SILVA FENNICA
Silva Fennica 45(5) review articles
www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

# Natural Forest Dynamics in Boreal Fennoscandia: a Review and Classification

Timo Kuuluvainen and Tuomas Aakala

**Kuuluvainen, T. & Aakala, T.** 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fennica 45(5): 823–841.

The aim here was to review and summarize the findings of scientific studies concerning the types of forest dynamics which occur in natural forests (i.e. forests with negligible human impact) of boreal Fennoscandia. We conducted a systematic search for relevant studies from selected reference databases, using search terms describing the location, structure and processes, and degree of naturalness of the forest. The studies resulting from these searches were supplemented with other known works that were not indexed in the databases. This procedure yielded a total of 43 studies. The studies were grouped into four types of forest dynamics according to the information presented on the characteristics of the native disturbance-succession cycle: 1) even-aged stand dynamics driven by stand-replacing disturbances, 2) cohort dynamics driven by partial disturbances, 3) patch dynamics driven by tree mortality at intermediate scales (>200 m$^2$) and 4) gap dynamics driven by tree mortality at fine scales (<200 m$^2$). All four dynamic types were reported from both spruce and pine dominated forests, but their commonness differed. Gap dynamics was most commonly reported in spruce forests, and cohort dynamics in pine forests. The studies reviewed provide the best obtainable overall picture of scientific findings concerning the characteristics and variability of the unmanaged boreal forest dynamics in Fennoscandia. The results demonstrate that the unmanaged Fennoscandian forests are characterized by more diverse and complex dynamics than has traditionally been acknowledged.

**Keywords** disturbance, age structure, stand replacement, cohort, gap, patch, natural disturbance emulation
**Addresses** University of Helsinki, Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland **E-mail** timo.kuuluvainen@helsinki.fi
**Received** 2 November 2010 **Revised** 7 November 2011 **Accepted** 16 November 2011
**Available at** http://www.metla.fi/silvafennica/full/sf45/sf455823.pdf

# 1 Introduction

Knowledge of the natural structure and dynamics of forests is important, both for basic understanding of ecosystem functioning as well as for practical reasons. Forest habitats shaped by natural forest development are those that the native species have adapted to during their evolutionary history. Knowledge of the characteristics of natural forest habitats and their spatiotemporal dynamics at different scales is therefore indispensable for all efforts to sustain forest biodiversity (Angelstam 1998, Bergeron et al. 2002). Activities using this knowledge include restoration of ecologically impoverished managed forest ecosystems (Vanha-Majamaa et al. 2007) and the development of forest management strategies and silvicultural prescriptions that seek to emulate natural forest dynamics (Angelstam 1998, Bergeron et al. 2002, Kuuluvainen 2009). For example, the debate on what constitutes ‘nature-based’ forestry (e.g. Diaci 2006, Larsen and Nielsen 2007) requires robust information on the structure and dynamics of the natural forest. Finally, it can be argued that a better understanding of the ecology of natural forests is needed in order to devise ways to mitigate and adapt to future climate change (Keane et al. 2009).

Currently in boreal Fennoscandia, the opportunities for studying natural forest ecosystems have become severely limited. The historical roots of the disappearance of natural forest lie in hundreds of years of diverse and intense forest exploitation. As a result of increasing population pressure during recent centuries, the most productive southern forest types were the first to be converted to permanent agricultural land. Other wide spread uses of the forest included slash-and-burn cultivation, tar production, forest pasturage, ship building and iron mining. The onset of forest industry in the 19th century further accelerated the disappearance of primeval forest cover. However, due to logistic restrictions, more remote areas remained unaffected until fairly recently. For example, as late as the mid-19th century a large part of the inland in southern and all of northern Finland was covered by natural or near-natural forests; this estimate was based on the first national-level assessment of forest resources by C.W. Gyldén of 1850 (Lindholm 2004).

Most of the remaining natural and old-growth forests of boreal Fennoscandia are located at northern, high-altitude and low-productivity sites (Aksenov et al. 1999). Fortunately, some large pristine forested landscapes still exist where research on a variety of spatial scales is possible. Some of the most notable remaining landscapes are located in Russian territory of eastern Fennoscandia (Aksenov et al. 1999, Kuuluvainen 2002a), although not all of these areas are protected, and thus face the threat of cuttings (Burnett et al. 2003).

In the southern Boreal Zone of Fennoscandia only a low percentage of the forest cover can be regarded as natural or near-natural, while considerably more remains in the middle and northern Boreal Zones. Often the few southern conservation areas are so small that the full range of forest dynamic processes cannot be expected to occur (Lilja and Kuuluvainen 2005). This consequently severely limits the opportunities to obtain representative regional understanding of the ecology of potential natural forests. For this reason, sustained efforts should be made to combine different methodologies and information sources to obtain a better understanding of the ecology of natural forests. Although some effort has already been made to synthesize information on natural forest dynamics in Fennoscandia (Kuuluvainen 1994, 2002b, Esseen et al. 1997, Engelmark 1999, Engelmark and Hytteborn 1999), no systematic review of the existing scientific literature has hitherto been carried out.

The aim here was therefore to conduct a systematic review (cf. Pullin and Stewart 2006, Pullin et al. 2009) of existing studies dealing with disturbance and successional dynamics of unmanaged forests in boreal Fennoscandia and to classify the forest dynamics reported according to predefined categories. Although the studies reviewed do not represent an unbiased or a representative sample of the prevalence of different forest dynamics types, they nevertheless can provide a large-scale picture of what has been reported on the characteristics and variability of natural forest dynamics in Fennoscandia.

# 2 Material and Methods

## 2.1 Geographic Scope of the Review

The study focused on boreal forests in the Fennoscandian Shield (henceforth Fennoscandia). Geographically, the area encompasses Norway, Finland, most of Sweden, as well as the Murmansk province and Republic of Karelia in Russia. Part of the Leningrad province in Russia also lies within Fennoscandia (see Fig. 1). The area of the Fennoscandian boreal forest stretches from 58°N in southern Norway and Sweden, to 69°N in northern Norway. Longitudinally, the area is demarcated by the Atlantic Ocean at the Norwegian coast at app. 5°E and the White Sea off the Kola Peninsula at 41°E.

Most of the bedrock in Fennoscandia is made up of Precambrian granites and gneisses, covered by young Quaternary and Holocene sediments, consisting mainly of podzolized moraines (Lidmar-Bergström and Näslund 2005). The area exhibits a varied topography. In the west the Scandes reach heights between 1000 and 2500 m above sea level (a.s.l.). A ridge at an elevation exceeding 200 m a.s.l. extends from the Scandes mountain range through northern Finland and the Kola Peninsula, along which the summits of the gently rolling hills (fells) rarely reach elevations above 1000 m. Finland and the southern part of Sweden are mainly lowland, whereas Norway only has a narrow strip of lowland lying along the coastline.

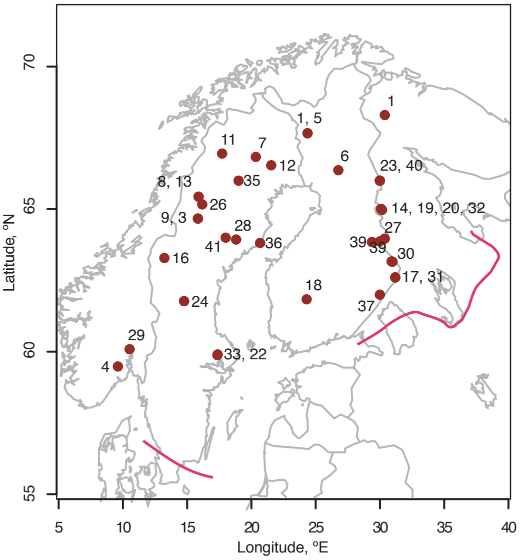

**Fig. 1.** Fennoscandia, with its eastern and southern limit, and the geographical distribution of sites of the studies reviewed. The numbers refer to the list of studies reviewed in Appendix 1. The studies at regional scales are not included. These include Uuttera et al. (1997) from the Ladenso forest inventory area in Russian Karelia, Sirén (1955), Aaltonen 1919 and Lassila (1920) in northern Finland, and Zackrisson (1977) in midnorthern Sweden. The following Russian studies also lack information on the exact location: Kazimirov (1971), Zyabchenko (1984) and Volkov (2003).

The main factor influencing the climate in Fennoscandia is its position between the Atlantic Ocean and Eurasia. The Scandes Mountains in the west give rise to major differences in precipitation particularly between the western and eastern parts of the region. The Norwegian coast is highly maritime, while the eastern parts of Fennoscandia are intermediate between maritime and continental. However, in all parts of the area at least moderate precipitation is recorded throughout the year. In the area covered by boreal forest, the mean temperature of the warmest month (July) ranges from 17 °C n the southern Sweden to 13 °C in some areas of Lapland. The mean temperature of the coldest month (February) varies from –3.5 °C in southern Sweden to –14.7 °C in northern Finland (FAO 2005). Precipitation also varies from over 2000 mm on the Norwegian coast to 450–500 mm in the interior of northern Lapland (Tikkanen 2005). In southwestern Norway 11% and in northern Sweden 38% of the precipitation comes as snow (FAO 2005).

The main forest-forming tree species in the region include Scots pine *Pinus sylvestris* L., Norway spruce *Picea abies* (L.) Karst., birches *Betula* spp., and aspen *Populus tremula* (L.). Of these, *Pinus sylvestris*, *Betula* spp., and *Populus tremula* are considered shade-intolerant pioneer species. *Picea abies* is a shade-tolerant species and often recruits under the canopy of the shade-intolerant species. *Pinus sylvestris* and *Picea abies* are able to form self-perpetuating stands, the former predominating at xeric and nutrient-poor sites and the latter at fresh and nutrient-rich sites.

The deciduous species are generally considered as dominant only in early successional phases. However, even in old conifer stands they are often able to maintain their presence.

## 2.2 Systematic Literature Searches

The search and selection of studies mainly followed the systematic review approach (e.g. Pullin and Stewart 2006, Pullin et al. 2009), as opposed to an approach in which the studies reviewed are selected subjectively by the authors. We conducted a systematic search for peer-reviewed scientific publications from several databases: the Previews Biological Abstracts (Biosis), CAB Abstracts, CSA Natural Sciences, and the ISI Web of Knowledge. We used different combinations of search terms in the title, abstracts and keywords. The aim was to retrieve studies describing the structure and/or processes in naturally dynamic boreal forests in Fennoscandia. The search terms thus included boreal forest, as well as different terms describing forest structure or dynamic processes, the location and the naturalness of the forest (Table 1). It was considered necessary to employ a large number of search terms, because the terminology used in the studies has changed over time.

The search results were supplemented with essential studies, identified based on our own and others' expert knowledge, and the references listed in the studies obtained through the systematic search. These mainly comprised older studies or studies reported in a language other than English, which were not indexed in any of the databases.

Since the studies from the Russian areas of Fennoscandia (Murmansk province, the Republic of Karelia and parts of the Leningrad province, see Fig. 1) are not indexed in any of the used databases and we did not have access to the original Russian studies, we supplemented our material with a recent review of Russian literature by Shorohova et al. (2009).

From the large number of studies fulfilling these criteria, selection was undertaken in two phases. First, based on the title and abstract, those that clearly did not fulfil our criteria were rejected. In many cases, the rejection was due to the focus of the studies on atypical species, on areas lying outside the Boreal Zone (e.g. southern Sweden), or on managed forests. In the second phase, all the remaining studies were carefully reviewed, and those that contained either inferences about forest dynamics or results suitable for making such inferences about the forest dynamics (such as tree age structures) were retained.

In all, this review was based on 43 studies, which are listed, with additional information, in Appendix 1. We are aware that studies probably exist outside this list that may contain relevant information with respect to the aim of the study. However, we believe that our search criteria and procedures (Table 1) yielded a representative set of studies conducted on the topic in question.

## 2.3 Classification of Forest Dynamics

The classification of forest dynamics was based on the characteristics of the predominant disturbance-succession cycle reported. Accordingly,

**Table 1.** Literature search term combinations used. Within each column, all terms are searched with the Boolean operator 'OR'. Asterisks denote wildcard search terms.

| | | Process / structure | | Location | | Naturalness |
|---|---|---|---|---|---|---|
| boreal forest | AND | disturbance*<br>tree mortality<br>stand structure*<br>forest structure*<br>stand dynamic*<br>forest dynamic* | AND | Fennosc*<br>Finland*<br>Finn*<br>Swed*<br>Norw* NOT Norway spruce<br>Karel*<br>Murmansk*<br>Scand* | AND | natural<br>pristine<br>unmanaged<br>virgin<br>old-growth<br>old<br>late-succes* |

**Table 2.** Key of forest characteristics used in the classification of forests into the four predetermined dynamics types.

| Type | Age structure | Spatial patterns | Spatial scale |
|---|---|---|---|
| Stand-replacing | Even | Uniform | Stand |
| Cohort | Multimodal | Diffuse | Stand |
| Patch | Multimodal | Aggregated | Aggregates $>200$ m$^2$ |
| Gap | Multimodal/all-aged | Aggregated | Aggregates $<200$ m$^2$ |

the reviewed studies were grouped into four types of forest dynamics (based on Angelstam and Kuuluvainen (2004)): (*type* 1) even-aged stand dynamics, initiated by stand-replacing disturbances, (*type* 2) cohort dynamics, driven by partial disturbances, (*type* 3) patch dynamics driven by tree mortality at intermediate scales ($>200$ m$^2$) and (*type* 4) gap dynamics driven by tree mortality at fine scales ($<200$ m$^2$). The main characteristics of these four categories of forest dynamics were defined as follows:

Studies were assigned to *type 1* (stand-replacing) if the influence of stand-replacing disturbance clearly dominated forest development and dynamics. Disturbance area was expected to be larger than one hectare.

Studies were classified as *type 2* (cohort dynamics), when explicitly mentioned (rarely), but more often using inferences from published tree age distributions. Studies reporting stands with multimodal age structures (i.e. age cohorts) were classified into this category. Studies that reported low-severity fires (i.e. fires with surviving trees) were classified into this category as well.

Studies were classified as *type 3* (patch dynamics) following the definition of McCarthy (2001), in which canopy openings larger than 200 m$^2$ but smaller than one hectare are considered as patches. The distinction between cohorts and patches was that the tree age cohorts were defined here as being more or less dispersed spatially within the stands, whereas the patches are spatially more distinct age or size classes of trees.

Studies were classified as *type 4* (gap dynamics), when single-tree or small tree group mortality or gap dynamics were mentioned as the factor driving stand dynamics. All-aged stands belonged to this category. The distinction between the gap and patch followed the definition of McCarthy (2001), in which gaps are canopy openings smaller than 200 m$^2$. The processes forming patches and gaps also differ: patches are larger canopy openings, often forming distinct patches in the forest, and are usually the result of allogenic, at times catastrophic, disturbances, whereas gap dynamics typically arise from tree senescent-related autogenic disturbance factors such as fungi and insects (Hytteborn et al. 1991, McCarthy 2001).

Each study was assigned to one of these categories, based mainly on the published results and information offered on tree age structure and spatial patterns, the characteristic spatial scale of the disturbance-succession processes (see Table 2). However, in cases where transparent statements or conclusions about forest dynamics were offered, despite a lack of relevant data (as was especially common in older studies), this was deemed '*expert opinion*', and the studies were included.

Probably owing to the scarcity of natural forests in Fennoscandia, many of the studies were conducted at the same sites. In the analyses each study site was considered to be one case. However, the results from studies at the same sites were considered complementary. For instance, if one study reported gap dynamics in the recent past (e.g. Aakala et al. 2009) while at the same area another study had documented patch dynamics in the more distant past (e.g. Caron et al. 2009), both results were taken as valid observations. In such cases the studies were considered to be complementary, thus revealing a more complete picture of the disturbance regime at that particular site.

## 2.4 Additional Information

In addition to assigning the studies to different forest dynamics categories, the studies were grouped according to their site type and the dominant tree species. Where more than one tree species was present, the dominant tree species was determined preferentially from volume data, or, if volumes were not available, from the number of trees. Where quantitative data were not available, a clear statement from the author was deemed acceptable.

Information was also recorded on the disturbance agents driving forest dynamics. For the analyses they were classified into the following categories: 1) fire, 2) wind, 3) biotic, 4) autogenic, 5) other and 6) undefined. The first two categories are self-explanatory. The biotic category included insects and fungi as the main disturbance agents. The category 'other' included more sporadic records of atypical disturbance factors, such as extreme weather events. In many studies, the force driving the forest dynamics was not specified, especially in the case of gap dynamics. These cases were classified under 'undefined'.

Other quantitative data were also extracted when available: absolute volumes of living and dead trees and species compositions. Sample plot size was also recorded. Finally, the studies were classified according to their spatial scale, considering either stand-level, landscape-level ($<10$ km$^2$) or if the study included more general inferences on a regional scale ($>10$ km$^2$).

**Table 3.** Locations of the study areas by dominant tree species and vegetation zones.

| | Pine | Spruce | Birch | Total |
|---|---|---|---|---|
| Northern boreal | 6 | 11 | 0 | 17 |
| Middle boreal | 9 | 15 | 1 | 25 |
| Southern boreal | 3 | 2 | 0 | 5 |
| Total | 18 | 28 | 1 | 48 |

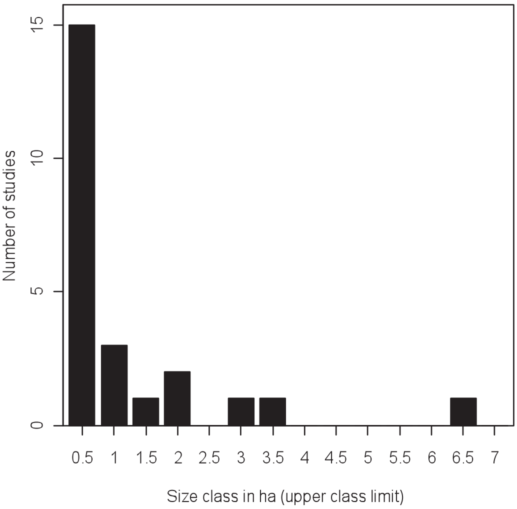

**Fig. 2.** Sample plot size distribution in the stand-scale studies reviewed.

# 3 Results

## 3.1 Geographic Distribution, Tree Species Dominance and Sampling Scale of Studies

Most of the studies reviewed were conducted in forests in the middle and northern Boreal Zones (Table 3, Fig. 1). Only five studies were carried out in the southern Boreal Zone. In the northern and middle Boreal Zones, spruce forests were more often studied than pine forests, whereas in the southern Boreal Zone both forest types were equally, albeit rarely, studied. Results from unmanaged deciduous forests were practically nonexistent, although they were included in the chronosequence study of Sirén (1955).

Most of the studies were conducted at stand scale. In the stand scale studies, the sizes of sample plots varied considerably. The mean sample plot size was 0.9 ha (SD = 1.4 ha), but the median was 0.3 ha, indicating that the studies were strongly inclined towards smaller sample plot sizes (Fig. 2).

## 3.2 Accumulation of Studies

The first significant investigations of primeval forests and forest ecology were conducted in the early and mid-20th century, when natural forests were still abundant in many areas. However, after the pioneering works of Aaltonen (1919) and Lassila (1920) in northern Finland, and Sernander

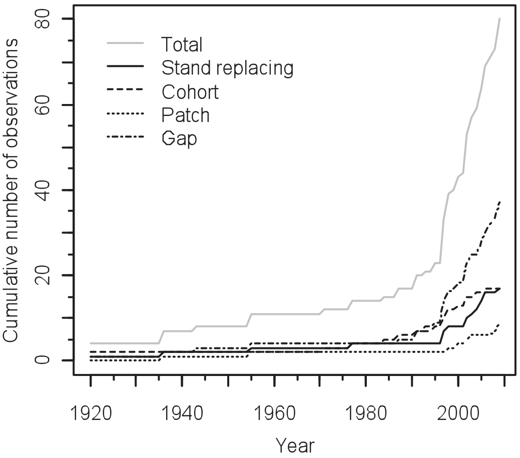

**Fig. 3.** Accumulation of studies dealing with natural forest dynamics in Fennoscandia during the period 1919–2009 in total and by forest dynamics type. (*type* 1) – stand-replacing disturbances and even-aged stand dynamics, (*type* 2) – cohort dynamics, driven by partial disturbances, (*type* 3) – patch dynamics driven by tree mortality at intermediate scale (>200 m$^2$) and (*type* 4) – gap dynamics driven by tree mortality at fine scale (<200 m$^2$).

(1936) and Arnborg (1943) in Sweden, new studies were published only sporadically: most significantly, Sirén's (1955) dissertation on primeval spruce forest dynamics in northern Finland and Zackrisson's (1977) classic study on forest fire dynamics in northern Sweden. It was not until the late 1990s when the number of published studies began to accumulate more rapidly. There has been an exponential increase in the cumulative number of studies since the 1990s and most of the studies related to natural forest structure and dynamics were published during the most recent decades (Fig. 3).

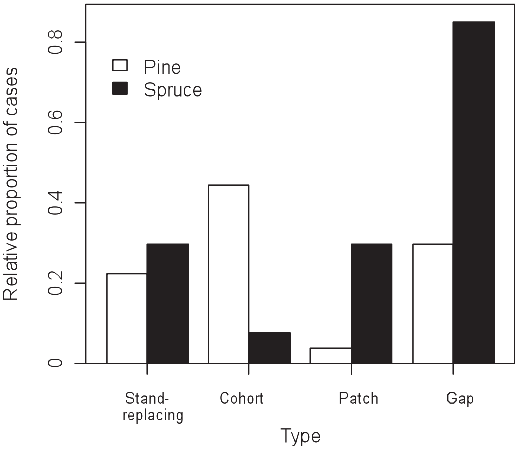

**Fig. 4.** Distribution of the forest dynamics type by dominant tree species in the studies reviewed.

The number of studies reporting gap dynamics has rapidly increased, especially since the mid-1980s. Overall, gap dynamics was in the studies reviewed the most commonly reported type of forest dynamics (Fig. 3). The number of studies reporting cohort dynamics, the second most commonly reported type of forest dynamics, has also increased. Studies reporting dynamics driven by stand-replacing disturbances were relatively rare, but their numbers have also increased in the last two decades. Patch dynamics studies have rarely been reported, but again their numbers have risen during the last decade (Fig. 3).

### 3.3 Types of Forest Dynamics by Dominant Tree Species

All four dynamic types have been reported in both spruce- and pine-dominated forests. Gap-dynamics, the most common type, was reported more than twice as often in spruce than in pine dominated forests (Fig. 4). Similarly, patch dynamics were much more common in spruce-dominated forests than in pine-dominated forests. The contrasting pattern was evident for cohort dynamics, which was most often reported for pine-dominated forests. Forest dynamics characterized by stand replacement was almost as commonly reported for pine- as for spruce-dominated forest (Fig. 4).

### 3.4 Disturbance Factors and Forest Dynamics

In both pine and spruce forests stand replacement occurred as a result of severe allogenic disturbances (Fig. 5, Appendix 1). In most cases, stand-replacement was due to high-severity forest fires. In spruce-dominated forests, windstorms also led to stand-replacing disturbances (Fig. 5). In Sirén's

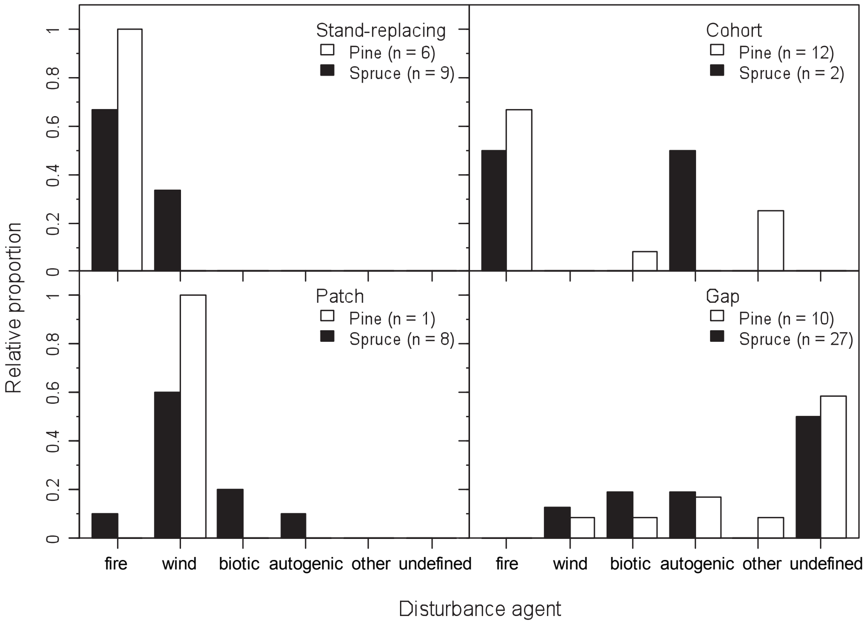

**Fig. 5.** Prevalence of documented disturbance agents in different categories of forest dynamics and as separated into pine- and spruce-dominated forests.

(1955) work, autogenic disturbance in the form of synchronized and total mortality of the dominant tree class of an old even-aged cohort was suggested to result in stand-replacing disturbance. However, this observation and its interpretation remain controversial, due to the lack of documentation and potential subjectivity of the sampling protocol used by Sirén (1955) (see Aakala et al. 2009, Aakala and Keto-Tokoi 2011).

Cohort dynamics was much more commonly reported in pine forests than in spruce forests (Fig. 4). The main driving factor of this type of forest dynamics was surface fires (Fig. 5). In one study (Engelmark et al. 1998), an insect outbreak (of *Diprion butowitsch)* killed a large proportion of younger pines in a stand. Kazimirov (1971, cited in Shorohova et al. (2009) also suggest that spruce forests may undergo cohort dynamics, apparently due to autogenic causes such as senescence-related weakening, and the consequent vulnerability to further disturbance agents. Short-term climatic variations have also been attributed as a driver of this type of forest dynamics. This could potentially occur through climate-induced dieback of trees, as reported in northern boreal pine forests (Kullman 1991). Under harsh conditions, climatic variations also interannually regulate highly variable seed crops, consequently creating cohort-type tree regeneration dynamics and age structures of trees (Steijlen and Zackrisson 1987).

Patch dynamics (disturbance-created openings larger than 200 m$^2$) was most commonly reported in spruce forests, but only once in a pine forest. In both types, patch dynamics was mainly driven by wind disturbances. However, small-scale fires in spruce-dominated forests can apparently also lead to patch formation (Wallenius et al. 2002).

The agents driving gap dynamics were often not well specified (Fig. 5; e.g. Hofgaard 1993, Karjalainen and Kuuluvainen 2002), or the authors merely stated that gap formation was due to small-scale treefalls related to the activity of pathogenic fungi and insects (e.g. Rouvinen and Kuuluvainen 2005). These general conclusions are supported by studies in which data on disturbance agents were explicitly gathered (e.g. Rouvinen et al. 2002). The typical agents driving small-scale tree mortality can be listed for some types of forest. This seems to be the case for northern boreal spruce forests, where stem rot typically weakens old trees so that they become more susceptible to wind- or snow-induced damage and stem breakage (Edman et al. 2007, Lännenpää et al. 2008, Aakala et al. 2009). The factors driving gap dynamics are especially varied and interact in complex ways, which often makes it difficult, or even impossible, to point out a single main causal tree mortality agent.

Although the above results were grouped by dominant tree species, it is noteworthy that stands usually also contain subordinate species and that there are clear differences in the modes of tree mortality among species in mixed stands. For instance, Hytteborn et al. (1987) reported that spruces were snapped in storms, while birches in the same stands died due to senescence. Sirén (1955) also suggested that birches that dominate the early successional stages of spruce forests die, primarily due to senescence-related autogenic causes.

# 4 Discussion

## 4.1 Development and Importance of Knowledge of Natural Forests

The properties of forest structure and dynamics under natural conditions (i.e. under negligible human influence) have been an issue of considerable debate and controversy over the years (Kuuluvainen 2009). One important reason for this is that despite the knowledge accumulated, our understanding of the variability of the ecology of natural boreal forests is still quite incomplete (see next chapter). There are several reasons for this. First, this research topic is highly demanding, requiring focus on temporal scales from years to hundreds or even thousands of years, and spatially from patches to stands and up to regional scales ($> 10$ km$^2$). The paucity of natural forests in many parts of Fennoscandia represents an additional problem: empirical studies of local characteristics of forest dynamics under unmanaged conditions are simply impossible in many areas (Aksenov et al. 1999). Finally, generalizations may be difficult, due to the inherent variability in forest ecosystem properties and the large spatial and temporal scales involved (however, see Pennanen (2002) for opportunities of modelling approaches).

In the societal and political arena, the definition of natural forest dynamics has also been a contested subject over time. In the absence of rigorous scientific information, various views and opinions were presented in the public debate as ‘final truths’. Part of this debate was related to the contest over defining what type of forest management can be called ‘nature-based’ or *naturnah* (in German), and hence sustainable or acceptable. In particular, forest managers supported the view that repeated stand-replacing fire and even-aged stand dynamics were the dominant natural cycle of boreal forest dynamics. This point of view was not surprising, considering that after WWII forestry in Fennoscandia switched to using clear-cutting as the dominant harvesting method, in contrast to previously practised selective cuttings (Siiskonen 2007).

There were also some pioneering studies that promoted the view of the dominance of stand-replacing disturbances (e.g. Sirén 1955); however, some of the results and their interpretations were later questioned (see Aakala and Keto-Tokoi 2011, for a discussion of this case). Nevertheless, such pioneering studies strongly influenced the thinking behind the emerging forest management practices, and especially in legitimizing the extensive introduction of the clear-cutting system and the neglect of other ways to harvest the forest.

From the point-of-view of sustainable forest management, there is now well-founded incentive to base our management practices on an adequate understanding of the ecology and natural variability of forest ecosystems (e.g. Landres et al. 1999, Keane et al. 2009). This especially applies to efforts to restore and safeguard biodiversity and in this way foster ecosystem resilience, which are widely accepted goals of modern sustainable forest management.

## 4.2 Types of Forest Dynamics and Disturbance Factors

With increasing numbers of studies carried out in unmanaged forests, evidence of the inherent multiscale variability of forest disturbance and structural dynamics in Northern Europe has rapidly been accumulating during recent decades (e.g. Angelstam 1998, Kuuluvainen 2002a, Shorohova et al. 2009, see Fig. 3). This conclusion was reinforced by this review (carried out following the systematic review principles, e.g. Pullin and Stewart 2006, Pullin et al. 2009) on the scientific literature concerning the characteristics and variability of types of forest dynamics in boreal Fennoscandia.

Although the studies reviewed are not a representative sample of the natural forests throughout Fennoscandia, and thus preclude us from making inferences about the areal extents or relative proportions of each dynamics types, there are several conclusions we can draw. All four forest dynamics types were found at varying sites, regardless of whether they were dominated by spruce or pine. Which forest dynamics types were most often reported at a particular forest site probably partly reflects the researchers' choices of study areas and tree species. However, it is noteworthy that the forest dynamics types described in the early literature were essentially the same as those described more recently, when research of natural forest has perhaps more purposefully targeted old-growth forests. For instance, Aaltonen (1919) and Lassila (1921) described fire-driven cohort dynamics in pine forests, and Sernander (1936) wind-driven gap dynamics in spruce forests. Both types of dynamics are commonly reported in the later studies. While much of the recent studies on natural forests have targeted old-growth forests, which makes it more difficult to document evidence of stand-replacing disturbances (but see Aakala et al. 2009), the older studies reviewed did not support the idea of the prevalence of stand-replacing disturbances either (except for Sirén 1955). The minor role of stand-replacing disturbances is suggested by the fact that such dynamics have rarely been documented in the Fennoscandian boreal forests, in contrast to the situation of in North American boreal forest (Payette 1992).

Among the studies reviewed, the number of papers reporting gap dynamics was clearly the highest and has been accumulating most rapidly (Fig. 3). The second most commonly reported type was cohort dynamics, followed by observations of stand-replacing and patch-scale dynamics. These studies together provide evidence of the existence of various types of nonstand-replacing forest dynamics, i.e. gap, patch and cohort dynamics in boreal Fennoscandia. Stand-replacing disturbances were also reported and they can obviously be of major importance locally. It should also be noted that when a stand-replacing disturbance occurs, it has far-reaching effects on the future development of the stands that may last for centuries (Aakala et al. 2009). Nevertheless, over wider spatial and longer temporal scales, stand replacement may play a smaller role in the overall disturbance regime compared with nonstand-replacing dynamics. This conclusion can also be drawn from the results of the only landscape-level simulation study focusing on unmanaged forest dynamics in boreal Fennoscandia by Pennanen (2002).

The common occurrence of nonstand-replacing disturbances and the consequent prevalence of complex stand structures and dynamics have been attributed to the semimaritime climate, fragmented landscape structure with abundant firebreaks (waterways and peatlands). Another important reason is that xeric sites, which may burn more often and are usually dominated by the fire-resistant pine (*Pinus sylvestris*), can be expected to exhibit cohort dynamics. (e.g. Shorohova et al. 2009).

The distribution of forest dynamics types by dominant tree species was, as could be expected, based on species ecological traits (Fig. 4). Gap dynamics was most common in late-successional spruce forests that had escaped major disturbances for long periods of time. In such forests, the disturbance process was typically driven by a complex interaction between tree senescence, fungi and insects (e.g. Lännenpää et al. 2008). In patch dynamic spruce forests, also wind appeared to be an important disturbance agent. Cohort dynamics, mostly driven by low-severity surface fires, was most common in fire-resistant pine-dominated forests. Stand-replacing disturbances were reported from both pine- and spruce-dominated forests. This could be related to the more or less random occurrences and/or large spatial scales of high severity disturbances, either fire or wind.

Fig. 6 provides an example of some of the documented tree age structures in cohort dynamics pine stands driven by surface fires. It is evident

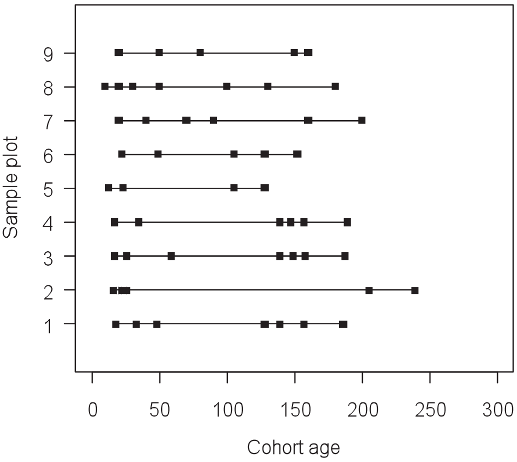

**Fig. 6.** Cohort dynamics can create complex tree age structures. An example of multiple tree age cohorts (black squares) documented in individual sample plots in northern boreal pine forests in Finland in the early 20th century by Lassila (1920).

that such forests represent complex multilayered canopy structures that were typical of pine forests over large areas before commercial forest exploitation (Linder and Östlund 1998, Axelsson and Östlund 2001, Kuuluvainen et al. 2002).

### 4.3 Problems of Interpretation

Potential problems and biases in classifying the forests studied into dynamics types were most likely related to 1) potential human impact in study areas described as ‘natural’ or ‘unmanaged’ (e.g. Josefsson et al. 2009), 2) differing research methodologies used over time, 3) different interpretations of the prevalence of the forest dynamics types in particular studies and/or 4) the varying spatial and temporal scales covered by the studies.

In this review we use the term ‘natural forest’ in a pragmatic manner, denoting a situation where human impact has been low or negligible and it can be assumed that the main natural features of forest dynamics remain. In the reviewed studies this assumption was based on the descriptions of the study sites. We acknowledge that the absence of direct signs of human impact is no proof of true naturalness. For example, long-term low-intensity land use by indigenous people, such as reindeer herding and the use of fire, may impact forest structure and dynamics at least locally (Josefsson et al. 2009). In this respect the reviewed studies may partly reflect historical range of variability of forest dynamics (Keane et al. 2009). However, in this review we preferred to use the term ‘natural’, indicating the assumption that low human populations did not significantly affect the dynamics of the forest (see Carcaillet et al. 2007).

In some of the older studies (e.g. Aaltonen 1919, Sirén 1955) the research methodology used may not have been up to current standards. This may be the reason for some controversies, e.g., concerning the inherent characteristics of the dynamics of northern spruce forests between older (Sirén 1955) and more recent studies (Hofgaard 1993, Aakala et al. 2009 and Caron et al. 2009 ; for a discussion see Aakala and Keto-Tokoi 2011). However, it was believed that even the more qualitative observations of older studies (e.g. Aaltonen 1919) are useful, especially since they concern ecosystems that were supposedly in a more natural state than some of the forests studied in later times (Jonsson et al. 2011). Overall, contradictory results were rare.

The type of forest dynamics was determined, based on the characteristics of the disturbance-succession cycle that was considered to have a dominant impact on forest structure. In this respect, a relevant question is how long it would take for a forest that is regenerated after a stand-replacing disturbance to enter into a qualitatively different mode of dynamics, e.g. patch or gap dynamics? According to the studies reviewed, the time taken for this to occur varies considerably, from 100 years in primary forest succession on the rising Baltic Sea coastline (Svensson and Jeglum 2001) to app. 300 years (Sirén 1955, Kazimirov 1971, Linder et al. 1997) or even 300+ years in the more northern forests (Aakala et al. 2009). This wide variability probably reflects true variations in climatic and other environmental conditions and their effects on the speed of forest succession, and thus should not be a problem from the point of view of this study.

The spatial and temporal scopes of the studies showed considerable variation. The spatial scale of the studies ranged from stand-level (e.g. Wallenius et al. 2002), to landscape-level ($< 10$ km$^2$, e.g. Pitkänen et al. 2003) and finally to studies at the regional scale ($> 10$ km$^2$, e.g. Sirén 1955). Similarly, the temporal scale ranged from structural snapshot data to hundreds (in dendroecological studies; e.g. Zackrisson 1977) and even thousands of years (in paleoecological studies, e.g. Bjune et al. 2009). Despite such variation in the 'depth and width' of the sampling window, we believe that, when combined and evaluated collectively, these studies build an informative and holistic picture of the natural variability of forest dynamics in boreal Fennoscandia.

### 4.4 Knowledge Gaps and Challenges of Research

Although our understanding of the structure and dynamics of natural forests has increased considerably, there are still serious shortcomings in the basic knowledge. First of all, there is a strong geographic bias in the distribution of studies (Table 3). The reviewed studies were strongly weighted towards middle and northern boreal forests, while data from the southern Boreal Zone were scarce. This is understandably based on the distribution of the remaining natural forests, but is, at the same time, unfortunate since the greatest challenges of biodiversity conservation reside in the southern Boreal Zone. The lack of knowledge is also apparent concerning the more rare types of natural forests. Most studies deal with either pine- or spruce-dominated forests, while practically nothing is known about the natural dynamic properties of forests dominated by deciduous tree species. Although many of these forests, which naturally occur at the richest sites, have been permanently converted to agricultural lands, we know that such unmanaged forests still exist (Raunio et al. 2008). The lack of results on deciduous forests is also due to the general focus on old forests, whereas early successional phases dominated by deciduous trees have been very little studied (but see Sirén 1955).

One of the biggest challenges in studying forest disturbance-succession cycles relates to determining meaningful spatial and temporal scales for characterizing the system dynamics (e.g. Habeeb et al. 2005). It is clear that the spatiotemporal scales commonly covered by studies are severely limited. Considering spatial scales, most of the studies reviewed were conducted at stand scale and within this observational scale the sample plot size distribution was strongly skewed towards small plots (see Fig. 2). However, we know that many important ecological processes may become visible only at landscape or even regional scales (Franklin 1993). Together with the small size of the natural forest remnants remaining in many regions, this may lead to the underestimation of rarely occurring meso-scale (i.e. landscape-scale) disturbances. However, longer-term and larger-scale reconstructions of disturbance history are common in forest fire history studies.

The challenge to cover meaningful temporal scales is perhaps even more daunting. Boreal forest systems develop slowly and are influenced by past events for a long time. For example in the study of Aakala et al. (2009), carried out in the wilderness of the Murmansk region, Russia, still after 317 years of post-fire succession the even-aged structure and dynamics of this northern boreal spruce forest reflected the past stand-replacing disturbance event. It was also estimated that in northern boreal spruce forests it may take at least 400 but possibly up to 1000 years of development without major disturbances before the classical quasi-equilibrating gap-phase dynamics emerge (Aakala et al. 2009). Due to such slow system dynamics and lack of data from long-term monitoring from permanent plots, the quantitative characteristics of natural forest successional trajectories and their variability in different ecological situations remain largely undocumented. However, this is essential ecological information.

Many of the studies have focused on specific disturbance agents (such as fires or windstorms), whereas simultaneous empirical assessments of all drivers of forest dynamics are rare. As a result, we lack information on the co-occurrence and relative importance of different disturbance factors. Moreover, the focus has mostly been on the structures created by disturbances at a single point of time, with somewhat weak inferences on the process drivers (cf. Rouvinen et al. 2002, Lännenpää et al. 2008). Processes have been somewhat better accounted for in disturbance reconstructions (Wallenius et al. 2004, Aakala et al. 2009, Caron et al. 2009,) or in chronosequence studies (Sirén 1955, Lilja et al. 2006). However, there are no studies based on long-term monitoring of forest structure and dynamics and the driving factors of change. Most of the studies are based on single snapshot data in time, disturbance reconstructions based on dendrochronological or paleoecological methods, or stand chronosequences.

To meet these serious research challenges, several approaches are needed. First, there is a need to more efficiently use existing multiple sources of information. By quantitatively synthesizing information from existing studies, historical sources and analyzing old forest inventory data can yield important new insights concerning the natural variability and historical states of the forest (for example, see Linder 1998, Axelsson and Östlund 2001).

Fortunately, there still remain some large intact forested landscapes in boreal Fennoscandia that provide unique opportunities to examine the ecology of the natural boreal forest at multiple and appropriate scales. Most of these forests are located in remote, high-altitude or border areas (Aksenov et al. 1999); unfortunately some of them remain under threat of logging. In this respect, one could highlight the unique forested landscapes in Russian Karelia along the Green Belt zone at the border of Finland and Russia (Burnett et al. 2003). These last intact forested landscapes should become the subject of detailed study, including long-term monitoring carried out at the landscape level. This is necessary for detecting slow and subtle changes in ecosystem structure and function, e.g. due to the impact of the anticipated climate change on forest ecosystem dynamics (Muller et al. 2010 ).

Finally, there is a need to develop modelling approaches that are associated with and validated by empirical research. Models are important, because they can synthesize and operationalize information from different sources (cf. Pennanen 2002, Pennanen and Kuuluvainen 2002). Modelling is also useful in pinpointing gaps in existing knowledge base. The models validated can then be used in scenario analyses on how the intact forests will respond e.g. to alternative climate change trajectories.

# 5 Conclusions

The studies reviewed can be considered to provide the best obtainable large-scale overview of what has so far been found concerning the characteristics and variability of natural forest dynamics in boreal Fennoscandia. These studies demonstrate the natural variability of types of forest dynamics in boreal Fennoscandia. The range of forest dynamics documented mostly included partial and small scale disturbances, and the following successions of different and complex types, whereas stand-replacing disturbances were less frequently documented. This documented variability and types of natural forest dynamics bear important implications for ecological conservation and ecosystem management of forested landscapes. Considering the current predominance of clear-cut harvesting in forest management, development of harvesting practices inspired by nonstand-replacing disturbances is needed for habitat and landscape restoration, and sustainable forest management.

# Acknowledgements

We thank Ruut Rabinowitsch-Jokinen for help in data analysis. The research was funded by the Ministry of Agriculture and Forestry in the Forest Biodiversity Research Programme of Southern Finland (METSO).

# References

Aakala, T. & Keto-Tokoi, P. 2011. The old Norway spruce forests of northern boreal Fennoscandia are alive and well: A review of Sirén (1955). Scandinavian Journal of Forest Research 26 (Suppl 10): 25–33.

— , Kuuluvainen, T., Wallenius, T. & Kauhanen, H. 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.

Aaltonen, V.T. 1919. Über die naturliche Verjungung der Heidewälder im finnischen Lappland. Communicationes ex Instituto Quaestionum Forestalium Finlandiae Editae 1. 319 p. (In Finnish with German summary).

Aksenov, D., Karpachevskiy, M., Lloyd, S. & Yaroshenko, A. 1999. The last of the last: the old-growth forests of boreal Europe. Taiga Rescue Network.

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in european boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9(4): 593–602.

— & Kuuluvainen, T. 2004. Boreal forest disturbance regimes, successional dynamics landlandscape structures – a European perspective. Ecological Bulletins 51: 117–136.

Arnborg, T. 1943. Granberget – en växtbiologisk undersökning av ett sydlappländskt granskogsområde med särskild hänsyn till skogstyper och föryngring. Norrländskt handbibliotek 14. (In Swedish with German summary).

Axelsson, A.-L. & Östlund, L. 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. Forest Ecology and Management 147: 109–122.

Bergeron, Y., Leduc, A., Harvey, B.D. & Gauthier, S. 2002. Natural fire regime: a guide for sustainable forest management of the Canadian boreal forest. Silva Fennica 36: 81–95.

Bjune, A.E., Ohlson, M., Birks, H.J.B. & Bradshaw, R.H.W. 2009. The development and local stand-scale dynamics of a Picea abies forest in southeastern Norway Source. Holocene 19(7): 1073–1082.

Burnett, C., Fall, A., Tomppo, E. & Kalliola, R. 2003. Monitoring current status of and trends in boreal forest land use in Russian Karelia. Conservation Ecology 7(2): 8.

Carcaillet, C., Bergman, I., Delorme, S., Hörnberg, G. & Zackrisson, O. 2007. Long-term fire frequency not linked to prehistoric occupations in northern Swedish boreal forest. Ecology 88(2): 465–477.

Caron, M.-N., Kneeshaw, D.D., De Grandpré, L., Kauhanen, H. & Kuuluvainen, T. 2009. Canopy gap characteristics and disturbance dynamics in old-growth Picea abies stands in northern Fennoscandia: Is the forest in quasi-equilibrium? Annales Botanici Fennici 46: 251–262

Diaci, J. 2006. Nature based forestry in central Europe. Alternatives to industrial forestry and strict preservation. Studia Forestalia Slovenica 126. 167 p.

Dolezal, J., Srutek, M., Hara, T., Sumida, A. & Penttilä, T. 2006. Neighborhood interactions influencing tree population dynamics in nonpyrogenous boreal forest in northern Finland. Plant Ecology 185(1): 135–150.

Edman, M., Jönsson, M. & Jonsson, B.G. 2007. Fungi and wind strongly influence the temporal availability o logs in an old-growth spruce forest. Ecological Applications 17(2): 482–490.

Engelmark, O. 1999. Boreal forest disturbances. In: Walker, L.R. (ed.). Ecosystems of disturbed ground. Ecosystems of the World 16. Elsevier, Amsterdam. p. 161–186.

— & Hytteborn, H. 1999. Coniferous forests. Acta Phytogeographica Suecica 84: 55–74.

— , Hofgaard, A. & Arnborg, T. 1998. Successional trends 219 years after fire in an old Pinus sylvestris stand in northern Sweden. Journal of Vegetation Science 9(4): 583–592.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16–47.

FAO. 2005. New_LocClim: Local climate estimator. Environment and Natural Resources, Working Paper 20. (CD-Rom).

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes. Ecological Applications 3: 202–205.

Fraver, S., Jonsson, B.G., Jönsson, M. & Esseen, P. 2008. Demographics and disturbance history of a boreal old-growth Picea abies forest. Journal of Vegetation Science 19(6): 789–798.

Habeeb, R.L., Trebilco, J., Wotherspoon, T. & Johnson, C.R. 2005. Determining natural scales of ecological systems. Ecological Monographs 75(4): 467–487.

Hofgaard, A. 1993. Structure and regeneration patterns of a virgin Picea abies forest in northern Sweden. Journal of Vegetation Science 4: 601–608.

Hörnberg, G., Ohlson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth Picea abies swamp-forests. Journal of Vegetation Science 6(2): 291–298.

Hytteborn, H., Packham, J.R. & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the virgin montane forest of Vallibäcken, northern Sweden. Vegetatio 72: 3–19.

— , Liu, Q.-H. & Verwijst, T. 1991. Natural disturbance and gap dynamics in a Swedish boreal spruce forest. In: Nakagoshi, N. & Golley, F.B. (eds.). Coniferous forest from an international perspective. SBP Academic Publishing, The Hague. p. 93–108.

Jonsson, B.G. 2000. Availability of coarse woody debris in a boreal old-growth Picea abies forest. Journal of Vegetation Science 11(1): 51–56.

— , Brumelis, G. & Kuuluvainen, T. 2011. Preface: Early classical studies of forest ecology in Northern Europe. Scandinavian Journal of Forest Research 26 (Suppl 10): 1–2.

Jönsson, M.T., Fraver, S., Jonsson, B., Dynesius, M., Rydgard, M. & Esseen, P. 2007. Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. Forest Ecology and Management 242(2–3): 306–313.

Josefsson, T., Hörnberg, G. & Östlund, L. 2009. Long-term human impact and vegetation changes in a boreal forest reserve: implications for the use of protected areas as ecological references. Ecosystems 12(6): 1017–1036.

Karjalainen, L. & Kuuluvainen, T. 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by Pinus sylvestris in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36(1): 147–167.

Kazimirov N.I. 1971. [Spruce forests of Karelia]. El'niki Karelii. Nauka, Leningrad. 140 p. (In Russian).

Keane, R.E., Hessburg, P.F., Landres, P.B. & Swanson, F.J. 2009. The use of historical range and variability (HRV) in landscape management. Forest Ecology and Management 258: 1025–1037.

Kullman, L. 1991. Cataclysmic response to recent cooling of a natural boreal pine (Pinus sylvestris L.) forest in northern Sweden. New Phytologist 117(2): 351–360.

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.

— 2002a. Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36(1): 5–12.

— 2002b. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36(1): 97–125.

— 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. Ambio 38: 309–315.

— & Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal Pinus sylvestris forest. Journal of Vegetation Science 9(4): 551–562.

— & Kalmari, R. 2003. Regeneration microsites of Picea abies seedlings in a windthrow area of a boreal old-growth forest in southern Finland. Annales Botanici Fennici 40(6): 401–413.

— , Mäki, J., Karjalainen, L. & Lehtonen, H. 2002. Tree age distributions in old-growth forest sites Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36(1): 169–184.

Landres, P.B., Morgan, P. & Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179–1188.

Lampainen, J., Kuuluvainen, T., Wallenius, T. H., Karjalainen, L. & Vanha-Majamaa, I. 2004. Long-term forest structure and regeneration after wildfire in Russian Karelia. Journal of Vegetation Science 15(2): 245–256.

Lännenpää, A., Aakala, T., Kauhanen, H. & Kuuluvainen, T. 2008. Tree mortality agents in pristine Norway spruce forests in northern Fennoscandia. Silva Fennica 42(2): 151–163.

Larsen, J.B. & Nielsen, A.B. 2007. Nature-based forest management – Where are we going? Elaborating forest development types in and with practice. Forest Ecology and Management 238: 107–117.

Lassila, I. 1920. Tutkimuksia mäntymetsien synnystä ja kehityksestä pohjoisen napapiirin pohjoispuolella. Acta Forestalia Fennica 14(3). 95 p.

Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (Picea abies (L.) Karst.) in 2 old-growth coniferous forests in central Sweden. Vegetatio 93(2): 157–165.

Lidmar-Bergström, K. & Näslund, J.-O. 2005. Major landforms and bedrock. In: Seppälä, M. (ed.). The physical geography of Fennoscandia. Oxford University Press, UK. p. 3–16.

Lilja, S. & Kuuluvainen, T. 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.

— , Wallenius, T. & Kuuluvainen, T. 2006. Structure and development of old Picea abies forests in northern boreal Fennoscandia. Ecoscience 13(2): 181–192.

Linder, P. 1998. Structural changes in two virgin boreal forest stands in central Sweden over 72 years. Scandinavian Journal of Forest Research 13(4): 451–461.

— & Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. Biological Conservation 85: 9–19.

— , Elfving, B. & Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. Forest Ecology & Management 98(1): 17–33.

Lindholm, T. 2004. Suomen metsät 1850. In: Kuuluvainen, T., Saaristo, L., Keto-Tokoi, P., Kostamo, J., Kuuluvainen, J., Kuusinen, M., Ollikainen, M. & Salpakivi-Salomaa, P. (eds.). Metsän kätköissä – Suomen metsäluonnon monimuotoisuus. Edita. 119 p. (In Finnish).

Lundqvist, L. & Nilsson, K. 2007. Regeneration dynamics in an uneven-aged virgin Norway spruce forest in northern Sweden. Scandinavian Journal of Forest Research 22(4): 304–309.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environmental Reviews 9: 1–59.

Muller, F., Baessier, C., Schubert, H. & Klotz, S. (eds.). 2010. Long-term ecological research. Springer. 456 p.

Niklasson, M. & Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology 81(6): 1484–1499.

Ohlson, M. & Tryterud, E. 1999. Long-term spruce forest continuity: a challenge for a sustainable Scandinavian forestry. Forest Ecology and Management 124(1): 27–34.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. & Bonan, G.B. (eds.). A systems analysis of the global boreal forest. Cambridge University Press, Cambridge.

Pennanen, J. 2002. Forest age distribution under mixed-severity fire regimes – a simulation-based analysis for middle boreal Fennoscandia. Silva Fennica 36: 213–231.

— & Kuuluvainen, T. 2002. A spatial simulation approach to the natural forest landscape dynamics in boreal Fennoscandia. Forest Ecology and Management 164: 157–175.

Pitkänen, A., Huttunen, P., Tolonen, K. & Jungner, H. 2003. Long-term fire frequency in the spruce-dominated forests of the Ulvinsalo strict nature reserve, Finland. Forest Ecology and Management 176(1–3): 305–319.

Pullin, A.S. & Stewart, G.B. 2006 Guidelines for systematic review in conservation and environmental management. Conservation Biology 20: 1647–1656.

— , Knight, T.M. & Watkinson, A.R. 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.

Raunio, A., Schulman, A. & Kontula, T. (eds.). 2008. The assessment of threatened habitat types in Finland – Part 1: Results and basis for assessment. Finnish Environment Institute, Helsinki. 264 p. (In Finnish with English summary). Available at: http://www.environment.fi/threatenedhabitattypes. [Cited 1 Oct 2010].

Rouvinen, S. & Kouki, J. 2002. Spatiotemporal availability of dead wood in protected old-growth forests: A case study from boreal forests in eastern Finland. Scandinavian Journal of Forest Research 17(4): 317–329.

— & Kuuluvainen, T. 2005. Tree diameter distributions in natural and managed old Pinus sylvestris-dominated forests. Forest Ecology and Management 208(1–3): 45–61.

— , Kuuluvainen, T. & Siitonen, J. 2002. Tree mortality in a Pinus sylvestris dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fennica 36(1): 127–145.

Sernander, R. 1936. Granskär och Fiby urskog. En studie över stormluckornas och marbuskarnas betydelse i den svenska granskogens regeneration. Acta Phytogeographica Suecica 8. 232 p.

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jogiste, K. 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: 201.

Siiskonen, H. 2007. The conflict between traditional and scientific forest management in the 20th century Finland. Forest Ecology and Management 249: 125–133.

Sirén, G. 1955. The development of spruce forest on raw humus sites and its ecology. Acta Forestalia Fennica 62: 1–363.

Steijlen, I. & Zackrisson, O. 1987. Long-term regeneration dynamics and successional trends in a northern

Swedish coniferous forest stand. Canadian Journal of Botany 65(5): 839–848.

Svensson, J. & Jeglum, J. 2001. Structure and dynamics of an undisturbed old-growth Norway spruce forest on the rising Bothnian coastline. Forest Ecology and Management 151(1–3): 67–79.

Tikkanen, M. 2005. Climate. In: Seppälä, M. (ed.). The physical geography of Fennoscandia. Oxford University Press, UK. p. 97–112.

Uuttera, J., Maltamo, M. & Hotanen, J. 1997. The structure of forest stands in virgin and managed peatlands: A comparison between Finnish and Russian Karelia. Forest Ecology & Management 96(1–2): 125–138.

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T. & Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. Forest Ecology and Management 250: 77–88.

Volkov, A.D. 2003. [The bio-ecological basics of exploitation of spruce forests in the north-west of taiga zone of Russia]. Bioekologicheskye osnovi ekspluatatsii el'nikov severo-zapada taezhnoy zony Rossii. Karelian Science Centre of Russian Academy of Sciences, Petrozavodsk. 250 p. (In Russian).

Wallenius, T., Kuuluvainen, T., Heikkilä, R. & Lindholm, T. 2002. Spatial tree age structure and fire history in two old-growth forests in eastern Fennoscandia. Silva Fennica 36(1): 185–199.

— , Kuuluvainen, T. & Vanha-Majamaa, I. 2004. Fire history in relation to site type and vegetation in eastern Fennoscandia, Russia. Canadian Journal of Forest Research 34: 1400–1409.

— , Pitkänen, A., Kuuluvainen, T., Pennanen, J. & Karttunen, H. 2005. Fire history and forest age distribution of an unmanaged Picea abies dominated landscape. Canadian Journal of Forest Research 35: 1540–1552.

Zackrisson, O. 1977. The influence of forest fires on North Swedish boreal forest. Oikos 29: 22–32.

— , Nilsson, M.-C., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. Journal of Ecology 83: 469–483.

Zyabchenko, S.S. 1984. [Pine forests of the European north]. Sosnovye lesa evropeyskogo Severa. Nauka, L. 248 p. (In Russian).

*Total of 87 references*

**Appendix 1.** Studies reviewed, their locations, dominant tree species and classified type of forest dynamics. Note that a single study may have documented two or more types of forest dynamics in different areas. Therefore, studies that include distinctly different areas, stand types, stand ages or species compositions are further indicated as a, b, c and d.

| ID | | Reference | Lat. | Lon. | Boreal zone | Dominant species | Dynamics type(s) |
|---|---|---|---|---|---|---|---|
| 1 | a | Aakala et al. 2009 | 67 | 24 | Northern | *P. abies* | Gap |
| 1 | b | Aakala et al. 2009 | 68 | 30 | Northern | *P. abies* | Stand-replacing |
| 2 | | Aaltonen 1919 | - | - | Northern | *P. sylvestris* | Stand-replacing, cohort, gap |
| 3 | | Arnborg 1943 | 64 | 15 | Northern | *P. abies* | Gap |
| 4 | | Bjune et al. 2009 | 59 | 9 | Middle | *P. abies* | Gap |
| 5 | | Caron et al. 2009 | 67 | 24 | Northern | *P. abies* | Patch, gap |
| 6 | | Dolezal et al. 2006 | 66 | 26 | Northern | *P. abies* | Patch, gap |
| 7 | | Engelmark et al. 1998 | 67 | 20 | Northern | *P. sylvestris* | Cohort, gap |
| 8 | | Fraver et al. 2008 | 65 | 16 | Northern | *P. abies* | Patch, gap |
| 9 | | Hofgaard 1993 | 64 | 15 | Northern | *P. abies* | Gap |
| 10 | | Hörnberg et al. 1995 | - | - | Middle-northern | *P. abies* | Gap |
| 11 | | Hytteborn et al. 1987 | 67 | 17 | Northern | *P. abies* | Gap |
| 12 | | Jonsson 2000 | 66 | 21 | Northern | *P. abies* | Patch, gap |
| 13 | | Jönsson et al. 2007 | 65 | 16 | Northern | *P. abies* | Gap |
| 14 | | Karjalainen and Kuuluvainen 2002 | 65 | 30 | Middle | *P. sylvestris* | Cohort |
| 15 | | Kazimirov 1971 | - | - | - | *P. abies* | Cohort |
| 16 | | Kullman 1991 | 63 | 13 | Northern | *P. sylvestris* | Cohort, gap |
| 17 | | Kuuluvainen and Juntunen 1998 | 62 | 31 | Southern | *P. sylvestris* | Patch |
| 18 | | Kuuluvainen and Kalmari 2003 | 62 | 24 | Southern | *P. abies* | Stand-replacing |
| 19 | | Kuuluvainen et al. 2002 | 65 | 30 | Middle | *P. sylvestris* | Cohort |
| 20 | | Lampainen et al. 2004 | 65 | 30 | Middle | *P. sylvestris* | Stand-replacing, cohort |
| 21 | | Lassila 1920 | - | - | Northern | *P. sylvestris* | Cohort |
| 22 | | Leemans 1991 | 60 | 18 | Middle | *P. abies* | Gap |
| 23 | a | Lilja et al. 2006 | 66 | 30 | Northern | *P. abies* | Stand-replacing |
| 23 | b | Lilja et al. 2006 | 66 | 30 | Northern | *P. abies* | Stand-replacing |
| 23 | c | Lilja et al. 2006 | 66 | 30 | Northern | *P. abies* | Stand-replacing |
| 24 | a | Linder 1998 | 61 | 14 | Middle | *P. sylvestris* | Cohort |
| 24 | b | Linder 1998 | 61 | 14 | Middle | *P. abies* | Gap |
| 25 | a | Linder et al. 1997 | - | - | Middle-northern | *P. abies* | Gap |
| 25 | b | Linder et al. 1997 | - | - | Middle-northern | *P. abies* | Stand-replacing |
| 25 | c | Linder et al. 1997 | - | - | Middle-northern | *P. sylvestris* | Stand-replacing, cohort, gap |
| 25 | d | Linder et al. 1997 | - | - | Middle-northern | *Betula* spp. | Stand-replacing, cohort, gap |
| 26 | | Lundqvist and Nilsson 2007 | 65 | 16 | Northern | *P. abies* | Gap |
| 27 | | Pitkänen et al. 2003 | 64 | 30 | Middle | *P. abies* | Cohort |
| 28 | | Niklasson and Granström 2000 | 64 | 18 | Northern | *P. sylvestris* | Cohort |
| 29 | | Ohlson and Tryterud 1999 | 60 | 10 | Southern | *P. abies* | Gap |

| ID | | Reference | Lat. | Lon. | Boreal zone | Dominant species | Dynamics type(s) |
|---|---|---|---|---|---|---|---|
| 30 | a | Rouvinen and Kouki 2002 | 63 | 30 | Middle | *P. abies* | Gap |
| 30 | b | Rouvinen and Kouki 2002 | 63 | 30 | Middle | *P. sylvestris* | Gap |
| 31 | a | Rouvinen and Kuuluvainen 2005 | 62 | 31 | Southern | *P. sylvestris* | Cohort, gap |
| 31 | b | Rouvinen and Kuuluvainen 2005 | 62 | 31 | Southern | *P. sylvestris* | Gap |
| 32 | | Rouvinen et al. 2002 | 65 | 30 | Middle | *P. sylvestris* | Gap |
| 33 | | Sernander 1936 | 60 | 18 | Middle | *P. abies* | Stand-replacing, patch, gap |
| 34 | | Sirén 1955 | - | - | Northern | *P. abies* | Stand-replacing, cohort, gap |
| 35 | | Steijlen and Zackrisson 1987 | 66 | 19 | Northern | *P. sylvestris* | Cohort |
| 36 | | Svensson and Jeglum 2001 | 63 | 20 | Middle | *P. abies* | Gap |
| 37 | | Uuttera et al. 1997 | 62 | 30 | Middle | *P. sylvestris* | Gap |
| 38 | | Volkov 2003 | - | - | - | *P. abies* | Gap |
| 39 | a | Wallenius et al. 2002 | 64 | 30 | Middle | *P. sylvestris* | Cohort |
| 39 | b | Wallenius et al. 2002 | 64 | 29 | Middle | *P. abies* | Stand-replacing, cohort |
| 40 | | Wallenius et al. 2005 | 66 | 30 | Northern | *P. abies* | Stand-replacing |
| 41 | | Zackrisson 1977 | 64 | 18 | Middle | *P. sylvestris* | Stand-replacing, cohort |
| 42 | | Zackrisson et al. 1995 | - | - | Northern | *P. sylvestris* | Cohort |
| 43 | | Zyabchenko 1984 | - | - | - | *P. sylvestris* | Cohort |