

Simulation of boreal forest landscape dynamics: modeling approaches and applications

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Academic dissertation

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Abstract

Boreal forests are dynamic, spatially heterogeneous ecosystems, and important reserves of biological diversity and timber resources. Spatially explicit simulation models of long-term and large scale forest dynamics are needed to make inferences about the historical structure of forest ecosystems, to project ecosystem dynamics under future conditions, and to simulate populations of forest-dwelling species in dynamic landscapes.

In this work two simulation approaches to forest landscape dynamics are described and tested, following the developmental line from the LANDIS model developed in Wisconsin, USA. The models describe the forest landscape as a square grid. On each grid cell, the tree layer is represented by cohorts, each cohort including trees of one species that belong to the same 10-year age class. In addition to patch-level processes of regeneration, growth and mortality, the models include landscape-level processes of tree seed dispersal and disturbance propagation and spread.

In the FIN-LANDIS model version, tree cohorts do not have quantitative attributes, such as basal area or volume, but are divided into two density classes, to facilitate simulation of partial disturbance and multi-layered stands. A new sub-model of forest fire initiation and spread was also developed. FIN-LANDIS was tested by attempting to reconstruct the current forest structure of the Ulvinsalo nature reserve in eastern Finland.

A sub-model of stand-level forest dynamics was developed to track quantitative attributes of tree cohorts, and linked to the landscape simulation framework. The resulting Q-LAND model was parameterized for the mixedwood boreal forests of Quebec, Canada. Simulations demonstrate that the stand dynamics submodel can be calibrated to produce realistic stand succession in accordance with specific targets. However, predictive applications requiring quantitative accuracy require more thorough parameterization and model testing.

FIN-LANDIS was used to examine how landscape-level forest age-class distribution is formed under mixed-severity fire regimes. When most fires are not stand-replacing, the theoretical steady state age-class distribution is either bell-shaped or bimodal, and dominated by old age-classes. Based on simulation results and the available empirical information, it is argued that, in middle boreal Fennoscandia, old-growth forests have dominated the historical unmanaged forest landscapes regardless of fire frequency.

FIN-LANDIS was coupled with a metapopulation model of an epiphytic lichen *Lobaria pulmonaria*. An extensive empirical study of aspen and epiphyte pattern was used to parameterize the host tree and epiphyte dynamics. The simulations suggest that the *Lobaria pulmonaria* population within the Teeri-Lososuo nature reserve is currently high relative to likely historical population levels, but the population is starting a sharp decline leading to local extinction, as the host trees regenerate poorly without disturbances to create stand-size openings.

Simulation results demonstrate the importance of late-successional forests, forests maintained by moderate intensity disturbance, and forests affected by stand-replacing disturbance. Assuming the goal of restoring natural forest structures to boreal Fennoscandian landscapes, both increasing the area set aside from commercial management and the increased use of harvesting methods that maintain multi-aged forest stands are required.

List of original articles

This thesis is based on the following research papers, which are referred to in the text using the Roman numerals:

- I** Pennanen, J., and Kuuluvainen, T. 2002. A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. *Forest Ecology and Management* 164: 157-175.
- II** Pennanen, J., Greene, D. F., Fortin, M.-J., and Messier, C. 2004. Spatially explicit simulation of long-term boreal forest landscape dynamics: incorporating quantitative stand attributes. *Ecological Modelling* 180: 195-209.
- III** Pennanen, J. 2002. Forest age distribution under mixed-severity fire regimes – a simulation-based analysis for middle boreal Fennoscandia. *Silva Fennica* 36: 213-231.
- IV** Snäll, T., Pennanen, J., Kivistö, L., and Hanski, I. 2005. Modeling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos*, in press.

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Contributions of the authors to the papers

In studies **I-III**, JP was the main writer and was responsible for planning and conducting the research, including the design and the implementation of the simulation models. In study **IV**, JP planned and implemented the landscape and metapopulation simulation models, and participated in planning the parameterization and simulation procedure, as well as in writing the paper. TK participated in planning the modeling and model testing approaches in study **I**, and gave comments on the manuscript. DG, M-JF, and CM participated in designing the simulation model and in writing the paper in study **II**. TS collected and analyzed the empirical data, participated in planning the parameterization and simulation approach, conducted the simulations, and was the main writer for study **IV**. LK was responsible for some of the empirical data collection for study **IV**. IH participated in study **IV** in all stages of planning and in writing the paper.

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1 Introduction

1.1 Need for simulation models

Boreal forests are dynamic and spatially heterogeneous ecosystems (Esseen et al. 1997, Kuuluvainen 2002). They are also biologically diverse (Hanski and Hammond 1994) and an important source of timber and various ecosystem services.

In Fennoscandia, most boreal forests are intensively managed and natural disturbance plays a small role. This has changed the structure and dynamics of forests greatly (Esseen et al. 1997, Linder and Östlund 1999). Hundreds of forest-dwelling species have been classified as threatened, and the actual number of threatened species has probably been underestimated (Hanski 2000, Rassi et al. 2001). In Canada and Russia, an increasing proportion of boreal forests is coming under systematic forest management. In all the regions, different means of protecting and maintaining forest biodiversity are being developed and implemented (Fries et al. 1998, Bergeron et al. 2002, Kuuluvainen 2002).

In managed forests, the natural variability approach is a central strategy for maintaining biological diversity (Bergeron et al. 1999, 2002, Niemelä 1999, Seymour and Hunter 1999, Kuuluvainen 2002, Perera et al. 2004). This means attempting to maintain patterns and processes typical of natural forests in the managed areas. Specific restoration measures may be needed when forest structure has already been strongly changed by human land use (Kuuluvainen et al. 2002a).

Maintaining or restoring natural forest patterns requires understanding how the landscape structure of boreal forests is formed under natural disturbance regimes and under the combined influence of anthropogenic and natural disturbance. Because of the broad scale of spatial forest processes (e.g. disturbance, seed dispersal), and the long temporal scale of forest succession, these questions are difficult to study empirically. Therefore, spatially explicit simulation models are needed to study the relationship between landscape-level processes and landscape pattern (Baker 1989, Mladenoff and Baker 1999, Messier et al. 2003, Fall et al. 2004, Keane et al. 2004, Mladenoff 2004). Spatially explicit output is also necessary for some model applications, such as coupling forest simulation with spatial metapopulation models.

Keane et al. (2004) define landscape fire succession models (LSFMs) as models which simulate fire and succession in a spatial domain, producing time-dependent, georeferenced results in the form of digital maps. Keane et al. (2004) found 44 LSFMs developed in different parts of the world. Because of the importance of fire in the boreal region (Wein and MacLean 1983), LSFMs include all models suitable for simulating boreal forest landscape dynamics under natural disturbance regimes. In terms of describing forest succession, LFSMs

range from simple fire simulators, where the only forest stand information is the time since last fire (Boyчук et al. 1997), to sophisticated individual tree based growth and yield models developed for forestry planning, augmented with submodels for fire simulation (Reinhardt and Crookston 2003).

LANDIS is a spatially explicit simulation model of forest landscape change and disturbance (Mladenoff et al. 1996, He and Mladenoff 1999, Mladenoff 2004). A forest landscape is described as a grid of square cells. Tree stands are described via the presence or absence of each tree species in 10-year age classes, without additional detail. It is suitable for simulating landscapes up to 1000s of km², with various types of disturbance. The advantage of the LANDIS approach, compared to other grid-based landscape simulation approaches, is that the description of forest succession incorporates individual tree species and forest age structure, while the model does not require laborious parameterization of tree growth, in contrast with the individual-tree and gap-phase models of succession (Mladenoff 2004). The generality and relative simplicity of parameterization made LANDIS applicable to any temperate or boreal region. From the software development point of view, the object-oriented design of LANDIS makes it suitable for modifications by extending and replacing modules describing different dynamic processes (He et al. 1999).

1.2 Fennoscandian natural forest landscapes

In middle boreal Fennoscandia few forest landscapes remain outside commercial forest management. What is more, fire regimes have varied because of human influence (Pitkänen and Huttunen 1999, Niklasson and Granström 2000), so that the current structure of unmanaged areas may differ from the historical or natural forest structure.

Empirical studies suggest that during the 19th century, middle boreal Fennoscandia had frequent forest fires, 40-70-year fire intervals being common (Lehtonen 1997, Pitkänen and Huttunen 1999, Niklasson and Granström 2000, Lehtonen and Kolström 2001). Between the 19th and 20th centuries, fires ceased quite abruptly, and during the last 100 years, fires have been negligible. Fires were also apparently less frequent prior to the 19th century (Pitkänen and Huttunen 1999, Niklasson and Granström 2000).

Although a general belief is that fires in the region have been of low intensity, there is no such data on fire severity that could be directly used to parameterize simulation models. However, according to the available empirical studies, frequent fires maintained landscapes dominated by multi-layered old-growth Scots pine (*Pinus sylvestris* L.) forests (Östlund et al. 1997, Linder and Östlund 1998, Axelsson and Östlund 2002, Kuuluvainen et al. 2002b). This information provides indirect evidence of the historical fire severities and can be used in selecting simulation scenarios that are consistent with observations.

Aims of the study

The general aim of this thesis was to develop and test modeling approaches for simulating natural forest dynamics, and for simulating the coupled dynamics of forests and forest-dwelling species, using LANDIS (Mladenoff et al. 1996) as a starting point. Secondly, the aim was to apply models to study the historical structure and dynamics of middle boreal Fennoscandian forest landscapes.

Specific aims were

- 1) to develop and test a spatial forest landscape simulation model, suitable for simulating Fennoscandian unmanaged forest landscapes under various fire regimes (Study **I**),
- 2) to develop and test approaches to adding stand-level information to the LANDIS model (Studies **I** and **II**),
- 3) to examine the age structure of natural forest landscapes under different fire regimes, particularly in middle boreal Fennoscandia under historical fire regimes (Study **III**), and,
- 4) to develop and parameterize a coupled model of forest landscape dynamics and the metapopulation dynamics of *Lobaria pulmonaria* L., an epiphyte lichen (Study **IV**).

2 Modeling approaches

2.1 Semi-quantitative approach

2.1.1 FIN-LANDIS model description

FIN-LANDIS model was developed and tested in study **I**. LANDIS was extended by developing a more mechanistic fire disturbance module, to expand the range of fire regimes and initial assumptions that can be studied. In addition, some detail was added to the tree stand description to facilitate the simulation of multi-layered stands created by non-stand-replacing fires.

LANDIS and FIN-LANDIS describe the forest landscape as a square grid of cells or sites. In this work, cell size is 20 m x 20m. Tree layer on each grid cell is described as a collection of *cohorts*, where each cohort includes all the trees of one species which established during one model time-step. Other site-specific data are the land type (ecological site type), which is static, and the time since the last disturbance events of each type (fire, harvest, wind).

In LANDIS, species identity and age are the only tracked cohort attributes. For FIN-LANDIS, we divided the cohorts into *dense* and *thin* cohorts, which represent cohorts with closed canopies, and cohorts representing open canopies or single trees, respectively. Specifically, in terms of model dynamics, dense cohorts do not allow regeneration of new cohorts with the same or a lower shade tolerance under them, while thin cohorts allow it. This solution makes it possible to simulate multi-layered stands and track sparse cohorts of single trees, without complicating the stand representation unnecessarily.

Processes simulated by FIN-LANDIS include 1) disturbance (fire) simulation, 2) tree seed dispersal calculation, 3) establishment of new cohorts, and 4) aging of cohorts, including thinning and removal of old cohorts. Simulation proceeds in 10-year (or user-defined) time-steps.

Fire ignition attempts occur randomly in the landscape. The number of ignitions per time-step is Poisson distributed around the mean value given as model input. After a successful ignition, fire spread is simulated, taking into account the landscape pattern of land types. Fires go out when the edge of burnable land types or the potential fire duration has been reached. Potential fire duration is generated for each individual fire from a truncated exponential distribution defined by the mean and maximum fire duration.

Fire intensity depends on the land type and the time since the previous fire. A stochastic component was added for some simulations of studies **III** and **IV**. Whether cohorts

die in fires, or dense cohorts become ‘thin’, depends on fire intensity, cohort age, and a species specific fire tolerance parameter.

The establishment of new tree cohorts in a grid cell depends on site type, time since fire, possible shading by existing tree cohorts, and the availability of seeds or asexual sprouts. A cohort of a specific species may only regenerate if *dense* cohorts of a species with the same or a higher shade tolerance are not present.

Seed availability is determined by the distance to the nearest sexually mature trees. The probability of seeds being present decreases with increasing distance to seed source. A dense cohort may only be established if the distance to seed source is less than the effective seeding distance (parameter EFFD). Otherwise the possible new cohort will be *thin*.

When seeds and sufficient light are available, the establishment probability is a function of species, site type, and time since last fire. There are 2 establishment parameters per species per site type. The first parameter gives the probability of establishment immediately after a fire. The second parameter determines establishment probability after the ground vegetation and the organic soil layer have recovered from the last disturbance, assumed to happen after the site type specific *recovery time* has passed. Generally, establishment probabilities are high immediately after a disturbance and then decrease.

Asexual reproduction is also possible. The probability of new cohort creation is $VEG \times c_1$, where VEG is a species specific resprouting parameter, and c_1 is the first species and site specific establishment parameter.

When the probability of the establishment of a new cohort is p , the probability of getting a dense or thin cohort is p^c or $p-p^c$, respectively. The exponent c determines the spatial aggregation of seedlings. If enough seeds are available for a thin cohort only, the new cohort is always thin.

Since cohorts do not have quantitative attributes, cohort ‘growth’ only means age increase by 10 years on every time step. Tree mortality occurs as the removal of a cohort or as cohort change from *dense* to *thin*. After cohort age reaches 50% of species specific maximum longevity, there is a positive, gradually increasing probability of thinning of dense cohorts. After 80% of longevity is reached, cohorts start dying entirely, so that when maximum longevity is reached, no cohort is alive.

2.1.2 FIN-LANDIS parameterization and testing

FIN-LANDIS was parameterized for middle boreal Fennoscandia, for the five most important forest trees, Scots pine, Norway spruce (*Picea abies* (L.) Karst.), aspen (*Populus tremula* L.), silver birch (*Betula pendula* Roth.), and pubescent birch (*Betula pubescens* Ehrh.). Essentially, parameters include life history parameters for the tree species (Table 1, Study I), establishment parameters defining species performance on different site types (Table 2, Study

I), as well as disturbance (fire) parameters. All parameter values could be set using information from literature, although sometimes only with qualitative accuracy.

Ulvinsalo strict nature reserve in eastern Finland was chosen for a test area. Ulvinsalo area is in a nearly natural state, and there was a fire history study available (Haapanen and Siitonen 1978). The extent, to which FIN-LANDIS could reproduce the current forest composition, based on the historical fire regime, and the generic tree life history parameters, was tested. Ulvinsalo site type configuration was derived from the GIS data collected and owned by Metsähallitus, a Finnish state enterprise managing state-owned forests.

Because there was no empirically based initial state for the landscape composition, the model run was initiated from an arbitrary state with all tree species present. The model was the run under the historical fire regime until a steady state forest composition was reached. After that, a 90-year period of fire suppression was added, because no fires practically occurred after 1910.

The simulated landscape composition for year 1990 was compared to the landscape composition based on the empirical GIS data. Forest composition was assessed by 2 methods: according to the occurrence of each tree species separately, and according to the distribution of forest stands by species composition. Assessments were based on attributes aggregated for the entire area of productive forest lands. The spatial distribution of forest attributes was not considered.

The presence of tree species on grid cells was assessed on a three level scale: not present, sparse, and abundant. In FPS data, the levels were determined by cohort basal area, in the simulated data by the dense/thin partitioning and cohort age.

The model test simulation yielded a landscape tree species composition quite similar to the observed one based on the FPS data. Species rankings based on species presence or abundant presence were similar in the simulated and the observed data (Fig. 3, Study 1).

The overall species composition was assessed by classifying the whole landscape first according to the dominant coniferous species, and secondarily according to the non-dominant species (Fig. 4, Study 1). The simulated coverage of the classes based on dominant conifers differed from the FPS observation by at most 5% in each three classes. However, especially in spruce-dominated forests, the presence of broadleaved species was not accurately predicted (Fig. 4, Study I).

Landscape level forest age structure was also considered by the cumulative forest age distribution based on the age of the oldest pine cohort present in each grid cell (simulation) or polygon (FPS data) (Fig. 7, Study I). While the median age of the simulated landscape was higher than observed, the proportion of forest less than 150 years old was also overestimated. Assuming the differences are meaningful (and not, e.g., due to inaccuracy of the FPS data), results suggest that the simulated tree mortality due to fires was overestimated. In any case,

both the simulated and observed age distributions show that a significant part of the fires were not stand-replacing.

2.2 Quantitative approach

2.2.1 Q-LAND model description

The obvious and intentional limitation of LANDIS and FIN-LANDIS models is the lack of quantitative stand data such as volume or basal area. In study **II**, a stand level submodel was developed and linked to the FIN-LANDIS framework, which has a quantitative description of tree cohorts and a quantitative treatment of seed dispersal and regeneration. The resulting Q-LAND model is summarized in a flow chart (Fig. 1, Study **II**).

Q-LAND derives quantitative cohort attributes from *growth tables* which give attributes, such as basal area, volume and tree dimensions, as a function of cohort age, tree species and site quality (Table 1, Study **II**).

The formulation of the stand submodel is based on a conceptual model where each grid cell consist of *territories*, each capable of lodging one full-grown tree. A cohort *occupies* a territory if the dominating canopy tree of the territory (the tree that will eventually be the sole occupant of the territory) belongs to the cohort. The territories are not explicitly simulated in the landscape model. Instead, we track the proportion of the territories occupied by each cohort with the cohort variable called *density*. The sum of the densities of all canopy cohorts is 1 or less. Cohort-level quantitative attributes such as basal area are derived by multiplying the values obtained from the growth table by cohort density, while tree level variables such as diameter are obtained directly from the growth tables.

With the above assumptions, a territory can be occupied by only one shade intolerant species at a time. However, shade tolerant trees may survive in the same territories as understory trees through the lifespan of the canopy trees. Therefore, in addition to the canopy cohorts, the simulation model has a separate set of understory cohorts for each cell. The density of understory cohorts also adds up to 1 or less.

Growth and mortality of trees depend on the competitive environment. This is implemented by controlling the rate of cohort development along the path defined by the growth table. For this purpose, each cohort has an attribute called *apparent age*, which may increase at a slower rate than actual age. Apparent age is used to index cohort attributes from the growth table.

The apparent age v_j of cohort j changes during a time step by

$$\Delta v = gT, \tag{1}$$

where T is the timestep length and g is the growth rate modifier that depends on the stand structure.

With the quantitative tracking of tree cohorts, seed production and dispersal can be simulated quantitatively. Empirical models by Greene and Johnson (1989, 1994, 1996, 1998, and unpublished data) were used to model seed production and seed dispersal between grid cells. Seed production is a species-specific function of source tree basal area. Dispersal is a function of species specific seed terminal velocity and the assumed wind conditions and canopy height.

On each model iteration, the density of sexual and asexual seedlings is calculated. Seedling survival, mediated by available seedbeds, is based on Greene and Johnson (1998). Subsequently, the proportion of territories in each cell containing seedlings is calculated. Non-random spatial pattern of seedlings is taken into account.

During a model iteration (Fig. 1, Study II), the establishment and release of cohorts begins by simulating the release of understory cohorts, followed by the creation of new canopy and understory cohorts from seedlings if growth space remains available. Competition between species is controlled by two ordinal scale parameters, specific to species and land type. These are juvenile growth rate and shade tolerance.

The release of understory cohorts proceeds as follows. The proportion of territories with no canopy layer trees is calculated as

$$D = 1 - \sum_k d_k, \quad (2)$$

where d_k is the density of cohort k , and k goes through the indexes of all canopy cohorts on the cell. Tree species are then considered one at a time, in the order of decreasing juvenile growth rates. For each species, proportion D of its understory cohorts will be released; i.e. the density d_k of each understory cohort k will change by

$$\Delta d_k = -d_k \cdot D, \quad (3)$$

where D is obtained from equation 2. Then a new canopy cohort of the same species is created, with density $d_j = \Delta d_k$, and having the same apparent age as the released understory cohort.

Establishment of new cohorts is based on the density of seedlings and asexual sprouts, and competition with other species. The proportion of territories of the cell that contain seedlings of a species is

$$q = r (1 - \exp(-b \cdot A \cdot N^c)), \quad (4)$$

where N is the number of seedlings of the species per square meter, A is the territory size in square meters and b and c are empirically fitted parameters describing the spatial patterns of

regeneration (D. Greene, unpublished data). A gap establishment coefficient, r , modifies the seedling density when the stand has not recently experienced a stand-replacing disturbance. The establishment coefficients are required to regulate stand dynamics, because within-cell spatial variation in light levels and other factors affecting tree establishment are not explicitly considered.

Tree species are again considered in the order of decreasing juvenile growth rate. The density of the new canopy cohort of species i is

$$d_i = q (1 - \sum_k d_k), \quad (5)$$

where q is obtained from equation 4, d_k is the density of cohort k , and k goes through the indexes of all the canopy cohorts on the cell. Values of d_k are updated between species, to account for new cohorts created.

New understory cohorts are created in a similar process, but space available for the understory cohorts of each species depends on the shade tolerance ranking of the species. The density for the new understory cohort of species i is

$$d_i = q (1 - \sum_m d_m) \sum_k d_k, \quad (6)$$

where q is obtained from equation 4, and d_m is the density of cohort m , and m goes through the indexes of already existing understory cohorts, and k goes through the indexes of the canopy cohorts of the species that have lower shade tolerance than species i .

Tree mortality is manifested as a decrease in cohort density. Cohort density may only decrease during its lifetime. When the density reaches zero, the cohort is removed. A deterministic decrease of density corresponds to tree death due to small scale disturbance and old age.

Growth tables given as model input give the cohort densities as a function of age. Because growth tables are for fully stocked cohorts, the density starts at 1.0, and ends at 0. During the simulation, the relative age-dependent decrease in the density of a cohort is the same as the relative density decrease according to the growth table, when the cohort's apparent age is used as index to the growth table.

The model derives the quantitative cohort attributes from the cohort's density, apparent age and the growth table. Attributes V such as basal area or volume are proportional to cohort density and are calculated as

$$V = V(v) \cdot d / d(v), \quad (7)$$

where d is cohort density, v is apparent age, $V(v)$ is the value of the attribute given in the growth table at age v and $d(v)$ is the density given by the growth table at age v . An attribute A

that is not directly related to cohort density, such as average tree height or diameter, is looked up directly from the growth table.

The number of tree cohorts tends to increase in a simulated stand during forest succession. When growing space is released in small amounts, cohorts with a very low density will be created. Cohorts also split when understory cohorts are partially released to the canopy cohort layer. Over time, a cell may contain hundreds of cohorts. This is problematic because computer memory requirement increases linearly with the number of cohorts.

To solve this problem we defined a minimum density, d_{\min} for new tree cohorts. If a new tree cohort, according to the description above, would have density $d < d_{\min}$, the cohort is actually created only with probability d/d_{\min} , and the density of a new cohort is set at d_{\min} . Increasing the minimum cohort density parameter will lead to a smaller number of cohorts, but on average should not affect stand composition and structure.

2.2.2 *Q-LAND parameterization and testing*

The simulation approach was tested in simulating the development of mixedwood boreal forests of Quebec, Canada. Stand development was simulated in 4 scenarios, starting after different types of stand-level disturbance events. The development of a single 1-ha grid cell was simulated. The length of each model run was 1500 simulation years. Growth tables from Pothier and Savard (1998) were used, choosing the tables for high-density stands with site quality indices 18 (coniferous species) and 21 (broadleaved species).

The first simulation scenario described the succession of a stand in the middle of a large burned area, starting from the situation immediately after the fire. During the succession, seed input from the stand's surroundings mimicked the situation where the neighbors are identical successional stands.

Scenario 1 was used to calibrate the gap establishment coefficients, which regulate tree regeneration under shaded conditions. The calibration target was defined as a certain steady state composition of old-growth stands, based on Kneeshaw and Bergeron (1998). Calibration of gap establishment coefficients required about 20 simulations. The final coefficients produced a steady state stand composition according to the target conditions (Fig. 3A, Study II). The simulated stand reached its steady state composition in about 500 years. Stand composition changed from broadleaf dominated to conifer dominated, balsam fir (*Abies balsamea* (L.) Mill.) and eastern white cedar (*Thuja occidentalis* L.) being the dominants at the late-successional stage.

In scenario 2 the set-up corresponded to a situation after a stand-replacing wind disturbance, the simulated stand being surrounded by old-growth forest. Stand development differed from scenario 1 because seed input from the surroundings is different, and seedling survival is different on undisturbed seedbeds. Trembling aspen (*Populus tremuloides* Michx.)

and white spruce (*Picea glauca* (Moench.) Voss.) were never abundant during the early part of stand development. White birch (*Betula papyrifera* Marsh.) dominated the stand initially, and was later replaced by balsam fir. Eventually the stand composition stabilized to the same steady state composition as in scenario 1.

Scenario 3 differed from scenario 2 in that the initial stand represented the result of a partial disturbance, which had left 30% of stems of the steady state stand determined in scenario 1. The essential difference in stand development was that the new cohorts grow slower as long as the pre-disturbance trees remain. White cedar increased quickly, due to its competitive advantage in shaded environments. Pre-disturbance cohorts disappeared from the stand in 160 years.

Scenario 4 added a chronic spruce budworm disturbance to scenario 1. The average mortality due to spruce budworm was set at 20% per 10-year iteration for balsam fir, and half of that for white spruce. The decadal mortality was chosen from a uniform distribution $U(0,2x)$, where x is the average mortality. Spruce budworm disturbance decreased balsam fir and white spruce abundance compared to scenario 1. White cedar took the dominant position in the steady-state stand. Aspen and birch also had relatively high basal areas in the late-successional stage.

After the single stand simulations, model performance and the effect of the minimum cohort density parameter were examined by simulating fire-mediated dynamics of a large landscape. The development of a 50 000-ha landscape was simulated over a period of 1500 years, using a cell size of 1 ha. Test runs showed that a minimum cohort density value of 0.02 produced the best balance between execution speed and realistic dynamics. Using this minimum cohort density value, a 1500-year simulation of the 50 000-ha landscape took a 30 mins of CPU time on a 2.4 GHz Pentium PC. Memory requirements were relatively constant at 140 Mb of RAM.

In conclusion, the stand submodel was shown to be flexible enough to be parameterized using the knowledge on steady-state old-growth composition as a calibration target. The emerging stand successional pathways were consistent with empirical studies. Model response to variation in initial and boundary conditions were plausible. However, the utility of the modeling approach in producing accurate predictions in general cannot be guaranteed, at the moment. The idea is to develop the formulation of the growth modifier function (equation 15, Study II) to make the model more accurate and general.

3 Model applications

3.1 Age structure of natural forest landscapes

3.1.1. Methods

Age structure is an important characteristic of forest landscapes. Attempts to maintain or restore natural forest structures on landscape level often concentrate on forest age distribution. We studied the age structure of unmanaged landscapes under various fire regimes using the FIN-LANDIS model.

First question considered was the theoretical equilibrium stand age class distribution of a forest landscape, assuming that the fire regime stays constant and fires are small compared to landscape size. If fires are not necessarily stand-replacing, the commonly applied negative-exponential age distribution (Van Wagner 1978) may not occur.

We also attempted to estimate the historical age structure of forest landscapes in middle boreal Fennoscandia under different fire cycles. It has been observed that frequently (every 50-70 y) burning landscapes have been dominated by multi-layered old-growth pine forests (Östlund et al. 1997, Linder and Östlund 1998, Axelsson and Östlund 2002, Kuuluvainen et al. 2002b). Taking this as a premise, we examine how lengthening the fire cycle changes the landscape age structure, taking into account that fire intensities may have been higher under longer fire cycles.

Simulations were divided into 4 simulation sets (Table 1, Study **III**). Sets I and II explored the shape of stand age distributions, when fire severity and fire frequency, respectively, were varied. Simulation set III investigated the average amount of old-growth forests in the landscape under varying fire regimes. Old-growth forests were defined as stands with tree cohorts at least 150 years old.

The first 3 simulation sets consisted of effectively nonspatial simulations, in which the size of fires was limited to one cell, tree seeds were assumed to be always present, and all 86 000 cells of the 'landscape' represented similar forest sites on mineral soil. Such schemes simulate collections of identical independently evolving stands whose attributes are aggregated in the model output.

Nonspatial simulations ignore site-dependent spatial variation in fire frequency and behavior, and limited seed dispersal. Therefore simulation set IV was conducted in a spatially explicit manner, with site type variation within the landscape and spatially explicit seed dispersal. Simulation set IV attempted to reproduce realistic dynamics of middle boreal forest landscapes under different fire frequencies.

3.1.2 Results

When fire severity changed from stand-replacing to low, the simulated steady state age-distributions changed from a distribution close to an exponential distribution to a bell-shaped distribution with the mode near the longevity of pine (Fig. 2, Study **III**). In contrast, changing the fire frequency under a medium-severity fire regime caused only small changes in the steady state age distribution; only the proportion of the youngest age classes was affected markedly (Fig 3, Study **III**).

Simulation set 3 examined specifically the amount of old-growth forests in a steady-state landscape, and the stand-replacement rate, i.e. the proportion of landscape burned in a stand-replacing fire per year. The amount of old-growth forest was high, except in the highest severity scenarios under short and medium fire rotations (Fig. 4, Study **III**). This reflects the pattern in stand-replacement rate, which was high in the high severity, short and medium rotation scenarios.

The spatially explicit simulations (simulation set 4) produced results similar to severity scenario 5 of simulations set **III**, with regard to the relationship between fire frequency and occurrence of old-growth forests (Fig. 5, Study **III**).

The spatially explicit simulations produced slightly bimodal age distributions that were quite flat for moderate or low fire frequencies (Fig. 6, Study **III**). The bimodality of stand age distributions based on spruce age (Figs. 6a-b, Study **III**) is related to spatial variation in fire frequency. The peak at high cohort age consists of climax-type old-growth spruce forests that occur on rarely burning spruce swamps or on sites that are isolated by mires. The spatial simulations also demonstrated how increased number of ignitions and increased fire frequency decrease the fire severity. The area burned increased with the number of ignitions, but not proportionally (Fig. 7a, Study **III**), and the mean fire severity decreases (Fig. 7b, Study **III**).

The simulations showed that under some circumstances it is possible that decreased fire frequency leads to a decrease in the abundance of old-growth forests, when longer time-since-fire leads to higher fire severity. However, this decrease in old-growth abundance was only slight even though a strong positive relationship between time-since-fire and fire severity was assumed. Simulation set IV gave a similar outcome, demonstrating that the result is not peculiar to a nonspatial model.

In summary, the simulations suggested that if old-growth forests dominate landscapes under frequent fires, old-growth dominance persists when the number of fires is decreased, even if this leads to higher average fire intensity. The same result was confirmed using an analytical model (Study **III**, Appendix 1). It was, however, assumed that the relationship between time-since-fire and fire severity remains the same when the number of fires changes.

3.2 Linking models of landscape change and population dynamics

A metapopulation model of the lichen epiphyte *Lobaria pulmonaria* was linked with FIN-LANDIS. FIN-LANDIS was suitable for the linkage, because it had already been parameterized for the region (Study I) and the 20m x 20m resolution was appropriate for lichen simulation. The aim of the study was to parameterize a dynamic model for a patch-tracking metapopulation based on only snapshot presence/absence data on the focal species and the landscape.

3.2.1 Methods

The study used an extensive empirical study of the occurrence patterns of the epiphyte and its host trees aspen (*Populus tremula*) and goat willow (*Salix caprea* L.) in and around Teeri-Lososuo nature reserve in eastern Finland (Fig. 2, Study IV). The density of aspen and goat willows in the study area was 7.1 and 1.8 stems/ ha, respectively. *Lobaria pulmonaria* occurred in 31% of the 1-ha-squares occupied by at least one of the host trees.

The parameterization approach is summarized in Fig. 1 (Study IV). Parameters of the metapopulation and forest landscape models are partly estimated from empirical data and literature, partly by adjusting parameters to achieve simulated host tree and *Lobaria* patterns that are consistent with the observations. Spatial patterns of host trees and epiphytes were analyzed using variogram models and Ripley's K-function (Diggle 1983, Diggle & Chetwynd 1991, Bailey and Gatrell 1995).

Landscape simulations were 2200 years long, corresponding to years 0-2200 AD. Simulations were started with random initial state, which developed under an assumed constant fire regime into a steady state landscape in 500 years. Fires were suppressed for the years 1850-2200.

FIN-LANDIS parameters defining the fire regime and host tree regeneration probability were adjusted in order to reach a host tree density and pattern consistent with the empirical data. The initial search for FIN-LANDIS parameter values made it evident that the observed aspen and goat willow densities and spatial patterns could be obtained with several different sets of disturbance and tree life history parameters. Two main landscape scenarios were recorded, as well as 9 replicate simulations with the parameter set giving the long fire return interval. The variation in predicted host tree dynamics and host tree densities and spatial autocorrelations (in year 2000) were analyzed.

Metapopulation dynamics consist of colonization and extinction of local populations in the raster cells. For each time step, the probability of epiphyte colonization of a raster cell with suitable host trees is

$$C = C_{\text{aspen}} + C_{\text{willow}} - C_{\text{aspen}}C_{\text{willow}}, \quad (8)$$

where C_{aspen} and C_{willow} are calculated as

$$C_{ts} = 1 - \exp(-c_{ts} S_i \text{Age}_i). \quad (9)$$

c_{ts} is a host tree specific ($_{ts}$) colonization parameter (c_{aspen} and c_{willow} , respectively) S_i is a measure of spatial connectivity, and Age_i is aspen or goat willow raster cell age, a surrogate for mean tree diameter. The spatial connectivity S_i is defined as

$$S_i = \beta \sum_{j \neq i} p_j \exp(-\alpha (\ln d_{ij})^2), \quad (10)$$

where α and β are parameters, d_{ij} is the distance between raster cells i and j , and $p_j = 1$ if cell j is occupied by an epiphyte population whose age exceeds the age of sexual or asexual maturity, otherwise $p_j = 0$ (see more details in Appendix 1, Study **IV**). Apart from the deterministic local extinction caused by all host trees in a raster cell falling, *L. pulmonaria* disappears randomly from an occupied cell with a probability E_i , which we set at 0.1 per decade.

The 1700-year-long metapopulation simulations were run over the recorded landscape scenarios, corresponding to years 500-2200 of the host tree simulations (step 8, Fig. 1, Study **IV**). Metapopulation parameters are listed in Table 1. The dispersal parameter α was estimated from the empirical data. The host tree specific colonization rate parameters (c_{aspen} and c_{willow}) were adjusted in repeated simulations, to find parameter values that would reproduce the empirical epiphyte patterns in the landscape in year 2000 (step 9). Because there were two main landscape scenarios with different fire regimes, two estimates of colonization parameters were obtained.

3.2.2 Results

The two main landscape scenarios produced densities and spatial patterns of aspen and goat willow that were similar to the empirical patterns (Figs. 3B and 4, Study **IV**). There was substantial variation in predicted host densities and autocorrelations between simulation replicates for a given parameter set (Figs. 3A and 4, Study **IV**).

In all simulations host tree density varied 2-3-fold over time, and occasionally fires reduced tree density even more (Fig. 3, Study **IV**). As fire suppression started in 1850, the host density first increased but subsequently declined. By year 2200 the host density was very low in all simulations. Small-scale density variation was generally higher in the empirical data than in the simulations in 2000, as indicated by low τ^2 estimates of the variogram models for simulated densities (Fig. 4, Study **IV**).

The metapopulation model successfully reproduced the empirically observed occupancy level and spatial aggregation in the landscape scenario with the long fire return interval and using the parameter values LOW in Table 1, Study **IV**. In 2000, the epiphyte was

predicted to occur on 29% of the ha-cells with host trees (Fig. 5A, Study IV) and the spatial pattern was similar to the empirical pattern (Fig 6, Study IV). Between ten replicate simulations there was little variation in predicted epiphyte dynamics, occupancy (0.25-0.52), and pattern.

The second main landscape scenario with the shorter fire return led to a 15% greater estimate of the colonization rate parameter (HIGH, Table 4, Study IV). However, the predicted spatial epiphyte pattern was now much more aggregated than the observed one (Fig 6, Study IV), and the predicted occupancy was close to zero for a long time before fire suppression (Fig. 5B, Study IV).

The number of raster cells occupied by the epiphyte was primarily determined by host tree dynamics, and severe reduction in tree density drove the lichen population density to a low level (Fig. 3B, Study IV). The level of occupancy tracked changes in the absolute number of raster cells with the epiphyte (Fig. 5A, Study IV). The occupancy level was very low before fire suppression (Fig. 5B, Study IV), coinciding with a period of reduction in host tree density (Fig. 3B, Study IV). The level of occupancy remained low during the initial increase in host tree density, but peaked later on, before reaching the empirically observed level in 2000. The epiphyte was predicted to go extinct before year 2200 in eight out of ten simulations using the LOW parameters in the landscape with long fire return interval.

The coupling between host tree dynamics and lichen metapopulation dynamics (Fig. 3B) is largely mediated by local extinctions caused by host tree mortality, which is typical for patch-tracking metapopulations (Snäll et al. 2003). The occupancy peak of the lichen following fire suppression is explained by the increasing population size of the lichen, which in turn increases overall connectivity and facilitates colonization, and by the increasing age of host trees.

For the landscape scenario leading to long (117 y) fire return interval it was possible to find epiphyte colonization parameters that produced the empirically observed occupancy level and spatial pattern. Therefore this set of parameters (LOW in Table 4, Study IV) is our best estimate of the metapopulation parameters. Unfortunately, the estimates of the colonization rate parameters were also sensitive to the assumed landscape dynamics.

According to our results, *L. pulmonaria* has an occupancy peak now but is predicted to go extinct from the reserve due to low colonization rate caused by falling numbers of occupied host trees and increasing distances to unoccupied host trees.

4 Discussion

4.1 Modeling approaches

4.1.1 FIN-LANDIS

Model testing (Study **I**) and applications (Studies **III**, **IV**) demonstrated that FIN-LANDIS is a useful model for spatial simulations of boreal forest landscape dynamics driven by forest fires. Compared to the original LANDIS model, the thin/dense characterization of cohorts makes it possible to model multi-layered stands maintained by low-severity fires, and the new fire module with its increased level of mechanistic detail allows analyzing the effects of changes in the mechanisms and parameters controlling the fire regime.

In the Ulvinsalo test, model fit was as good as could be reasonably expected. The occurrence of each tree species and the major stand composition classes were very close to the observed ones. The test was not very stringent, because of the inaccuracies related to the empirical data and the problems with transforming data between the formats used in the empirical data and in the model. Also, spatial landscape patterns in forest structure were not considered in the testing. The differences between model output and actual landscape composition highlight certain issues that need further attention, such as the effect of site type and stand structure on flammability and fire intensity, and the processes affecting the regeneration of broadleaved trees.

The Ulvinsalo model test was rigorous in the sense that model parameterization and initialization, as well as the procedures for data conversion and comparison, were independent of the test data by Metsähallitus. Model was not fitted to the test data by any parameter adjustments.

FIN-LANDIS was well suited for the study of forest age structure in relation to fire regimes. A related study used a simpler model of forest age classes without species level description of tree stands (Wimberly et al. 2000). Species level tracking of stand structure in FIN-LANDIS makes it possible to analyze the effects of the interaction between stand structure and fire behavior in more detail, in addition to dispersal effects and species-specific output.

The semi-quantitative data structure of FIN-LANDIS has certain limitations. Apart from the obvious, it is not very easy to link model input and output with empirical data, which rarely has comparable resolution, in terms of plot size or stand vertical structure. The thin/dense characterization is functional, characterizing the threshold between the cohorts that allow regeneration of light demanding species under them, and those which do not. This is

suitable for qualitative exploration, but a linkage with empirical data requires ad-hoc assumptions (Study I).

FIN-LANDIS model was originally used with a relatively high spatial resolution of 20 m x 20 m (Study I). This made it possible to derive estimates of the occurrence and abundance of the non-dominant tree species such as aspen and goat willow, which was necessary in study IV. The resolution is also compatible with many satellite based GIS data. Similar patch sizes have been successfully used in gap model (Bugmann 2001). It can be questioned, whether it is realistic to simulate tree establishment and growth on such patches without considering competition from trees in the neighbouring grid cells. However, since FIN-LANDIS does not simulate tree growth quantitatively, the problem is smaller than in the case of quantitative gap models.

A resolution of 100 m x 100m, or coarser, is suitable for examining landscape structure in terms of the age structure of the dominant conifers. In study III, 1-ha grid cells were used when studying the distribution of stand age classes.

In the Teeri-Lososuo study (IV), FIN-LANDIS was used to generate a plausible landscape history for the study area. Model was run repeatedly with varying fire regime parameters, until the density and spatial pattern of aspen and goat willow were similar to observed. Even with one parameter set, stochastic variation in fire regime resulted in very different host tree patterns in each replication (Appendix H, Study IV). The high variability means that one cannot actually constrain the historical dynamics very well. If a spatially explicit study of the disturbance history of the study area existed, FIN-LANDIS would be suitable for reconstructing the forest history of the area.

4.1.2 Q-LAND

Using the minimum cohort density parameter, Q-LAND model was computationally efficient, making it possible to simulate a landscape of the order of 10^5 grid cells with quantitative stand information for each cell.

Apart from the value of quantitative model output, the quantitative tracking of cohorts made it possible to use quantitative models of seed production, dispersal and regeneration (Greene et al. 1999). This is an important advantage over the semi-quantitative approach, in studying the role of dispersal and regeneration on landscape dynamics. While the published implementation (study II) uses a simplified dispersal model, it is straightforward to implement a more detailed model based on the given equations (equations 2-4, study II).

Already with the limited effort spent on model parameterization, Q-LAND is useful for exploratory work in applications, where quantitative output on stand structure across the landscape is needed. It is also suitable for theoretical investigation of, e.g., the role of dispersal and regeneration processes in shaping forest landscapes.

The growth table approach has the advantage that stand development in terms of tree quantity such as volume is constrained to a reasonable range. Error propagation cannot lead to huge errors in cohort quantities, even if parameterization data is inaccurate.

If sufficient information on multi-species and multi-cohort stand development is available, for instance, in the form of a validated detailed simulation model of stand level forest dynamics, it is possible to refine Q-LAND parameters and behavior. Rigorous parameterization requires very comprehensive data on the development of complex-structured stands or a well validated stand-level model capable of producing such data.

The following procedure is suggested for improving Q-LAND model accuracy to make it suitable for practical applications: 1) Define the input growth tables according to the development of even-aged single-species stands on each site type. 2) Apply data on the development of conifer understories in mixed stands to define the growth modifier so that broadleaf-spruce or broadleaf-fir stands are appropriately simulated. 3) Use data on late-successional stands and stands after partial disturbance events to further refine the growth modifier function (equation 15, Study II).

The growth table approach of course has strong limitations. What level of accuracy and generality in stand simulation can be achieved, can only be resolved by parameterizing the model for specific applications and testing model behavior under a sufficient number of conditions.

4.1.3 Metapopulation modeling on a dynamic landscape

FIN-LANDIS was used to produce plausible landscape scenarios for the Teeri-Lososuo area, with realistic past dynamics of aspen and goat willow (Study IV). Replicate simulations showed that knowledge of tree life-history and disturbance regime parameters is not sufficient to accurately predict the long-term dynamics of the trees in the study area. Stochastic variation in the occurrence and pattern of fires leads to great variation in landscape pattern even if the long-term occurrence and mean size of fires is given. Each simulated landscape pattern can be considered as an independent 2086 ha observation from a region with a certain mean fire regime. Empirically, the fire history of areas of that size varies considerably (Niklasson and Granström 2000).

Our attempt to parameterize models of both the forest landscape and the focal species metapopulation, based on snapshot data, illustrate a number of difficulties in the approach. Most importantly, it is hard to obtain high-resolution snapshot data for an area of thousands of hectares, and even then information in a single snapshot without knowledge of past landscape dynamics is quite limited. Nonetheless, it was encouraging that the model predicted consistent metapopulation dynamics of *Lobaria pulmonaria* for a specific landscape history. This

suggests that rigorous parameter estimation would be possible if sufficiently detailed data for the landscape history were available.

The metapopulation simulation was run on the landscape grid with 182 500 cells. In order to improve model performance, an aggregation scheme was designed (Appendix 1, Study IV). A similar scheme may be useful in other simulations of dispersal on a grid. For instance, it could be used in simulating tree dispersal in the Q-LAND model.

4.1.4 General modeling and validation issues

LANDIS has turned out to be a good platform for developing new simulation models of forest landscape dynamics. It was possible to extend the cohort-based data structure by adding cohort attributes and thereby increasing model detail, as was proposed by He et al. (1999). The object-oriented programming style of the LANDIS program code further facilitated model extensions, which did not require changing the overall architecture of the program.

While study II suggested that it is possible to implement quantitative cohort attributes, the simpler approach used in FIN-LANDIS has advantages. The model applications in studies III and IV show that the semi-quantitative approach is in many cases sufficient. In a study such as the age structure study (Study III) it is simpler to formulate the alternative assumptions when there is no need to consider the quantitative details of stand structure.

Fire is the only disturbance agent that was explicitly simulated by FIN-LANDIS and Q-LAND models. More detailed models of disturbance agents, such as harvesting (Gustafson et al. 2000) or biological disturbance (Sturtevant et al. 2004), have been linked to LANDIS. Such models can also be linked to FIN-LANDIS or Q-LAND models.

Validating or evaluating complex models is difficult, because of the complexity of model output and the richness of internal model mechanisms (Gardner and Urban 2003). In the case of forest landscapes, this is augmented by the large spatial and temporal scales which make empirical reference data hard to acquire. The FIN-LANDIS test (Study I) appears to be the first published test, where the output of a spatially explicit forest landscape model is compared with the structure of a natural boreal forest landscape.

Because complex models can rarely be ‘validated’ in any absolute sense, model performance should be tested in the context of specific applications and research problems. Sensitivity analysis can be used in order to find out the modeling assumptions that any conclusions are sensitive to. One way to assess sensitivity of predictions to model assumptions is to compare the predictions of different simulation models.

Policy-relevant predictions and other inferences are made by model users, with models as one tool for managing ecological knowledge. When considering the correctness of such predictions, the users should take into account the evidence on the model behavior produced by any evaluation procedures.

Models are useful even if they have not been thoroughly validated. They can be used for exploratory work and studying the implications of variable assumptions (Canham et al. 2003). Models may also serve in setting priorities for empirical research by suggesting the parameters that are the most important in determining the dynamics of forest landscapes.

Modeling work in this thesis was not data-driven, but driven by a need to progress towards useful simulations of the complex forest landscape dynamics. Lack of data regarding many key processes meant that ad-hoc model assumptions and parameter estimates were needed. At the same time, the models did produce useful results that appeared sufficiently robust despite the uncertainties (specifically Study **III**). The models developed are already usable in applications but continuous testing and refinement of the models in the context of new applications is needed.

Concurrently with this study, various other approaches to simulating forest landscape disturbance and succession have been developed and are being developed (Garman 2004, Keane et al. 2004, Scheller and Mladenoff 2004, Schumacher et al. 2004). Most modeling approaches are not fully developed, and model tests, comparisons, and applications have been limited. Therefore it is too early to say which approaches will turn out most practical in applications and most fruitful in stimulating further advances in model development.

4.2 Forest dynamics and biodiversity management

4.2.1 Mixed-severity fire regimes

A lot of theoretical work has addressed the question of forest age distribution as a function of fire regime (Van Wagner 1978, Johnson and Van Wagner 1985, Boychuk et al. 1997, McCarthy et al. 2001). However, it has been assumed that fires are all stand-replacing, meaning that stand age equals time-since-fire. Yet, non-stand-replacing fires are typical in many regions (Agee 1998), and occur even under the so-called crown fire regimes (Bergeron et al. 2002).

When a significant proportion of fires were non-stand-replacing, FIN-LANDIS simulations produced bell-shaped or bimodal steady state age distribution shown in Figs 2-3 (Study **III**). A simple conceptual model describes how such age-class distributions arise (Fig. 8, Study **III**). Stands can be divided into those in which the oldest cohort was established after a stand-replacing disturbance and those in which the currently oldest cohort was released when an earlier cohort died of senescence. Stands where the oldest cohort has established after a stand-replacing fire have a decreasing age distribution, youngest age classes being the largest. On the other hand, the age distribution of the stands dominated by released cohorts is concentrated at the high end of the age scale. The frequency of stand-replacing disturbances determines the relative importance of the two types of stand.

Simulations were used to produce the steady state proportion of old-growth forests as a function of fire regime (Fig. 4, Study **III**). The overall shape of the response surface, showing that old-growth occurrence is high unless fires are both severe and frequent, is intuitively simple. However, fire frequency may interact with fire severity (Schimmel and Granström 1996). This interaction may decrease the abundance of old-growth forests, when longer fire intervals lead to increased fuel loads, and to higher fire intensities. It was shown that this effect exists, but the effect is rather small, both in the non-spatial and spatial simulations, and in an analytical model (Appendix 1, Study **III**), despite an assumed strong positive relationship between potential fire severity and time since the previous fire.

Simulations that produced forest age distributions assumed that fire size is small in relation to landscape size. In reality, large fires occur, and age-class distributions are hardly near equilibrium even on large landscapes (Wimberly et al. 2000). However, the theoretical results are relevant when the age-class distribution is averaged over large enough areas or over long enough periods of time.

4.2.2 Conservation issues in middle boreal Fennoscandia

The main conclusion of Study **III** was that, assuming that frequent fires maintained landscapes dominated by old-growth pine forests, and that changes in fire frequency have been based on changes in numbers of human ignitions, old-growth forests have dominated historical Fennoscandian forest landscapes regardless of fire intervals. Figure 6 (Study **III**) show plausible forest landscape age structures under different fire return intervals.

This conclusion depends on the assumption that climate stayed similar while fire frequencies changed. Niklasson and Granström (2001) found no evidence to suggest that climatic effects would have caused any decrease in fire severity when approaching the 19th century. Fire sizes did decrease while fire numbers increased, and the simulations demonstrate (Study **III**) how this effect easily arises.

It should be noted that the simulations of Study **III** were based on a strong, possibly exaggerative assumption about the positive relationship between time-since-fire and potential fire intensity. At low times-since-fire such relationship has been observed (Schimmel and Granström 1996), but the trend does not necessarily extend to higher times-since-fire. If model assumptions were exaggerated, that strengthens the conclusion that a decrease in the number of fires cannot greatly decrease the occurrence of old-growth forests.

When policy-relevant predictions based on complex simulation models are made, it is important to consider the limitations and uncertainties of the modeling approach (Pielke 2003). In study **III**, several simplifications and approximations in FIN-LANDIS set-up are considered and our conclusion is that, although the quantitative details of simulation results have uncertainties, the qualitative main results are not affected.

Simulations of forest development in and around Ulvinsalo (Study I) and Teeri-Lososuo (Study IV) nature reserves showed the effect of the century-long suppression of forest fires. The unmanaged forests have changed from multi-layered old-growth pine forests to old-growth spruce forests. The occurrence of broadleaved trees and pine continues to decrease when the fire-origin cohorts die from old age. This trend has been observed in empirical studies (Linder et al. 1997, Kouki et al. 2004).

While fires obviously belong to the natural forest landscape, the increase of old-growth spruce stands in nature reserves is not necessarily a problem. Old-growth spruce forests were more common when fire intervals were longer, than during the 19th century when the number of human ignitions was the highest. However, the structure of old-growth forests in nature reserves does not necessarily reflect the typical structure of late-successional stands in natural landscapes. Current old-growth forests are rather even-aged due to the very frequent fires of the 19th century.

The lack of forest fires has, according to simulation results, had a strong effect on the *Lobaria* epiphyte population in the Teeri-Lososuo area (Study IV). It appears that the *Lobaria* population has currently an abundance peak. Now, approximately 150 years since last fires, large aspens and willows are abundant, and the trees have had sufficient time to get colonized by *Lobaria*. However, the host trees are already dying, and their populations are in a steep decline, probably leading to extinction of *Lobaria* in the area. Lack of aspen regeneration in nature reserves threatens also other species dependent on large aspen trees (Kouki 2004).

A fire rotation time of 92 years led to a low level of *L. pulmonaria* occupancy in the Teeri-Lososuo simulations (Study IV). This rotation is similar to the cutting rotation time in the managed middle boreal forests of Finland (Statistical yearbook ... 2002). Because of uncertainties in model assumptions, it is not possible to determine the persistence threshold for *L. pulmonaria* in terms of rotation time, but nevertheless the result suggests that the persistence of *Lobaria* populations may also be sensitive to harvest rotation times in the managed forests.

Old-growth forests, as defined in Study III, based on the age of the oldest tree cohorts, include a wide range of forest structures. The simple definition used emphasizes the most obvious difference between natural and uniformly managed landscapes. While late-successional forests that have escaped logging are rare in the managed landscape, the open, recently disturbed old-growth stages maintained by fire are even more exceptional (Linder et al. 1997, Östlund et al. 1997).

Apart from the destruction of certain spatially confined habitat types, the most detrimental effects of forest management have been the elimination of old, dying, and dead trees, the critical components of old-growth structure (Esseen et al. 1997, Jonsell et al. 1998, Rassi et al. 2001). Of course, stand-replacing disturbances are not harmful as such. Early- and mid-successional habitats, such as broad-leaved stands often created by stand-replacing fires

(Sirén 1955), are an essential part of the natural variability of forest landscapes (Esseen et al. 1997, Martikainen et al. 1998).

The prevalence of old-growth forests in the natural landscape suggests that old-growth structures should be maintained and restored. Setting aside protected areas is probably the most cost-effective method to protect late-successional, spruce-dominated forests, and species that are sensitive to stand-replacing disturbance and do not disperse effectively between isolated or short-lived habitat patches. On the other hand, as long as only a low proportion of forests is reserved primarily for the maintenance of biodiversity, it may be most efficient to use such areas to accommodate late-successional stands.

A considerable proportion of threatened forest species do not require late-successional stands, however, but prefer open stands with a good supply of dying and dead trees (Jonsell et al. 1998, Martikainen 2001, Rassi et al. 2001). Such conditions are found in old-growth forests maintained by frequent fires of moderate severity. Maintaining open, multi-aged old-growth forests may require management through logging, since reintroducing natural fire regimes on an extensive scale is difficult. This would require the use of harvesting methods which that leave a considerable proportion of trees permanently unharvested, instead of the conventional terminal cutting methods (Seymour and Hunter 1999, Bergeron et al. 2002, Kuuluvainen 2002).

5 Concluding remarks

In this thesis, new modeling approaches were developed for simulating boreal forest dynamics on landscape scale and over long term. FIN-LANDIS is a suitable tool for qualitative exploration of landscape and disturbance dynamics, and for reconstructing historical landscape patterns.

A submodel of stand level forest dynamics was developed for tracking quantitative tree stand data within the LANDIS landscape simulation framework. The resulting Q-LAND model is currently being parameterized and developed into a ‘forest restoration simulator’ for the Finnish conditions.

Simulations emphasized the importance and prevalence of old-growth forests in the natural Fennoscandian forest landscapes. The old-growth forests include both late-successional forests that have escaped large-scale disturbance, and multi-aged pine-forests maintained by low to moderate severity fires. On the other hand, simulations of *Lobaria* lichen epiphyte metapopulation showed the importance of occasional stand-replacing disturbance in maintaining sufficient amounts of certain forest habitats, in this case the microhabitats of aspen and willow trunks.

Late-successional, spruce-dominated old-growth forests are probably preserved most cost-effectively in areas set aside from commercial forestry. On the other hand, maintaining

significant amounts of open, multi-aged pine-dominated stands may require management by partial logging, since extensive reintroduction of fires is difficult. Therefore, assuming the goal of restoring natural forest structures to boreal Fennoscandian landscapes, both increasing the area set aside from commercial management, and the increased use of harvesting methods that maintain multi-aged forest stands are required. The survival of species dependent on large aspen and goat willow host trees may require restoration measures concentrated around areas with high current host tree densities.

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