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# Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996

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**Abstract**

Changes in the structure and composition of 123 000 ha of boreal forests in Sweden, were analysed using historical records. These forests had not been commercially logged when the first forest surveys took place in the late 1800s, so the earliest surveys provide unique data on structure of the natural boreal forest. The pre-exploitation forests had many large-diameter living and standing dead trees (*Pinus sylvestris* L. and *Picea abies* (L.) Karst.), and were dominated by stands > 200 years old. Commercial exploitation in the late 1800s, subsequent intensive forest management and fire protection have generated a forest landscape dominated by relatively young and dense stands, totally different from the pre-exploitation forests. Since the late 1800s, both the number of large trees and the volume of snags have been reduced by about 90%, and the area of old stands has diminished to < 1%. These fundamental changes have reduced the number of habitats for many red-listed species considerably. We conclude that the essential characteristics of the natural forest landscape have to be re-created in order to restore and maintain natural biodiversity. 

*Keywords:* Forest history; Old-growth forest; Stand structure; Red-listed species; Dead trees

## 1. Introduction

Present forest management practice is changing the structure and dynamics of forest ecosystems to an ever increasing extent. In addition, fire protection has changed the rate of natural disturbances in most forests. We believe that efforts to maintain ecosystem function and biodiversity must be based on sound understanding of the primeval forest's structure and processes (cf. Anon., 1993, 1995). For this reason, and in order to understand the present status of forest ecosystems in relation to the primeval state, there is a need for historical analysis (Christensen, 1989).

Recently, increasing attention has been paid to the large number of threatened species in forest ecosystems. In Sweden there are 1487 forest species on the national red-data lists (Berg et al., 1994). About 40% are found in the boreal forest, which is the dominant forest type, comprising almost 70% of the forest in the country.

Stand factors such as age and density, and habitat elements such as old trees, snags and downed logs are of vital importance for the forest species on the Swedish red-data list (Berg et al., 1994). However, the quantity of these ecologically important habitat elements has been reduced in the boreal part of Sweden (Kohh, 1975; Linder and Östlund, 1992; Ericsson, 1997; Östlund et al., 1997), due to more intensive forest management during the last 150 years. There are few estimates of the magnitude of these changes, but some of these characteristics have been investigated in forest reserves, and compared with the state in the managed forest landscape (Lämås and Fries, 1995; Majewski et al., 1995). However, such comparisons have an obvious weakness since all protected forests in boreal Europe lack natural fire disturbance.

So far, most retrospective analyses of the Swedish forests have had their starting point in the late 1920s, when the Swedish National Forest Survey was started (SOU, 1932:26). Data from the first, and subsequent, surveys give a general illustration of the changes that have taken place within Swedish forests during the last 70 years. While the National Forest Survey provides a comprehensive record of changes that have occurred in the forest during most of the present century, it does not give any information on the forest structure before the

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late 1920s. It also lacks important ecological data concerning typical characteristics of old-growth forests. This means that there is a general shortage of retrospective data on forest stand properties that are essential for threatened species. Forest records covering a longer period than the National Forest Survey are kept at some large forest holdings, for instance the records of the Orsa Forest Common, Hamra State Forest and Älvdalen Forest Common, which form the basis of this study. A 'forest common' is collectively owned forest land belonging to the landowners of a particular parish. These records are unique in that they are very detailed and they include forest stand data from the time when most of these forest landscapes were largely in a virgin state, before cutting operations had begun. Therefore, they can provide valuable information on the structure of the natural boreal forest landscape. They can also be used for comparisons with present records to reveal the magnitude of the structural changes that forest exploitation and forest management have brought about.

### 1.1. The aim of the study

The major goal of this study was to assess the nature and magnitude of structural changes that have taken place since the first large-scale logging operations in the boreal forest landscape. We have focused on structural components which were distinctive features of the primeval boreal forest landscape, i.e. the abundance of large-diameter trees, standing dead trees (snags), and old forest stands. We have also examined changes in standing volume and tree species composition of the forests. We discuss ecological implications of our findings for the forest fauna and flora, and suggest necessary changes in forest management practices, in order to restore important ecological processes, and to maintain biological diversity in boreal Scandinavia.

## 2. The study area

### 2.1. General description of the forests

Three large forest holdings with a well-documented forest history were selected; Orsa Forest Common (Orsa) and Hamra State Forest (Hamra) are situated in the north-east of the county of Dalarna, and Älvdalen Forest Common (Älvdalen) is situated c. 70 km southwest of these areas (Fig. 1). Additional information about the physical settings are found in Table 1. These forests are located within the main boreal zone (Ahti et al., 1968) and together they contain almost 7% of the total forested area of Dalarna. The dominant tree species are Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) Karst, hereafter referred to as pine and spruce respectively. The most common deciduous broad-leaved trees are hairy birch *Betula pubescens* Ehrh. and silver birch *B. pendula* Roth.; there are also scattered aspen *Populus tremula* L., grey alder *Alnus incana* L., rowan *Sorbus aucuparia* L. and goat willow *Salix caprea* L.

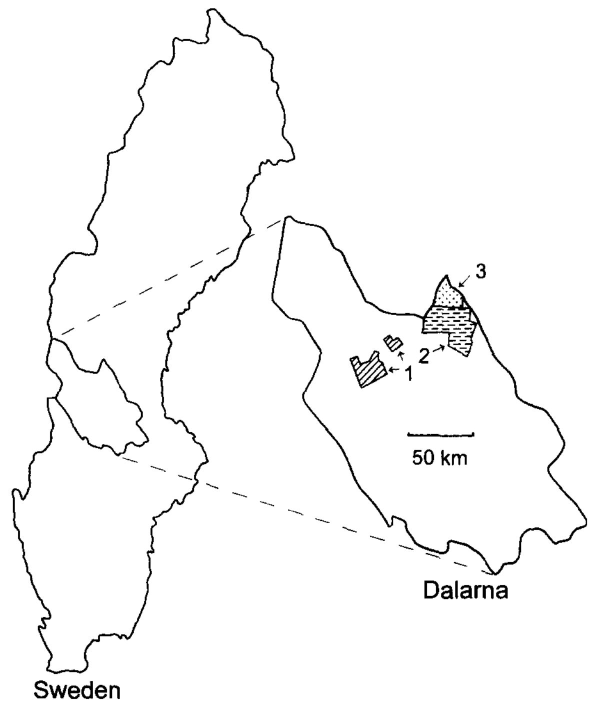


Fig. 1. Location of the province of Dalarna in Sweden and the studied forest landscapes: (1) Älvdalen Forest Common, (2) Orsa Forest Common, and (3) Hamra State Forest.

### 2.2. General history of the area

In the studied forest landscapes, large scale logging was introduced in the late 1800s, much later than in

Table 1
General information on the studied forests

| Study area | Geographic location | Area of forest land (ha) | Altitude[a] (m a.s.l.) | Bedrock[a] |
|---|---|---|---|---|
| Orsa | 61° 35′ N, 14° 50′ E | 53 000 | 250–550 | gneiss, granite (sandstone, porhory) |
| Hamra | 61° 45′ N, 14° 45′ E | 28 000 | 350–660 | gneiss, granite |
| Älvdalen | 61° 10′ N, 13° 40′ E | 49 000 | 270–760 | porphory (sandstone) |

[a] According to Holmgren (1938); Tamm and Wadman (1945); Lundqvist (1951); Kolmodin (1953); Hjelmqvist (1966).

most of boreal Sweden. Furthermore, in contrast to most other forests in boreal Sweden, forest surveys preceded the first logging of the forest (Östlund, 1993).

Most of the people living in this area prior to the 1900s were farmers, and their economy was primarily based on cattle husbandry, which depended on winter fodder from natural meadows and grazing in the vast forests during the summer. Farmers commonly had summer pasture in the forest for their cattle relatively far from the villages (Frödin, 1925; Veirulf, 1953). Various forest resources for domestic uses such as wood for fuel, bark for food and fodder, wood for fencing, etc., were generally harvested from the immediate surroundings of the villages. Further away, cattle grazed, and occasional burning was undertaken in the forests to improve grazing. In the 1500s and 1600s, farmers from Finland started to establish new settlements in some areas in the inner parts of northern Sweden (Tarkiainen, 1990). These were generally located in remote parts, far away from the older villages. The Finnish settlers had a different agricultural tradition from that of the local farmers. They relied more on slash-and-burn agriculture in the forest, in combination with cattle herding. They also usually chose to establish their settlements at higher elevations (Jonsson, 1970; Tarkiainen, 1990). The impact of these settlements on the forest landscape was probably rather small. Descriptions from the Hamra State Forest from the early 1900s claim that human impact on the forest was restricted to the immediate surroundings of the Finnish settlements (Andersson and Hesselman, 1907). However, their slash and burn technique may have influenced the fire regime.

In the 1700s, farmers from some of the villages also sold locally-produced charcoal to blast furnaces and iron works. In 1864, the forest within the Orsa parish was inspected by forest officials from the National Board of Forestry. They commented on the state of the forest and concluded that the forest near the villages was intensively used in contrast to the forest in the northern part of the parish, which was described as virgin at that time (Riksarkivet Skogsstyreleen EIIIb:1). This northern part of the parish would later become Orsa Forest Common and Hamra State Forest.

Forest fires have been a recurrent disturbance factor in the boreal forest. In Älvdalen State Forest, a large forest holding bordering Älvdalen Forest Common, there was a mean fire interval of 67 years in the period 1400–1850 (Kohh, 1975). Analysis of old trees and stumps from Hamra State Forest and Orsa Forest Common have indicated similar mean fire intervals (Linder, in press and Niklasson, unpublished data). These data also indicate that most fires were surface fires, which mainly killed spruce, deciduous trees and small pines, but not the larger trees. When large scale logging was introduced in the late 1800s, effective fire protection of the forests was organised. Fire watchtowers were built, telephone lines were erected, and firefighters were hired during the summer. This resulted in a sharp decline in forest fires within a short period of time (Pettersson, 1909; Holmgren, 1938).

The forest commons and the State Forests were established in the late 1800s, when delineation (separation of private and public land) and enclosure (division of land among the different landowners in the villages) were carried out in this part of the county (Nordenstedt, 1928). Most of the unclaimed forest land was allotted as forest commons to landowners in existing villages, but some parts were designated State Forests under the administration of the National Forest Service. The forest commons were to be used on a communal basis, and the income from the selling of timber was used for collective needs, or split among the villagers according to their relative share of the village assessment units.

In 1885 and 1888, after the delineation of the forest properties, the landowners of the forest commons assessed the amount of timber trees within the forest. These surveys produced unique sets of data on forest structure before the onset of commercial logging, especially in the case of Orsa Forest Common and Hamra State Forest, both of which were described as un-logged, virgin forests at the time (Andersson and Hesselman, 1907; Schotte, 1913; Kolmodin, 1953). However, in Älvdalen Forest Common, some high-grading had occurred before the first forest surveys (Holmgren, 1938).

Between 1887 and 1895, the forest commons investigated in this study sold logging contracts including large timber trees at public auctions (Holmgren, 1938; Kolmodin, 1953). This resulted in an almost total loss of large diameter trees in these two areas. In Hamra State Forest, the large diameter trees were gradually exploited according to strict regulations imposed by the Forest Service (Nilsson, 1933). The regulations implied that consideration should be paid both to the sustainability of the existing timber resources, and to the regeneration of the new forest.

In the early 1900s, new forest management practices were gradually introduced, including different silvicultural systems; small clear cuts, single tree selection and group tree selection combined with natural regeneration, soil scarification, sowing and planting (Pettersson, 1909; Holmgren, 1938; Kolmodin, 1953). However, until the 1940s, natural regeneration without any soil treatment was the most common regeneration technique. Commercial and pre-commercial thinning of stands, with the intention of creating evenly-aged stands was also introduced, as was the draining of wetlands and (later) nitrogen fertilisation, to increase stand productivity. Until the 1990s, dead standing trees (snags) were removed from the forests, since they were seen as a source of dispersal of unwanted wood-living fungi and insects, which might attack healthy trees. From the 1950s, clearcutting was the dominant felling system, which in most cases was followed by planting of tree-seedlings. In the 1960s and 1970s, the clearcuts increased in size, and efforts were made to reduce the presence of broadleaf trees in young stands, by spraying with herbicides for instance. In the 1990s, silvicultural practices have been directed towards the promotion of more natural conditions so the size of clearcuts has decreased, natural regeneration has increased, and a larger proportion of broadleaf trees has been encouraged.

## 3. Material and methods

### 3.1. Sources

This study is primarily based on published reports and unpublished records from the archives of the three forest holdings. The most important records are the forest surveys. The first surveys included only the presence of large trees, i.e. trees larger than 33 cm DBH (Orsa and Älvdalen) and trees larger than 30 cm DBH (Hamra). The surveys were completed in 1885 (Orsa), 1888 (Älvdalen) and 1891 (Hamra) and were conducted as total stem counts in Orsa and Älvdalen, and as a strip survey in Hamra. In Orsa and Älvdalen all large trees were recorded in 1-inch classes, while in Hamra only the total number was recorded. A total of >2·8 million trees was recorded in Orsa (Gyllenhammar, 1886), and 1·6 million in Älvdalen (Collén, 1888). The forest commons were divided into operational logging areas, which ranged in size between 140 and 1300 ha. Subsequently, strip surveys were conducted in the early 1900s and, later, a series of sample plot surveys. The surveys in the 1900s also included delimitation of individual forest stands, and descriptions of stand characteristics such as stem volume and tree species composition (Orsa: Pettersson, 1909; Orsa besparingsskogs arkiv, 1896–1904, 1919–1920, 1939–1940, 1956, 1966, 1971–1972, 1981–1982 and 1991; Hamra: Arkivhuset, Falun. Domänverkets arkiv, 1905–1911, 1920–1921, 1937, 1953, 1966; ASSI/Domän Hedemora förvaltning (Skogsindelningsregistret), 1991; Älvdalen: Älvdalens besparingsskogs arkiv (Skogsindelnings handlingar), 1906, 1915–1917, 1936, 1965, 1984, 1996). Up until the years 1936 (Älvdalen), 1937 (Hamra), and 1939 (Orsa), the forest surveys only recorded trees larger than 10 cm DBH, but all trees were included in later surveys.

Records, forest maps, and descriptions of logging and the general state of the forest, have been used to corroborate and supplement the information from the forest surveys (Orsa: Gyllenhammar, 1886; Pettersson, 1909; Orso besparingsskogs arkiv, skogsindelnings handlingar 1896–1904; OBA 1919–1920; Kolmodin, 1953; Hamra: Andersson and Hesselman, 1907; Schotte, 1913; SOU 1922:22; Nilsson, 1933; Fredenberg, 1936; Älvdalen: Holmgren, 1938; Aldemark, 1988). National Forest Survey records from the county of Dalarna have also been analysed to compare the results from the holdings with those covering a larger area (SOU 1932:26; Hagberg, 1949; Nilsson and Östlin, 1961; Arman, 1969; Svensson et al., 1989; Anon., 1996).

### 3.2. Analysis

Since the first surveys only included number of trees, diameter (DBH) and species (in Orsa and Älvdalen, but not Hamra), it was not possible to reconstruct total standing volume or tree species composition from their data. Therefore we had to use logging records, covering the time span between the first and the second survey, and data from the second survey, to reconstruct standing volume and species composition prior to the first exploitation. Accordingly, to estimate the standing volume in the late 1800s, we used the records of standing volume and tree species composition from the second survey, added the volume of the logged trees and snags, and subtracted the growth recorded between the first and second surveys. The late 1800s tree species composition in Orsa and Älvdalen was calculated in the same way. However, in Hamra, no record was kept of the species logged, so we assumed that the species composition of the large trees was the same in 1891 as in the second survey. We also assumed that the abundance and species composition of trees smaller than 30 cm DBH was the same in 1891 as found in the second survey.

## 4. Changes in forest structure

The structure of the forests, including standing volume, age class distribution, tree species composition, and the presence of old-growth structures such as large trees, snags and downed logs has drastically altered since the late 1800s. The complex interactions between a gradual logging of old-growth forests, introduction of silviculture and fire-elimination are the driving forces behind the transformation of the forest (cf. Langston, 1995). In the studied forests, old-growth has been turned into managed forest within the course of a century. Larger proportions of fast-growing young stands have been gained but, at the same time, the forest has suffered severe losses of important ecological niches and biodiversity.

### 4.1. Standing volume

The standing volume at the time of the first forest surveys was 120 $m^3 ha^{-1}$ in Orsa, 141 $m^3 ha^{-1}$ in Hamra, and 95 $m^3 ha^{-1}$ in Älvdalen. Since Orsa and Hamra were described as virgin forests at the time, we believe that their figures are representative of the natural forest landscape of this part of the boreal forest. The lower standing volume in Älvdalen is presumed to be primarily due to lower site productivity, but also partly due to commercial cutting of timber that took place in the mid-1800s. Consequently, the recorded average volume is probably lower than what could be expected in this area under natural conditions.

In Orsa and Älvdalen, the standing timber volume was drastically reduced by the first large cuttings in the late 1800s, while only a minor decrease occurred in Hamra at the same time (Fig. 2). After the initial exploitation, the standing volume has gradually increased in the forest commons, due to intensive silvicultural measures and cessation of browsing by domestic animals. However, in Hamra, the standing volume decreased successively until the 1970s. It should be noted that the volume estimates exclude trees smaller than 10 cm DBH for the period 1885 to the 1930s, and deciduous trees for the period 1885–1920s. Therefore the actual standing volume in the first surveys was somewhat larger than recorded. Consequently, the present timber volumes are still lower than they were in the natural state (Fig. 2).

The timber volume in Hamra State Forest very slowly decreased after the initial exploitation in the late 1800s, indicating a more gradual change of the forest landscape in Hamra than occurred in the forest commons. The changes in standing volume for the county of Dalarna as a whole since 1923 were similar to those recorded for the forest commons (Fig. 2).

### 4.2. Number of large trees

At the time of the first forest surveys, the number of large-diameter trees was 77 trees $ha^{-1}$ in Hamra, 38 $ha^{-1}$ in Älvdalen, and 53 $ha^{-1}$ in Orsa. The surveys at the forest commons also showed that only a very small fraction of the landscape had < 20 large trees per ha (Table 2). Pine was the dominant species among the large trees in both Orsa and Älvdalen, constituting 90 and 91% of the large trees, respectively, the rest being spruces. In Hamra, there were no data on tree species composition from the first survey, but in 1911, 68% of the large trees were pines.

Due to intensive logging during the late 1800s to the mid-1900s, and the present silvicultural practices, with rotation periods of about 120 years in this region, large trees are very scarce in the forest landscape today. The latest surveys including data on large-diameter trees recorded 13, 4 and 7 $ha^{-1}$ of them in Hamra (in 1966, DBH > 30 cm), Älvdalen (in 1984, DBH > 35 cm) and Orsa (in 1991, DBH > 34 cm), respectively—about 15–20% of the densities of large trees found in the 1880s.

The discrepancy between the present forest landscape and the natural forest landscape is even more striking when the largest trees are considered, i.e. trees larger than 50 cm DBH. Such trees are totally absent in the studied forests today (Fig. 3). This is also a general feature of the present Swedish boreal forest landscape. According to the National Forest Survey for the period 1990–1994, the number of trees larger than 50 cm DBH was c. 0·2 trees $ha^{-1}$ in the county of Dalarna (Anders Lundström, pers. comm.).

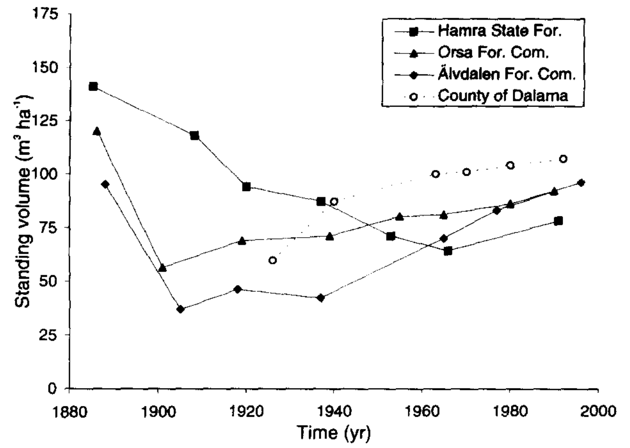


Fig. 2. Changes in standing volume between the 1880s and the 1990s in the studied forests, and for the county of Dalarna since 1923. (Before 1940 only coniferous trees > 10 cm DBH were included, thereafter all trees were included.)

### 4.3. Number of snags

Large numbers of dead standing trees (snags) were a characteristic of the natural forest landscape of northern Sweden, according to reports of travellers and foresters from the 1700s until the 1950s (Näsström, 1925; Holmgren, 1950; Uggla, 1953). There were 11–13 $m^3 ha^{-1}$ of snags in the studied forests in the late 1880s. Since that time, the quantity has diminished considerably (Fig. 4). A similar development was also reported from the nearby Älvdalen State Forest, where there was 8·3 $m^3 ha^{-1}$ of snags in 1922, and 0·8 $m^3 ha^{-1}$ in 1952 (Kohh, 1975).

The quantity of snags has not been recorded in the studied forests since the 1950–1960s because of their low

Table 2
The distribution of forest land for different density classes of large-diameter trees (DBH > 33 cm) in two forest commons in the late 1880s

| Area | Total forest land (ha) | % of forest land for different density classes ($ha^{-1}$) | | | | |
|---|---|---|---|---|---|---|
| | | < 20 | 20–40 | 40–60 | 60–80 | > 80 |
| Orsa | 53 000 | 0·3 | 17·9 | 57·3 | 20·2 | 4·3 |
| Älvdalen | 49 000 | 1·2 | 59·7 | 35·6 | 3·4 | — |

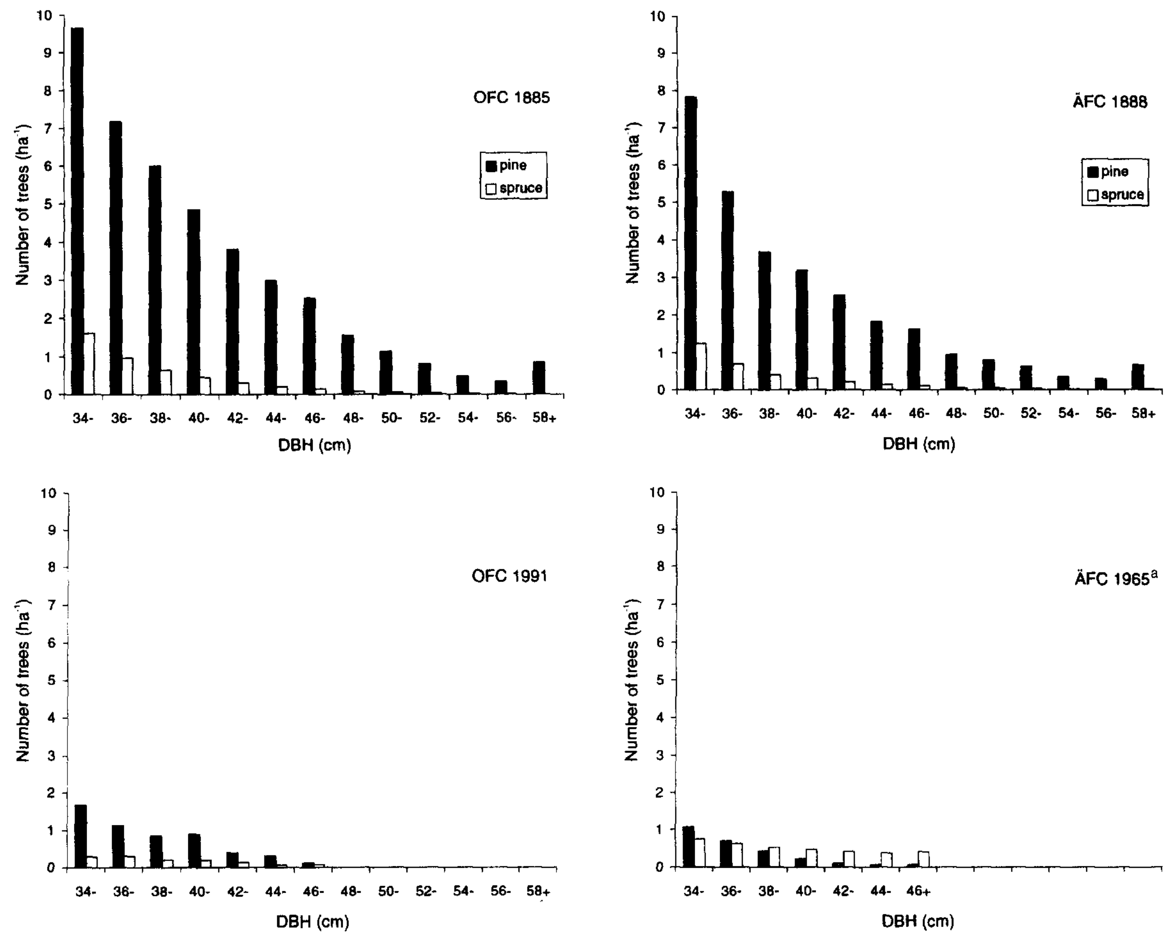


Fig. 3. Comparison of the number of large diameter trees in 1885 and 1991 in Orsa (OFC), and in 1888 and 1965[a] in Älvdalen (AFC). ([a] The last comparable survey (with diameters recorded in 2 cm classes) was conducted in 1965. The latest survey with diameter data, in 1984, only collated data in 5 cm classes. The number of large pines was then about 20% higher, while the number of spruces was 80% lower than the numbers found in 1965.)

abundance. However, their present volume is probably comparable to the quantities reported by the National Forest Survey for the county of Dalarna as a whole (Fig. 4), which means that the quantity of snags has been reduced by more than 90% since the late 1800s. According to the National Forest Survey, the volume of snags suitable for fire wood has been relatively stable, at *c.* 1 $m^3 ha^{-1}$, from the 1920s until the present time in the county of Dalarna (Fig. 4). This clearly shows that the major changes in the boreal forest landscape occurred before the 1920s.

The very low quantities of dead trees during most of the 1900s is due to the fact that snags and logs have been continuously removed from the forests, partly for use as fire-wood and for log-driving constructions in the rivers (Ericsson, 1997), and partly to 'clean up' unwanted trees from the forests (Öckerman, 1993). Directions in the Forestry Act of 1979, for example, recommended that all damaged trees should be removed from the forest (SKSFS, 1979:3). Today, a more liberal view is applied, and up to 5 $m^3 ha^{-1}$ of newly dead or wind-thrown trees is tolerated (SKSFS, 1993:2).

### *4.4. Stand age*

From the time of the first loggings, there are only imprecise descriptions of forest age. In Orsa, the trees in pine-dominated stands were generally 225–250 years old, although much older trees could be found. The trees in the spruce-dominated stands were generally younger, c. 160 years old (Kolmodin, 1953). In Hamra, about 80% of the forest consisted of older stands, generally 200–300 years old at the beginning of this century (Schotte, 1913), but no descriptions are available from Älvdalen. More detailed information on age distributions of the forests is provided from the second forest surveys, which show that the proportion of old stands was about 30–60% of the total area (Table 3). However, the age records from the two forest commons were criticised for underestimating the age of the stands (Orsa besparingsskags arkiv, skagsindelningshardlingar, 1919–1920). At that time, most of the stands were unevenly aged, making it difficult to determine their age (Orsa besparingsskags arkiv, skagsindelningshardlingar, 1896–1904). It was not only these particular forests that were dominated by unevenly aged stands at that time; 35% of the forest land in the county of Dalarna and close to 50% of the forest land in all northern Sweden was classified as unevenly aged in the 1920s (SOU, 1932:26).

The proportion of old stands in the studied areas has decreased substantially since the beginning of this century (Table 3). The same pattern is also recorded for the entire State Forest in boreal Sweden, where 44% of the area (mountainous forest dominated by old-growth forests excluded) consisted of stands older than 150 years in 1915 (SOU, 1922:22), while in 1990 the corresponding figure (mountainous forest included) was only 7% (ASSI Domän, Stockholm skogsindelningsregistret 1990; ASSI Domän, Jokkmokks förvaltning skogsindelningsregistret 1991).

## 5. Changes in tree species composition

The tree species composition in the late 1880s differed markedly between the investigated areas (Fig. 5). We believe that this was mainly due to different soil and hydrology conditions, which resulted in different fire regimes. Nevertheless, the major changes since the late

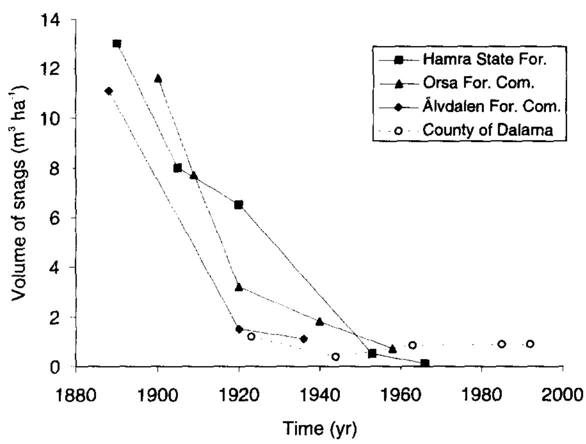


Fig. 4. Changes in the volume of standing dead trees since the late 1800s at Hamra State Forest, Orsa Forest Common, Älvdalen Forest Common, and since 1923 in the county of Dalarna.

Table 3
Changes in the abundance of old forest stands in the studied areas during the 1900s

| Area | Year | % of older forest |
|---|---|---|
| Orsa | 1919 | 57[a] |
| | 1991 | 11[a] |
| Hamra | 1921 | 44[b] |
| | 1991 | 1[b] |
| Älvdalen | 1916 | 29[c] |
| | 1996 | 1[c] |

[a] > 120 years.
[b] > 140 years.
[c] > 150 years.

1880s have been similar in all areas; the proportion of pine decreased during the rapid exploitation phase, while the proportion of spruce increased. Such changes have also been described for other parts of the boreal Swedish forest (Örtenblad, 1894; Kempe, 1909; Tirén, 1937). However, after the 1920s the trends have changed, and pine has increased at the expense of spruce

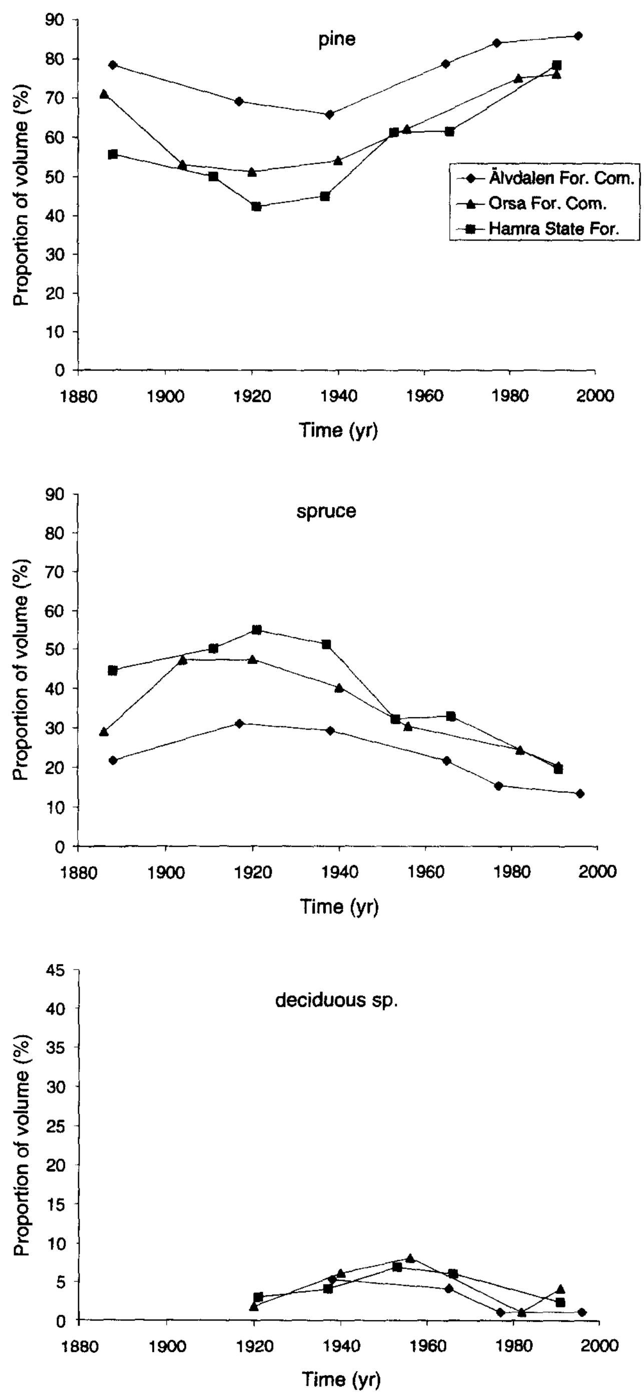


Fig. 5. Changes in tree species composition for the studied forests since the late 1880s based on stem volume figures of living trees. Data on deciduous trees were not available before 1920 for Hamra and Orsa. In Älvdalen , the first data on deciduous trees were recorded in 1936.

(Fig. 5). This is a well-documented shift which has occurred throughout the Swedish boreal forest landscape (Lindroth, 1995), due to silvicultural measures such as thinning in favour of pine, and large scale planting of pine seedlings.

From the surveys conducted in the 1920s, and onwards, there is also data on the proportion of deciduous trees, which tended to increase from the 1920s to the 1950s, and thereafter declined (Fig. 5). The early increase was mainly due to the introduction of clear-cutting on a large scale, which favoured pioneer species such as hairy birch, and the later decrease was a result of the 'battle against deciduous trees' that was initiated in Sweden around 1950, and effected throughout the 1960s and 1970s by various means including extensive use of herbicides (Öckerman, 1993). A consequence of this development was a drastic reduction of older deciduous trees (Östlund et al., 1997).

Today, several large Swedish forest companies are trying to increase the proportion of deciduous trees in forests to about 10–20%, to improve the survival for species which depend on them, since there is a general assumption that the 'natural proportion' of deciduous trees is much higher than the present proportion (Angelstam et al., 1993; Bernes, 1994). This may be true for some forest landscapes, but our data from the 1920s indicate that deciduous trees accounted for only 2 and 3% of the standing volume in Orsa and Hamra, respectively, indicating a low natural abundance of deciduous trees in these landscapes. In this context, it is important to note that there is a general lack of information about the abundance of deciduous trees in the Swedish primeval boreal landscape. Older descriptions of a large abundance of deciduous stands (e.g. Lovén, 1901; Zackrisson, 1977) do not necessarily reflect natural conditions. They may, equally likely, have been a result of human activity, such as burning for pasture and temporary cultivation.

## 6. Discussion

### *6.1. The effect of structural changes on flora and fauna*

The disappearance of natural forest stands and their ecological niches have undoubtedly impaired the survival for species associated with old-growth structures. The most dramatic structural change is the removal of dead trees. Berg et al., 1994 estimated that about 47% of the forest species on the red data list are dependent on snags or logs. Such species include many highly specialised species of, for example, crustose lichens, liverworts, wood-living fungi and insects (Heliövaara and Väisänen, 1984; Söderström, 1988; Tibell, 1992; Aronsson, et al., 1995; Bader, et al., 1995). It has also been shown that the abundance of dead trees is the most important variable explaining biological diversity in boreal old-growth swamp forests (Ohlson et al., 1997).

Another problem is the general loss of old-growth stands. Several species of the original bird community in the boreal forest, including the Siberian tit *Parus cinctus* L., crested tit *P. cristasus* L., Siberian jay *Perisoreus infaustus* L. and three-toed woodpecker *Picoides tridactylus* L., have decreased drastically since the 1940s in northern Finland due to the loss, and fragmentation, of old forest stands (Väisänen et al., 1986). The loss of natural forest stands has also brought a decrease in the abundance of epiphytic lichens; lichen biomass being significantly lower in managed boreal stands than in old-growth stands (Esseen et al., 1996). The numbers and biomass of invertebrates living in the tree canopy is also larger in old-growth boreal spruce forests than in managed forests, which may reduce foraging possibilities for passerine birds (Pettersson et al., 1995).

The density of the forest is an important, but often overlooked, aspect for fauna and flora. We have shown that the average standing volume is still lower today than that of the natural state, but most predictions assume a further increase in the future (Lindroth, 1995). Consequently, the standing volume will probably be of the same magnitude as it was in the late 1800s, within the next 20 years. But the number of large diameter trees is only a fraction of what it was then, which means that the forests of today and the near future, will contain a much higher number of trees than would be found in the natural state. The resulting trend towards denser forests is a general phenomenon in both boreal and hemiboreal Swedish forests (Anon., 1996), and is very inhibitory for light-demanding, competition-sensitive species, such as the vascular plants *Anemone vernalis* L. and *Chimphila umbellata* L. Barton (Ingelög et al., 1987), and for warmth-demanding animals like the sand lizard *Lacerta agilis* L. (Berglind, 1995a; Ahlen and Tjernberg, 1996). Many invertebrates also suffer in dense forest conditions (Heliövaara and Väisänen, 1984; Berglind, 1995b), and several threatened wood-inhabiting insects have been found in large numbers on dead trees in exposed sites, including cut sites, illustrating the ecological importance of such features (Ahnlund and Lindhe, 1992; Ahnlund, 1996). The increased tree density may also explain the decline of bird species such as the nightjar *Caprimulgus europaeus* L. and wood lark *Lullula arborea* L. (Stolt, 1972; Roos, 1974), which both prefer open forest habitats (Stolt, 1972; Valkama and Lehikoinen, 1994).

The trend towards denser forests occurs not only in managed forests but also in forest reserves in Scandinavia, since most reserve regulations include both exclusion of cutting operations and forest fires (Linder, 1998 in press; Linder et al., 1997). This increase in density must be acknowledged by conservationists, or forest reserves will attain unnaturally high stand densities.

This phenomenon could also explain the lower numbers of insects found in the field- and bottom-layers in forest reserves than in managed forests (Biström and Väisänen, 1988; Niemelä et al., 1988).

The disappearance of large and old trees represents a loss of one of the key characteristics of a natural forest, with serious implications for the fauna and flora. For example, it reduces the possibilities of finding suitable nesting trees for large raptors such as the golden eagle *Aquila chrysaëtos* L., which needs tree crowns consisting of coarse branches, a feature that only develops in very old trees, for its nests (Tjernberg, 1983). Another species which suffers from the decrease of large and old trees is the black woodpecker *Dryocopius martius* L., whose nests are mostly excavated in pines larger than 50 cm DBH and almost never in trees with DBH less than 35 cm (Hågvar et al., 1990; Johnsson, 1993). Since many other birds and mammals use these holes as nests and hiding places, the decrease of larger trees could also have negative consequences for a wide range of other species (Esseen et al., 1997). There is also a large number of beetles that only appear on large and old trees, depending on the particular bark and wood structures present (Ehnström and Waldén, 1986).

### 6.2. Management implications

Our results show that many ecologically important structures have been severely reduced in the studied forest landscapes since the late 1800s. To reduce the threat to red-listed species, all remaining old-growth characters must be kept. Furthermore, all remaining old-growth stands below the mountainous areas, and all older stands which will develop such characters in the near future, must be protected. In the long term, the proportion of really old stands must increase from the present very low level. Furthermore, measures to promote the renewed occurrence of large-diameter trees and snags must be introduced on a large scale in the forest landscape, i.e. significant numbers of storm-hardy trees must be left at cut sites. Prescribed burning should be carried out to a much greater extent than today for regeneration purposes, with the aim of getting a more diverse tree species composition in the new stands, simultaneously producing more snags and, in the longer run, more downed logs. This method should also be used in mature stands to mimic fire disturbance in older stands, with the aim of producing more natural multistoried pine stands (cf. Östlund et al., 1998). In general, fire is essential to sustain basic ecosystem functions in the boreal forest (Zackrisson et al., 1996). Felling machines, or special explosives (so called blasting clamps), could also be used to produce snags from living trees, especially trees with stem rot in the lower parts, which seems to be a prerequisite for several red-listed wood-living fungi (Renvall, 1995).

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