CHAPTER

Dynamic Landscape Metapopulation Models and Sustainable Forest Management

18

Sarah Bekessy, Brendan Wintle, Ascelin Gordon, Ryan Chisholm, Lisa Venier, and Jennie Pearce

Sustainable forest management is a widely held international goal (Mulder et al. 1999, Smith and Zollner 2005) and in many cases a legislated mandate (Commonwealth of Australia 2001). One component of sustainable forest management involves assessing the impact of management on biodiversity, which is frequently carried out using individual species as indicators (Mulder et al. 1999). However, the choice of indicators and determination of how they should be monitored is far from resolved. The urgency with which meaningful, practical, and immediate assessments of sustainability must be developed is highlighted by national and international sustainable forest management certification systems that are expanding rapidly and influencing market demand (Kanowski et al. 1999) and the rate of timber harvesting in forests is continuing at substantial levels (Canadian Council of Forest Ministers 2000).

The use of indicators is often associated with long-term and broad-scale monitoring of populations to assess population trends and inform management in an adaptive manner (Walters and Holling 1990, Johnson 1999, Elzinger et al. 2001). However, there is increasing evidence that long-term monitoring alone, especially at broad scales, is unable to provide useful information to address the most immediate concerns of forest management for sustainability (Temple and Wiens 1989, Ralph et al. 1995). This is partly because monitoring programs require long time frames to identify change (Green and Hirons 1991). It is often difficult to use broad-scale monitoring data to establish whether real and important changes are occurring in populations (Temple and Wiens 1989), especially at scales necessary to inform sustainable forest management. Broad-scale programs are suited to detecting changes over long time periods and over large areas.

Long-term, broad-scale monitoring has also been criticized because it is difficult to assign a cause to changes that are measured. Morrison (1986) suggested that species respond to change, but not uniquely to specific changes; therefore, it becomes difficult to identify the responsible mechanisms unless the data are collected within carefully designed experiments. Population trends, in and of themselves, do not help identify cause-and-effect relationships and therefore do not help identify management options (Ralph et al. 1995). The general lack of controls in large-scale monitoring programs is also problematic because of the pervasive impacts of large-scale disturbances, such as climate change. Information about underlying causes of change are more likely to be obtained through intensive local-scale studies (Venier and Pearce 2004). The major drawback of such studies is that they are not as likely to provide as widely applicable results as broader scale studies.

Alternative indices of sustainability such as vegetation structural indicators have been proposed (Lindenmayer et al. 2000) on the basis that they do not suffer from the specific concerns identified for taxon-based indicators. Structural indicators are appealing because they are relatively easy to measure, and the structural consequences of forest management are easier to predict than individual species and demographic responses. Structural complexity maintenance, forest connectivity, and spatial heterogeneity in stand structure are important aspects of forest management and should be included as criteria for sustainable forest management. Such criteria would be relatively easy to monitor. However, the link between species persistence and structural metrics is seldom clear, and structural indices may not be a good indicator of species richness or persistence (Abensperg-Traun et al. 1997).

An important aspect of sustainable forest management is maintaining viable populations of associated organisms (Noss 1990, Poiani et al. 2000, Smith and Zollner 2005), and measuring structural metrics does not ensure that management achieves this outcome. The measurement of structural metrics alone does not assist managers in balancing the ecological, economic, and social values of a forest because it does not answer the question of how much connectivity, heterogeneity, and complexity is enough to ensure species persistence and the maintenance of biodiversity in a region. The question of how much of these structural attributes in a landscape is enough can only be properly answered in the long term through carefully designed biodiversity monitoring strategies within an adaptive management context. Even so, such a system provides no immediate guidance and no forecasting of the likely consequences of current actions and management alternatives. Options for exploring alternatives are required in the short term, even if a comprehensive and reliable monitoring system is in place.

Recently, there has been an increasing emphasis on exploring indicator responses through habitat models (Mulder et al. 1999) where habitat relationships are assessed based on small-scale studies and expert opinion (e.g. Yahner 1992, Petranka et al. 1994). Predictions of the future distribution of habitat together with known habitat occupancy rates provide an approximation of the future abundance of a species under alternative management approaches (e.g., Gustafson et al. 2001). Such approaches are more appealing than simple structural indicators and abundance measurements because they make explicit use of available knowledge about habitat requirements to make predictions about the local persistence of a species. Often these requirements incorporate forest structural attributes, but in a way that is more biologically meaningful than simply measuring the structural attributes themselves. However, some of these methods do not consider environmental and demographic stochasticity explicitly. Further, some do not account for the spatial attributes of a species' biology that may occur at broader scales such as dispersal dynamics and Allee effects. Some of these methods are also constrained by inadequate estimates of detection probability and the ability to confidently determine absence (Wintle et al. 2005*b*). Consequently, these methods may be unable to capture the potential landscape-scale effects of forest management activities on habitat composition and configuration and temporal fluctuations in habitat occupancy that in turn affect population persistence (Andren 1994, McGarigal and McComb 1995, DesRochers and Hannon 1997, Schmiegelow et al. 1997).

Metapopulation models can be used to address these additional concerns. They incorporate the dynamic consequences of dispersal among local populations and the conditions that lead to regional persistence of a species (Hanksi 1998). They provide a mathematical representation of the demographics within populations and dispersal between populations, and allow predictions of population size over time. Metapopulation models have been used widely in endangered species management (Boyce 1992, Akçakaya et al. 1995), but not in more general management problems, though the potential for such an application has been recognized (Burgman and Possingham 2000). The predictions of metapopulation models for a range of indicator species may provide a useful means of evaluating the sustainability of current and alternative forest management activities and predicting ecological changes.

Metapopulation models have been used in conservation planning under the umbrella of population viability analysis (PVA; Akçakaya et al. 1995; Lindenmayer and Possingham 1996; Burgman and Lindenmayer 1998; Akçakaya and Brook, this volume; Beissinger et al., this volume). Population viability analysis has been described as any systematic attempt to understand the processes that make a population vulnerable to decline or extinction (Gilpin and Soulé 1986, Burgman and Lindenmayer 1998) and may be used to assess the likelihood that a population will persist for some arbitrarily chosen time into the future (Shaffer 1990, Boyce 1992, Smith and Person 2008). It is an interactive process of model construction, parameterization, sensitivity analysis, and validation (Akçakaya 2000, Burgman and Possingham 2000). While there is considerable uncertainty associated with using population viability models to predict actual risks of extinction (Taylor 1995, McCarthy 1996, Beissinger and Westphal 1998, Fieberg and Ellner 2000), PVA models appear to be useful for predicting changes in population size and ranking the severity of the effect of different management strategies (Boyce 1992, Beissinger and Westphal 1998, McCarthy et al. 2003). The models allow the available data and information to be integrated in a manner that is comprehensive, explicit, and repeatable, which then allows a transparent assessment of the consequences of different management strategies (McCarthy et al. 2004).

The development of a species metapopulation structure involves the identification of habitat requirements including the finer scale dependencies derived from habitat studies (e.g., Yahner 1992, Petranka et al. 1994, Smith et al. 2004, Smith and Person 2008) and the ecosystem stresses it responds to. Metapopulation models may predict change in habitat attributes or structural indicators in a way that directly addresses the impact of such changes on populations of forest-dependent species in terms of their probability of decline or loss. Moreover, it provides a way to incorporate available information about specific spatial and demographic requirements of species. Demographic models also allow the comparison of management scenarios that do not explicitly change forest structure or habitat quality indices but may impact on biodiversity, such as hunting or the application of herbicides and pesticides.

A modeling approach also addresses the need for more immediate information to make informed management decisions. The nature of the system can be hypothesized, model predictions can be generated, and the impacts of management can be measured using metrics such as minimum expected population size. Models can provide the capacity to compare alternative management options using the best information available and to quantify the uncertainty in what we know.

Constructing metapopulation models under a range of management scenarios requires a dynamic landscape model (Burgman et al. 1993; Holt et al. 1995; Mladenoff and Baker 1999; He, this volume) to characterize future changes in landscape vegetation composition and structure resulting from each management scenario. Dynamic landscape models predict the vegetation composition and structure of future landscapes by incorporating the effects of deterministic and stochastic disturbance (such as timber harvesting and fire) and succession. Successional processes may be described on the basis of establishment and persistence probabilities for individual vegetation species or vegetation types (Mladenoff and He 1999). Linkages between dynamic landscape models and metapopulation models are very recent and pose a number of challenges including software and computing challenges. Previous studies manually linked outputs from dynamic landscape models with habitat suitability models or population models (Larson et al. 2004, Shifley et al. 2006). More sophisticated packages devoted to these approaches are emerging. The case studies described here and one other study (Akçakaya et al. 2004) have used the dynamic landscape metapopulation (DLMP) modeling software package RAMAS Landscape (Akçakaya et al. 2003).

Further challenges to sustainability assessments are brought about by the multitude of scales at which forest management takes place. Cumulative effects of forest management on ecosystem composition and function arise from activities at the level of prescription (usually stands and management units) to the level of resource allocation (usually regions, license areas, and provinces). Assessment of sustainable management should therefore encompass the influences of both prescription- and allocation-level decisions. Dynamic landscape metapopulation models have the flexibility to be developed at multiple scales and to incorporate influences at multiple scales.

INDICATOR SPECIES

Monitoring a few indicator species is an intuitively appealing method of measuring the ecological sustainability of forest management because it is impossible to measure and monitor the effects of forest management on all species or environmental conditions of interest (Landres et al. 1988; Noon et al., this volume). Lindenmayer et al. (2000) define seven types of indicator species: (1) species whose presence indicates the presence of a set of other species; (2) keystone species (*sensu* Terborgh 1986) whose addition to or loss from an ecosystem leads to major changes; (3) species whose presence indicates human-created abiotic conditions such as air or water pollution (Spellerberg 1994); (4) dominant species that provide much of the biomass or number of individuals in an area; (5) species that indicate particular environmental conditions such as certain soil or rock types; (6) species thought to be sensitive to, and therefore serve as an early warning of, environmental change (also called indicator species); and (7) management indicator species, which reflect the effects of a disturbance regime or the efficacy of particular efforts to mitigate disturbance (Milledge et al. 1991).

These seven types of indicator species can be effectively classified into three classes of indicators: (1) biodiversity, (2) environmental, and (3) ecological. Biodiversity indicators indicate the presence of a set of other species (Noss 1990, Gaston and Blackburn 1995, Flather et al. 1997) and therefore provide a descriptive function. Environmental indicators are also descriptive in that they indicate changes in the state of the abiotic environment directly. Ecological indicators demonstrate the effects of environmental change on the biotic systems including species, communities, and ecosystems (Meffe and Carroll 1994), which provides an indication of change in the functioning of the system. Biological indicators of sustainable forest management are ecological indicators in that they must provide information on the effects of forest management on the functioning of the forest ecosystem to be useful. They can be keystone species, dominant species, sensitive species, or species that reflect the ecological effects of a disturbance regime. To be most effective, some must target anticipated stresses that are known to result from current or potential forest management approaches (Mulder et al. 1999, Venier et al. 2007). Examples of such stresses might include the truncation of older forest tree cohorts (e.g., McRae et al. 2001) or reduction in coarse woody debris in the form of snags or fallen logs.

The choice of a wide range of indicator species that target a range of potential ecosystem stresses would increase the likelihood that changes in ecosystem process resulting from forest management would be detected in monitoring systems. Indicators should also be chosen that represent a full range of spatial scales from local to regional, and a range of life history characteristics to capture as much of the ecological spectrum as possible. The rarity and detectability of an indicator species is likely to influence its effectiveness as an indicator of sustainable forest management. A characteristic of rare species is that suitable habitat may remain unoccupied for long periods of time. This creates problems for model-based assessments of sustainability due to difficulties in estimating initial population size, identifying habitat requirements, and describing metapopulation structure. We recommend the use of relatively common, widespread species, as they will serve as a better index of ecosystem condition over a greater proportion of the region and not just in the areas in which they exist.

The principle behind the use of indicator species implies a shift toward an ecosystem approach to management and monitoring. In our framework, indicator species are chosen because they reflect the ecosystem conditions necessary for their persistence. A change in the status of indicator species indicates a change in the state of the system. Likewise, no change in indicator species infers that an ecosystem is healthy. However, this second assertion will hold only if a sufficient number of indicator species are chosen on the basis that they target a variety of different ecosystem stressors predicted to arise from management activities. Using multiple species may also limit the problem of regional ecological differences weakening the effectiveness of indicator species (Smith et al. 2005).

Although the use of indicator species is attractive and could be a valuable management tool (Roberge and Angelstam 2004), there have been several major criticisms of current approaches to using biological indicators to inform sustainable forest management. These include the long time frames required to produce useful information, the lack of cause-and-effect linkages between management and indicator responses (Andelman and Fagan 2000, Smith et al. 2005), and the lack of transparency in the process. The indicator species approach is fraught with the difficulty of defining threatening processes, the species most sensitive to each process, and the manner in which species are affected by each process (Lindenmayer et al. 2002). These difficulties are compounded by complicated interactions between threatening processes and biases in biological data toward well-known vertebrates (Lindenmayer et al. 2002). The indicator species approach, like other taxon-based surrogate schemes, is based on the implicit assumption of nestedness among species; that is, the response of a certain species is assumed to be representative of the response of a broader range of species. Surrogate approaches that rely on single species, or aggregations of a few species, have been criticized because qualitatively similar species may have substantially different responses to environmental change (Lindenmayer et al. 2002; Noon et al., this volume). In a study by Andelman and Fagan (2000), taxon-based surrogate schemes were shown to be no more effective than species selected at random for capturing species or protecting habitat. Moreover, combining multiple assessments of impacts across species remains a significant challenge (Wintle et al. 2005*a*; Noon et al., this volume).

Effective use of indicator species approaches requires an understanding of the relationships between the response of surrogate species and the response of broader biodiversity to management actions (Bekessy et al. 2008). Indicator species can be used to guide habitat-based approaches to biodiversity planning and can be incorporated into population process-based assessments. If an indicator species approach is adopted, the consequences of given management scenarios for individual species persistence need to be understood. Of course, species can also be the focus of modeling or planning because of concern or interest in a particular species, and not because they are to be used as indicators. In this chapter, we propose the development of DLMP models of biological indicators for assessing the sustainability of forest management and guiding forest management decisions at various scales as a means of addressing current criticisms. We define ecological sustainability here as the maintenance of forest-dependent species within the managed forest estate. We review the practical advantages and problems of these methods based on our experiences gained through case studies and provide recommendations for appropriate implementation of the method in an adaptive management setting.

CONSTRUCTING AND INTERPRETING DLMP MODELS FOR INDICATOR SPECIES

Dynamic landscape metapopulation models integrate information on forest succession, natural disturbance regimes, and forest management actions to provide a spatial representation of the landscape and how this landscape changes through time. These models integrate dynamic landscape models with models of the population dynamics of the indicator species, representing the response of the species to this spatially and temporally variable environment. This holistic modeling approach allows prediction of future population sizes of the indicator species under a range of forest management scenarios. Thus, a DLMP model is an integration of modeling techniques currently applied in forest management and conservation planning including habitat modeling, landscape modeling, and metapopulation modeling. The landscape model and the population model are linked via a habitat model, which identifies areas in the landscape that may be suitable for occupation by indicator species. The habitat model provides information for the metapopulation model regarding the location and quality of habitat "patches" and the number of individuals of an indicator species that each patch is likely to support. The landscape dynamics model describes how habitat availability changes through time due to succession and disturbance.

Developing the Model

A DLMP model is developed in five steps (Wintle et al. 2005*a*):

1. Build a habitat suitability map relating species presence and abundance to environmental variables. A habitat model may take various forms and is simply a description of how a species' presence or abundance is related to the landscape. It may be defined by a regression model (e.g., Pereira and Itami 1991; Buckland and Elston 1993; Ford et al. 2004; Niemuth et al., this volume), a classification tree (e.g., Hastie et al. 2001), a Habitat Suitability Index (e.g., Rand and Newman 1998; Burgman et al. 2001; Dijak and Rittenhouse, this volume), a machine learning algorithm, or any other statistical function. This model is extrapolated across the landscape using a geographical information system (GIS; e.g., Menzel et al. 2006), to produce a continuous map of habitat suitability.

2. Develop a population dynamic model for indicator species describing demographic attributes such as age or stage-specific birth and death rates through time. A population model allows predictions of population size over time by modeling the demographic attributes of a species (e.g., Smith and Person 2008). The structure of the population is specified in terms of survival, fecundity, and mortality among juvenile and adult life stages. Demographic stochasticity is included by specifying each parameter as a mean value with a standard deviation.

3. Develop a metapopulation model by linking the population dynamic model to the habitat suitability model to reflect spatial dynamics across time and space. The landscape model and the population model are linked via the habitat model. Patches of contiguous habitat are defined as populations, with carrying capacities. Discrete habitat patches are identified using estimates of species' range movements and a threshold of habitat suitability below which cells would be considered unsuitable and therefore unoccupied. Dispersal rates between populations are specified by the user and describe the degree of interaction between populations. Lindenmayer et al. (1995) provide a review of metapopulation modeling methods.

4. Develop a forest dynamic model to describe how forest composition and structure are expected to change over time given natural and anthropogenic disturbance regimes. A sucession model describes the tree species composition of the landscape and how this composition changes through time, based on species life-history attributes, site conditions, disturbance regimes, and management. Life-history characteristics considered include longevity, age at sexual maturity, shade and fire tolerance, and seed dispersal distance of each tree species. Disturbance regimes include natural processes, such as fire and windthrow, and anthropogenic processes such as timber harvesting and prescribed burning and the extent to which anthropogenic disturbance influences the likelihood of natural disturbance.

5. Link the dynamic forest model to the metapopulation model. The resulting model then provides a spatially and temporally explicit representation of habitat and population dynamics. The succession model is linked to the habitat model to describe habitat availability through time. Changes in fecundity and survivorship, as well as presence or absence of the species, are developed to reflect changing landscape conditions (e.g., survivorship can be set lower in areas buffering harvesting activities). The metapopulation model uses this information to describe population sizes through time.

DLMP Model Software

The five steps outlined in the preceding section are implemented in a new software package called RAMAS Landscape (Akçakaya et al. 2003). RAMAS Landscape is the only standalone software package that is currently designed to implement DLMP models (Akçakaya et al. 2004), and it does this by linking the dynamic landscape modeling package LANDIS 3.7 (Mladenoff and He 1999) with the metapopulation modeling package RAMAS GIS 4 (Akçakaya and Root 2002). The software allows managers to integrate ideas about species habitat, population dynamics, landscape dynamics, and management.

The RAMAS GIS module of RAMAS Landscape simulates species metapopulation dynamics over time. The RAMAS GIS module is composed of various submodules designed to identify the metapopulation patch structure; specify the population model parameters, catastrophes, and management actions; and implement Monte Carlo simulations to evaluate predictive uncertainty. The user must specify the structure of the population in terms of survival, fecundity, and mortality rates among juvenile and adult life stages. Simulations are stochastic in that population parameter estimates, and catastrophic events are specified from a distribution of possible values with the mean and standard deviation of distributions specified by the user.

The LANDIS module simulates forest change by modeling tree species in 10-year age classes (He, this volume). It 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 include longevity, age at sexual maturity, shade and fire tolerance, and seed dispersal distance of each tree species. Any number of tree species can be included in the model. Site conditions are encapsulated by “land types,” which can be derived from climatic, physiographic, and edaphic properties. The LANDIS model incorporates natural processes (fire, windthrow, succession, and seed dispersal) and anthropogenic processes (e.g., timber harvesting and prescribed burning). It allows many different silvicultural treatments such as thinning, selection, gap harvesting, and clearcut harvesting to be modeled.

A detailed discussion of the theory, design, and implementation of RAMAS Landscape, RAMAS GIS, and the LANDIS model are provided elsewhere (He et al. 1996; Mladenoff and He 1999; Akçakaya and Root 2002; Akçakaya et al. 2003; Akçakaya and Brook, this volume; He, this volume).

Interpreting Model Predictions

The DLMP model estimates the expected metapopulation size at each time step of the simulation and presents this as a population trajectory, with time on the x-axis and population size on the y-axis (e.g., Fig. 18-3B). A population trajectory illustrates fluctuations in population size over time in response to environmental changes and demographic processes. Uncertainty in metapopulation model predictions is characterized by running the model many times and generating predicted population trajectories for each run of the model to form a distribution of predictions. The shape and spread of the predictive distribution defines the magnitude and type of uncertainty inherent in model predictions.

The response of indicator species population size to alternative management scenarios may be defined in terms of the risk of decline, measured by change in the expected minimum population size (EMP; McCarthy and Thompson 2001) between a reference state (e.g., a “natural” or base model with no anthropogenic disturbance) and the particular scenario being evaluated. The EMP is defined as the mean of the predicted minimum population sizes from all simulations of a given model and provides a representation of the lowest population size expected over the duration of a simulation under each management scenario. The EMP has been recommended as a suitable single metric for comparing population trajectories that is easily interpreted and more meaningful than other metrics such as mean population size or quasiextinction probability (McCarthy and Thompson 2001). The change in EMP can be calculated as

$$S_i = \frac{EMP_i - EMP_b}{EMP_b} \times 100 \tag{1}$$

where S_i is 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.

Results may also be graphically represented as risk curves. These describe the probability that the population will decline below a given threshold value over the course of the simulation. They are constructed by plotting simulation results, such as the minimum population size observed in a replication, as a cumulative probability function of population size (e.g., Fig. 18-1). Management scenarios may be compared in terms of the added risk of the species declining below a particular population size under each scenario relative to some reference state such as a “no timber harvesting” scenario.

The combination of predicted population trajectories, risk curves, expected minimum population size and sensitivity analysis provides a range of options for interpreting the predictions of a DLMP model and ranking management options. A particularly useful method for ranking management options is by comparing their EMPs and by assessing the sensitivity of each option compared with a

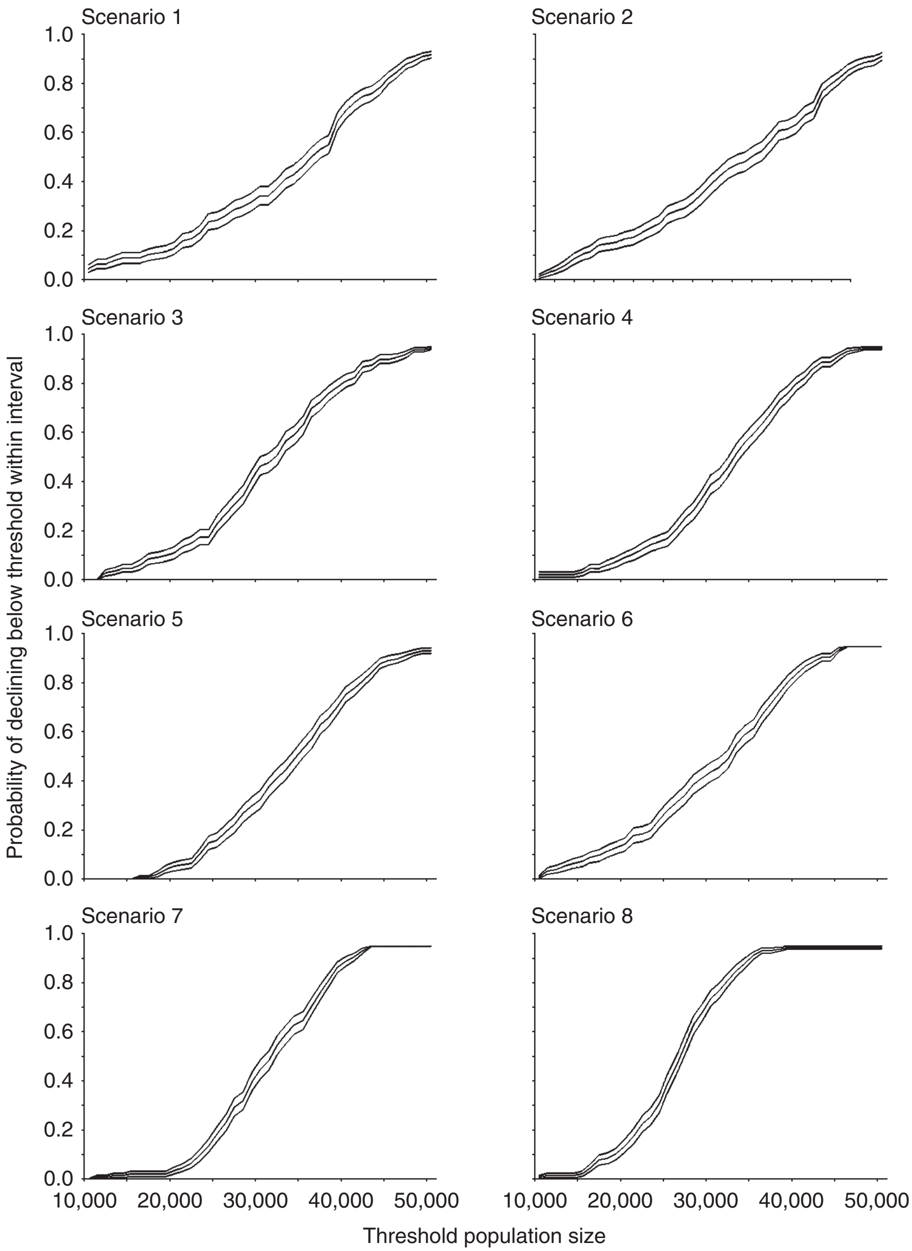

FIG. 18-1

Interval extinction risk curves for the brown creeper population model for eight scenarios (see Table 18-1). On each graph, the middle line shows the estimated probability of declining below the threshold value, while the upper and lower lines show one standard error from this estimate (from Wintle et al. 2005*a*, *b*). The shift in the risk curve for each scenario, relative to the base scenario, represents the increased risk of smaller population sizes resulting from each scenario.

reference state such as a "no timber harvesting" management option (McCarthy and Thompson 2001). While quantitative comparisons of the impacts of various options are appealing, caution is recommended due to the multitude of uncertainties inherent in predictions (Beissinger and Westphal 1998, McCarthy et al. 2003). For the same reason, ranking of management options is preferred to interpretation of absolute predictions.

SUMMARY OF CASE STUDIES

Study Area

We conducted case studies in north central Ontario, Canada, in a 150 km^2 section of the White River management area (Fig. 18-2), which has been actively managed for timber production for approximately 35 years. The northeast corner of Pukaskwa National Park was also included in the study area. As of 1972, approximately 83% of the research area was covered with mature closed-canopy forest, of which 43% was dominated by conifer forest, 33% by deciduous forest, and 25% dominated by mixed forest. The main tree species in the study area were jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* Mill.), trembling

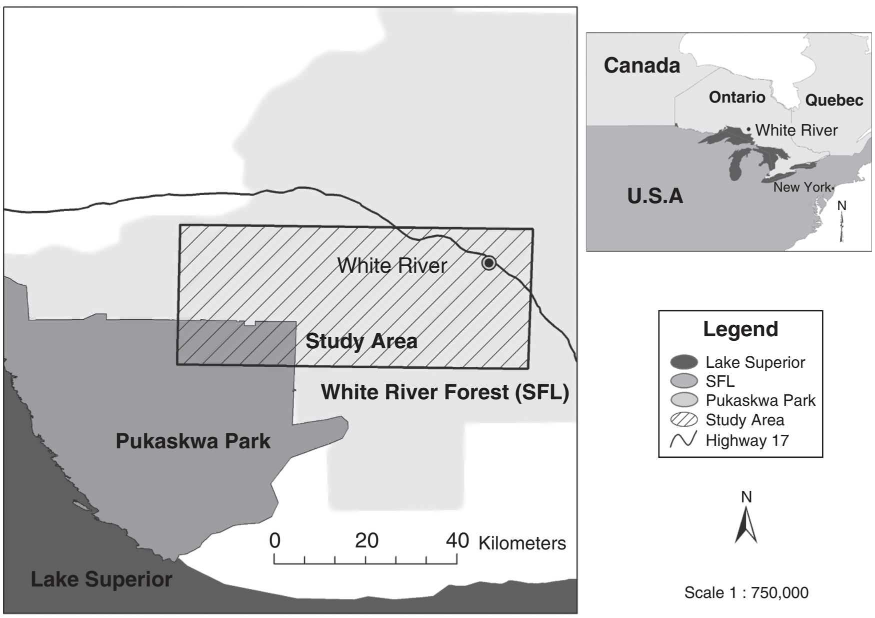

FIG. 18-2

Map of the study area in north central Ontario, Canada.

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). Harvesting activities within the White River management area have concentrated on harvesting mature jack pine or jack pine mixed-wood stands. As of 1998, approximately 21% of the forested portion of the research area had been harvested and replanted principally to jack pine (although sometimes to black spruce, or natural regeneration).

Species

We chose three species for this exercise: the brown creeper (*Certhia americana*), the red-backed salamander (*Plethodon cinereus*), and the red-backed vole (*Clethrionomys gapperi*). We chose these species as potential indicators for three reasons. First, they are dependent on components of the forest that may be affected by forest management. Second, they have very different life histories, allowing us to explore how easily different aspects of a species' biology may be incorporated in DLMP models. Third, each species uses habitat at different scales.

The brown creeper is a monogamous, territorial species that is dependent on snags and old trees for nesting and foraging (Hejl et al. 2002). It is known to be sensitive to timber harvesting that degrades these old growth characteristics (Hobson and Schieck 1999). The red-backed salamander is highly sensitive to environmental change or disturbance due to a strong reliance on their environment for temperature and moisture regulation (Welsh and Droege 2001). They occupy small activity ranges, are quite long-lived, and breed biennially. The red-backed vole is dependent on old, moist forest sites with woody debris and is potentially sensitive to timber management practices that may alter understory conditions (Thompson et al. 2003). They undergo large population fluctuations, are short-lived, and are polygynous breeders.

Details on parameter estimates are provided in Pearce and Venier (2004*a*, 2005, in prep) and Wintle et al. (2005*a*), Venier and Pearce (2005, 2007), and Gordon et al. (in prep). All three species are considered relatively common in the region. Hence, we evaluate their relative abundance and changes in EMP under different management scenarios, rather than their risk of extinction.

Modeling Approach and Scenarios Evaluated

We developed an integrated DLMP model for the three species using RAMAS Landscape. We developed habitat models to describe the presence-absence (brown creeper) and abundance (red-backed salamander, red-backed vole) as a function of forest age, forest composition, microclimate, and elevation. Using these parameters, we developed metapopulation models for each species based on information from biologists and the literature. The succession model was based on Forest Resource Inventory (FRI) maps interpreted from aerial photographs, and tree life history parameters provided by Farrar (1995). The model for each species was used to rank the sustainability of eight forest management scenarios in terms of their impact on the abundance of each species during two timber rotations spread over 160 years (brown creeper) or 100 years (red-backed salamander and red-backed vole). The eight alternative forest management scenarios modeled ranged in intensity from “no timber harvesting and a natural fire regime” to “intensive timber harvesting with salvage logging after fire” (Table 18-1). For the brown creeper, fifty landscape realisations and three population replicates per landscape realisation were conducted for each scenario. Fifty landscape replicates and three population replicates were

Table 18-1 Details of the Four Forest Management Approaches Modeled. Two Fire Regimes were Modeled. The First was a Natural Fire Regime (Scenarios 1, 3, 5, and 7; Fire Size Return Time Parameters were Set to Match Current Estimates), and the Second Assumed Fire Suppression (Scenarios 2, 4, 6, and 8; Fire Return Times were Set to 320 Years for Jack Pine Dominated Forest, and 700 Years for Mixed Forests. The Fire Size Distribution was Set to a Mean of 8,000 ha, an Upper and Lower Limits of 10,000 and 6,000, Respectively) (From Venier et al. 2007)

Scenarios	Harvesting Regime
1 and 2	No timber harvesting
3 and 4	Harvesting according to Natural Disturbance Emulation guidelines (NDE; OMNR 2001). Under these guidelines, 20% of the harvested area in the region is allowed to regenerate naturally to mixed forest, with the remainder replanted to jack pine. Ten percent of the stands nominated for harvesting are retained in one-hectare blocks as wildlife habitat and are not harvested. Replanted areas remain as jack pine for the length of the simulation. The total area harvested is approximately 18,000 ha in each of two rotations. The first rotation starts at the beginning of the simulation. All 18,000 ha are harvested within the first 20 years (salamander and vole) or the first 40 years (creeper) of the simulation. Harvesting in the second rotation is completed between the 90th and 100th year (salamander and vole) and the 90th and 130th year (creeper) of the simulation. Other prescriptions within the NDE standards and guidelines (OMNR 2001) were not modeled due to a lack of data.
5 and 6	Similar to scenario 3, but involves an increase in the intensity of silviculture. The timing of harvesting events is the same as in scenario 3. All areas nominated for harvesting are clearcut and replanted to jack pine. All replanted areas remain as jack pine for the duration of the simulation.
7 and 8	Similar to scenario 4, though the total harvested area effectively increases, as areas burned by wild fire are then salvage logged. Harvested and burnt areas are replanted with jack pine. No salvage logging occurs in Pukaskwa National Park.

conducted for each scenario. This particular ratio of landscape replicates to population replicates was established using the results of an investigation into the relative contributions of landscape and population stochasticity on DLMP predictions. For the red-backed salamander and red-backed vole models we refined our analysis and developed software that iteratively calculated the number of population replicates per landscape realisation (the Repeater package [Chisholm and Wintle 2007]; see below). Full details of model development, management scenarios, and uncertainty analysis are provided elsewhere (Pearce and Venier 2004, Wintle et al. 2005*a*,*b*, Venier et al. 2007).

Sensitivity analysis was conducted to determine if the results of the model were sensitive to estimates of parameter values and other key assumptions. S_i, the change in EMP relative to Scenario 1, was used to compare the sustainability of the various management scenarios.

Key Findings

The results of this case study illustrate that, under the assumptions made in the models, the current style of forest management (most closely resembling scenario 4) is expected to result in a 9% to 25% decrease in the expected minimum population size of the species modeled over the next 100/160 years compared to the option of no timber harvesting (Table 18-2). The threat of local extinction is close to zero for all species under all scenarios. The differences between natural disturbance emulation (scenarios 3 and 4) and more intensive styles of logging (scenarios 5 and 6) were mixed, with the brown creeper showing greatest sensitivity to intensive logging (Table 18-2). Salvage logging led to at least a 15% increase in the area harvested and had a substantial impact on all species modeled (Tables 18-1 and 18-2). Fire was also an important variable for all species, with scenarios including large, infrequent fires increasing the risk of decline in many cases (Table 18-2). Each model incorporated our current knowledge of landscape succession, disturbance regimes, and indicator species biology.

As such, these models provided a synthesis of our current knowledge base and identified information needs, and allowed us to explore the impact of model uncertainties on predicted outcomes of forest management. Therefore, this approach provided a transparent and explicit statement of the predicted cost of management actions in terms of predicted population change, within stated bounds of certainty. The decisions about whether such costs are unacceptable are inevitably value-based, but this method provides a means to describe the risks more clearly. For example, model results indicate that under a fire suppression regime, the additional cost of salvage logging is between a further 1% to 11% decrease in expected minimum population size over the next 100/160 years (Table 18-2). Model results also help to guide future research. For example, all three species' models were sensitive to the specification of density dependence, highlighting that this parameter is a priority for future research, and variations in this parameter should be considered when comparing scenarios.

Table 18-2 Summary of the Population Decline and Carrying Capacity of All Study Species Due to Anthropogenic Disturbance. The Values Presented Represent the Percentage Decline in Expected Minimum Population Size Relative to Scenario 1 (No Anthropogenic Disturbance) and the Minimum Carrying Capacity as the Percentage of the Original Carrying Capacity

		Scenario							
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Brown creeper (*Certhia americana*)*	% Decline in EMP		8.51	15.20	24.50	23.27	23.99	21.24	31.64
	Minimum K	99.33	75.46	89.01	77.59	90.56	73.56	76.68	51.96
Red-backed salamander (*Plethodon cinereus*)*	% Decline in EMP		5.9	7.0	9.2	5.9	17.0	27.0	28.4
	Minimum K	100.00	100.00	92.3	90.6	93.5	95.7	72.4	73.7
Red-backed vole (*Clethrionomys gapperi*)#	% Decline in EMP		0.5	15.1	16.8	15.5	18.1	20.3	19.0
	Minimum K	96.4	95.2	90.7	88.5	90.2	88.9	86.3	83.6

**160 year simulation; #100 year simulation*

The relative insensitivity of the red-backed salamander to harvesting scenarios (Table 18-2) was unexpected, as terrestrial salamanders have been widely recommended as bioindicators (e.g., deMaynadier and Hunter 1995, Welsh and Droege 2001). Very few population parameters were sensitive to misspecification within this model, suggesting that sufficient connected habitat is available on the landscape to maintain salamander populations, irrespective of forest management actions. However, before accepting these findings, the habitat model needs to be validated. Key microhabitat features expected to be relevant to red-backed salamanders were not included in the habitat model. Although this model was based on data collected within the study area, and represented our best understanding of salamander distribution there, this habitat model had poor predictive performance, suggesting that it did not adequately capture environmental features important to salamanders. Many potentially important predictors were not available in mapped form; others that were available and considered important within other parts of the salamander's range were not significant within the study area. It is likely that including these key habitat attributes would increase the sensitivity of the model to timber harvesting, as refining the distribution of the salamander is expected to reduce the amount of habitat available.

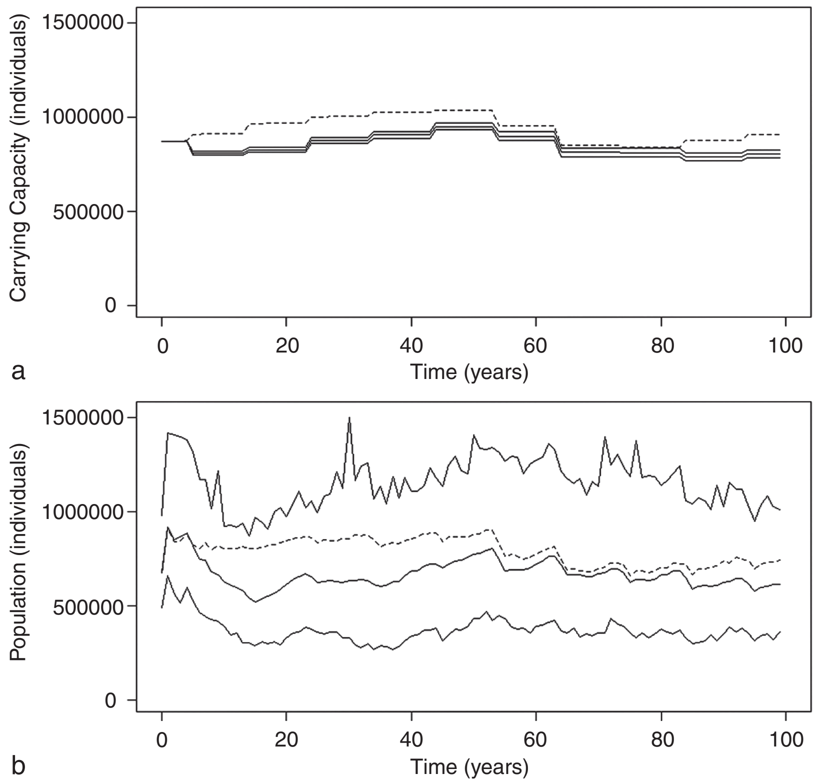

FIG. 18-3

(A) Carrying capacity and (B) population trajectory for the red-backed vole under scenario 3 (natural disturbance emulation with small, frequent fires). The middle line shows the mean carrying capacity or population size, while the upper and lower lines show one standard deviation from the mean. The dashed line shows the mean value of scenario 1.

Although the red-backed salamander model may be more sensitive to habitat availability than any other feature, DLMP models have the capacity to provide greater information on species decline than would be obtained from habitat supply models on their own (Akçakaya et al. 2003). For example, the population trajectory for the red-backed vole under scenario 3 (Fig. 18-3B) followed a substantially different pattern to the predicted habitat availability (expressed in terms of carrying capacity, Fig. 18-3A). This is most likely related to the tendency of populations of red-backed voles to fluctuate in response to disturbance (Fryxell et al. 1998). Short-term loss of habitat is followed by rapid recovery due to the high population growth rate of the species. In this case, predictions based purely on habitat would be optimistic, as including demographic considerations led to a greater estimated risk of decline. Other spatial factors, such as dispersal and connectivity, also affect habitat use and make the predictions of habitat

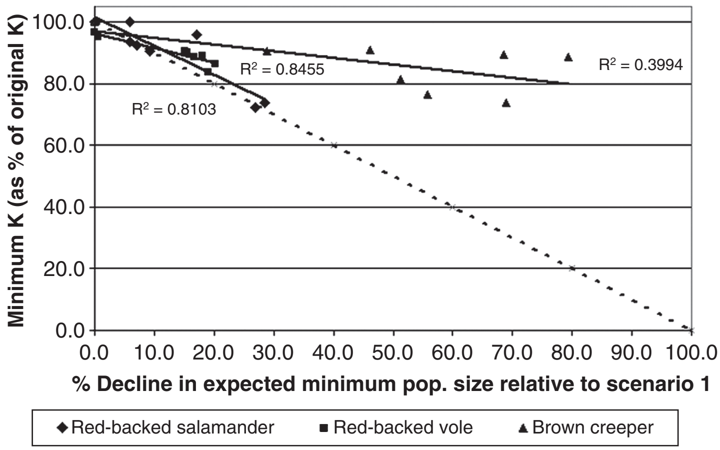

FIG. 18-4

Regressions of decline in expected minimum population size relative to scenario 1 and the minimum carrying capacity as a percentage of the original carrying capacity. Data are presented for three indicator species: the red-backed vole, brown creeper, and red-backed salamander. The dashed line indicates a perfect correlation for comparison.

supply models overly optimistic. For example, if habitat connecting two populations is harvested, it may have a greater impact than simply reducing the total extent of habitat.

Table 18-2 presents a summary of the predicted impact of the eight management scenarios on the three case study species in terms of habitat availability and EMP, and Fig. 18-4 presents the regression between these predictions. Regressions varied substantially among species, with the predictions of the population model for the red-backed salamander most closely following habitat supply and the predictions of the brown creeper least well correlated (Fig. 18-4). Importantly, the ranking of management scenarios based on habitat supply was considerably different for all species when compared with the ranking based on the population models. This result provides some evidence to suggest that habitat supply maps may not be adequate to describe the response of all species to alternative management scenarios.

How Feasible and Realistic Are DLMP Models?

The modeling methods were generally straightforward to apply, especially with the advent of the commercially supported software, RAMAS Landscape. DLMP models can be implemented, however, by manually linking outputs from independent landscape models and population models. The reliability of DLMP model predictions depends on the realism of landscape, habitat, and metapopulation models and assumptions. These, in turn, rely on the quality of available data and limits to understanding of ecological processes and stressors acting on indicator species populations. Model development therefore requires biologists and foresters to work together to parameterize the model and ensure realism within the bounds of data availability. For a similar study conducted in production forest in Tasmania, Australia, researchers developed software and found the programming and debugging elements debilitating for routine applications. With RAMAS Landscape, some data preparation is required outside the package (i.e., GIS data) although it is predominantly standalone and relatively straightforward to use.

The DLMP model adequately met our goal of considering the ecology of the whole forest system when assessing sustainability of forest management. We were able to build a succession model, represent the stochasticity in natural disturbance patterns, and consider indicator species persistence and viability within this system. Using this model, we were then able to consider the additional impact of forest management actions on population persistence, and rank management actions in terms of their impact on the indicator species. Although no forest management actions in the case studies predicted the local extinction of the indicator species, several forest management actions substantially reduced the population of the indicator species relative to a natural disturbance regime. For widespread and abundant indicator species, this is the type of reaction we expect. Thus indicator species demonstrate that the management action under consideration has a large negative impact on the forest system relative to natural disturbance, and is therefore potentially unsustainable. Decisions regarding whether this level of ecological unsustainability warrants a change in management is ultimately a value-based decision, taking into account other social, economic, and ecological values.

The greatest asset of this approach is that DLMP models allow us to incorporate environmental variability into the model, providing a distribution of predictions, rather than a single value. This is a significant advancement over existing sustainability assessment methods such as trend monitoring and habitat supply analysis. We were also able to consider uncertainty in our estimates of metapopulation model parameters, and thus identify areas of the model requiring further study. Parameterization of the metapopulation model is often done with "expert guesses" due to a lack of detailed life history information for most species. Sensitivity analysis allowed us to question and explore these model assumptions and measure how these estimates impacted model predictions.

Do DLMP Models Provide More Information Than Habitat Supply Models?

The relationship between species persistence and forest habitat structure and complexity is an important issue. If model results are simply an index of habitat availability, then this supports the use of habitat supply maps for forest management purposes, rather than a DLMP that includes demographic considerations. Demographic information is expected to be of most importance when habitat patches are isolated through habitat management, habitat becomes limiting through forest management, the indicator species is nonterritorial and polygamous, or when nonhabitat-related influences such as hunting or high periodic mortality rates from environmental stochasticity are important.

One method to assess the importance of habitat availability versus demographic information is to compare the population trajectory with the trajectory of habitat supply. If model results were simply an index of habitat availability, then the population trajectories would be expected to follow the pattern of change in carrying capacity, which is a function of habitat quality and quantity. As already noted, the trajectories for the red-backed vole differed markedly (Fig. 18-3). The lack of a strong correlation between the predictions based on habitat supply and population models for some species (Fig. 18-4) and the difference in ranking of management scenarios based on the two measures (Table 18-2) suggest that DLMP models do provide more information than habitat supply models.

While we argue that the inclusion of spatial metapopulation dynamics adds important elements to the interpretation to sustainability assessments for forest management, we accept that the information required to undertake these studies will only be readily available for a small number of species without substantial investment in data collection. Furthermore, the trade-off between realism and simplicity needs to be carefully examined with respect to the availability of data, as more complex models are not automatically more informative (Beissinger and Westphal 1998; Millspaugh et al., this volume). Attempts to include more details than can be justified by the quality of the available data may result in decreased predictive power (Ginzburg and Jensen 2004).

Limitations of the DLMP Software, RAMAS Landscape

Given the extent to which the habitat map determines model outcomes (including patch structure, population abundance, response to management scenarios, etc.), the results may be highly dependent on our ability to map habitat supply adequately. Our ability to model the habitat relationships of the case study species was unknown but may be low. This is primarily due to a lack of research within the study area defining habitat relationships, the paucity of mapped predictor variables, and the coarse resolution of many of the mapped variables that are available. A primary concern with the RAMAS Landscape package is the practical difficulty associated with incorporating sensitivity analysis on the spatial attributes, such as the habitat supply map, the succession model parameters (e.g., tree species establishment probabilities), and the natural disturbance model parameters (e.g., fire size and frequency). Currently, a full investigation of these forms of uncertainty would involve a long and tedious process of manually simulating stochasticity in such parameters.

This issue is a significant limitation in the current version of RAMAS Landscape. In particular, fire and succession regimes have a stochastic element, but these sources of prediction uncertainty are not linked with the representation of uncertainty in the metapopulation model. The model currently uses a single realization of the landscape for calculating species persistence, with multiple realizations of the species response to this single landscape examined to rank management scenarios. In our examples, fire regimes could not be held constant between scenarios because of the interaction between harvesting history and fire. For example, if an area was burned early in the simulation, it was unavailable for harvesting. Similarly, recently harvested areas were less likely to be burned by wildfire. While this is a realistic basis on which to model fire and harvesting, it limits the generality of results based on a single run of the landscape dynamics model. To overcome this we built our own software (the Repeater package, Chisholm and Wintle 2007) to automate the process of running the metapopulation model over multiple landscape realizations. This software enables the magnitudes of landscape- and demographic-induced variance in model outcomes to be separated, and iteratively calculates the optimal number of metapopulation realizations per landscape to minimize the combined landscape- and demographic-induced variance. This enabled assessment of the impact of the stochastic landscape simulation in our DLMP model. The Repeater software is freely available from <http://www.esapubs.org/archive/appl/A017/013/suppl-1.htm>.

RAMAS Landscape has a number of other limitations that impinge on its versatility in forest management settings. First, LANDIS was developed in the United States to be generalizable to a range of landscape settings. While the way in which the landscape is described meets this criterion of generality, it does not easily allow for incorporation of planning maps used in a specific area. For example, in northern Ontario, FRI maps, derived from interpretation of aerial photographs, are used for planning to describe the vegetation composition and structure of the landscape. Vegetation types are described in terms of the proportion of each tree species present. However, LANDIS cannot use this information. LANDIS describes vegetation types in terms of species presence or absence on each pixel, and dominance is assigned based on the relative age of the trees present. Although FRI information can be transformed into presence-absence form, significant information is lost. The realism of RAMAS Landscape would be enhanced by allowing base maps of vegetation type to be imported directly into LANDIS, and the vegetation types defined automatically based on these maps. Currently, all vegetation types must be specified manually, which is quite tedious.

The second problem we encountered was the inability to model more than 500 populations of the indicator species over the life of the simulation. This limitation meant that we needed to reduce the number of years that could be simulated or limit the spatial extent of the study. This assumption may be realistic for rare and endangered species for which RAMAS GIS was originally developed, but was not a realistic expectation for a DLMP model used to assess forest management over large areas using common and widespread species. Applied Biomathematics should address this concern if it is to continue promoting RAMAS Landscape for use in forest management.

CONCLUSIONS

The modeling approach we present in this chapter is proposed as a fundamental component of sustainable forest management. Dynamic landscape metapopulation models allow forest managers to explore aspects of the ecological sustainability of management actions before they take place. Management decisions are therefore made on the basis of anticipated impacts rather than as a reactive measure following environmental harm.

The DLMP model also helps to focus monitoring efforts by identifying important knowledge gaps. These gaps may be in terms of both species biology and ecosystem functioning. Construction of the DLMP model also highlights both environmental and model uncertainties, and incorporates them directly into the decision-making process. The DLMP model clarifies the causal linkages between management actions and indicator response.

The DLMP model may be used to assess the sustainability of forest management in cases where forest planning is done spatially or aspatially. It is most effective when used as part of an adaptive management system. Both models and strategic monitoring are used to iteratively design and evaluate forest management actions that minimize ecological harm, while maximizing social and economic gain from forest resources.

The models must be a component of an adaptive management system in which the results of monitoring are used iteratively to refine model parameters and predictions. The aim of using DLMP models is to stay a step ahead of environmental harm by prospectively assessing the sustainability of management options (Mulder et al. 1999). Data obtained by the monitoring system are used to improve models, which are in turn used to focus monitoring programs by describing the causal relationship between population processes and environmental stressors (Mulder et al. 1999).

SUMMARY

Sustainable forest management is a widely held international goal and in many cases a legislated mandate. Reliable, practical, and affordable means of assessing the sustainability of forest management remain elusive. Monitoring of biological indicators is an important element, but sufficiently powerful monitoring strategies are expensive and monitoring alone may not provide answers in time to avoid irreversible environmental or ecological damage.

We proposed a model-based approach to assessing sustainability using indicator species of ecosystem condition (as distinct from indicators of biodiversity or species richness) to provide timely feedback to managers about the sustainability of current and alternative forest management options, and to support the development of better-targeted and more relevant monitoring systems. Dynamic landscape metapopulation (DLMP) models integrate spatial models of forest change (also known as landscape dynamic models or forest succession models) with metapopulation models, which describe demographic and biological attributes of species and the dynamic consequences of dispersal and habitat change. We reviewed some of the benefits and criticisms of the indicator species approach and the advantages and problems associated with using DLMP models of indicator species to evaluate the sustainability of forest management options. We drew on results of a case study in northern Ontario, Canada, that utilized three indicator species to explore the sustainability of competing forest management scenarios. We compared those results with other recent studies undertaken in Australia and the United States that explored the utility of DLMP models in forest planning. Based on case study results, DLMP models of indicator species appear to be useful for assessing and ranking the sustainability of management options, quantifying the stresses placed on ecosystems by particular management activities, and targeting future research and data collection. Dynamic landscape metapopulation models have the potential to play an important role in assessments of sustainability, and we propose that such models should be considered a fundamental adaptive management tool. Such models will complement monitoring studies by providing a context for interpreting observed population fluctuations, identifying sensitive parameters and biologically important effect sizes, thereby supporting ecologically meaningful and cost-effective monitoring systems.

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