

Even-Aged and Uneven-Aged Forest Management in Boreal Fennoscandia: A Review

Timo Kuuluvainen, Olli Tahvonen, Tuomas Aakala

Received: 19 October 2011 / Revised: 25 January 2012 / Accepted: 11 April 2012 / Published online: 12 May 2012

Abstract Since WWII, forest management in Fennoscandia has primarily been based on even-aged stand management, clear cut harvesting and thinning from below. As an alternative, uneven-aged management, based on selection cutting of individual trees or small groups of trees, has been proposed. In this review we discuss the theoretical aspects of ecology and economics of the two management approaches. We also review peer-reviewed studies from boreal Fennoscandia, which have aimed at comparing the outcomes of uneven-aged and the conventional even-aged forest management. According to a common view the main obstacle of practicing uneven-aged forestry is its low economic performance. However, the reviewed studies did not offer any straightforward support for this view and several studies have found uneven-aged management to be fully competitive with existing even-aged management. Studies on the ecological aspects indicated that selection cuttings maintain mature or late-successional forest characteristics and species assemblages better than even-aged management, at least at the stand scale and in the short term. We conclude that although the number of relevant studies has increased in recent years, the ecological and economic performance of alternative management methods still remains poorly examined, especially for those stands with multiple tree species and also at wider spatial and temporal scales. For future research we advocate a strategy that fully takes into consideration the interdisciplinary nature of forest management and is better connected to social goals and latest theoretical and methodological developments in ecology and economics.

Keywords Even-aged forestry · Uneven-aged forestry · Biodiversity · Optimal harvesting · Forest economics · Natural disturbance emulation

INTRODUCTION

Since the birth of industrial-scale forestry, timber harvesting throughout the circumboreal forest has been based on clear cutting, which has been seen either as a logistically efficient way to extract pristine timber resources (Canada, Russia) or as a means to organize sustained-yield forestry when most of the original pristine forests are logged (Norway, Sweden, Finland). However, recent policy demands for more sustainable forestry, including its ecological, economic and social goals, have raised questions about the dominant role of clear cutting and resulted in an increased interest in alternative forest management systems (Kohm and Franklin 1997; Bergeron et al. 2002; Gauthier et al. 2009; Puettman et al. 2009). From the management point of view, the question is: What should be the roles and functions of different silvicultural systems in future forestry? Before addressing this question it is useful to take a brief look at how timber harvesting practices have developed in Fennoscandia over time.

The methods and principles of forest harvesting in Fennoscandia have undergone drastic changes during the past century. Initially, timber extraction was based on selective harvesting (Östlund et al. 1997; Siiskonen 2007). This was practical as forests, which mostly had originated from natural processes, were in general plentiful and the demand of timber was primarily for specific domestic purposes, such as construction and fuel. Prior to industrialized forestry some forest uses, especially iron mining, potash and tar extraction, and slash-and-burn cultivation practices were extensive (Heikinheimo 1915; Östlund et al. 1998; Östlund and Roturier 2011). For example, the mining for iron in Mid-Sweden created large clear cuts already in the eighteenth century. From around the mid-nineteenth century, timber was increasingly cut for the booming

sawmill industry, which targeted the largest trees of the best quality (Östlund 1995; Siiskonen 2007). With diminishing numbers of large high quality trees for sawn logs, smaller and smaller trees had to be harvested. Finally, the rise of the pulp industry enabled the large-scale utilization of even smaller diameter trees. All these developments led to high demands for timber and diminishing timber resources in many areas of Fennoscandia (Esseen et al. 1997; Östlund et al. 1997).

As a response, the leading foresters and state authorities expressed their increasing criticism against selective logging practice (Siiskonen 2007). Selective logging was indeed basically resource extraction with little or no consideration of long-term sustainability of the resource base, for regeneration of the forests. In particular, diameter limit cuts were considered to be the main cause of the deteriorated condition and growth of the forests. There were also fears of genetic deterioration of the trees due to the selective harvesting of the best quality trees. This led to the official banning of selective diameter limit cuts, for example in Finland in the late 1940s (Appelroth et al. 1948), and in the state forests in Sweden in 1950. Forestry authorities deemed the practice of diameter limit cuts as an unsustainable way to manage the forests. As a result, the strengthened forestry administration steered a swift transition from selective cutting practice to clear cut harvesting and even-aged management, which incorporated thinning from below. This transition was also partly enabled by the availability of improved machinery and inexpensive fossil fuels (Esseen et al. 1997). The main motivation for the change to even-aged management was to ensure continued and increasing raw material supply for the nationally important forest industries.

This focus on sustained-yield forestry through even-aged forest management also had a strong and far-reaching influence on the development and orientation of forest sciences (Jalonen et al. 2006). A major part of forest research has hitherto focused on issues that are directly related to the implementation and practice of the even-aged management system. In contrast, other management systems have received little or no attention. Moreover, for example, in Finland applying these other practices has been made very difficult or impossible by the forest legislation (Siiskonen 2007). One unfortunate consequence of this narrow policy orientation is an inadequate development of more general theory and knowledge of various silvicultural possibilities (Jalonen et al. 2006). However, this knowledge is indispensable for developing novel forest management scenarios in the rapidly changing ecological and socio-economic environment.

It is evident that past forest harvesting and management practices have mostly been dictated by resource needs and limitations, mediated by technological innovations to intensify forestry. However, the even-aged management

system has been criticized because of its adverse ecological effects (Esseen et al. 1997; Kuuluvainen 2002). Moreover, in a centralized forest policy regime the economic objective of forestry was taken to be the maximum sustainable yield. In addition, the broader environmental values of forests were given little attention. In the global context the importance of tropical areas in pulp and paper industry is growing at the expense of northern areas. In Europe the use of woody biomass for energy is rapidly increasing. The changing operational environment and changes in social values make it essential to re-evaluate silvicultural practices as tools for attaining specific goals set by forest owners and by society.

In the discussion regarding the pros and cons of different silvicultural alternatives the main focus has been in making a comparison between two contrasting approaches: uneven- and even-aged forest management (Fig. 1). Even-aged forest management is characterized by stands with even tree age structures, resulting from forest regeneration through clear cutting usually followed by single species planting and by intermediate thinnings from below. Currently in Fennoscandia this management system is dominant and it is applied with a low number of live retention trees left on the clear cuts (low retention management). The retention of live trees (typically 5–10 trees ha⁻¹) is due to forest certification (PEFC, FSC) standards (Vanha-Majamaa and Jalonen 2001; Gustafsson and Perhans 2010).

In contrast, uneven-aged forest management creates stands with uneven tree age structure (Fig. 1). This age structure is maintained through selection cuttings, in which trees can be removed individually (single tree selection) or as groups (group selection) (e.g., Nyland 2002). Thus, uneven-aged forest management can actually be regarded to consist of a range of methods, in which the forest cover is only partially removed (see Fig. 2). It is noteworthy that in this definition of uneven-aged management the tree age distribution does not necessarily conform to the reverse J-shaped form (all-aged forest) and an uneven-aged forest can also consist of spatially segregated groups of tree age classes (cohorts) created by the group selection method. This broader group of uneven-aged management methods is also sometimes referred to as continuous cover forestry (Pommerening and Murphy 2004).

The main purpose of this study is to review and synthesize research comparing even- and uneven-aged forest management in boreal Fennoscandia. To this end, we first consider the management systems from a theoretical point of view, and then focus on the ecological and economic performance of the two management systems, in addition to a more general evaluation of the studies that have reported these findings. With this approach, we aim to point out gaps in the knowledge and shortcomings of past studies in order to make recommendations regarding future research.

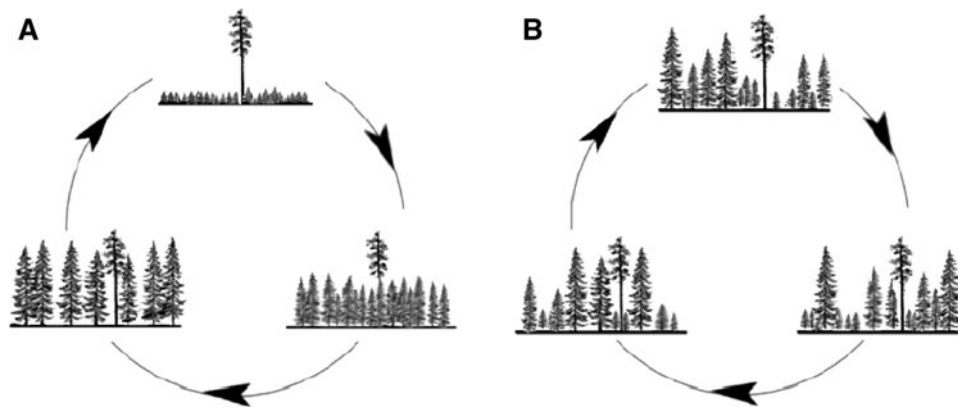


Fig. 1 An illustration of the two forest management systems to be compared in this study: the even-aged (a) and uneven-aged (b) forest management. At stand level, even-aged management comprises a clear and repetitive cycle of distinct phases, including the regeneration, growing, and thinning, and final harvesting where typically a low number of live retention trees are left on the clear cuts. In uneven-aged management the cyclic phases occur at smaller scale and

are thus mixed in space and time at stand level. Here harvesting can be done either by removing individual trees uniformly throughout the stand or in small groups when the created small gaps provide microenvironments suitable for regeneration. Note that irrespective of the management system, permanent retention is a prerequisite if biodiversity conservation is a goal of forest management (Drawing: Tuomas Aakala)

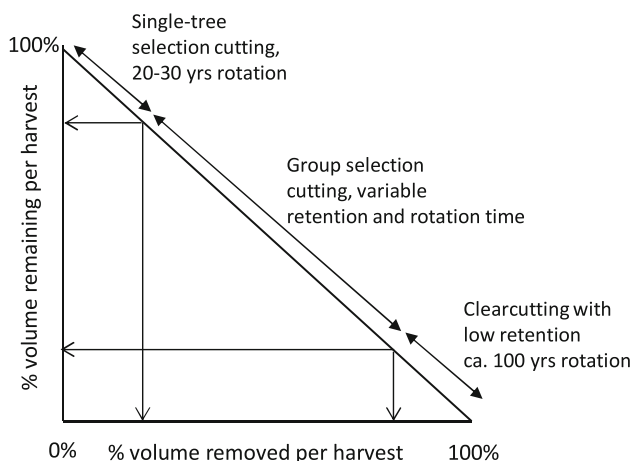


Fig. 2 An illustration of the relationships between different forest management alternatives at stand level in terms of proportion of timber removed and retained at each cutting event. It is noteworthy that the two conventional management systems, the uneven-aged management under single tree selection system and the clear cutting system, represent two extreme cases in the continuum of removed versus retained timber at each cutting event. Between these extremes there exists a wide range of potential stand structures in which the forest cover remains more or less continuous, although sometimes patchy and partly open to facilitate regeneration. These structures can be created by leaving variable retention and can be broadly classified under the concept of uneven-aged or continuous cover forest management. The conventional silviculture thus only utilizes a small part of potential range stand structures to realize different management goals, whether economic, ecological, or social ones (see also Franklin et al. 1997)

SELECTION OF THE REVIEWED STUDIES

We used a systematic approach for the selection of the studies for review (Pullin and Stewart 2006; Pullin et al. 2009). Four databases were interrogated in terms of

targeting the title, abstract, and keywords of the indexed studies: the BIOSIS, CAB Abstracts, CSA Natural Sciences, and the ISI Web of Science. We used a set of predefined search terms (Table 1), which describe the diverse array of terms used for uneven-aged forest management, and the locations (limited to boreal Fennoscandia). The studies were published prior to May 2011. Only peer-reviewed studies were accepted, as a quality control measure.

The resulting studies were screened, based on their title and abstract contents, to exclude the studies that either did not include comparisons between the two management systems, or were outside the region of interest. The following information was extracted from the remaining

Table 1 The used literature search term combinations

Forest zone	Structure/procedure	Location
boreal forest	AND uneven age* uneven size* partial cut* alternative harvest* alternative cut* alternative felling* selection felling* single tree selection selection harvest* gap cut* gap felling* gap harvest*	AND Fennoscand* Finland Finnish Swed* Norw* Murmansk Karelia Leningrad

Within each column all terms are searched with the Boolean operator “OR”

* Wildcard search terms

studies (when applicable): location, type of study (empirical, experimental, simulation, or a review), dominant tree species, site type, spatial scale, temporal scale, connection with natural disturbances, and the percentage of trees removed.

The studies were categorized according to their focus, namely ecological effects, timber production, forest economics, and societal aspects of forest management. In the following, we focus on the ecological effects and forest economics. Timber production was evaluated as a part of the evaluation of the forest economics as it is an implicit part of those assessments. The literature searches revealed that societal aspects of the forest management system were very rarely evaluated, and were thus not considered here. Some of the experimental studies included several cutting intensities. We focused our comparisons on selection cutting and clear cutting, with the former typically the lightest cutting treatment within experimental designs.

The literature searches returned 26 studies that fulfilled our screening criteria. Ecological aspects were treated by 12 studies whereas timber production or economic performance was considered by 14 studies. The number of studies has increased in the recent years. Most of the studies (18) have been conducted since 2000. This reflects the increase in the number of research reports published in general, and also in their better indexing (i.e., the newer the study the more likely it is that it is indexed in literature databases). However, it is most likely to be indicative of an increased interest in the topic.

Most studies have focused on forests dominated by the shade-tolerant Norway spruce *Picea abies* (L.) Karst. This is probably because shade-tolerance has often been considered a pre-requisite for managing forests through selection cuttings (O'Hara 2002). However, it should be noted that such a restriction seems to be unnecessary as unmanaged Scots pine *Pinus sylvestris* L. forests are known to be typically characterized by uneven-aged or cohort age structures (Shorohova et al. 2008; Kuuluvainen and Aakala 2011). Accordingly, Pukkala et al. (2009) developed growth models for uneven-aged Scots pine and birch (*Betula pendula* Roth., *Betula pubescens* Ehrh.) forests in Finland.

ECOLOGICAL EFFECTS AND PERFORMANCE

Theoretical Aspects and Evaluation Criteria

The ecological impacts of tree harvesting in Fennoscandia and elsewhere can most logically be considered within the framework of forest *disturbance ecology* (Sousa 1984; Clark 1989; Attiwill 1994). It is generally acknowledged that tree mortality, viz., disturbance, whether natural or anthropogenic, has a profound impact on a forest ecosystem, its

community structure and processes, and its species richness (Attiwill 1994). The variability in the extent, severity and frequency of disturbances maintain the structural heterogeneity of forests. This heterogeneity creates habitat variability, which is fundamental for species diversity and ecosystem processes (Kuuluvainen 2002). A logical outcome of an increased understanding of the central importance of disturbances in forest ecosystems is the *natural disturbance emulation* (NDE) hypothesis in forest management. This hypothesis states that most components of biodiversity can be protected and ecosystem resilience secured when forest management maintains the key characteristics of natural habitats by imitating the repeatability, severity, and extent of natural disturbance events (e.g., Bergeron et al. 2002; Perera et al. 2004; Drever et al. 2006).

The NDE hypothesis is closely linked with two commonly used and inter-related ecological and management concepts: the *natural range of variability* (NRV, Landres et al. 1999; Keane et al. 2009) and the *coarse and fine filter* metaphor (Hunter et al. 1988). It is assumed that stand and landscape structures can be kept within their NRV by implementing management that emulates natural disturbances. This is essentially the same as realizing the coarse filter principle, i.e., maintaining the essential parts of the structural variability and the processes characteristic to the natural forest at a particular site. This in turn is hypothesized to maintain the associated components of biodiversity. However, this approach will probably not be sufficient for maintaining the most demanding species, and thus it needs to be complemented by the fine filter, e.g., a network of strict forest reserves or restored habitats (Hunter et al. 1988).

With the NDE approach the guiding principle is the creation and retention of natural habitat structures, for which organisms are adapted and which positively influence their long-term survival (Bergeron et al. 2002; Gauthier et al. 2009). Within this framework selection cuttings represent an important silvicultural tool that can be used to imitate natural disturbances, especially in ecosystems where partial or small-scale disturbances are prevalent (Kuuluvainen 1994; McCarthy 2001; Raymond et al. 2009).

This is particularly relevant in boreal Fennoscandia, where natural forest dynamics are suggested to be characterized by partial and small-scale disturbances, whereas stand-replacing disturbances appear to be less common (Gromtsev 2002; Shorohova et al. 2009; Kuuluvainen and Aakala 2011). Thus, selection cuttings under this approach would be justified as a way to mimic the process of tree mortality at the scale of individual or small groups of trees. This would imitate a gap creation and subsequent gap filling processes that occur in response to tree mortality in natural conditions (Kuuluvainen 1994). On the other hand, in the NDE-framework clear cutting would then represent stand-replacing disturbances.

Moreover, other specific ecological hypotheses and theories have been proposed with regard to the effect of spatial and temporal scale of disturbances on species richness. Probably the most relevant of these is the *intermediate disturbance hypothesis* (Connell 1978). This hypothesis states that species richness is maximal under intermediate levels of disturbance. This is based on the assumption that under intermediate disturbances both early- and late-successional species can survive, which will result in high diversity. Here ‘intermediacy’ can refer to frequency, intensity, extent or duration of disturbance and the spatial scale of observation from stand to landscape (Roxburgh et al. 2004; Shea et al. 2004). In general, the intermediate disturbance hypothesis can be interpreted to represent the outcome of a between-patch spatial meta-population process (Wilson 1994).

When considering the intermediate disturbance hypothesis for the comparison of even- and uneven-aged management, the disturbance extent, such as gap size, becomes important. According to the theory, the proportion of shade-intolerant pioneer species can be expected to increase with increasing disturbance (gap) size whereas the proportion of shade-tolerant species decreases (Runkle 1982). With intermediate gap sizes, or over a range of gap sizes, both shade-tolerant and shade-intolerant species are able to co-exist. What IDH basically hypothesizes is that if management based on natural disturbance emulation (NDE) succeeds to maintain the patch dynamics within its natural range of variability (NRV), it will also safeguard native species populations and their dynamics.

Intermediacy can also be considered in terms of the *severity of disturbance*. The severity of disturbance may affect the regeneration mechanisms, such as buried seeds, sprouting or advance regeneration, and thus the community species composition. Thus, the variability of disturbance severities can also dictate species richness (Oliver and Larson 1990). This may be relevant when variable retention is used (Jalonen and Vanha-Majamaa 2001). Furthermore, *disturbance frequency*, or time since a disturbance, can vary but less so in managed forests.

It is evident from the foregoing that the *scale* is crucial when evaluating ecosystem impacts of tree harvesting disturbance. Scale in this context refers to the spatial or temporal dimension of an object or a process (Turner et al. 2001). Forest management takes place and impacts upon forest structure across a range of spatial and temporal scales. Two factors are important to distinguish: the scale of the disturbance per se and the scale of observation at which the outcomes of these disturbances can be detected (Shea et al. 2004). In forest management, the former refers to the size and repetition of harvesting, whereas the latter depends on the intrinsic scale of the object or process of interest. For example, the impact of cutting practices on common sessile plant species may be studied at the stand

scale, whereas the impact on rare mobile animal species requires a larger landscape-scale approach (Wilson 1994). In addition to spatial scales, the temporal scale is highly relevant for ecological processes. In boreal forests, the influence of alterations in the stand and landscape structures occurs over the long term, on temporal scales extending from decades to centuries (Aakala et al. 2009). Consequently, often there is a delay between habitat loss and degradation and its influence on species populations (Hanski 2000). Therefore, the impacts of forest management need to be considered over similar time scales.

We therefore have distinguished a number of crucial questions or criteria, against which to assess the validity of the findings of earlier studies, regarding the comparison of the performance of even- versus uneven-aged management systems or their respective associated silvicultural methods (clear cutting vs selection cutting). For forest ecological considerations the evaluation criteria are as follows: (1) Are the spatial scales of the study relevant for the study questions? (2) Are the temporal scales of the study relevant for the study questions? (3) Have the study and its hypotheses been linked to respective theoretical framework? The relevant spatial and temporal scales are to some extent dependent on the study questions, and were based on our own judgment.

STUDIES ON ECOLOGICAL PERFORMANCE

Forest Structure and Ecological Processes

The question in the ecological studies that needs to be addressed is, whether there are differences between selection cutting and clear cutting in chosen response variable(s), such as species abundance/richness, stand structure, and ecological processes (Table 2). Particular attention should be paid to selection cuttings which can be expected to better maintain forest conditions to resemble those of late-successional forests. Such conditions include the more or less continuous presence of big trees and associated canopy cover, which acts to reduce variations in microclimatic conditions and stand structure, i.e., habitat availability (Atlegrim et al. 1997). In contrast, after clear cutting the changes in microclimatic conditions are expected to lead to a reduction in shade-tolerant late-successional species and increase in pioneer species (Jalonen and Vanha-Majamaa 2001).

Lähde et al. (2002) examined the structural development of stands following thinning from below compared to selection felling. As was to be expected, thinning from below reduced structural diversity compared to selection cuttings that were aimed at creating an uneven-sized structure. In general, the issue of ingrowth has been considered as the most challenging component of uneven-aged

forest management (Smith et al. 1997), and it is also central in retaining structural diversity.

Atlegrim and Sjöberg (2004) measured deadwood volumes near Vilhelmina, Sweden, in selection cut (single tree selection) forest and compared it with a clear cut forest. They concluded that after the cuttings, deadwood volumes were higher in the selection cut forest. However, the study covered a relatively short time period. Thus, the authors cautioned that in a longer time period continued selection harvesting may not solve the problem of declining availability of dead wood in managed forests. Finally, the authors refer to landscape-level forest dynamics and raise the issue that selection cuttings can be used to mimic small-scale gap disturbances and maintain the forest conditions created by such dynamics (Atlegrim and Sjöberg 2004).

Microclimatic differences between the two management systems could be expected to lead to differences in deadwood decomposition rates, given that the decomposition rates measured *in vitro* have shown dependence on the temperature and moisture conditions (Shorohova et al. 2008). However, contrary to these expectations, after measuring stump decay rates for different treatments, Shorohova et al. (2008) concluded that the retention levels in cuttings had no effect on the stump decay rates. They considered the interaction of temperature and moisture as a plausible explanation for this result. They found that while exposure to sunlight following cutting episodes increases, the effects of the subsequent temperature increase are countered by the decrease in substrate moisture (Shorohova et al. 2008).

Plant Species

Only two of the studies selected for this review reported vegetation changes, and both found that, in the short term, the changes in the under-storey species composition (Jalonen and Vanha-Majamaa 2001) and abundance (Atlegrim and Sjöberg 1996a) were smaller in selection versus clear cutting. In their experiment, Atlegrim and Sjöberg (1996a) reported that 4 years after harvesting, selection felling (removing 30% of the number of trees) had a smaller impact on blueberry *Vaccinium myrtillus* abundance compared to clear cuttings. They suggested that selection cuttings and better maintenance of blueberries, a major food source for many herbivores, is beneficial for the maintenance of biodiversity associated with mature forest conditions.

Similarly, Jalonen and Vanha-Majamaa (2001) studied the immediate effects of harvesting on understorey vegetation at stand scale and reported that within a year of cuttings, selection cutting (33% of trees removed) retained late-successional plant species better than clear cutting or clear cutting with retention (93% of trees removed). They concluded that if late-successional plant species are to be maintained at the stand level, treatments must be less

intense than clear or low retention felling (Jalonen and Vanha-Majamaa 2001).

Invertebrates

A majority of the ecological studies (7/12) focused on the effects of cutting events on invertebrate species assemblages (Table 2). It is noteworthy that cutting events can have both a direct influence on the species and an indirect effect through the changes in vegetation.

Matveinen-Huju and Koivula (2008) studied the changes in spider assemblages for different treatments (clear cuts, retention fellings, gap fellings, and thinnings), over 2.5 years in south-central Finland. Their thinning treatment was, in effect, similar to selection cuttings found in most other studies, in that the removal of between 11 and 34% of the trees was done to retain an uneven-sized structure. The thinning treatment led to only minor changes in spider assemblages compared to the uncut control. In contrast, clear cutting and retention felling led to drastic changes, whereas group selection within an uneven-aged management technique led to mixed responses. They concluded that cuttings that aimed at an uneven-aged forest structure, appear to maintain spider assemblages efficiently and similar to that found in the mature forest (Matveinen-Huju and Koivula 2008).

Siira-Pietikäinen et al. (2003) studied the changes in macroarthropods over three years in the same experiment as described by Matveinen-Huju and Koivula (2008). The changes in community structure correlated with harvesting intensity in such a way that macroarthropods were the most affected by clear cutting and the gap cuttings, whereas the selection cuttings had smaller impacts on their populations (Siira-Pietikäinen et al. 2003). Siira-Pietikäinen et al. (2001) studied the short-term response of microbial assemblages and found no changes after selection cuttings, whereas changes were found after gap and clear cuttings. Nevertheless, in their two studies Siira-Pietikäinen et al. (2001, 2003) concluded that both the decomposer and macroarthropod communities were relatively resistant to the environmental changes that resulted from harvesting. Siira-Pietikäinen and Haimi (2009) resampled the soil fauna 10 years after the cuttings in a follow-up of their earlier study and concluded that no changes were observed for the selection cuttings. Moreover, they stated that in the more intensive cutting treatments the fauna had not recovered within the 10-year period.

Koivula (2002) found that cutting treatments, by which 10–30% of trees were removed and which aimed at uneven-aged stands, retained forest-floor carabid assemblages well. In contrast, clear cutting benefitted generalist and open-habitat species, and slightly influenced the forest-species. In a 4-year study Atlegrim et al. (1997) reported no significant effects on carabid assemblages in response to different cutting treatments, except for a higher abundance of open-habitat species

Table 2 Studies comparing the ecological aspects of the two management systems, and their evaluation against the criteria on spatial and temporal scales, and the linkage to a theoretical framework

Study	Theoretical framework	Study type	Temporal scale ^a	Spatial scale	Study focus
Atlegrim et al. (1997)	None	Inventory after harvesting	Short	Stand	Ground beetles
Atlegrim and Sjöberg (2004)	None	Inventory after harvesting	Short	Stand	Deadwood and deciduous trees
Jalonen and Vanha-Majamaa (2001)	None	Inventory before/after harvesting	Short	Stand	Plant species diversity and cover
Matveinen-Huju and Koivula (2008)	Natural disturbance emulation	Inventory before/after harvesting	Short	Stand	Ground-dwelling spiders
Siira-Pietikäinen et al. (2003)	None	Inventory before/after harvesting	Short	Stand	Macroarthropods
Siira-Pietikäinen et al. (2001)	None	Inventory before/after harvesting	Short	Stand	Soil decomposers
Atlegrim and Sjöberg (1996a)	None	Inventory after harvesting	Short	Stand	Blueberry abundance
Atlegrim and Sjöberg (1996b)	None	Inventory after harvesting	Short	Stand	Blueberry-feeding larvae
Koivula (2002)	Natural disturbance emulation	Inventory before/after harvesting	Short	Stand + adjacent habitat matrix	Carabids
Siira-Pietikäinen and Haimi (2009)	None	Re-inventory of earlier harvesting	Medium	Stand	Soil decomposers
Shorohova et al. (2008)	None	Decay modeling	Medium	Stand	Stump decay rates
Lähde et al. (2002)	Natural disturbance emulation	Inventory before/after harvesting	Medium	Stand	Structural diversity

^a Short time-scale: 0–5 years; medium time-scale 5–15 years

in clear cuts compared to the selection treatment. In a review of Finnish case studies Koivula and Niemelä (2002) argued that selection cuttings are beneficial for local (stand level) maintenance of carabid beetle assemblages.

An example of the indirect effects of cuttings on fauna is provided by the study of Atlegrim and Sjöberg (1996b), who reported the relative abundances of blueberry-feeding larvae after selection cutting or clear cutting in the same areas in which they also studied blueberry abundances (Atlegrim and Sjöberg 1996a). Clear cutting inversely affected blueberry and associated larvae, whereas selection cuttings had little effect on blueberry abundance and blueberry-feeding larvae. In the selection felled stands blueberry was patchily distributed, but the abundance of blueberry was high in these patches. Atlegrim and Sjöberg (1996b) also suggested that selection cuttings are potentially beneficial to the vertebrates feeding on the larvae.

Summary of Studies on Ecological Performance

As seen above, hitherto there have been only a handful of rather short-term empirical studies that focus on comparing the ecological performance of even- versus uneven-aged management approaches (Table 2). Three of these studies

considered forest structure and ecological processes, two studies covered plant species and seven studies focused on invertebrates. Overall, the reviewed studies suggest that selection cuttings maintain mature or late-successional forest characteristics and species assemblages better than even-aged stands at least at stand scale and in the short term. A major limitation is that the limited spatial and temporal scales investigated in these studies hamper conclusions related to long-term maintenance of biodiversity. It is also noteworthy that none of the studies made the effort to link the results to some established theoretical framework, such as the intermediate disturbance hypothesis. Some of the studies mention a suggested forest management strategy, the natural disturbance emulation (NDE), but the link between this and the study results was not elaborated further.

VOLUME PRODUCTION AND ECONOMIC OUTPUT

Theoretical Aspects and Evaluation Criteria

Forest management has numerous economic, ecological, social, and cultural consequences, which imply that the

forest management research should be a pluralistic, interdisciplinary investigation. In this review social sciences are represented by natural resource and forest economics which have rather close connections with forest production ecology but not perhaps with forest ecology more broadly defined.

Timber can be produced by using methods that rather poorly mimic the development of natural forests described above (Smith et al. 1997). This leaves many options for the design of the forest management systems that optimally achieve various timber production objectives under the prevailing biotechnical and ecological constraints. A large part of forest science literature is based on the view that the suitable aim in forestry is the Maximum Sustainable Yield (MSY) (Puettmann et al. 2009). The same MSY objective applies to biological population harvesting in general (Begon et al. 2011, p. 450). Given such policy aim, even-aged forest management, artificial regeneration, and thinning from below have been generally accepted as superior forest management methods. For example, in Finland the MSY approach has been considered adequate especially at the national level (Kuusela 1999). In contrast to the MSY policy the objectives of private forest owners have been taken to include short-sighted tendencies. This discrepancy has formed one of the main challenges in forest policy leading to various silvicultural restrictions in forest legislation and to government subsidy programs for promoting forest regeneration and “noncommercial” silvicultural activities. However, such policy appears rather problematic from the economics point of view; instead of MSY the reasonable economic aim in timber production is maximizing economic surplus, i.e., prices, cost and interest rate should be taken into account.

With only a handful of exceptions, forest economic research has concentrated on applying the optimal rotation model which dates back to Faustmann (1849). The generic version of this model is based on assumptions such as the forest owner’s monetary income (or profit) as being the sole aim of forest management, perfect capital markets (unlimited amounts of money can be loaned or borrowed with constant interest rate) and the rotation period as the only variable to be optimized (e.g., thinning is neglected). As special cases the model includes maximizing sustainable yield and maximizing average annual net revenues or “forest rent”.

A major part of forest economic research has produced various theoretical extensions to the generic optimal rotation model, such as adding “non-timber” environmental values, but one subset of multidisciplinary studies has developed ecologically detailed specifications. These specifications include thinning and the initial density of the stand among the management variables. In this approach the stand growth is described by models taken directly from forest production ecology and the results have been utilized in designing practical silvicultural guidelines (Tapio 2006). Typical models have applied statistical–

empirical single tree models (Valsta 1992), but some economic studies have applied detailed process-based models (Niinimäki et al. 2012).

As shown by Haight (1985, 1987) and also by Getz and Haight (1989) the theoretically sound approach for specifying economically optimal uneven-aged forestry requires that the problem is specified as a dynamic optimization model. In these models the objective is to maximize the present value of net revenues over an infinite horizon. The optimized variables are the cutting of trees from each size class in any period. The numerical solution for such a model is more complicated than for the even-aged model. In even-aged management infinite horizon is obtained as a chain of similar finite horizon rotation periods. For uneven-aged management the problem is to apply a time horizon that is long enough (e.g., 200 periods) for finding a solution that converges to a steady state or a stationary cycle. Several studies have tried to circumvent this somewhat demanding optimization problem. Some early strategies were to compute the optimal steady states as static optimization problems (“investment efficient steady states”) or base dynamic solutions on some predefined steady states that were required to be reached within a given time period (“fixed or equilibrium endpoint problems”). In addition, many early simulation studies used the silvicultural q -value principle (Puettmann et al. 2009), the aim of which was to maintain the reverse J-shaped tree size class distribution. All these simplifications yield deviations from the theoretically sound results and may over or underestimate the true economic performance of uneven-aged management.

Most ecological growth and yield models for Norway spruce and Scots pine stands are specified and estimated for the purposes of even-aged management (e.g., Hynynen et al. 2002). Nevertheless, the models may be restrictive even for this purpose because the forest structures represented in the existing empirical data may be too narrowly guided by past forestry practices. An example of this is the question of thinning type; growth models are the most reliable at describing thinning from below because this has been taken to mimic natural mortality in dense stands due to competition. However, there are clear economic reasons to favor thinning from above but it has been a somewhat open question as to whether the available growth models were able to describe stand development after removing the dominant trees. In addition, economic optimization in uneven-aged management requires growth models that are derived for the purposes of uneven-aged management or models that are able to describe forest growth under both management systems. These models may be individual tree models or transition matrix models (Getz and Haight 1989). For Fennoscandian tree species such models are still rare the exceptions being Kolström (1993), Bollandsås et al. (2008), and Pukkala et al. (2009).

A crucial element in uneven-aged growth models is the specification of the natural regeneration process. In the transition matrix and the single tree models natural regeneration is specified as “ingrowth”, i.e., as the number of trees that enter the smallest size class in each period. Another ingrowth model, which originated from Usher (1969), specifies ingrowth as a function of harvested trees and their size. Both of these specifications have been used for Norway spruce stands in addition to an assumption of fixed regeneration per time period.

Detailed even-aged models apply different harvesting cost specifications for thinnings and clear cuts since clear cutting is less expensive per unit of volume. This suggests that uneven-aged solutions should be computed by using a harvesting cost model suitable for this purpose instead of simply applying the same stumpage prices or the same harvesting cost models for both alternative management approaches.

In line with the MSY policy much of the earlier silvicultural literature compares even- and uneven-aged systems in terms of produced timber volume. From the economic point of view these studies do not reveal the true performance of the management methods because volume output is not a reasonable economic objective either at national or at forest owner level and because harvesting is specified by applying ad hoc rules without any optimization. A theoretically sound setup defines some initial stand state and computes the optimal uneven-aged management solution that converges to some steady state (or stationary cycle) or switches to even-aged management (Getz and Haight 1989, Haight and Monserud 1990). This requires that the ecological growth model is general enough to describe both management alternatives accurately. Another approach is to take the optimal even-aged management solution and the related bare land value from studies specialized for even-aged management.

We specify five different criteria that can be used to evaluate the economic studies on the relative economic performance of even- and uneven-aged management. These criteria are: (1) Is the optimization framework theoretically correct? (2) Does the investigation include detailed harvesting cost submodels? (3) Is the analysis based on valid growth models? (4) What kind of ingrowth (regeneration) model was applied? (5) What is the origin of bare land value used in computing the even-aged management alternative?

STUDIES ON VOLUME PRODUCTION AND ECONOMIC PERFORMANCE

Volume Production

Several studies focused on comparing the potentials of the two management systems for timber volume production

(Table 3). The results obtained were mixed. Mikola (1984) reviewed older selection cutting experiments in Norway spruce forests in southern Finland, in which the volume growth during a 25-year period in two experiments were 3.1 and 3.9 m³ a⁻¹ ha⁻¹. He concluded based on growth and yield tables that this level of growth is approximately half of what could be expected from an even-aged forest at a similar site and location. On the other hand, Lähde et al. (1994) analyzed National Forest Inventory data collected in the 1951–1953 period, and concluded that although the density of all-sized (assumed uneven-aged) stands was much higher, the average volume growths did not differ between even- and all-sized plots. It should be emphasized that the management system of the stands was not known, and the all-sized structure of the stands may have developed naturally as much as due to any management actions. When comparing stands with the same volume, growth was estimated to be higher in all-sized stands. Lähde et al. (2002) made comparisons for an 11-year period, for which it was found that timber production in Norway spruce forests was higher after selection cuttings (5.4 m³ a⁻¹ ha⁻¹) compared to thinning from below (4.6 m³ a⁻¹ ha⁻¹). In a recent study, Lähde et al. (2010) reported 48% higher diameter increment in uneven-sized Norway spruce forests compared to even-sized forests during a 15-year period. The uneven-sized forest was treated with selection cuttings and the even-sized forest with thinning from below.

Studies that use growth and yield models presented a somewhat more uniform picture on volume production. Pukkala and Kolström (1988) used a transition matrix model to compare volume production between even- and uneven-aged forest management. Transition matrix models have been widely used for studying uneven-aged management in the United States and elsewhere (Liang et al. 2005). According to the specification given by Pukkala and Kolström (1988), ingrowth depends on the gaps left by harvested trees (cf. Usher 1969). These authors used simulations in which a fixed fraction of trees were removed from each size class. They concluded that uneven-aged management is capable of producing 5 m³ a⁻¹ ha⁻¹, which they presumed to be inferior to that of even-aged management (7.8 m³ a⁻¹ ha⁻¹). Later Kolström (1993) applied a similar model and approach with new empirical data and computed that an uneven-aged Norway spruce stand may produce up to 8 m³ a⁻¹ ha⁻¹ on medium to high fertility sites with a temperature sum of 1200 degree days (d.d., defined as the annual sum of the daily average temperatures over the 5 °C threshold value). Pukkala et al. (2009) developed growth models for uneven-aged stands. The harvesting strategy is based on simple rules of thumb and the models for uneven stands predicted volume growth that was 0.5 m³ a⁻¹ ha⁻¹ less than that of even-aged forest management in southern and central Finland. In addition to these studies volume production

Table 3 Some main properties of studies comparing the economic or timber production performance between even- and uneven-aged management

Study	Optimization framework	Harvesting cost specification	Growth model	Ingrowth model	Source of BLV	Volume output ^c	Economic output ^c
Mikola (1984) ^a	None	None	Case data	None	None	EA > UEA	–
Pukkala and Kolström (1988) ^a	None	None	Transition matrix	Usher-type	None	EA > UEA	–
Kolström (1993) ^a	None	None	Transition matrix	Usher -type	None	–	–
Lähde et al. (1994) ^a	None	None	Inventory data	None	None	EA < UEA	–
Wikström (2000)	Several	None	Single tree	Fixed ingrowth	Same framework	EA > UEA	EA > UEA
Andreassen and Øyen (2002)	None	Empirical experiment	Case data/ even-aged model	Case data	External source	EA > UEA	EA > UEA
Lähde et al. (2002) ^a	None	None	Case data	None	None	EA < UEA	–
Gobakken et al. (2008)	None	Same for both alternatives	Single tree	Various explanatory variables ^b	Same framework	EA < UEA	Depends on initial stand state
Lexerød and Gobakken (2008)	None	Same for both alternatives	Single tree	Various explanatory variables ^b	Same framework	EA < UEA	Depends on initial state and discounting
Tahvonen (2009)	General dynamic	None	Transition matrix	Usher -type	Same framework	–	EA < UEA
Pukkala et al. (2009) ^a	None	None	Single tree	Function of density	None	EA > UEA	–
Pukkala et al. (2010)	Static	None	Single tree	Function of density	External source	–	Depends on site fertility and discounting
Tahvonen et al. (2010)	General dynamic	Separate for even and uneven	Transition matrix	Function of density	Same framework, external sources	EA > UEA	EA < UEA
Lähde et al. (2010) ^a	None	None	Case data	None	None	EA < UEA	–

^a Compares volume yield scenarios only

^b Altitude, latitude, site index, age class, number of trees, dominant species

^c EA refers to even-aged management and UEA to uneven-aged management

results have been reported as secondary output in economic studies which are reviewed next.

Economic Performance

Wikström (2000) used a single tree growth model constructed using data obtained from six separate studies. The model simulates the number of trees and their diameter development but takes tree height as a function of the diameter. The model is suitable for zones in which the temperature sum is between 1100 and 1200 d.d. Furthermore, Wikström referred to an earlier study by Kolström (1993) and specified regeneration to be independent of stand density and sets ingrowth for every 5 years to be

equal to 50 trees ha⁻¹ with an average diameter of 5 cm. Harvesting cost was assumed to be independent of the management method. The uneven-aged solutions were restricted to keep the stocking level above 150 m³ ha⁻¹. The study applied various optimization approaches and the interest rate was set to 3%.

Wikström (2000) specified three initial stands. Two of the stands were outcomes from even-aged management and the third stand represented a reverse J-shaped diameter distribution. The study compared the economic performance of even-aged management to an approximate infinite horizon dynamic problem and to an equilibrium endpoint and fixed endpoint problems. The approximation was based on 41 5-year periods and the fixed endpoint

solution specified the endpoint (or target) stand structure with a reverse J-shaped diameter distribution. The infinite time approximation yielded 88–96% of the present value net revenues of the even-aged solution, whereas the equilibrium endpoint yielded 78–96% and the fixed endpoint formulation was 70–96%. Even-aged solution yielded an average volume output of $6.3\text{ m}^3\text{ a}^{-1}\text{ ha}^{-1}$ whereas the uneven-aged solution yielded $3.2\text{ m}^3\text{ a}^{-1}\text{ ha}^{-1}$. Basal area varied between 22 and $15\text{ m}^2\text{ ha}^{-1}$ and trees were cut when they reached the 19–25 cm diameter class.

Andreassen and Øyen (2002) performed an empirical experiment for comparing clear cutting, tree selection, and group selection in six initially mature Norway spruce stands. Data for the initial cuttings were obtained from the experiments and the future harvests were computed by a simulator originally designed for even-aged stands. The authors simply assumed that selection forests would yield 85% of volume increment of the even-aged management. Selection cuttings were designed subjectively in order to maintain irregular stand structure and they removed about 30–40% of stand basal area after each sequential 20-year periods. The experimental cuttings indicated that selection harvesting increased the harvesting cost by about 10% compared to clear cutting. Given an interest rate equal to 2%, the selection system was found to yield about 15% lower net present value (NPV) benefits compared to even-aged management. Using a 3% interest rate the difference was 25% in favor of the even-aged stands.

Gobakken et al. (2008) developed an individual tree forest simulator and used it to study both even- and uneven-aged management. The simulator included mortality and growth models but the tree height was given as a function of age and site index. Data source was the permanent plots of the Norwegian Forest Inventory system. The study specified six initial stands; four of them were uneven-sized stands with varying q -ratios, one stand had a uniform diameter distribution and one a normal diameter distribution. The simulator did not include any optimization as such; instead the solutions were chosen from some predefined set of management alternatives. Harvesting costs were independent of management method and the interest rate was set at 3%. Under the uneven-aged management there was a cutting every 30 years which removed all trees with diameter equal to or above 30 cm.

According to the results (Gobakken et al. 2008) the selection cutting method was superior when the initial stand had an uneven-aged structure whereas even-aged management dominated when the initial tree distribution was uniform or normal. Results were similar both for Norway spruce and Scots pine. Surprisingly, uneven-aged management yielded higher volumes than the even-aged solutions based on uniform or normal initial tree distributions (ibid.).

A study by Lexerød and Gobakken (2008) used the same simulator which was further developed but it was still based on somewhat artificial silvicultural actions (for example, the thinning algorithm removed trees randomly). The initial stand age in their simulations varied between 64 and 189 years, the initial volume between 84 and $335\text{ m}^3\text{ ha}^{-1}$, and the basal area between 16 and $40\text{ m}^2\text{ ha}^{-1}$. According to the results selection cutting yielded higher present value revenues with low interest rates (1–2%) whereas even-aged management became superior with higher interest rates. For Norway spruce uneven-aged stand management yielded higher volumes, whereas for Scots pine the results were slightly the reverse.

Tahvonen (2007, 2009) used the growth model of Kolström (1993) for dynamic economic optimization for maximizing present value stumpage revenues over infinite horizon (3% interest rate, harvest every 5 years). The optimal steady state volume output became $7\text{ m}^3\text{ a}^{-1}\text{ ha}^{-1}$, the diameter of harvested trees was 26 cm and the after harvest basal area was $17\text{ m}^2\text{ ha}^{-1}$. In a stylized comparison (e.g., assuming zero regeneration cost) the economic outcome from uneven-aged management was found to be clearly higher than that of even-aged management. It is important to recognize that the regeneration specification by Kolström (1993) yielded an excessive number of seedlings, and it became optimal to thin the smallest size class rather heavily. However, the superiority of uneven-aged management remained until the ingrowth was decreased to as low as 8% of the original ingrowth level given in Kolström (1993).

Pukkala et al. (2010) utilized the growth data from Pukkala et al. (2009) with the aim of solving optimal steady state stand structures to develop management instructions for Norway spruce and Scots pine stands. Pukkala et al. (2010) based their economic model on the ideas by Duerr and Bond (1952), Chang (1981), and Bare and Opalach (1987). This led them to solve for the post-thinning steady state stand structures that maximize NPV defined as:

$$\text{NPV} = \frac{\text{NR}_T}{(1+r)^T - 1} - (\text{NR}_{\text{cc}} - \text{NR}_{\text{pc}}), \quad (1)$$

where NR_T is the roadside revenues net of harvesting costs (or stumpage revenues) obtained every T periods, the term $(1+r)^T - 1$ reflects the infinite time horizon (r is the rate of interest), NR_{cc} is the net revenues if the steady state stand is clear cut, and NR_{pc} is the net revenues if the stand is cut to the state that enables to continue the steady state uneven-aged cuttings. The interpretation of this investment efficient steady state by Getz and Haight (1989, pp. 269–272) and Pukkala et al. (2010) and others, is that $\text{NR}_{\text{cc}} - \text{NR}_{\text{pc}}$ is considered to be an opportunity cost or investment cost to stocking needed for uneven-aged forestry. The

maximization of Eq. (1) requires solving for the number of trees and their diameters over the cycle periods taking the stand growth model as a constraint. To simplify this problem Pukkala et al. (2010) followed Bare and Opalach (1987) and assumed that the post-harvesting stand structure could be represented by a Weibull distribution function. The problem could then be computed by taking the parameters of the Weibull function as the variables to be optimized instead of the number of trees directly.

Their method yielded a reverse J-shaped post-thinning stand structure with the property that trees larger than 18–20 cm are cut. Typically, the removal consists of about 50 % of pulpwood. In comparing even- and uneven-aged management the latter turned out to be superior both for Scots pine and Norway spruce. The only exception was in the case of Norway spruce growing on mesic *Myrtillus* site type with 1300 d.d. temperature sum and with 1 % interest rate, which showed that an even-aged management yielded slightly higher profitability.

The study by Tahvonen et al. (2010) used a nonlinear transition matrix model for studying uneven-aged management of Norway spruce. The ecological model was estimated for sites with rather high fertility, i.e., between *Oxalis-Myrtillus* and *Myrtillus* site types, and a temperature sum of 1200 d.d. Harvesting costs were specified separately for even- and uneven-aged management, the latter being 15 % higher per m³ when the harvested trees were similar (Surakka and Siren 2004). The solutions were computed applying the dynamic optimization approach. When the aim was volume maximization, even-aged management with artificial regeneration and thinning from above produced higher volume than uneven-aged management. However, when comparing the economic superiority of forest management forms, it was found that uneven-aged management was superior to even-aged management, although at low interest rates the differences became small.

Summary of Studies on Volume Production and Economic Performance

The number of reviewed volume production and economic studies is 14. Of these five studies analyze field experiments or inventory data whereas nine are based on empirically estimated growth models that are integrated with economic factors (Table 3). Six studies reported that volume production was higher in even-aged management compared to uneven-aged management whereas five studies obtained the converse result. Economic performance was compared in seven studies. In two studies even-aged management was found to be superior, in another two the result was the converse and in the remaining three studies it depended on thermal zone and variables such as the interest

rate and the stand initial state. The differences between the study results can be understood to follow from the differences in the economic setup and growth models. Four studies used some economic optimization approach (two include restrictive features) whereas in others the uneven-aged management is defined by applying ad hoc principles. In general, economic studies suffer from the limiting availability of growth models suitable for uneven-aged management.

DISCUSSION

Ecology

The concept of ecosystem-based forest management incorporates the idea that when extracting timber resources, the natural structures, processes and species assemblages of ecosystems, and hence the ecosystem services they provide, are simultaneously safeguarded (Gauthier et al. 2009). Improved understanding of the intrinsic features of forest structure and dynamics, and comparisons with those of managed forests, have provided the impetus for critical re-evaluations of forest management strategies for all of the circumboreal forest (Esseen et al. 1997; Bergeron et al. 2002; Puettmann et al. 2009; Cyr et al. 2009; Kuuluvainen 2009; Shorohova et al. 2009). The traditional view was that stand-replacing disturbances (mainly fire) and the resulting even-aged stand dynamics are dominant natural phenomena for all of the circumboreal forest. In such a case, clear cutting would essentially emulate natural forest dynamics. However, this view has been abandoned now and the unveiling picture of disturbance and ecosystem dynamics of the natural boreal forest reveals much more diversity than the traditional view (Gauthier et al. 2009; Shorohova et al. 2008; Kneeshaw et al. 2011; Kuuluvainen and Aakala 2011).

The accumulating evidence points in the direction that under Fennoscandian conditions the natural forest is characterized by highly heterogeneous stands and landscape structures and dynamics, which are mainly driven by a variety of non-stand-replacing disturbances (Kuuluvainen 2009). Partial disturbances, i.e., cohort and gap dynamics due to wind, insects, pathogens and factors that are endogenous to trees, appear to be prevalent and these help maintain the forest on a more or less continuously covered basis (Kuuluvainen and Aakala 2011). Such structures and habitats of the natural Fennoscandian forest strongly differ from those created by the current clear cutting practice (Esseen et al. 1997, Östlund et al. 1997, Kuuluvainen 2009). From the disturbance ecology point of view what has taken place since WWII is that forest management has implemented a disturbance regime that is divergent from

what the ecosystem has encountered before under ‘natural’ or historic conditions and hence could not have adapted to. The mismatch between the spatio-temporal scales of natural versus human-induced disturbances in Fennoscandia has had and obviously continues to have serious ecological consequences, including continuous decline of biodiversity (Hanski 2000; Auvinen et al. 2007; Raunio et al. 2008; Rassi et al. 2010).

It is evident that many ecologically detrimental changes in habitat conditions, such as a decline in dead wood, are related to the amount of timber extraction per se. However, adverse changes are probably also associated with *how* the timber extraction is done, i.e., what is the management system implemented (Fig. 1; Kuuluvainen 2002, Bergeron et al. 2002). A crucial question is: Can uneven-aged management provide an alternative that would allow a better emulation of the dynamics and habitats that naturally occur? The ecological results of the reviewed studies contain a weak positive signal regarding the possibility of maintaining habitat conditions and species populations associated with gap-phase dynamic late successional forests in versatile selection cuttings. Importantly, this is also in accordance with predictions based on the intermediate disturbance hypothesis. This would suggest that changing the spatial scales and temporal dynamics of timber harvesting to resemble those created by natural disturbances factors could be a way to better sustain ecological values (Gauthier et al. 2009).

However, the information from studies that address ecological questions is fragmentary both geographically, and in terms of study focus: in particular some species or species groups are considered, whereas others are not. Results from long-term and large-scale experiments are also missing. It is therefore not yet possible to properly evaluate the differences between the two management systems in this respect. For instance, the finding that thinning from below reduced structural diversity more than selection felling in short-term experiments (Lähde et al. 2002), is prone to uncertainty in its longer-term effects, because of the critical role of ingrowth of younger and smaller trees in maintaining the desired structural diversity. Even so, the reviewed experimental studies are an important first step, and with time these and other studies will yield more and more valuable results, as exemplified by the case of the re-inventory study by Siira-Pietikäinen and Haimi (2009) of the experimental cuttings first inventoried by Siira-Pietikäinen et al. (2003).

It needs to be stressed that the uneven-aged management cannot be considered as the sole solution to ecosystem-based management and biodiversity protection, because the natural disturbance dynamics under Fennoscandian conditions is known to be highly variable (Kuuluvainen and Aakala 2011). It should also be borne in mind that uneven-aged

management as such does not solve the problems of deadwood-dependent species, and a proper tree retention management plan is necessary to ensure the availability of these habitats. However, uneven-aged forests have the advantage over their even-aged counterparts in that larger diameter deadwood can be created continuously. Such an advantage is not possible over a long time period after clear cutting, unless retention trees are left. It seems that uneven-aged management can be used in natural disturbance emulation (NDE) and it can be an important component of a coarse filter management strategy for biodiversity maintenance (Gauthier et al. 2009). However, it is not a substitution for an adequate forest reserve network, which would be the fine filter, necessary for the maintenance of species which are most sensitive to alterations in their habitats conditions.

The large spatial and long temporal scales of involved ecological phenomena make research on this topic very demanding, especially as related to questions of biodiversity. The problems associated with the short time scales were usually mentioned in the reviewed ecological studies. The short time scales in experimental studies are understandable, given that the interest in alternative forest management strategies has increased only quite recently. However, it is evident that forest dynamics operate on time scales of decades or even centuries, and phenomena such as species diversity also depend on landscape-level habitat mosaics. The potentially long time lags in ecological responses were illustrated by the study of Sippola et al. (2001), in which stand structure and species diversity in forests logged selectively 50–100 years ago had still not recovered in comparison to those found in unmanaged forests. However, in some other studies an opposite result was obtained (Lilja and Kuuluvainen 2005; Lommi et al. 2009).

Conducting experiments on large scales is expensive and time-consuming (Peterson and Anderson 2009). It was therefore not surprising that the ecological studies that relied on experiments were conducted on a stand scale. This experimental strategy may be sufficient for addressing the differences between the two management regimes for some of the study questions, such as the effects on blueberry abundance (Atlegrim and Sjöberg 1996a), soil fauna (Siira-Pietikäinen and Haimi 2009), stand structure (Lähde et al. 2002), or stump decay rates (Shorohova et al. 2008) that are not strongly influenced by landscape-scale interactions. However, it is clear that for most study questions the quality of the surrounding landscape is important, e.g., for species dispersal and movement (Wintle et al. 2005). The study by Koivula (2002) was the only investigation that explicitly considered the quality of the adjacent stands.

Because it is impractical, expensive, or even impossible to perform many large-scale experiments, a feasible approach is to tackle the large spatial and long temporal scales involved by the use of simulation models to

complement experimental studies. Such simulations would also help in designing empirical studies. For example, it has been shown that models for forested landscapes can be coupled with species metapopulation models (i.e., habitats and species), and the effects of different forest management alternatives simulated (Wintle et al. 2005). Such simulations could also be used to formulate testable hypotheses when designing for experimental studies. Studying the effects of uneven-aged management for larger, more mobile species for which stand scale manipulations bear little significance, could also be enhanced by simulations. Similarly, a more systematic approach for studying species or species group responses would be needed, or at least substituted by indicator species, to assess the utility of NDE approach in effectively maintaining species diversity.

The reviewed ecological studies on selection cuttings and uneven-aged forest management also suffer from the lack of multi-disciplinary approaches and links to a more general theoretical basis. For example, in those studies that address the ecological aspects of forest management probably the most relevant theoretical framework, the intermediate disturbance hypothesis, was not even mentioned. In addition, the integration of these studies to a more holistic forest management strategy, such as that provided by the natural disturbance emulation (NDE) (Attwill 1994, Bergeron et al. 2002) has been poor, although three of the studies loosely connected the use of selection cuttings to the idea of NDE. Somewhat similar problems can be found in forest economic studies which are considered next.

Timber Production and Economy

The major drawback in the studies that analyzed timber production volumes is that they do not apply any common systematic setup in making this comparison. Two of the studies (Lähde et al. 1994, Lähde et al. 2002), in which volume production was found to be higher in uneven-aged management, were experimental studies with very short time intervals (11 and 15 years) and they actually compare thinning from above to thinning from below. As such the result that thinning from above may yield higher volume yield compared to thinning from below is not surprising in the light of studies on even-aged-management (Vuokila 1970; Valsta 1992; Niinimäki et al. 2012). However, the crucial question is whether this result carries over to the long-term for uneven-aged management solutions based on natural regeneration.

The remaining studies on higher volume production in uneven-aged management (Gobakken et al. 2008; Lexerød and Gobakken 2008) did not interpret their results, but Gobakken et al. (2008) gave the impression that their results may be the outcome of the initial stand state.

In studies that compared the economic performance only Wikström (2000), Tahvonen (2009), and Tahvonen et al. (2010) applied a similar optimization procedure. The fact that their results did not coincide may be due to the after harvest stocking constraint ($>150\text{ m}^3\text{ ha}^{-1}$) used in Wikström (2000). The author did not justify the constraint but it may have originated from the Swedish forest legislation. In the study by Tahvonen et al. (2010) the optimal stand volume after harvest was about $40\text{ m}^3\text{ ha}^{-1}$ and was even lower with a positive interest rate. The low density was a consequence of the sensitivity of natural regeneration to the basal area level and adding the restriction used by Wikström (2000) would clearly decrease the economic output. Moreover, in Wikström's (2000) study the high stocking did not create problems in regeneration because regeneration was fixed at 50 new seedlings per 5 years per ha. In the study by Tahvonen (2007, 2009) regeneration was based on the specification made by Kolström (1993). This was independent of density and it produced high regeneration and lead to high economic performance. We note that the level of natural regeneration in the study by Kolström (1993, see also Pukkala and Kolström 1988), is much higher than in any other growth model.

The studies of Lexerød and Gobakken (2008) and Andreassen and Øyen (2002) produced results suggesting that the relative performance of uneven-aged management decreases with discount rate, whereas Tahvonen et al. (2010) and Pukkala et al. (2010) reported the opposite result. In Andreassen and Øyen (2002) the initial states represented mature stands and in even-aged management there was an immediate clear cut, whereas in uneven-aged management (ad hoc) harvesting removed a rather moderate fraction of trees every 30 years or so. Under this setup it is to be expected that the relative performance of uneven-aged management would decrease with interest rate. Those authors pointed out that their results were influenced by the initial stand states that favoured immediate clear cutting, especially with higher interest rates. Tahvonen et al. (2010) found that, it may be optimal to clear cut an initially mature stand once and start the transition of the stand toward uneven-aged management later. Even in this case a higher discount rate works against the clear cutting solution. The interpretation of their results is that clear cutting is followed by regeneration investment and the investment cost increases with interest rate, which imply lower competitiveness against free (but scanty) natural regeneration.

The investment efficient steady state that was used in Pukkala et al. (2010) study had been previously analyzed by Getz and Haight (1989, pp. 269–272) and Tahvonen and Viitala (2006) where it was shown to lack a sound theoretical basis. A major problem was the ad hoc economic valuation of forest stands. As a consequence both the steady state stand structure and the economic profitability

of the uneven-aged management were found to deviate from their theoretically correct solutions. The deviation may be significant (Tahvonen and Viitala 2006). The other question is how does the optimization of the Weibull function parameters affect the optimal solution? A priori it can be expected that it decreases the profitability results for uneven-aged management since it brings additional restrictions to the optimization.

A problem in many economic studies is the lack of theoretical specification behind the computations or the heterogeneity of the theoretical specifications applied. This problem reflects the fact that applying the correct economic approach of solving a nonlinear, nonconvex infinite horizon optimization problem is computationally demanding. The other main problem is the low number of ecological models that describe the growth of heterogeneous uneven-aged stands. The existing growth models have some weaknesses like the ingrowth specification that gives the number of trees that enter to the smallest size class. These specifications include density dependence but implicitly assume the existence of some stock of seedlings independently of stand history. From the economic point of view the growth models should include the most important tree species simultaneously and they should be general enough to allow the analysis of both even- and uneven-aged management. In addition, knowledge on many practical details such as damages on sapling in selection harvesting is poor or even nonexistent.

A major part of forest economics does not recognize that even-aged management is only one of a number of possible forest management systems (see Fig. 2). Models of uneven-aged management can be regarded as special cases of age and size structured models in the general context of managing biologically regenerating natural resources (Getz and Haight 1989). Studies on uneven-aged management should apply sufficiently general optimization methods. The erroneous belief that the reasonable economic aim in forestry is maximum sustainable yield has influenced model development in forest production ecology. This has led to development of ecological growth models that are excellent in describing forest management based on clear cutting and artificial regeneration and thinnings from below, but which may perform less reliably if thinning is made from above, for example. From the economic point of view it is essential to keep these types of management choices a priori open and subject to analysis by optimization models. Fruitful interdisciplinary research in forestry requires that these two sciences complement and integrate with each other.

In silviculture the classic selection harvesting system suggests removing trees from all size classes (e.g., Smith et al. 1997, Nyland 2002). This is closely related to the goal of maintaining a balanced uneven-aged structure depicted

by the reverse J-shaped tree size distribution. However, these traditional views are problematic in the light of economic studies and are questioned in a recent study by Tahvonen (2011). Given the Fennoscandian conditions the critical factor is the low level of natural regeneration. Thus, it is normally not optimal to harvest small size classes; instead removal is targeted toward trees with lower relative value growth and stronger density effects. Simultaneously the stand density is kept at a level where natural mortality is low and regeneration is maintained.

There was a clear difference in the implementation between ecological and economic studies. All but one ecological study relied on experimental set-ups, whereas most economic studies used simulation approaches and models. As a result, there was a major difference in the time scales involved in the assessments. The ecological studies considered only short time periods that ranged from immediate post-treatment effects up to 10 years, whereas the economic models applied an infinite time horizon. On the other hand, economic models seldom included spatial dimension.

CONCLUSIONS

According to a widely held view the main obstacle of applying uneven-aged forestry is its poor economic performance. However, the existing studies do not offer any straightforward support for this view and indeed several studies have found uneven-aged management to be fully competitive with existing even-aged management systems. The reviewed ecological studies suggest that selection cuttings maintain late-successional forest characteristics and species assemblages better than even-aged stands at least at the stand scale and in the short term. These results give some promise for using uneven-aged management as a component of a forest management strategy that adequately serves both economic and ecological goals. However, it is amply clear that more studies are needed.

We conclude that there remain considerable gaps in our knowledge regarding the ecological and economic outcomes and applicability of the two forest management alternatives in Fennoscandian conditions. In the future, studies would greatly benefit from multidisciplinary research settings and from linking the studies better to theory. Moreover, the connection between empirical and modeling work should be strengthened.

Acknowledgments We thank Ruut Rabinowitsch-Jokinen for help in data analysis and two anonymous reviewers who commented on an earlier version of the manuscript. The research was partly funded by the Ministry of Agriculture and Forestry as part of the Forest Finnish Biodiversity Programme (METSO). Olli Tahvonen is grateful to the Maj and Tor Nessling foundation and Academy of Finland for financial support.

REFERENCES

- Aakala, T., T. Kuuluvainen, T. Wallenius, and H. Kauhanen. 2009. Contrasting patterns of tree mortality in late-successional *Picea abies* stands in two areas of northern Fennoscandia. *Journal of Vegetation Science* 20: 1016–1026.
- Andreassen, K., and B.-H. Øyen. 2002. Economic consequences of three silvicultural methods in uneven-aged mature coastal spruce forests of central Norway. *Forestry* 75: 483–488.
- Appelroth, E., O. Heikinheimo, E.K. Kalela, E. Laitakari, J. Lindfors, and R. Sarvas. 1948. Julkilausuma. *Metsätaloudellinen Aikakauslehti* 65: 315–316 (in Finnish).
- Atlegrim, O., and K. Sjöberg. 1996a. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management* 86: 39–50.
- Atlegrim, O., and K. Sjöberg. 1996b. Effects of clear-cutting and single-tree selection harvests on herbivorous insect larvae feeding on bilberry (*Vaccinium myrtillus*) in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management* 87: 139–148.
- Atlegrim, O., and K. Sjöberg. 2004. Selective felling as a potential tool for maintaining biodiversity in managed forests. *Biodiversity and Conservation* 13: 1123–1133.
- Atlegrim, O., K. Sjöberg, and J.P. Ball. 1997. Forestry effects on a boreal ground beetle community in spring: Selective logging and clear-cutting compared. *Entomologica Fennica* 8: 19–26.
- Attiwill, P.M. 1994. The disturbance of forest ecosystems—the ecological basis for conservative management. *Forest Ecology and Management* 63: 247–300.
- Auvinen, A.-P., M. Hildén, H. Toivonen, E. Primmer, J. Niemelä, K. Aapala, S. Bäck, P. Härmä, et al. 2007. Evaluation of the Finnish National Biodiversity Action Plan 1997–2005. *Monographs of the Boreal Environment Research* 29: 1–55.
- Bare, B.B., and D. Opalach. 1987. Optimizing species composition in uneven-aged forest stands. *Forest Science* 33: 958–970.
- Begon, M., C.R. Townsend, and J.L. Harper. 2011. *Ecology: From individuals to ecosystems*. Oxford: Blackwell.
- Bergeron, Y., A. Leduc, B.D. Harvey, and S. Gauthier. 2002. Natural fire regime: A guide for sustainable forest management of the Canadian boreal forest. *Silva Fennica* 36: 81–95.
- Bollandsås, O.-M., J. Buongiorno, and T. Gobakken. 2008. Predicting the growth of stands of trees of mixed species and size: A matrix model for Norway. *Scandinavian Journal of Forest Research* 23: 167–178.
- Chang, S.J. 1981. Determination of the optimal growing stock and cutting cycle for an uneven-aged stand. *Forest Science* 27: 739–744.
- Clark, J.S. 1989. Ecological disturbance as a renewal process: Theory and application to fire history. *Oikos* 56: 17–30.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillet. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* 10: 519–524.
- Drever, C.R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? *Canadian Journal of Forest Research* 36: 2285–2299.
- Duerr, W.A., and W.E. Bond. 1952. Optimum stocking of a selection forest. *Journal of Forestry* 50: 12–16.
- Esseen, P.-A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal forests. *Ecological Bulletins* 46: 16–47.
- Faustmann, M. 1849. Berechnung des Wertes welchen Waldboden sowie noch nicht haubare Holzbestände für die Waldwirtschaft besitzen. *Allgemeine Forst- und Jagdzaitung* 15: 441–455.
- Franklin, J.F., D.E. Berg, D.A. Thornburgh, and J.C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: Variable retention on harvest systems. In *Creating a forestry for the twenty-first century: The science of ecosystem management*, ed. K.A. Kohm, and J.F. Franklin, 111–139. Washington, DC: Island Press.
- Gauthier, S., M.-A. Vaillancourt, A. Leduc, L. DeGardpre, D. Kneeshaw, H. Morin, P. Drapeau, and Y. Bergeron. 2009. *Ecosystem management in the boreal forest*. Québec: Les Presses de l'Université du Québec.
- Getz, W.M., and R.G. Haight. 1989. *Population harvesting: Demographic models for fish, forest and animal resources*. Princeton, NJ: Princeton University Press.
- Gobakken, T., N.L. Lexerod, and T. Eid. 2008. A forest simulator for bioeconomic analysis based on models for individual trees. *Scandinavian Journal of Forest Research* 23: 250–265.
- Gromtsev, A. 2002. Natural disturbance dynamics in the boreal forests of European Russia: A review. *Silva Fennica* 36(1): 41–55.
- Gustafsson, L., and K. Perhans. 2010. Biodiversity conservation in Swedish forests: Ways forward for a 30-year-old multi-scaled approach. *AMBIO* 39: 546–554.
- Haight, R.G. 1985. A comparison of dynamic and static economic models of uneven-aged stand management. *Forest Science* 31: 957–974.
- Haight, R.G. 1987. Evaluating the efficiency of even-aged and uneven-aged stand management. *Forest Science* 33: 116–134.
- Haight, R.G., and R.A. Monserud. 1990. Optimizing any-aged management of mixed-species stands. II: Effects of decision criteria. *Forest Science* 36: 125–144.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: Modeling the consequences of different approaches to biodiversity conservation. *Annales Zoologici Fennici* 37: 271–280.
- Heikinheimo, O. 1915. Kaskiviljelyksen vaikutus Suomen metsiin [Effect of swidden cultivation on forests in Finland]. *Acta Forestalia Fennica* 4: 1–264 (in Finnish).
- Hunter Jr., M.L., G.L. Jacobson, and T. Webb. 1988. Paleocology and coarse filter approach in maintaining biological diversity. *Conservation Biology* 2: 375–385.
- Hynynen, J., R. Ojansuu, H. Hökkä, H. Siipilehto, H. Salminen, and P. Haapala. 2002. Models predicting stand development in the MELA system. Finnish Forest Research Institute, Research Papers 835.
- Jalonen, R., I. Hanski, T. Kuuluvainen, E. Nikinmaa, P. Pekonen, P. Puttonen, K. Raitio, and O. Tahvonen. 2006. *Uusi metsäkirja [The new forest book]*. Helsinki: Gaudeamus (in Finnish).
- Jalonen, J., and I. Vanha-Majamaa. 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. *Forest Ecology and Management* 146: 25–34.
- Keane, R.E., P.F. Hessburg, P.B. Landres, and F.J. Swanson. 2009. The use of historical range and variability (HRV) in landscape management. *Forest Ecology and Management* 258: 1025–1037.
- Kneeshaw, D., Y. Bergeron, and T. Kuuluvainen. 2011. Forest ecosystem structure and disturbance dynamics across the circumboreal forest. In *The Sage handbook of biogeography*, ed. A.C. Millington, M.B. Blumler, and U. Schickhoff, 263–280. Los Angeles: Sage.
- Kohm, K.A., and J.F. Franklin (eds.). 1997. *Creating a forestry for the twenty-first century: The science of ecosystem management*. Washington, DC: Island Press.
- Koivula, M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management* 167: 103–121.
- Koivula, M., and J. Niemelä. 2002. Boreal carabid beetles (Coleoptera, Carabidae) in managed spruce forests—a summary of Finnish case studies. *Silva Fennica* 36(1): 423–436.

- Kolström, T. 1993. Modelling the development of an uneven-aged stand of *Picea abies*. *Scandinavian Journal of Forest Research* 8: 373–383.
- Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: A review. *Annales Zoologici Fennici* 31: 35–51.
- Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36: 97–125.
- Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. *AMBIO* 38: 309–315.
- Kuuluvainen, T., and T. Aakala. 2011. Natural forest dynamics in boreal Fennoscandia: A review and classification. *Silva Fennica* 45: 823–841.
- Kuusela, K. 1999. *Metsän leiviskät*. Jyväskylä: Atena kustannus.
- Lähde, E., T. Eskelinen, and A. Väänänen. 2002. Growth and diversity effects of silvicultural alternatives on an old-growth forest in Finland. *Forestry* 75: 395–400.
- Lähde, E., O. Laiho, and J. Lin. 2010. Silvicultural alternatives in an uneven-sized forest dominated by *Picea abies*. *Journal of Forest Research* 15: 14–20.
- Lähde, E., O. Laiho, Y. Norokorpi, and T. Saksa. 1994. Structure and yield of all-sized and even-sized Scots pine-dominated stands. *Annals of Forest Science* 51: 111–120.
- Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9: 1179–1188.
- Lexerød, N., and Gobakken, T. 2008. Economic efficiency of selective cutting under different timber price scenarios. In *Planning, management and economy of selective cutting in Norway*, ed. N. Lexerød (PhD thesis). Ås: Norwegian University of life sciences.
- Liang, J., J. Buongiorno, and R.A. Monserud. 2005. Growth and yield of all-aged Douglas-fir—western hemlock forest stands: A matrix model with stand diversity effects. *Canadian Journal of Forest Research* 35: 2368–2381.
- Lilja, S., and T. Kuuluvainen. 2005. Structure of old *Pinus sylvestris* dominated forest stands along a geographic and human impact gradient in mid-boreal Fennoscandia. *Silva Fennica* 39: 407–428.
- Lommi, S., H. Berglund, M. Kuusinen, and T. Kuuluvainen. 2009. Epiphytic lichen diversity in late-successional *Pinus sylvestris* forest along local and regional forest utilization gradients in eastern boreal Fennoscandia. *Forest Ecology and Management* 259: 883–892.
- Matveinen-Huju, K., and M. Koivula. 2008. Effects of alternative harvesting methods on boreal forest spider assemblages. *Canadian Journal of Forest Research* 38: 782–794.
- McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environmental Reviews* 9: 1–59.
- Mikola, P. 1984. Selection forestry. *Silva Fennica* 18: 293–301.
- Niinimäki, S., O. Tahvonen, and A. Mäkelä. 2012. Applying a process based model in Norway spruce management. *Forest Ecology and Management* 265: 102–115.
- Nyland, R.D. 2002. *Silviculture. Concepts and applications*. Boston: McGraw Hill.
- O'Hara, K.L. 2002. The historical development of uneven-aged silviculture in North America. *Forestry* 75: 339–346.
- Oliver, C.D., and B.C. Larson. 1990. *Forest stand dynamics*. New York: McGraw-Hill Publishing.
- Östlund, L. 1995. Logging the virgin forest of northern Sweden in the early 19th century. *Forest History and Conservation* 39: 160–171.
- Östlund, L., and S. Roturier. 2011. Forestry historical studies in the province of Västerbotten, Northern Sweden: a review of Lars Tirén (1937). *Scandinavian Journal of Forest Research* 26(Suppl. 10): 91–99.
- Östlund, L., O. Zackrisson, and A.-L. Axelsson. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27: 1198–1206.
- Östlund, L., O. Zackrisson, and H. Strotz. 1998. Potash production in northern Sweden: History and ecological effects of a pre-industrial forest exploitation. *Environment and History* 4: 345–358.
- Perera, A.H., L.J. Buse, and M.G. Weber (eds.). 2004. *Emulating natural forest landscape disturbances*. New York: Columbia University Press.
- Peterson, C.E., and P.D. Anderson. 2009. Large-scale interdisciplinary experiments inform current and future forestry management options in the U.S. Pacific Northwest. *Forest Ecology and Management* 258: 409–414.
- Pommerening, A., and S.T. Murphy. 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77: 27–44.
- Puettman, K.J., K.J. Coates, and C. Messier. 2009. *A critique of silviculture: Managing for complexity*. Washington, DC: Island Press.
- Pukkala, T., and T. Kolström. 1988. Simulation of the development of Norway Spruce stands using a transition matrix. *Forest Ecology and Management* 25: 255–267.
- Pukkala, T., E. Lähde, and O. Laiho. 2009. Growth and yield models for uneven-sized forest stands in Finland. *Forest Ecology and Management* 258: 207–216.
- Pukkala, T., E. Lähde, and O. Laiho. 2010. Optimizing the structure and management of uneven-sized stands in Finland. *Forestry* 83: 129–142.
- Pullin, A.S., T.M. Knight, and A.R. Watkinson. 2009. Linking reductionist science and holistic policy using systematic reviews: Unpacking environmental policy questions to construct an evidence-based framework. *Journal of Applied Ecology* 46: 970–975.
- Pullin, A.S., and G.B. Stewart. 2006. Guidelines for systematic review in conservation and environmental management. *Conservation Biology* 20: 1647–1656.
- Rassi, P., E. Hyvärinen, A. Juslén, and I. Mannerkoski, eds. 2010. *The 2010 Red List of Finnish Species*. Helsinki: Ympäristöministeriö & Suomen ympäristökeskus, 685 p.
- Raunio, A., A. Schulman, and T. Kontula, eds. 2008. Assessment of threatened habitat types in Finland. The Finnish Environment 8/2008, Parts 1 and 2, 264+572p (in Finnish with English summary).
- Raymond, P., S. Bédard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. *Journal of Forestry* 107: 405–413.
- Roxburgh, S.H., K. Shea, and J. Bastow Wilson. 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology* 85: 359–371.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533–1546.
- Shea, K., S.H. Roxburg, and S.J. Rauschert. 2004. Moving from pattern to process: Coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7: 491–508.
- Shorohova, E., E. Kapitsa, and I. Vanha-Majamaa. 2008. Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. *Forest Ecology and Management* 255: 3606–3612.
- Shorohova, E., T. Kuuluvainen, A. Kangur, and K. Jogiste. 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: A review with special reference to Russian studies. *Annals of Forest Science* 66: 1–20.

- Siira-Pietikäinen, A., and J. Haimi. 2009. Changes in soil fauna 10 years after forest harvestings: Comparison between clear felling and green-tree retention methods. *Forest Ecology and Management* 258: 332–338.
- Siira-Pietikäinen, A., J. Haimi, A. Kanninen, J. Pietikäinen, and H. Fritze. 2001. Responses of decomposer community to root-isolation and addition of slash. *Soil Biology & Biochemistry* 33: 1993–2004.
- Siira-Pietikäinen, A., J. Haimi, and J. Siitonen. 2003. Short-term responses of soil macroarthropod community to clear felling and alternative forest regeneration methods. *Forest Ecology and Management* 172: 339–353.
- Siiskonen, H. 2007. The conflict between traditional and scientific forest management in the 20th century Finland. *Forest Ecology and Management* 249: 125–133.
- Sippola, A.-L., T. Lehesvirta, and P. Renvall. 2001. Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. *Ecological Bulletins* 49: 243–254.
- Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1997. *The practice of silviculture: Applied forest ecology*, 9th ed. New York: Wiley.
- Sousa, W.P. 1984. The role of disturbances in natural communities. *Annual Review of Ecology and Systematics* 15: 353–391.
- Surakka, H., and M. Siren. 2004. Selection harvesting: state of the art and future directions (in Finnish). *Metsätieteen Aikakauskirja* 4: 373–390 (in Finnish).
- Tahvonen, O. 2007. Optimal choice between even- and uneven-aged forestry systems. Finnish Forest Research Institute. Working Papers 60.
- Tahvonen, O. 2009. Optimal choice between even- and uneven-aged forestry. *Natural Resource Modeling* 22: 289–321.
- Tahvonen, O. 2011. Optimal structure and development of uneven-aged Norway spruce forests. *Canadian Journal of Forest Research* 41: 2389–2402.
- Tahvonen, O., T. Pukkala, O. Laiho, E. Lähde, and S. Niinimäki. 2010. Optimal management of uneven-aged Norway spruce stands. *Forest Ecology and Management* 260: 106–115.
- Tahvonen, O., and E.-J. Viitala. 2006. Does Faustmann rotation apply to regulated forests? *Forest Science* 52: 23–30.
- Tapio. 2006. *Instructions for good silviculture*. Helsinki: Metsäku-stannus (in Finnish).
- Turner, M.G., R.H. Gardner, and R.V. O'Neill. 2001. *Landscape ecology in theory and practice*. New York: Springer.
- Usher, M.B. 1969. A matrix model for forest management. *Biometrics* 25: 309–315.
- Valsta, L. 1992. An optimization model for Norway spruce management based on individual-tree growth models. *Acta Forestalia Fennica* 232: 1–20.
- Vanha-Majamaa, I., and J. Jalonen. 2001. Green tree retention in Fennoscandian forestry. *Scandinavian Journal of Forest Research* 16: 79–90.
- Vuokila, Y. 1970. Selection from above in intermediate cuttings. *Acta Forestalia Fennica* 110: 1–45.
- Wikström, P. 2000. A solution method for uneven-aged management applied to Norway spruce. *Forest Science* 46: 452–463.
- Wilson, J.B. 1994. The 'intermediate disturbance hypothesis' of species coexistence is based on patch dynamics. *New Zealand Journal of Ecology* 18: 176–181.
- Wintle, B.A., S.A. Bekessy, L.A. Veneir, and J.L. Pearce. 2005. The utility of dynamic landscape meta-population models for sustainable forest management: The Brown Creeper. *Conservation Biology* 19: 1930–1943.

AUTHOR BIOGRAPHIES

Timo Kuuluvainen (✉) is Associate Professor and docent in forest ecology at the Department of Forest Sciences, University of Helsinki, Finland
 Address: Department of Forest Sciences, University of Helsinki, P. O. Box 27, 00014 Helsinki, Finland.
 e-mail: timo.kuuluvainen@helsinki.fi

Olli Tahvonen is Professor of forest economics at the Department of Forest Sciences, University of Helsinki, Finland
 Address: Department of Forest Sciences, University of Helsinki, P. O. Box 27, 00014 Helsinki, Finland.
 e-mail: Olli.Tahvonen@helsinki.fi

Tuomas Aakala is a post-doctoral researcher in forest ecology at the Department of Forest Sciences, University of Helsinki, Finland
 Address: Department of Forest Sciences, University of Helsinki, P. O. Box 27, 00014 Helsinki, Finland.
 e-mail: Tuomas.Aakala@helsinki.fi