenario was set at 320 years for jack pine and 700 years for mixed species. The fire size distribution increased in the second scenario so that the mean size was 8000 ha. This scenario was developed to represent an upper bound on the future fire size distribution.

LAND TYPES

Land types are used in the LANDIS module to describe site conditions (usually based on substrate and topographic features) that lead to spatial variation in tree species establishment probabilities and fire-return intervals. We identified two generic land types: (1) those with shorter fire-return intervals that are generally conducive to jack pine establishment and (2) those with longer fire-return intervals that are generally dominated by mixed conifer and deciduous forest (where jack pine comprised < 50% of the canopy). Fire-return times for the two land types were set according to the forest-specific estimates described above. Seedling establishment probabilities were set so that floristic composition remained stable over time under natural fire conditions. The probability of seedling

establishment in landtype 1 was 0.9 for jack pine and 0.1 for other species. Landtype 2 probabilities were 0.25 and 0.5, respectively.

LANDSCAPE MODEL PREDICTIONS

The LANDIS module generates predictions of forest species composition and structure as a time series of raster maps (1-ha grid cell size) at 10 yearly intervals for the duration of the simulation (160 years in this case). Default outputs include a time series of raster maps representing forest species composition and the age of the dominant strata in each 1-ha cell. Each cell may be assigned to a forest type depending on the tree species it contains. The Brown Creeper is thought to avoid pure jack pine and black spruce forest, so both were included as separate forest types. A series of mixed forest types was also defined to provide the LANDIS forest classification algorithm with a range of options similar to those used by managers in the area (OMNR 1997).

LINKING THE METAPOPULATION MODEL TO A FOREST-DYNAMICS MODEL

The RAMAS Landscape program links the metapopulation model and the forest-dynamics model by creating a time series of habitat maps based on forest age and composition maps produced by LANDIS. Sixteen age and composition maps were created (one for each decade). The movement of individuals between populations in any time step depends on the quality and spatial arrangement of habitat.

Defining and Testing a Range of Forest Management Scenarios

We simulated four silvicultural scenarios in LANDIS based on various combinations of mean harvest size, tree-retention rates, and salvage-logging practices (Appendix). Each scenario was subject to the two alternative fire regimes described above. For each of the eight combinations of harvest and fire scenario we developed a separate LANDIS model and used it to predict the future floristic composition and age structure of the forest over 160 years. We used these predictions as the basis for the Brown Creeper DLMP model, which was run for 160 years with 50 landscape replicates and three population replicates on each landscape. This particular ratio of landscape replicates to population replicates was established based on the results of an investigation into the relative contributions of landscape and population stochasticity on DLMP predictions (R.C. & B.W., unpublished data).

Sensitivity Analysis

We conducted sensitivity analyses for 19 DLMP model parameters to determine whether model predictions were

sensitive to particular estimates, their standard deviations, and other key assumptions. Sensitivities were evaluated by the change in expected minimum population size (EMP; McCarthy & Thompson 2001) resulting from a given change to a single parameter or assumption. Where possible, parameter changes were made on the basis of observed upper and lower bounds or biologically plausible ranges, although this approach is difficult in the case of poorly understood parameters such as the spatial autocorrelation function, in which a standard range of $\pm 20\%$ was used for sensitivity analysis. The EMP for each sensitivity was estimated following the method described above for the alternative silvicultural scenarios: 50 landscape replicates with three population replicates on each landscape.

The sensitivity of parameters investigated was calculated as

$$S_i = \frac{EMP_i - EMP_b}{EMP_b} \times 100, \quad (4)$$

where S_i is the sensitivity of model i (the model being investigated), EMP_i is the expected minimum population size of the model i , and EMP_b is the expected minimum population size of the base model. Sensitivity calculated in this way provides an indication of both the magnitude and direction (positive or negative) of the change in EMP. Most sensitivity analyses were conducted using the base model scenario (scenario 1: no timber harvesting, natural fire regime). The sensitivity of results to R_{max} , however, was tested across all management scenarios to see whether the rank order of scenario EMPs changed with alternative parameterizations.

Results

Impact of Scenarios on Habitat Availability

The impact of each scenario on the availability of habitat for the Brown Creeper may be expressed in terms of changes in K in the study region over 160 years in response to each management scenario (Fig. 1). Carrying capacity is linearly related to the amount and quality of habitat in the region. Carrying capacity was highest in the base model and lowest under the scenarios that involved salvage logging (scenarios 7 and 8, Fig. 1). Scenarios in which conversion to jack pine was undertaken only on the areas already scheduled for logging (scenarios 3–6) showed similar K s over the 160 years of the simulation. Variation in K over 160 years was greater in scenarios involving fire suppression (scenarios 2, 4, 6, and 8) because of the larger mean fire sizes. In scenarios that did not involve salvage logging, the variability associated with fire

regime was comparable to or greater than the relative influence of the different timber harvesting options.

Impact of Scenarios on Brown Creeper Population Size

The population trajectories constructed represent population size fluctuations over the simulation period for each of the eight scenarios (Fig. 2). Examination of the mean tendency for the base scenario (no timber harvesting and no fire suppression; top left box in Fig. 2) revealed that the Brown Creeper population in the study area was predicted to be relatively stable over 160 years, fluctuating around a mean population size of approximately 70,000 individuals. Trajectories for the Brown Creeper under alternative management scenarios differed from the base model, with declines predicted as the intensity of disturbance increased. Scenarios 7 and 8 were the most intensely disturbed scenarios, as indicated by the continual decline in K below levels of the other scenarios (Fig. 1). Both of these scenarios showed the strongest and most consistent decline in population size throughout the simulation (Fig. 2). Under most scenarios the predicted minimum population size was not in direct proportion to the change in K over the simulation, indicating that population processes, beyond simple habitat availability, were influencing model results.

No scenario indicated a possible decline to extinction, although there were differences between scenarios in the relative risk of decline to various threshold population sizes (Fig. 3). For example, the risk of decline to 30,000 individuals under the base model was approximately 0.2, whereas the risk of decline to a population size of 30,000 individuals under scenario 8 was approximately 0.7. The difference between the base model EMP and alternative scenario EMPs tended to increase with increasing intensity of disturbance, although the relationship was not perfect (Table 3). The EMP was 34,131 individuals for the base model. The EMPs for scenario 2 (fire suppression, no harvest) was 8% lower than the base model, whereas the highest impact scenario (scenario 8) had no greater impact on EMP than scenario 6 (fire suppression with jack pine planted after harvest). The rank order of population sizes at the end of the simulation (N_{160}) followed our expectations given the relative impact of scenarios on K .

Sensitivity Analysis

The Brown Creeper model was sensitive to the choice of vital rates affected by density dependence (Table 2). Under the worst-case scenario, in which density dependence affects all vital rates, large fluctuations in population size resulted in a low predicted EMP (1,305; $S = -96\%$). This was the only assumption to which the model was notably sensitive. Results were not sensitive to our estimate of R_{max} .

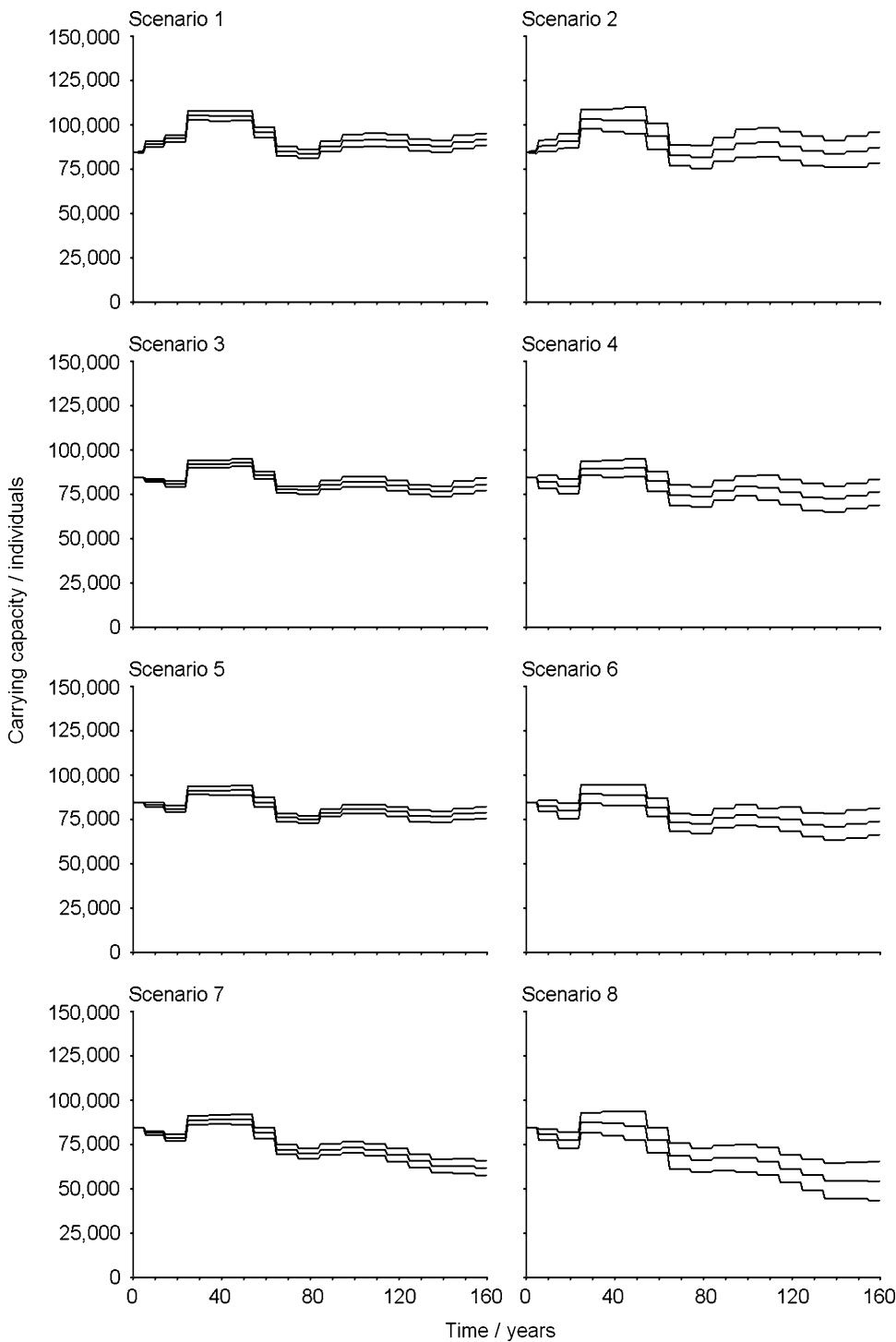


Figure 1. Changes in carrying capacity (K) for the Brown Creeper model over 160 years under each management scenario (see Appendix for description of management scenarios). Carrying capacity is the total K over all populations in the region. On each graph, the middle line shows mean K and the upper and lower lines show one standard deviation from mean K.

Discussion

Implications of the Case-Study Results

The Brown Creeper was sensitive to the differences between forest management scenarios. Results of the risk assessment indicated that, when landscape stochasticity is considered, the EMP was approximately 15% lower under the highest impact scenario compared with the lowest.

The other silvicultural management options fell between these two extremes.

The results of this case study illustrate that, under the assumptions made in the model, the current style of forest management (most closely resembled by scenarios 4 and 6) results in a predicted 18–20% decrease in population size after 160 years, with a 12–15% decrease in EMP (Table 3) compared with the option of no timber harvesting. This result is not unexpected, given that approximately

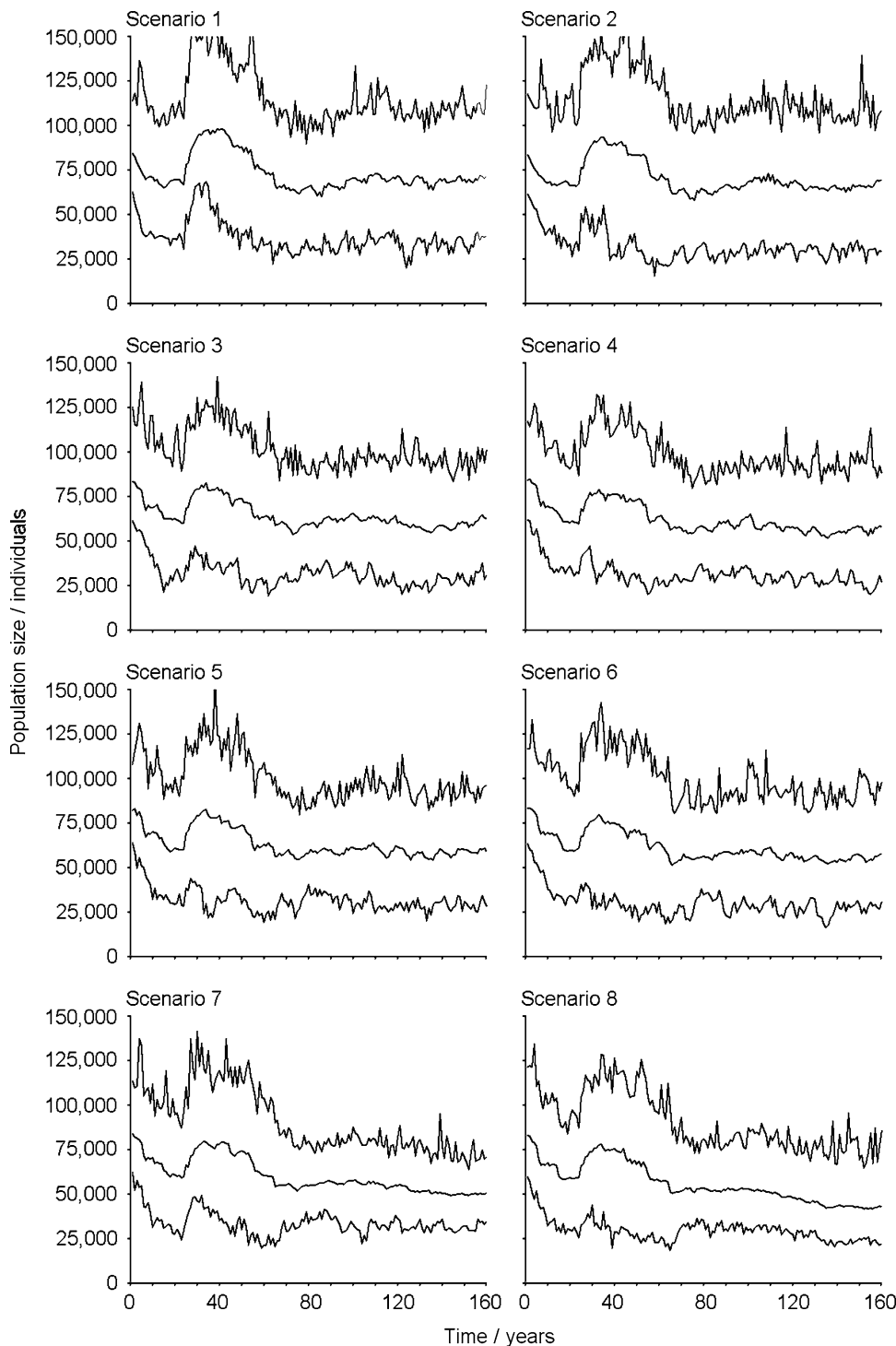


Figure 2. Trajectory summaries for the Brown Creeper population model under eight alternative management scenarios (see Appendix for description of management scenarios). On each graph, the middle line shows the mean population size and the upper and lower lines show the maximum and minimum observed population sizes in 150 simulations (three population simulations on each of 50 landscapes).

11–14% of the landscape was harvested in scenarios 4 and 6. The threat of local extinction is close to zero (Fig. 3). These results provide a transparent statement of the predicted cost of management actions in terms of population outcomes. Salvage logging incurs a further 20–22% decrease in predicted population size at 160 years when compared with current practices (Table 3). The decision about whether such a cost is unacceptable is a social one,

but DLMP model results provide a means to define the stakes more clearly.

Users of the DLMP model are encouraged to consider the robustness of the model assumptions. The results of the sensitivity analysis were encouraging, in that the model was not particularly sensitive to changes in most population parameter estimates. Although an alternative assumption about the mechanism of density dependence

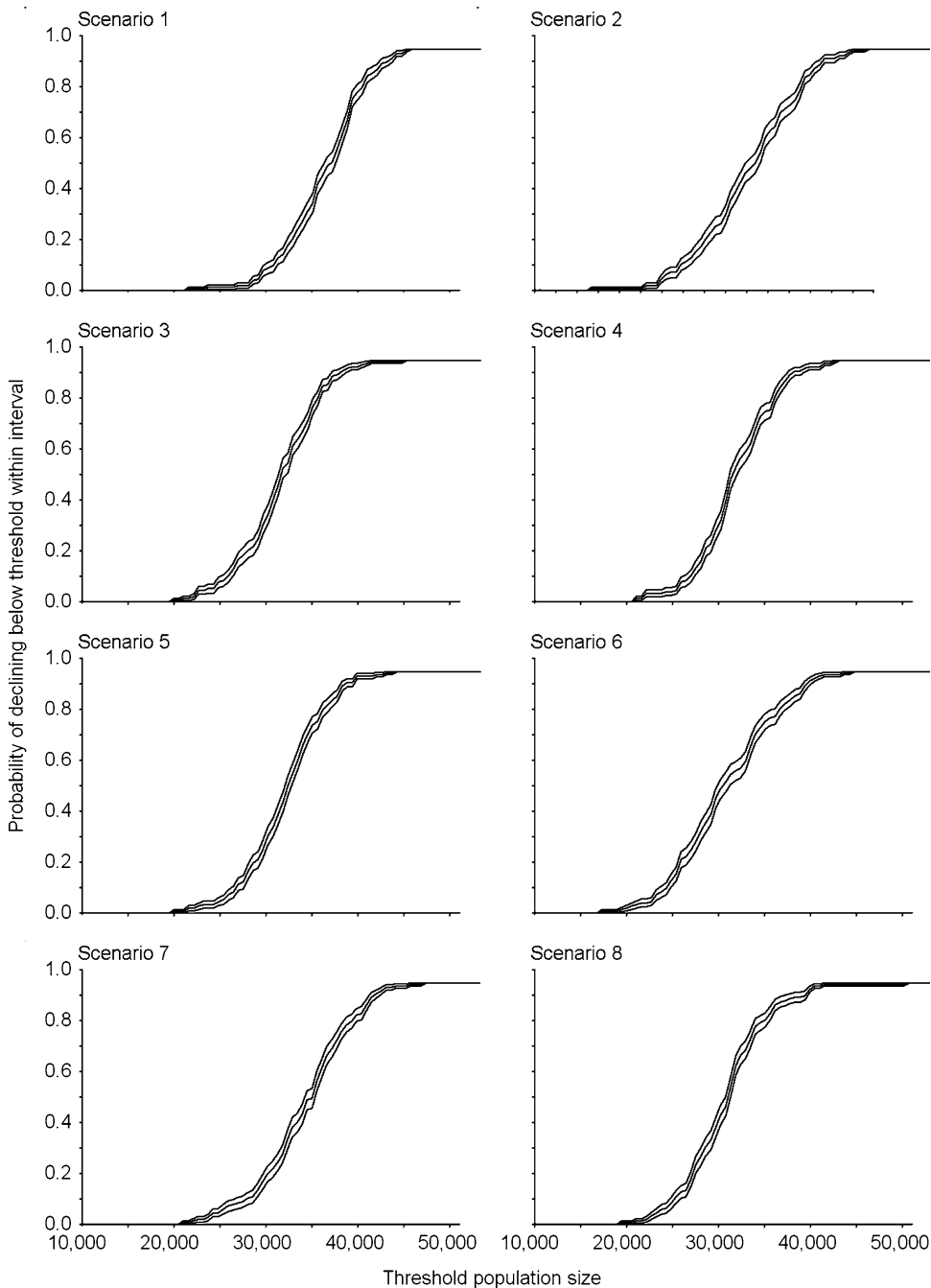


Figure 3. Interval extinction risk curves for the Brown Creeper population model under eight management scenarios (see Appendix for description of management scenarios). On each graph, the middle line shows the estimated probability of declining below the threshold value, whereas the upper and lower lines show one standard error from this estimate.

resulted in a substantial change in EMP (Table 2), the relative ranking of the scenarios did not change (B.W., unpublished data), suggesting that the general result was robust to this assumption. The maximum population growth rate R_{\max} is a particularly important parameter when density dependence is modeled with contest competition (Akçakaya & Root 2002). Our sensitivity analysis, however, indicated that results were not particularly sensitive to our choice of R_{\max} .

The statistical model defining the relationship between stand age and Brown Creeper occurrence was used in

combination with vegetation type to define the spatial distribution of suitable habitat. The statistical model explained a relatively small amount (15%) of the variation in Brown Creeper observation data, and this is commonly the case in habitat studies that use survey data in statistical analyses (e.g., Loyn et al. 2001). Previous studies and expert knowledge add support to the relationship we used to define suitable habitat. A common alternative to a statistical habitat model is the use of expert opinion alone to specify a habitat suitability index, though the explanatory power of the index is unknown. The uncertainty in

Table 3. Comparison of scenarios for the Brown Creeper model based on three population repetitions on each of 50 landscapes for each scenario.

Simulations	N_{160}^a		MP^b		S^c
	mean	$SE(\text{mean})$	mean	$SE(\text{mean})$	
Scenario 1 no harvest (base model)	71438	1587	34131	491	
Scenario 2 fire suppression, no harvest	70045	2186	31249	657	-8
Scenario 3 natural disturbance emulation	62649	1734	29609	509	-13
Scenario 4 natural disturbance emulation with fire suppression	58265	1576	29896	486	-12
Scenario 5 conversion to jackpine after harvest	59205	1546	30234	474	-11
Scenario 6 conversion to jackpine after harvest with fire suppression	58112	1747	28936	605	-15
Scenario 7 harvest with salvage logging	50479	864	32229	581	-6
Scenario 8 harvest with salvage logging and fire suppression	42757	1456	28960	535	-15

^aPopulation at end of simulation (after 160 years).

^bMinimum population size.

^cSensitivity of this scenario compared with the base model, as determined by Eq. 4.

habitat relationships used in metapopulation models may contribute a substantial source of prediction uncertainty and is an important area of future research.

It is possible that this case study provided optimistic predictions under logging scenarios because some potential impacts were not incorporated. The influences of herbicide application and edge effects around harvested sites (Brand & George 2001) were not included. Ideally the model would include the possibility of reduced fecundity in a buffer zone around harvested sites, but this impact is challenging to implement. The assumption of a constant mortality rate in the nonbreeding season may be problematic because there is evidence that survival rates of adults may be lower following wet, cold winters (Peach et al. 1995). Incorporating environmental stochasticity and standard deviation around survival rates ought to have captured most of this variation. The assumption that no further areas would be harvested after 2010 may also be optimistic. To improve confidence in model predictions, further research is needed to clarify sensitive assumptions such as the mechanisms of density dependence (Table 2).

Future work might investigate the influence of additional biodiversity prescriptions, including the preservation of old trees, snags, and coarse woody debris on logged sites; longer rotation lengths; and alternative harvesting designs. This may help define silvicultural approaches for improved biodiversity outcomes.

The Utility of Indicators and the Use of DLMP Models in their Evaluation

Substantial controversy surrounds the use of single-species indicators in assessing sustainable forest management, and alternatives have been proposed (Noss 1990; Lindenmayer et al. 2000). Single-species indicators, however, continue to be one of the most common means of interpreting and inferring ecological sustainability (Commonwealth of Australia 1998). We did not set out to resolve the validity of indicators but to provide a workable

interpretation for assessing sustainability. Our approach has several advantages over long-term monitoring programs, including the relatively low cost, the immediacy of the information, the explicit treatment of uncertainty, and the flexibility of the method to provide predictions about future management scenarios. Importantly, model-based approaches also allow numerous species to be modeled and provide a representative sample of the ecosystem response to management. Future implementation of model-based approaches will require a means to aggregate results of several species' models to enable a multispecies evaluation of management options or the state of the system.

Models may provide an early warning on unsustainable practice where monitoring cannot. Model-based approaches, however, must be supported by monitoring studies because the latter are critical to developing biological knowledge, testing predictions, and refining parameters (Walters & Holling 1990).

The utility of the modeling method we used was assessed in terms of practicality, generality, sensitivity, and realism. The RAMAS Landscape program was practical to apply. Although some data preparation is required outside the package (i.e., GIS data), RAMAS Landscape is predominantly stand-alone and is relatively straightforward to use. Primary concerns about the method include the practical difficulties associated with incorporating Monte Carlo simulation of fire and vegetation successional processes (see below). Other technical problems include the limitation of 500 populations and difficulties associated with the introduction of initial age-class and floristic data. The current LANDIS model output makes it difficult to evaluate the proportional dominance of vegetation species in cells.

DLMP modeling has generality in that it has the potential to be applied to many species that use a range of habitats at different spatial scales. We developed similar models for two other species in the boreal forests: the red-backed salamander (*Plethodon cinereus*) and the red-backed vole (*Clethrionomys gapperi*) (S.B. et al., unpublished). Species were selected as bioindicators because they were likely to respond to ecosystem stresses induced

by harvesting. The applicability of the method will vary from species to species depending on life history and habitat specificity. Long-lived plant species, species with habitat requirements that are difficult to map, or species with unique density-dependence mechanisms present particular challenges. The relevance of DLMP to such species requires further research.

The model predictions were sensitive to the differences between management scenarios, indicating that these methods are useful for assessing and ranking the sustainability of forest management options. An important aspect of the realism of the models is the ability to graphically represent processes such as forest succession and the incidence of fire. This facility enables visual verification of model parameters by experts. Exploring model assumptions has an important role in introducing sufficient realism to a metapopulation model. RAMAS Landscape appears to be sufficiently flexible to facilitate the development of realistic models, although further applications of the model in case studies are required.

Modeled and Ignored Forms of Uncertainty in the Current Method

The RAMAS GIS software appears well equipped to model the various forms of uncertainty associated with demographic parameters. Most model parameters are specified with an expected value and an expression of uncertainty in terms of standard deviations or upper and lower bounds. In the integration of RAMAS GIS and LANDIS, however, important forms of uncertainty may go largely untested without substantial and tedious effort.

The RAMAS Landscape software does not provide a simple means for incorporating the uncertainty in model predictions associated with landscape model assumptions and parameter estimates such as fire size distribution, fire frequency, tree-species establishment probabilities and other life-history traits, the initial composition and structure of the forest, and the assumed species habitat relationships. Landscape stochasticity and its influence on model predictions are also difficult to quantify. In our study, fire regimes could not be held constant between scenarios because of the interaction between logging history and fire. Preliminary results indicated that the variation in EMPs arising from landscape model stochasticity was at least as large as the variation attributable to alternative management scenarios. Thus we had to perform a large number (50) of landscape repetitions for each scenario to account for this variation. Although at least one research project has attempted to use the RAMAS Landscape package to assess the relative importance of landscape and demographic uncertainty (Akçakaya et al. 2005), the impracticalities of performing this procedure manually led us to develop software to automate the landscape repetitions. This software is freely available from the authors.

Conclusions

We present one of the first attempts to produce a metapopulation model of species dynamics coupled with a forest-dynamics model (see also Akçakaya et al. 2004). This approach is proposed as a fundamental component of sustainable forest management. The DLMP models allow forest managers to explore aspects of the ecological sustainability of management actions before the actions take place and it makes the causal link between management actions and indicator responses clear. Management decisions are therefore made on the basis of anticipated impacts rather than as a reactive measure following environmental harm, encouraging managers to stay a step ahead by prospectively assessing the sustainability of management options. The DLMP models highlight both environmental and model uncertainties and encourage the incorporation of uncertainty in the decision-making process.

The DLMP models also help focus monitoring efforts by identifying important knowledge gaps. These gaps may pertain to both species biology and ecosystem functioning. In our case study, sensitivity analysis indicated that a better understanding of the mechanism of density dependence should be a research priority for the Brown Creeper.

The models represent one component of an adaptive management system in which the results of monitoring are used iteratively to refine model parameters and predictions. Both models and strategic monitoring may be used iteratively to design and evaluate forest management actions that minimize ecological harm while maximizing social and economic gain from forest resources.

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Appendix . The eight forest management scenarios implemented, including forest composition, fire, and harvesting regimes.*

<i>Scenario</i>	<i>Fire regime</i>	<i>Harvesting regime</i>
1. No timber harvesting and a natural fire regime	fire size and return time parameters set to match current estimates	no timber harvesting
2. No timber harvesting with fire suppression	fire-return times set to 320 years for jack-pine-dominated forest and to 700 years for mixed forests; fire size distribution set to a mean of 8,000 ha, with upper and lower limits of 10,000 and 6,000 ha, respectively	no timber harvesting
3. Natural-disturbance-emulation harvesting guidelines with natural fire regime	same as scenario 1	harvesting according to natural-disturbance-emulation guidelines (NDE; OMNR 2001), i.e., 20% of harvested area allowed to regenerate naturally to mixed forest, remainder replanted to jack pine; 10% of stands nominated for harvesting retained in 1-ha blocks as wildlife habitat and not harvested; replanted areas remain jack pine for the length of the simulation; total area harvested approximately 18,000 ha in each of two rotations; first rotation starts at the beginning of the simulation; all 18,000 ha harvested within the first 40 years of the simulation; harvesting in the second rotation completed between the 90 th and 130 th year of the simulation; other prescriptions within the NDE standards and guidelines (OMNR 2001) not modeled because of a lack of data
4. Natural-disturbance-emulation harvesting guidelines with fire suppression	same as scenario 2	same as scenario 3
5. Intensive harvesting with a natural fire regime	same as scenario 1	similar to scenario 3, but involves an increase in the intensity of silviculture; timing of harvesting events same as in scenario 3; all areas nominated for harvesting clearcut and replanted to jack pine; all replanted areas remain jack pine for duration of the simulation
6. Intensive harvesting with fire suppression	same as scenario 2	same as scenario 5
7. Intensive harvesting with natural fire regime and salvage logging in burned loggable areas	same as scenario 1	similar to scenario 4, except total harvested area effectively increases because areas burned by wild fire are salvage logged; 20% of salvage-logged area allowed to regenerate naturally and remainder planted with jack pine; no salvage logging occurs in Pukaskwa National Park
8. Intensive harvesting with fire suppression and salvage logging in burned forest under an altered fire regime	same as scenario 2	same as scenario 7

*In all eight scenarios forest composition and structure at the first time step reflects that of 1970 according to historical forest inventory maps. Forest composition and structure changed according to successional processes driven by tree species and life-history traits.

