Forest Age Distribution under Mixed-Severity Fire Regimes – a Simulation-Based Analysis for Middle Boreal Fennoscandia

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A simulation model was used to study the age structure of unmanaged forest landscapes under different fire regimes. Stand age was defined as the age of the oldest tree cohort in a stand. When most fires are not stand-replacing, the theoretical equilibrium stand age distribution is either bell-shaped or bimodal and dominated by old age-classes. Old-growth forests (oldest cohort > 150 y) dominate the landscape unless fires are both frequent and severe. Simulation results and analytical calculations show that if a regime of frequent fires (about every 50 y) maintains landscapes dominated by old-growth forests, then old-growth dominance persists when the number of fires is decreased, despite the associated increase in fire severity. Simulation results were applied to *Pinus sylvestris*-dominated landscapes of middle boreal Fennoscandia, which according to empirical results were dominated by old-growth forests when fires were frequent during the 19th century. Since the changes in the fire regime can be plausibly explained by changes in the number of human-caused ignitions, old-growth forests have evidently also dominated the landscapes earlier when fires were less frequent. The simulation model is used to produce plausible age distributions of middle boreal Fennoscandian forest landscapes under different historical fire regimes. In summary, the frequency of large-scale disturbance alone predicts forest landscape dynamics poorly, and the roles played by fire severity and residual stands need to be considered carefully. Maintaining and restoring old-growth structures is essential to regaining the natural variability of Fennoscandian forest landscapes.

Keywords age structure, disturbance, forest fire, modeling, landscape
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1 Introduction

Maintaining or restoring the natural range of variability in boreal forest ecosystems is a widely approved approach to protecting biodiversity and other nontimber values (Haila et al. 1994, Angelstam and Pettersson 1997, Fries 1997, Landres et al. 1999, Niemelä 1999, Bergeron et al. 2002, Kuuluvainen 2002). A specific application of the natural variability concept is to manage for landscape-level forest age-class distributions that occur in natural, fire-controlled forests (Bergeron et al. 1999, 2002, Niku et al. 2000). A prominent issue related to forest age structure is the maintenance of old-growth forests and structures. Old-growth structures, as used here, are old and large living, dying, and dead trees. Old-growth forests are broadly understood as stands in which these structures are present, whether or not the majority of the trees are old.

Designing management based on natural variability requires information on the historical age structure of unmanaged landscapes, but reconstructing past landscape structure and dynamics is never straightforward (Swetnam et al. 1999). Field studies, inventory data, and dendroecological methods can only be used to study landscape structures that prevailed in relatively recent times. These patterns have been shaped by disturbance regimes that may be different from the regimes of the more remote past. Finding unmanaged landscapes for empirical studies in Northern Europe is difficult, and thus there is little empirical data on their age structure.

Past landscape patterns may be estimated using knowledge of past fire regimes. Forest age-class distributions have commonly been considered in terms of time-since-fire distributions, using several theoretical approaches (Van Wagner 1978, Johnson and Van Wagner 1985, Boychuk et al. 1997, McCarthy et al. 2001). Simple analytical models of equilibrium dynamics yield exponential or Weibull distributions of fire interval length, from which the corresponding time-since-fire distributions are easily derived (Johnson and Van Wagner 1985). More or less erratic age-class distributions produced by random fires, which may be large in relation to landscape size, have also been simulated (Boychuk and Perera 1997, Boychuk et al. 1997).

Several studies have shown that in the 19th century middle boreal Fennoscandian landscapes displayed a regime of frequent fires, with mean intervals of about 50 y (Lehtonen 1997, Pitkänen and Huttunen 1999, Niklasson and Granström 2000, Lehtonen and Kolström 2001). Fire intervals were longer in the more remote past. Niklasson and Granström (2000) demonstrated by dendroecological means a gradual increase of fire frequency in northern Sweden from the 17th century onward. Fire frequencies peaked in the 19th century prior to a rapid onset of the current regime of very infrequent fires. Niklasson and Granström (2000) also argue that the increase in fires between the 17th and 19th centuries was primarily caused by a growing number of human-caused ignitions. In eastern Finland a similar trend of gradually increasing fires appears to have prevailed for the last 2000 y, according to estimates based on peat and sediment stratigraphies (Pitkänen 1999, 2000, Pitkänen and Huttunen 1999, Pitkänen and Grönlund 2001). The estimated fire frequencies for the past few centuries are very similar in the two areas of Finland and Sweden. Studies suggest fire intervals of 40–70 y in the 1800s, about 130 y in the 1600s and about 200 y around 1700 y BP, but it is not clear over what regions such figures could be extrapolated (Pitkänen and Huttunen 1999, Niklasson and Granström 2000, Pitkänen and Grönlund 2001). The longest fire intervals have been observed on spruce swamps (Hörnberg et al. 1995), in northern high-elevation forests (Steijlen and Zackrisson 1987, Hyvärinen and Sepponen 1988), and in European Russia outside Fennoscandia (Syrjänen et al. 1994, Wallenius 2002).

Using theoretical time-since-fire distributions to model landscape age structure would result in the conclusion that old-growth forests do not persist under regimes of frequent fires. For example, in the exponential model with a mean fire interval of 50 y the proportion of forests older than 150 y is $\exp(-150/50) \approx 0.05$. In contrast, frequently burning middle boreal Fennoscandian landscapes were dominated by multiaged, old-growth pine forests (Linder and Östlund 1992, 1998, Östlund et al. 1997, Axelsson and Östlund 2000, Lehtonen and Kolström 2001, Karjalainen and Kuuluvainen 2002, Kuuluvainen et al. 2002). The obvious explanation is that fire severity has been low. Accordingly, it appears that stand-replacing fires have been rare in Fennoscandia (Saari 1923, Zackrisson 1977, Zackrisson and Östlund 1991, Engelmark et al. 1994), and development of frequently burning stands may resemble gap dynamics (Kuuluvainen 1994). In many other ecosystems throughout the world low-severity fires are also common or prevalent (Agee 1998), and fires usually leave living trees even in systems that are considered crown fire-dominated (Bergeron et al. 2002).

The existence of frequently burning old-growth pine forests shows that models of forest age structure and old-growth forest occurrence should take account of fire severity, in addition to fire frequency. A distinction should be made between time-since-fire and stand age. Using time-since-fire distributions in timing terminal cuttings to mimic natural disturbance patterns (e.g. Niku et al. 2000) may result in landscape structures that are far outside the natural range of variability.

In the present study, computer simulations and analytical arguments are used to explore landscape age structure, in terms of actual tree or cohort age, in response to variation in the fire regime. The ecosystems targeted are Scots pine (*Pinus sylvestris* L.)-dominated forests of the middle boreal zone (Ahti et al. 1968) of Fennoscandia.

The theoretical research question is how the shape of stand age distribution and the abundance of old-growth forests are determined under mixed-severity fire regimes. The more practical problem is what can be inferred about the forest age structure of natural Fennoscandian landscapes. The main difficulty in estimating the structure of past landscapes is the lack of direct data on the severity of past fires. However, empirical studies suggest that frequent fires have maintained old-growth-dominated landscapes. This information can be used as a constraint when choosing simulation scenarios that are consistent with empirical data. One specific question considers, whether old-growth forests were also dominant when fire frequency was lower. The answer is not obvious, because longer fire intervals increase the mean time-since-fire, which may increase the severity of fires.

2 Methods

2.1 Modeling Approach

Simulations were conducted using FIN-LANDIS, which is a spatially explicit, grid-based model of forest landscape dynamics, tailored for Fennoscandian conditions. The model simulates landscape change in 10-y time steps, and operates on raster maps derived through GIS. Stand development is driven by seed availability based on spatially explicit seed dispersal, competition between cohorts, and fire events. Ignition and spread of forest fires are simulated dynamically during each time step. The model is based on the LANDIS model (Mladenoff et al. 1996, He and Mladenoff 1999, He et al. 1999). FIN-LANDIS has been described in detail and tested elsewhere (Pennanen and Kuuluvainen 2002). In this section, we describe the most relevant aspects of model structure, and the assumptions incorporated in these parameter values that were common to all simulations conducted in this study.

In the simulations, the landscape is a collection of stands represented by grid cells. Stands contain cohorts of different species and age. A stand may accommodate several tree species, and several cohorts of the same species but different ages. Tree cohorts have no quantitative attributes apart from age, but are divided into thin and dense cohorts.

The modeling approach is rule-based rather than quantitative, meaning that the dynamics is mostly based on defining conditions under which transitions of state occur instead of equations determining change in state variables (Pennanen and Kuuluvainen 2002). For instance, new cohorts are established if requirements related to shading, seeding, and seedbed are met. The processes involved are the establishment of new cohorts and the death of cohorts. In addition, cohorts may be converted from dense to thin cohorts, but not the other way around, and the cohort age increases by 10 y in each iteration.

The tree species explicitly considered in this study are Scots pine and Norway spruce (*Picea abies* Karst.). In forests on mineral soil, with abundant seeds present, regeneration occurs as follows: pine always regenerate in dense cohorts, but only immediately after fires, and if there are

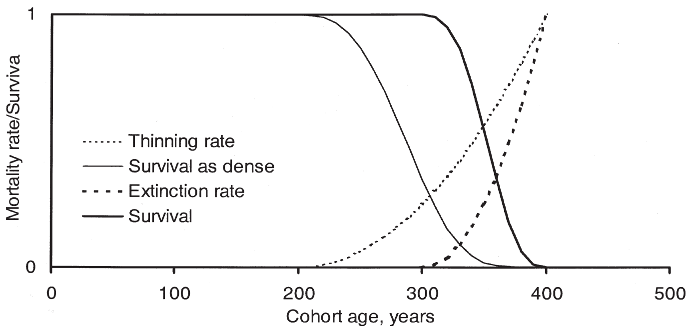

Fig. 1. Mortality and thinning of pine cohorts due to senescence, as assumed in the simulations. Survival curves describe the fate of entire cohorts, not of single trees. Time of 'thinning' or death of cohorts is assumed to approximate a normal distribution. Mortality or thinning rates give the fraction of cohorts thinned or removed per 10-y time step.

no dense cohorts of any species already present. Spruce also regenerate after fires, but are indifferent to the presence of other cohorts. After 10 y since last fire, spruce establishment probability drops to a lower value (0.25 per cell and iteration). Spruce cohorts may be thin from the beginning, but this has no feedback on model behavior, since regeneration of species other than spruce is not considered in the late-successional stands. The decrease in establishment probabilities with increasing time-since-fire, which is especially clear for pine, has been confirmed empirically (Sirén 1955, Agee 1998).

Dense tree cohorts will eventually disintegrate due to senescence. After tree cohorts attain half the maximum longevity of their species, they begin turning into thin cohorts with increasing probability (Fig. 1). Cohorts above 80% of the maximum age begin to die entirely with increasing probability (Fig. 1). The longevity of individual cohorts is assumed to be approximately normally distributed, which holds if the deaths of individual trees are not too correlated. A maximum age of 400 y was used for pine and 350 y for spruce. At these ages the contribution of the cohort to the stand volume would be negligible (Norokorpi 1979, Nikolov and Helmisaari 1992, Kuuluvainen et al. 2002).

Fire severity is defined through tree mortality and is represented by positive integer values. Spruce cohorts are killed in any fire, while the mortality of pine cohorts is dependent on cohort age. The susceptibility of pine cohorts changes at age thresholds of 24, 56, 120, and 200 y, which give the maximum ages of cohorts that are killed by fires of severity classes 1–4 respectively. Fires of class 5 or higher kill all cohorts. Dense cohorts in the 2 highest susceptibility classes that survive a fire become thin cohorts, e.g. a class 1 fire thins pine cohorts up to 120 y of age.

2.2 Simulation Runs

Simulations were divided into 4 simulation sets. Differences between simulation sets are summarized in Table 1. Sets I and II explored the shape of stand age distributions under varying fire regimes, using simple assumptions. Simulation set III investigated the average amount of old-growth forests in the landscape under varying fire regimes. Simulation set IV attempted to reproduce realistic dynamics of middle boreal forest landscapes under different fire frequencies, consistent with the empirical knowledge of historical Fennoscandian forest structure.

Theoretical exploration of landscape dynamics is simpler when not considering spatially explicit dynamics. Therefore, simulations of the first 3 simulation sets were conducted as effectively nonspatial simulations, in which the size of fires was limited to one cell, tree seeds were assumed

Table 1. Summary of differences between simulation sets.

Simulation set	Number of simulations	Parameters varied between simulations	Other model assumptions	Output examined
I	4	Fire severity (4 levels)	Fire severity and hazard independent of time-since-fire	Shape of age distribution
II	4	Fire interval (4 levels)	Fire severity and hazard independent of time-since-fire	Shape of age distribution
III	35	Fire severity (7 levels), fire interval (5 levels)	Fire severity and hazard dependent on time-since-fire	Amount of old-growth, stand-replacement rate
IV	10	Number of ignitions (10 levels)	Spatially explicit simulation in a realistic landscape	Forest age distribution, fire severity distribution

to be always present, and all cells represented similar forest sites on mineral soil. Such schemes simulate collections of identical independently evolving stands whose attributes are aggregated in the model output. These nonspatial model runs were conducted on a 'landscape' of 86 056 cells.

Nonspatial simulations ignore several aspects of actual landscape dynamics, such as site-dependent spatial variation in fire frequency and behavior (Engelmark 1987). Limited seed dispersal could also affect the stand age distribution. The last simulation set IV was conducted in a spatially explicit manner, using explicit seed dispersal of tree species and fires that spread according to a spatially explicit algorithm.

In simulation sets III and IV it was assumed that fire severity increases with time-since-fire and that most fires are stand-replacing if time since the previous fire is long enough. Such assumption is reasonable (Schimmel and Granström 1996), but the detailed form of the relationship is not known. The assumption was made to investigate whether it is possible that decrease in the number of fires could lead to decrease in the abundance of old-growth forests. This would be possible if the lengthened mean time-since-fire would increase fire severity strongly. If fire severity and fire frequency were independent, the amount of old-growth forests and fire frequency would obviously be negatively correlated.

Output from each simulation was recorded after running the model for at least 100 iterations (1000 y). It was separately assessed that the simulations were lengthy enough to eliminate the effect of initial conditions. The results thus represent theoretical steady state landscape structures.

When interpreting the simulation results, stand age means the age of the oldest tree cohort, which is a suitable indicator for describing the structural diversity of the stand when the focus is on the occurrence of old-growth structures. Stand age distribution means the frequency distribution of stand ages in the landscape.

2.2.1 *Simulation Set I*

Simulation set I examined the effect of fire severity on stand age distribution in 4 scenarios. In the first simulation run fire severity was always 5, in the second run fire severity was a random number between 1 and 5, and in the third a random number between 1 and 3. The last scenario assumed that fires always thin pine cohorts but never kill them completely. The probability of burning was 0.1 per site and decade, corresponding to a mean fire interval of 95 y. To keep the assumptions and the interpretation of results simple, fires occurred randomly, and the probability of burning and fire severity were independent of time-since-fire and stand structure.

2.2.2 *Simulation Set II*

Simulation set II examined the effect of mean fire interval on stand age distribution under a moderate-severity fire regime. The mean fire intervals in the 4 simulation runs were 40, 50, 70, and

150 y. In all runs, the severity of each fire was a random number between 1 and 3. Fire occurrence and severity were independent of time-since-fire and stand structure.

2.2.3 Simulation Set III

Simulation set III examined the combined effect of fire frequency and fire severity on the abundance of old-growth forests and on the frequency of stand-replacing fires. Experimenting with 5 values of mean fire interval and 7 fire severity scenarios yielded $5 \times 7 = 35$ simulations. The phrase 'severity scenario' is used because fire severity and fire frequency were not independent, since fire severity was assumed to increase with time since previous fire in the stand. Each scenario corresponds to a specific form of the relationship between fire severity and time since last fire.

The severity scenarios were labeled with numbers from 1 to 9, giving the maximum fire severity that could be attained under any conditions. The potential fire severity increased linearly with time-since-fire, so that it reached the maximum at a time-since-fire of 90 y and remained constant after that. The actual severity of each fire was randomly chosen from the integers between 0 and the potential severity determined by the severity scenario and the time-since-fire. Severity class 0 corresponded to a failed ignition. The stochastic component in the determination of fire severity corresponds to variations in weather conditions, which influence fire behavior (Bessie and Johnson 1995, Schimmel and Granström 1996). Empirical evidence shows that fire severity (Schimmel and Granström 1996) and the probability of burning (Lehtonen 1997, Niklasson 2000) increase with time-since-fire. Fire probability also increases in the simulations with time-since-fire, since the occurrence of discarded 'fires' of severity class 0 decreases when potential fire severity grows.

2.2.4 Simulation Set IV

For spatially explicit simulation set IV, most tree life history attributes were chosen as in Pennanen and Kuuluvainen (2002). The landscape used in the simulations was an actual eastern Finnish landscape, and was represented by a site-type map with the following site-type distribution: 30% dryish sites, 30% mesic sites, 10% spruce swamps, and 30% pine bogs, open mires, and waters. This distribution is similar to the average vegetation of the Eastern middle boreal Finland (Salminen and Salminen 1998).

On mesic and dryish sites, pine and spruce regenerated as described in section 2.1. In spruce swamps establishment probabilities for pine and spruce were 1.0 and 0.5 immediately after fires and 0 and 1.0 later, respectively. In pine bogs the respective probabilities were 1.0 and 0 after fires, and 0.5 and 0 later. The flammability of swamp and bog forests was assumed to be 10 times lower, and the flammability of mesic sites 2 times lower than the flammability of dryish sites (Engelmark 1987, Hörnberg et al. 1995). Flammability corresponds to the probability of a site being burnable during a fire (Pennanen and Kuuluvainen 2002).

Fire spread is determined in FIN-LANDIS by setting the mean fire duration and defining the rate-of-spread in relation to fire severity (Pennanen and Kuuluvainen 2002). The rate of spread was of the form $c \cdot 2^I$, where I is fire severity class. Potential fire severity was set to increase with time-since-fire (until time-since-fire of 100 y) and with the age of the oldest spruce cohort present (until age of 175 y), spruce age having twice as strong an effect as time-since-fire.

The goal of simulation set IV was to reproduce realistic dynamics of middle boreal forest landscapes under different fire frequencies. Consistency with empirical studies required that, when the mean fire intervals were 50–70 y, the majority of the forests were old-growth pine forests (Zackrisson 1977, Zackrisson and Östlund 1991, Östlund et al. 1997, Axelsson and Östlund 2000, Lehtonen and Kolström 2001, Kuuluvainen et al. 2002). Therefore, the parameters determining fire severity were adjusted until simulations yielded old-growth-dominated landscapes under mean fire intervals of 50–70 y. Simulation parameters were such that when time-since-fire was high, fires were severe and frequently stand-replacing.

The simulation set consisted of 10 simulations. The only parameter varying between the simulations was the number of ignition attempts, which was doubled between each simulation. Thus the frequency and severity of fires were not determined externally as in the nonspatial simulations. It was therefore possible to investigate the relationship between the number of ignitions and the fire regime.

3 Results

3.1 Stand Age Distributions in Relation to Fire

Different fire severity scenarios with a mean fire interval of 95 y gave rise to strongly varying age-class distributions (simulation set I, Fig. 2). Stand-replacing fires produced an approximately exponential age distribution with a cutoff due to the limited longevity of trees (Fig. 2a). Under a low-severity fire regime the stand age distribution was bell-shaped, with the mode near the maximum longevity of pine (Fig. 2d). The distributions were in all cases unimodal with the mode either at the youngest or near the oldest age-classes. Age distributions based on spruce cohorts were approximately exponential in all cases because of the assumed zero tolerance to fires (Fig. 2). The smooth shape of the age distributions demonstrates that the number of stands used in the nonspatial simulations was high enough to eliminate the effect of stochastic variation in the aggregated output.

Age distributions dominated by old age-classes (Fig. 2c–d) represent landscapes with multi-layered pine stands. These arise when fires are not stand-replacing, but thin stands and facilitate regeneration of new cohorts. When the oldest cohort dies of old age, younger cohorts

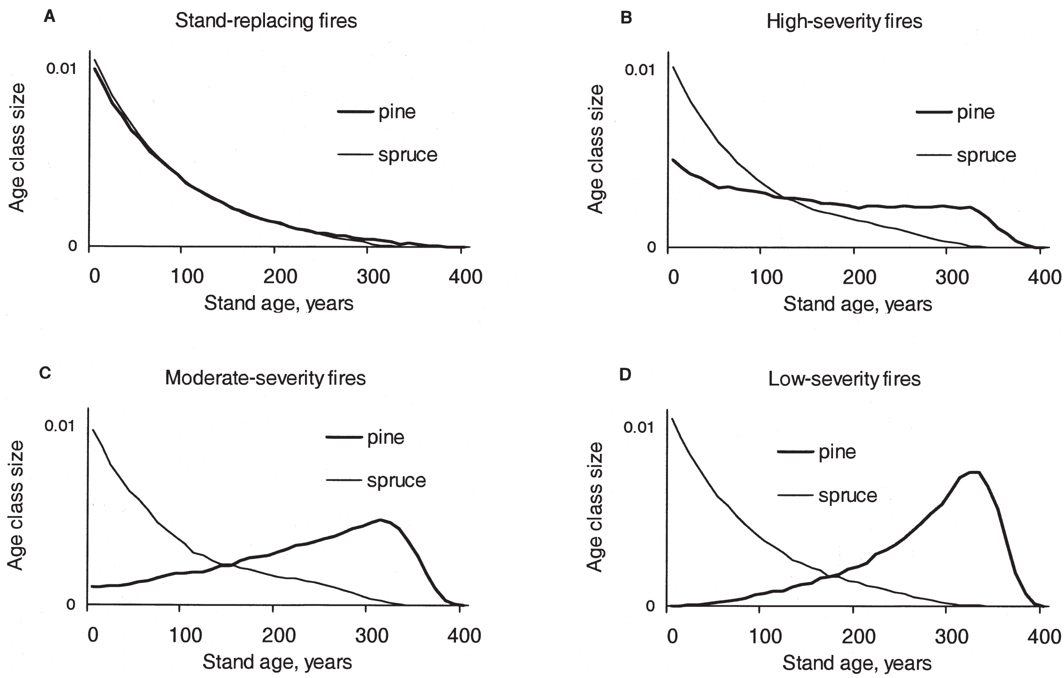

Fig. 2. Steady state stand age distribution in response to fire severity. Stands are classified separately according to age of the oldest spruce cohort and the age of the oldest pine cohort. Mean fire rotation is 95 y (0.1 fires/decade at each site). A) Fires are always stand-replacing (severity class 5). B) Any severity from 1 to 5 is equally probable. C) Any severity from 1 to 3 is equally probable. D) Fires always thin pine cohorts but never kill them completely.

Fig. 3. Stand age distribution under a moderate-severity fire regime in response to mean fire interval. Fire severity takes values from 1 to 3 with equal probability. Fire severity is assumed to be independent of time-since-fire.

are released under them, and stand age remains high.

When fire frequency was changed in the moderate-severity fire scenario, only the occurrence of the youngest age-classes was notably affected (simulation set II, Fig. 3). Shortened fire rotation increased the abundance of young stands, resulting in bimodal stand age distributions under high-frequency fire regimes.

In simulation sets I and II, both the probability of burning and the fire severity were independent of time since previous fire. In reality, both appear to be lower at the early stages of succession (Schimmel and Granström 1996, Niklasson and Granström 2000). This may increase the occurrence of young age-classes in the simulations, because the high occurrence and severity of fires during early succession make it less likely that young stands survive to old age and become less susceptible to fires.

3.2 Occurrence of Old-Growth Forests

The results of simulation set III were summarized by plotting the occurrence of old-growth forests and the frequency of stand-replacing fires against mean fire interval and the fire severity scenario (Fig. 4). Old-growth forests were defined as stands that are at least 150 y of age. 'Stand-replacing fires' are fires that actually destroy all existing cohorts, so whether a fire is stand-replacing, is dependent not only on fire severity but also on the stand structure prior to the fire. Old-growth forests were primarily defined based on the age of the oldest cohort in a stand (Fig. 4a), but also based separately on the age of the oldest pine cohorts (Fig. 4c) and the oldest spruce cohorts (Fig. 4d). The occurrence of old-growth forests is high except when fires are frequent in the high-severity fire scenarios (Fig. 4a), which alone supports a high stand-replacement rate (Fig. 4b).

In the scenarios where frequent fires maintain old-growth-dominated landscapes, the proportion of old-growth forests decreases slightly when mean fire rotation increases from 50 to 200 y (scenarios 1–5 of Fig. 4a). However, old-growth dominance still persists under all fire rotations in these scenarios. The reason for decreased old-growth occurrence is the increased fire severity caused by longer mean time-since-fire.

The occurrence of old-growth pine forests peaks at the combination of low severity and high frequency of fires (Fig. 4c). As fire interval increases, the old-growth pine forests are gradually replaced by old-growth spruce forests (Figs. 4c,d). Since fires were assumed to be always lethal to spruce, the mean fire severity does not influence the pattern of old-growth spruce (Fig. 4d).

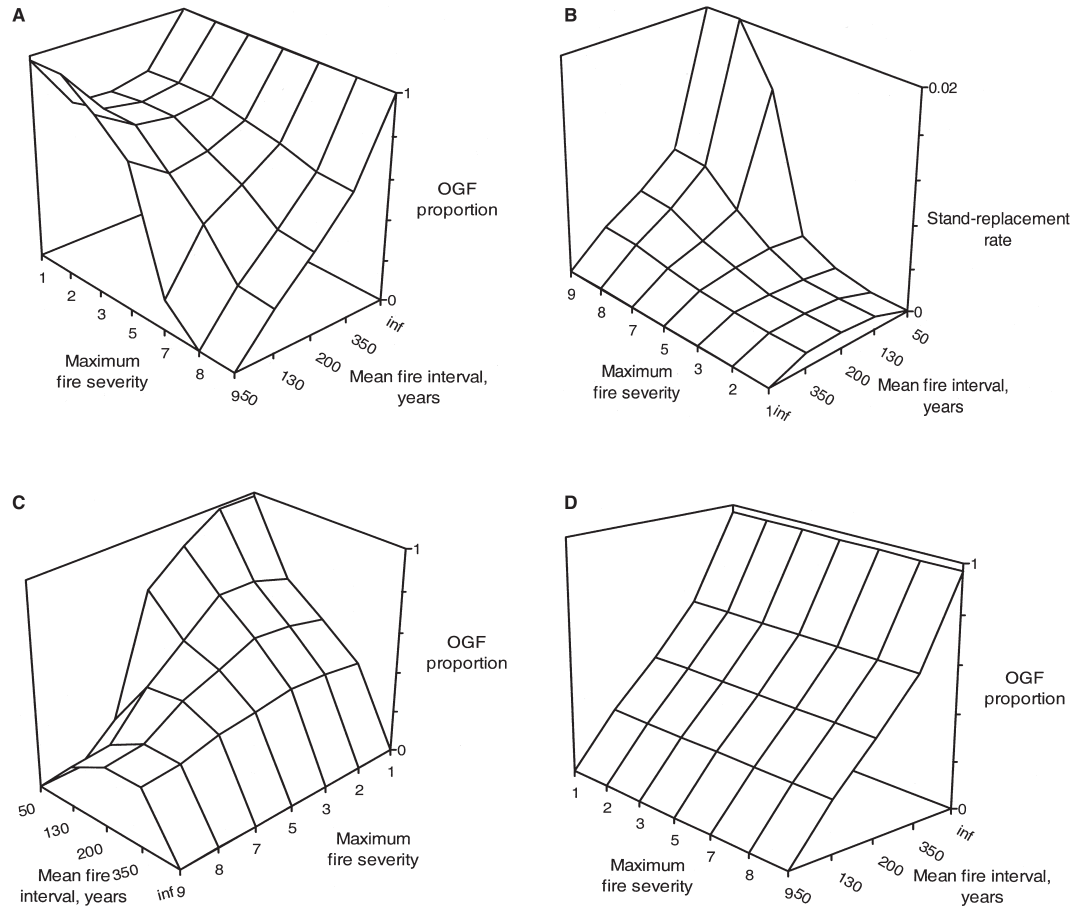

Fig. 4. Landscape properties under varying fire severity scenarios (labeled by maximum potential fire severity) in response to mean fire interval, based on simulation set III. A) Proportion of old-growth forests (OGF, oldest cohort > 150 y) in the landscape. B) Stand replacement rate (mean yearly proportion of landscape suffering a stand-replacing fire). C) Proportion of stands with oldest pine cohort > 150 y of age. D) The proportion of stands with oldest spruce cohort > 150 y of age.

3.3 Spatially Explicit Simulations

The spatially explicit simulations (simulation set IV) 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). In both scenarios the proportion of old-growth forests is high regardless of mean fire frequency.

The spatially explicit simulations produced slightly bimodal age distributions that were quite flat for moderate or low fire frequencies (Fig. 6). The bimodality of stand age distributions based on spruce age (Figs. 6a,b) 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. Such old-growth spruce forests are important in actual landscapes with intermediate fire frequencies (Zackrisson and Östlund 1991, Hörnberg et al. 1995, Esseen et al. 1997).

The spatial simulations also demonstrate how increased number of ignitions and increased fire

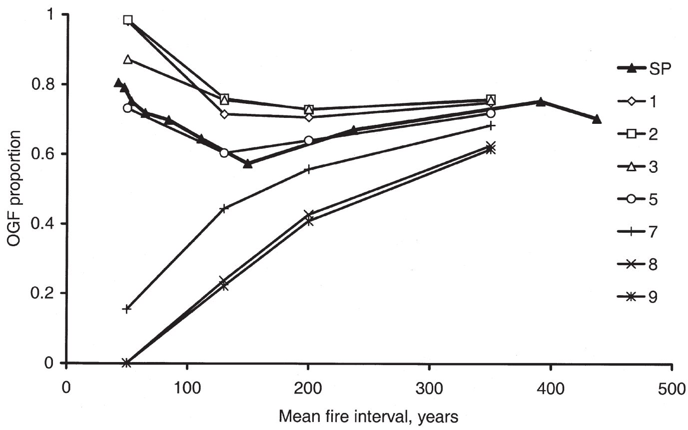

Fig. 5. Proportion of old-growth forests (OGF) in the landscape in response to mean fire interval according to spatially explicit simulation set IV (SP), and to scenarios of nonspatial simulation set III (1–9).

frequency decrease fire severity. The area burned increases with the number of ignitions, but not proportionally (Fig. 7a), and the mean fire severity decreases (Fig. 7b). Changing the area burned 3-fold, from 0.5%/y to 1.5%/y, requires a 16-fold increase in the number of ignitions (Fig. 7a).

As an example of the simulation fire regime, in a simulation with an annual burn rate of 0.7%, the mean fire size was 0.5% of the burnable landscape area. Most of the burned area was due to fires larger than 2% of the area, while the largest fire covered 43% of the landscape.

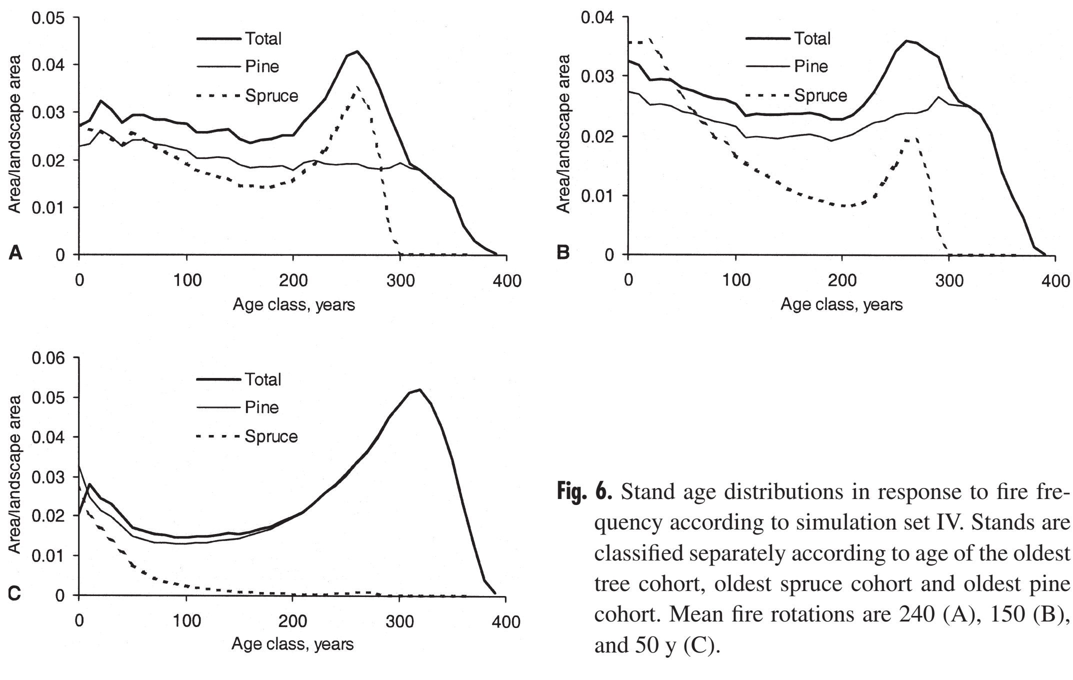

Fig. 6. Stand age distributions in response to fire frequency according to simulation set IV. Stands are classified separately according to age of the oldest tree cohort, oldest spruce cohort and oldest pine cohort. Mean fire rotations are 240 (A), 150 (B), and 50 y (C).

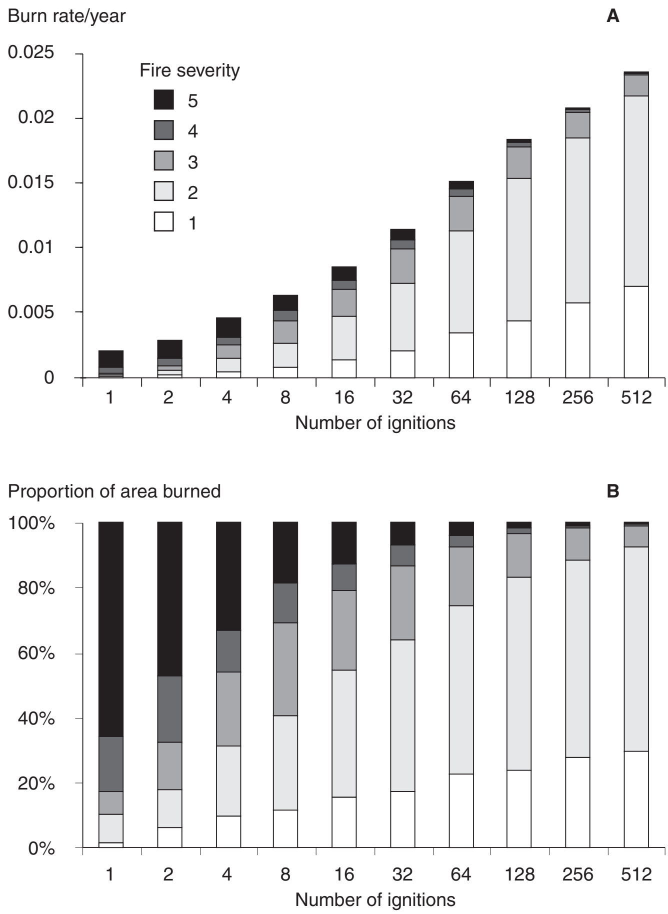

Fig. 7. Fire regime in relation to number of ignition events per time step (unit arbitrary) in spatially explicit simulation set IV. A) Annual burn fraction. Area burned is divided according to fire severity class. B) Proportion of area burned in each fire severity class.

4 Discussion

4.1 Shape of Age Distributions

The simulations demonstrated that when fires are not always stand-replacing, stand age distributions differ considerably from time-since-fire distributions. Theoretical time-since-fire distributions of equilibrium landscapes (exponential, Weibull, or any other) are always monotonously decreasing and dominated by stands that are young in relation to mean disturbance interval (McCarthy et al. 2001). However, stand age distributions based on actual tree age may be dominated by old stands and be unimodal or bimodal, regardless of the fire interval (Figs. 2–3).

A simple conceptual model clarifies how the age-class distributions observed in the simulations (Figs. 2–3) arise (Fig. 8). 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. The shape of the age distribution

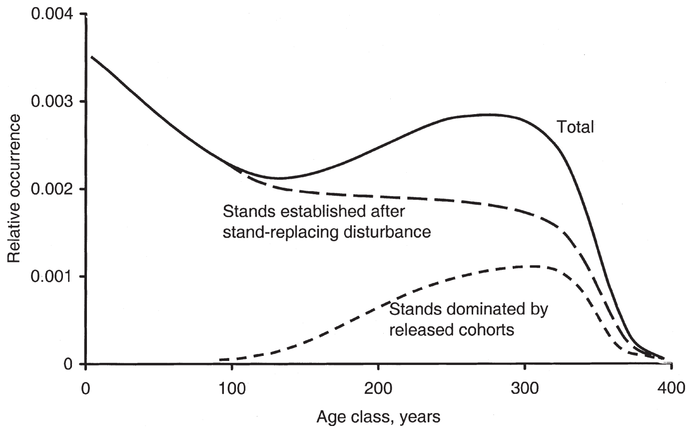

Fig. 8. Conceptual model of stand age distribution in a Scots pine-dominated forest landscape. Stands can be divided into 2 classes: Stands in which the oldest cohort was born after a stand-replacing disturbance, and stands whose oldest cohort was released when an earlier cohort died. It is assumed that cohorts older than 120 y survive fires. New cohorts are only created after fires.

of those stands established after stand-replacing fires (Fig. 8) arises because cohorts are most susceptible to fires at young age. On the other hand, the age distribution of the stands dominated by released cohorts is concentrated at the high end of the age scale (Fig. 8), because when an old cohort dies, the next oldest cohort is formed of trees that regenerated under the dying cohort, when it 'thinned' in a low-severity fire or due to old age. The frequency of stand-replacing disturbances determines the relative importance of the 2 types of stand, producing different unimodal and bimodal age distributions.

4.2 Old-Growth Forests under Mixed-Severity Fires

The results of simulation run III demonstrate a relationship between the fire regime and the mean occurrence of old-growth forests in a forest landscape. Old-growth forests are rare when fires are frequent in the high-severity scenarios, but otherwise they dominate the landscape (Fig. 4a).

The simulations show 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 suggest that if old-growth forests dominate landscapes under frequent fires, old-growth dominance persists under all fire rotations. The simulations assumed that the relationship between time-since-fire and fire severity remains the same when fire frequency changes. This requires that both the climate and the successional pathway that stands follow remain constant.

The simulations assumed that the increase in potential fire severity occurs gradually during the stand succession after a fire. However, it is conceivable that the nonlinear dynamics of fire propagation could produce 'catastrophic' changes in fire behavior in response to change in parameters such as stand structure (Hesseln et al. 1998), e.g. at the point where the spruce canopy becomes developed enough to support crown fires. Such system behavior could make fire severity even more sensitive to mean fire intervals than was

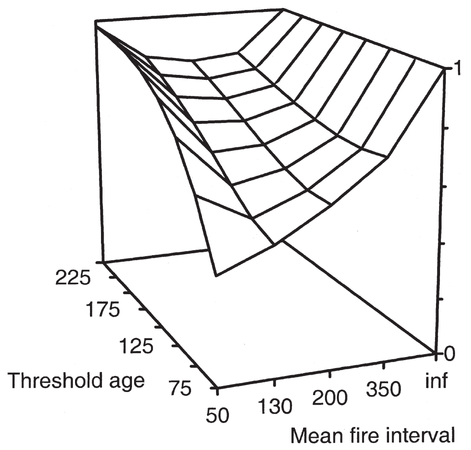

Fig. 9. Theoretical proportion of old-growth stands in a landscape. Fire severity is assumed to be determined so that fires are stand-replacing if time since the previous fire exceeds the threshold age, and otherwise they are not. Old-growth forests are stands where time since last stand-replacing fire is at least 150 y. 'Inf' stands for infinite fire interval (no fires). See Appendix 1 for details.

assumed, increasing the stand-replacement rate and decreasing the occurrence of old-growth forests at intermediate fire frequencies. Therefore it should be determined if the results are very sensitive to detailed assumptions of the temporal pattern of fire severity.

Let us consider the hypothetical case that is most favorable to the occurrence of old-growth forests at high fire frequencies and least favorable at intermediate fire frequencies. Assume that there is a sharp threshold at a certain time-since-fire, separating the young stands that do not sustain stand-replacing fires from older stands that do support them. Using some simplifying assumptions it is possible to calculate analytically the occurrence of old-growth forests in this extreme scenario (Appendix 1). It appears that as long as old-growth forests clearly dominate at short fire intervals (50 y) the old-growth stands cover the majority of forests at any fire frequency (Fig. 9). We conclude that the pattern of Fig. 4a appears robust even under extreme assumptions of fire behavior.

In fact, there is no necessary clear successional trend in crown fire behavior (Bessie and Johnson 1995). Therefore, it is possible that the relationship between fire frequency and fire severity in simulation sets III and IV was unrealistically strong. If the relationship between fire frequency and mean fire severity were weaker, the general pattern of Fig. 4a would remain the same, but the decrease in old-growth forest abundance at intermediate fire frequencies would be shallower.

The nonspatial simulations assumed a uniform 'landscape' of forest stands with identical mean fire intervals. In an actual landscape the susceptibility of different sites to fires varies (Engelmark 1987). Given a certain mean fire interval for a landscape, the age distribution of the entire landscape would be the sum of the age distributions at each site. This would decrease further the sensitivity of the landscape age distribution to the mean fire interval.

4.3 Historical Fennoscandian Landscapes

Empirical knowledge can be used to link the previous theoretical picture with the actual historical dynamics of middle boreal Fennoscandian forest landscapes. The main difficulty is that there is no direct evidence for the severity of fires at those times. However, several studies have shown that when fire intervals have been short (about 50–70 y), landscapes have been dominated by multi-aged old-growth pine forests (Zackrisson 1977, Zackrisson and Östlund 1991, Östlund et al. 1997, Axelsson and Östlund 2000, Lehtonen and Kolström 2001, Kuuluvainen et al. 2002). This implies, according to the previous discussion, that old-growth forests have also dominated landscapes when fire intervals were longer, if the climate and the succession of vegetation after fires have been relatively constant.

The conclusion on landscapes constantly dominated by old-growth forests would be in question if the climate was much more favorable to severe fires prior to the 19th century. However, Niklasson and Granström (2000) found no correlation between climate proxies and the fire regime. The drop in mean fire size between the 17th and 19th centuries (Niklasson and Granström 2000) could indicate a change in climatic conditions, but the spatially explicit simulations (set IV) show that decreased fuel loads resulting from more frequent fires can well explain the change in fire size. The reason is that the increasing area burned decreases the mean time-since-fire in the landscape. This decreases the mean fire severity (Fig. 7b), leading to lower rates of fire spread and consequently to smaller fire size. This relationship between number and size of fires was earlier suggested by Niklasson and Granström (2000).

Fire frequencies appear to have increased steadily for the last 2000 y until they peaked in the 19th century (Pitkänen and Huttunen 1999). This does not suggest that forests have been significantly more fire-prone in older times. In summary, it seems plausible that the trend in fire frequency has followed the number of human-caused ignitions and the unmanaged middle boreal Fennoscandian forest landscapes have been constantly dominated by old-growth forests.

Wimberly et al. (2000) have previously used a simulation model incorporating non-stand-replacing fires and multicohort stands to investigate the historical amount of old-growth forests and its temporal variability. They had an empirical estimate of fire severity available, but due to lack of data they had to assume that fire intervals and fire severity were independent. For the present study, no direct data on fire severity were available, but empirical data on the structure of frequently burning landscapes could be used instead to infer realistic fire intensity scenarios.

4.4 Limitations of the Modeling Approach

The basic limitation of the modeling approach is the assumption of equilibrium dynamics. In real landscapes fires that are large in relation to landscape size may be common, producing irregular and erratic time-since-fire distributions (Baker 1989, Cumming et al. 1996, Boychuk et al. 1997). Therefore the simulation results must be interpreted as theoretical mean age distributions.

Non-stand-replacing fires have been typical under Fennoscandian conditions, and large fires are spatially heterogeneous, with fire severity varying inside each burned area. Therefore the effect of spatially correlated disturbance on the stand age distribution is lower than on the time-since-fire distribution. Furthermore, since the old-growth forests include a wide range of age-classes, their occurrence is considerably less sensitive to the influence of nonequilibrium dynamics than the exact shape of the age distribution. However, Wimberley et al. (2000) showed that variability in the amount of old-growth forests may be very high, even on landscape level. Even under nonequilibrium dynamics, the previous conclusion could be rephrased that unmanaged landscapes have most of the time, and on a regional scale perhaps constantly, been dominated by old-growth stands.

The shape of the age-class distribution produced by a simulation model is dependent on the model structure and the chosen parameter values; thus it is useful to consider how sensitive the results are to changes in the assumptions incorporated. Moderate changes in the assumptions governing the establishment, thinning, and death of cohorts would only affect the width and exact location of the peak in age distributions (Fig 8). The results regarding old-growth occurrence are therefore also insensitive to these parameters, as long as the maximum age of the species is considerably higher than the old-growth threshold of 150 y. Regarding the effect of fires on age distribution, the assumption that mortality decreases with cohort age is realistic (Ryan and Reinhardt 1988, Kolström and Kellomäki 1993). The assumption that cohorts in the 2 lowest fire tolerance classes above the survival threshold will be thinned by a fire is more arbitrary. This assumption affects the regeneration of understory cohorts and, therefore, influences indirectly the mean age of cohorts released when the oldest cohort dies. Altering the assumption would change the exact shape of the peak in the age distribution under low fire severities, but would not change the general pattern.

Relating the simulation results to quantitative forest data would require defining the size of grid cells and setting up quantitative thresholds defining ‘thin’ and ‘dense’ cohorts. Such thresholds would obviously be specific to species, cohort age, and site type. However, in the present study such quantitative comparisons are not made, and the actual values of the thresholds are not relevant to the conclusions, as long as the rules defining model behavior are qualitatively correct.

The inferred domination of old-growth stands under all fire frequencies is specific to landscapes in which the fire-resistant Scots pine is abundant and to the conditions of middle boreal Fennoscandia. However, the theoretical conclusions may generalize to other regions where mixed-severity fire regimes prevail.

5 Conclusions and Management Implications

The main results of this study are the following:

1) When not all fires are stand-replacing, theoretical stand age distributions of forest landscapes may be roughly bell-shaped or bimodal and qualitatively different from the time-since-fire distributions. Actual forest landscapes may follow such equilibrium distributions when averaged over sufficiently wide areas or sufficiently long times.
2) If old-growth forests dominate landscapes when fires are frequent, old-growth dominance persists when the number of fires is decreased, even if longer fire intervals increase the severity of fires.
3) Assuming, in accordance with empirical studies, that frequent fires maintained landscapes dominated by old-growth pine forests and that historical trends in fire frequency were due to human-caused ignitions, middle boreal Fennoscandian forest landscapes have been consistently dominated by old-growth forests and stand-replacing fires have been rare.
4) Fig. 6 shows plausible age distributions of historical Fennoscandian forest landscapes under varying fire frequencies corresponding to empirical observations (Pitkänen and Huttunen 1999, Niklasson and Granström 2000, Pitkänen and Grönlund 2001). Changes in fire frequency have mostly influenced the abundance of old-growth spruce stands.

Old-growth forests, defined as here, based on the age of the oldest tree cohorts, include a wide range of forest structures, varying in species composition, density, and spatial pattern. The simple definition used emphasizes the most obvious difference between unmanaged and uniformly managed production landscapes. Late-successional forests that have escaped logging are rare in the managed landscape today, and the open, recently disturbed old-growth stages maintained by fire are even more exceptional (Linder et al. 1997, Östlund et al. 1997).

The observed structure of unmanaged forests may be misleading, when determining the natural range of variability in the forest landscape. Fire regimes have varied fundamentally during the history of Fennoscandian forests. Therefore, current late-successional forests are denser than the open stands maintained by frequent fires of the 19th century. On the other hand, the conversion to late-successional spruce forests (Linder et al. 1997) may bring back spruce-dominated stand types that were more common before the 19th century, when fires were less frequent (Pitkänen and Huttunen 1999, Niklasson and Granström 2000). For the same historical reasons, the present even-aged old-growth spruce stands may not resemble the old-growth spruce forests of historical or 'natural' landscapes, in which more open 'climax' structures are common (Norokorpi 1979, Syrjänen et al. 1994, Kuuluvainen et al. 1998).

The habitat requirements of the species classified as threatened in Finland suggests that, 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 and the importance of such forests to biodiversity suggest that old-growth structures should be maintained and restored. Since late-successional stands are not easily maintained in the context of commercial management, setting aside protected areas is probably the most cost-effective method to protect species that are sensitive to stand-replacing disturbance and do not disperse effectively between isolated or short-lived habitat patches. For the same reason, 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 may be found in old-growth forests maintained by frequent fires of moderate severity. Maintaining such open, multiaged old-growth forests could require management through logging, since reintroducing natural fire regimes on an extensive scale is difficult. Restoring old-growth structures would require management scenarios that avoid conventional terminal cuttings, such as variable-retention and group selection schemes that leave a considerable proportion of trees permanently unharvested (Seymour and Hunter 1999, Bergeron et al. 2002, Kuuluvainen 2002).

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Appendix 1

Assume that fires occur randomly with time-homogenous Poisson distribution. The mean fire interval is $1/b$, and the probability density function (p.d.f.) for the length of fire intervals t is e^{-bt} (Van Wagner 1978). Parameter b is approximately the annual probability of burning for a specific site. Fire severity is assumed to be determined so that fires are stand-replacing if time since the previous fire exceeds a threshold value m, and otherwise they are not. Stand age will be defined as the time since last stand-replacing fire.

Assume that a stand-replacing fire occurs at time $t=0$, and denote the probability that the stand survives until year a (i.e. does not burn in a stand-replacing fire before that) by $F(a)$. Obviously, $F(a)=1$ when $a \le m$. The derivative $F'(t)=-f(t)$, where $f(t)$ is the p.d.f. of the random variable giving the time of the next stand-replacing fire. The first stand-replacing fire after $t=0$ occurs at time a if and only if the stand burns at time a, the stand has not burned in the time interval $[a-m, a[$, and the stand has not suffered a stand-replacing fire during the time interval $]0, a-m[$. Since fires occur randomly, these 3 events are mutually independent. The probability that a stand does not burn during a period of m years is e^{-bm}. Combining these facts, we obtain, for $a>m$,

$$F'(a) = -f(a) = -be^{-bm}F(a-m) \quad (1)$$

Integrating Equation 1 we obtain, for $a>m$,

$$F(a) = F(m) + \int_m^a F'(t)dt = 1 - be^{-bm}\int_0^{a-m} F(t)dt \quad (2)$$

The survival function F can now be solved from Equation 2 inductively for any $a>0$. The solution is

$$F(a) = \sum_{i=0}^{[a/m]} \frac{(-1)^i}{i!} b^i e^{-ibm}(a-im)^i \quad (3)$$

where $[a/m]$ means the largest integer less than or equal to a/m.

The survival curve $F(a)$ is by definition normalized so that $F(0)=1$. To obtain the p.d.f. for the equilibrium stand age distribution in the landscape, $F(a)$ must be multiplied by the rate at which stands burn in stand-replacing fires, i.e. be^{-bm}. Thus stand ages are distributed according to the p.d.f. $A(t)=be^{-bm}F(t)$. Now the proportion of forest stands that are more than a years of age is

$$M_{b,m}(a) = 1 - \int_0^a A(t)dt = 1 - be^{-bm}\int_0^a F(t)dt \quad (4)$$

Comparing Equations 2 and 4 we see that, in fact,

$$M_{b,m}(a) = F_{b,m}(a+m) \quad (5)$$

Substituting Equation 3 into Equation 5, we obtain

$$M_{b,m}(a) = \sum_{i=0}^{[a/m]+1} \frac{(-1)^i}{i!} b^i e^{-ibm}(a+m-im)^i \quad (6)$$

Fig. 9 shows $M_{b,m}(150)$, i.e. the proportion of stands that are at least 150 y of age, for different values of mean fire interval $1/b$ and threshold age m. For a given m, $M_{b,m}(a)$ is minimized by maximizing the stand-replacement rate be^{-bm} through setting $b=1/m$, i.e. when the mean fire interval coincides with the threshold age. This can be confirmed by evaluating the derivative

$$\frac{\partial M_{b,m}(a)}{\partial b}.$$

All the calculations could be repeated and solved numerically using a more realistic assumption that the probability of stand replacement is determined as a continuous function of time since the last fire. However, the actual tree cohort age structure would still be ignored, which is one of the reasons that a simulation approach was used in this study.