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Forest history and the development of old-growth characteristics in fragmented boreal forests

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Abstract

Questions: Can small and isolated high-conservation value forests (e.g. designated woodland key habitats) maintain old-growth forest characteristics and functionality in fragmented landscapes? To what extent have past disturbances (natural and anthropogenic) influenced the development of old-growth characteristics of these forests? How long does it take for selectively cut stands to attain conditions resembling old-growth forests?

Location: Southern boreal zone of central Sweden.

Methods: We linked multiple lines of evidence from historical records, biological archives, and analyses of current forest structure to reconstruct the forest history of a boreal landscape, with special emphasis on six remaining core localities of high-conservation value forest stands.

Results: Our reconstructions revealed that several of these stands experienced wildfires up to the 1890s; all had been selectively harvested in the late 1800s; and all underwent substantial structural and compositional reorganization over the following 100-150 years. This time interval was sufficient to recover considerable amounts of standing and downed dead wood (mean $60.3\,m^3\,ha^{-1}$), a range of tree ages and sizes (mean basal area $32.6\,m^2\,ha^{-1}$), and dominance of shade-tolerant spruce. It was insufficient to obtain clearly uneven tree age structures and large (>45 cm diameter) living and dead trees. Thus, these forests contain some, but not all, important compositional and structural attributes of old-growth forests, their abundance being dependent on the timing and magnitude of past natural and anthropogenic disturbances. Our landscape-level analysis showed marked compositional and structural differences between the historical forest landscape and the present landscape, with the latter having a greater proportion of young forests, introduction of non-native species, and lack of large trees and dead wood.

Conclusions: The remnant high-conservation value stands were not true representatives of the pre-industrial forests, but represent the last vestige of forests that have regenerated naturally and maintained a continuous tree cover. These traits, coupled with their capacity for old-growth recovery, make them valuable focal areas for conservation.

Keywords: Coarse Woody Debris; Dendrochronology; Fire Ecology; Historical Records; Land-Use History; *Picea Abies*; Southern Boreal Zone; Stand Dynamics; Stand Reconstruction; Sweden; Woodland Key Habitats.

Abbreviations: WKH = woodland key habitat; NFI = National Forest Inventory.

Introduction

The human influence on the boreal forest biome has varied considerably over time. Nowhere has the biome been as dramatically transformed as in Fennoscandia (Lloyd 1999). For example, the structurally diverse, multi-age, old-growth forests, which once dominated the northern Swedish landscape, have today been replaced by young, largely single-age and even-size monocultures (Östlund et al. 1997; Axelsson & Östlund 2001). At present, only a small percentage of Fennoscandian old-growth forest remains, and this dramatic landscape change has created serious conservation threats to many specialized forest-dependent species. In Sweden, some 100 forest-dependent species are already recorded as regionally extinct and approximately 2000 are currently red-listed (Gärdenfors 2005).

With inadequate areas of old-growth forest remaining, it is clear that strategies for preserving forest biodiversity must consider restoration and conservation in managed forest landscapes. In the Nordic countries and the Baltic States, considerable efforts and resources have been allocated to delineate and set aside remnant high-conservation value forest areas within the managed forestland. These areas are often referred to as *woodland key habitats* (WKHs). All productive forestland in Sweden has been subjected to WKH inventory. WKHs have no direct legal protection, but should be preserved and restored according to the Swedish Forest Stewardship Council (FSC, Anon 2005a). Despite being small (typically just a few ha) and isolated, WKHs are intended to: (1) host or potentially host red-listed species (Sweden, Baltic States); (2) exhibit a low degree of exploitation; (3) contain important structures or other qualities considered valuable for maintaining biodiversity; and/or (4) serve as sources of dispersal to other forests (e.g. Nitare & Norén 1992; Aasaaren & Sverdrup-Thygeson 1994; Tenhola & Yrjönen 2000; Sohlberg 2004). Hence, the set aside of WKHs provides one of the most important forest biodiversity conservation measures outside traditional protected areas.

Recent studies demonstrate that many WKHs and other proposed protected areas in the region cannot be considered remnants of old-growth forests, but, rather, are forest fragments resulting from selective logging, fire suppression and abandonment by modern forestry during the 20th century (Bendiksen & Svalastog 1999; Ericsson et al. 2005). Much remains unknown about the combined influence of anthropogenic and natural disturbances on the development of old-growth forest structure and composition in boreal forests. Long-term studies that include both anthropogenic and natural disturbances are quite uncommon, yet are needed for several reasons. First, they are more likely to provide insights on the character of future forest change when compared to models based purely on autogenic succession. Second, they provide an assessment of the rate of structural development and old-growth habitat renewal, which is essential when evaluating management requirements, restoration efforts, and the potential to sustain species populations. In addition, there is a need for understanding these processes at the landscape scale, where high-conservation value forests are evaluated as components of functional habitat networks (Angelstam et al. 2005; Mikusiñski & Edenius 2006). Thus, stand developmental information needs to be linked to overall changes within the landscape to determine if present-day high-conservation value forests resemble forest compositions, structures, and functional attributes that were typical of the historical forest. Such retrospective studies can provide important guidelines concerning where and in which forest types restoration may be needed in order to maintain representative and well-connected functional habitat networks.

Methods available for long-term retrospective studies include the use of historical records (e.g. timber ledgers, maps, forest surveys), biological archives (e.g. methods of dendrochronology, pollen analysis), and analyses of current forest structures and processes. Each method has limitations and advantages, and subsequently most studies benefit from using multiple approaches (Foster et al. 1996). In the present study, we combined several of the above methods to reconstruct the composition and structure of six spruce-dominated WKHs within a southern boreal forest landscape of central Sweden. This combination of techniques and scales allowed us to address the following research questions: (1) Can small and isolated high-conservation value forests (e.g. designated woodland key habitats) maintain old-growth forest characteristics and functionality in fragmented landscapes? (2) To what extent has past disturbance (natural and anthropogenic) influenced the development of old-growth composition (e.g. diverse communities of trees and saplings), structure (e.g. large, old trees, snags, and woody debris), and functional attributes (e.g. small-scale disturbance dynamics) of these forests? (3) How long does it take for selectively cut stands to attain conditions resembling old-growth forests?

Methods

Study area

The study was conducted within a 16 km × 24 km area (approximately 384 km^2, centered at 62°43′N, 17°10′E) in Västernorrland County, in the southern boreal zone of Sweden (Fig. 1). Elevations range from approximately 50-440 m a.s.l., mean annual temperature is around 3 °C, and the region receives mean annual precipitation of around 700 mm. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the two dominant tree species in the study area. Six WKHs were included in the study (representing a random subset of spruce-dominated WKHs in the study area), ranging in size from 3 to 25 ha and separated by distances of 1-17 km (Fig. 1). *Picea* is the dominant tree species in all WKHs, with *Pinus* and birch (*Betula* spp.) as subordinate species.

The study area has been inhabited since prehistoric times, but the earliest detailed accounts of colonization are tax records from the mid 15th century, when a total of 33 households were registered

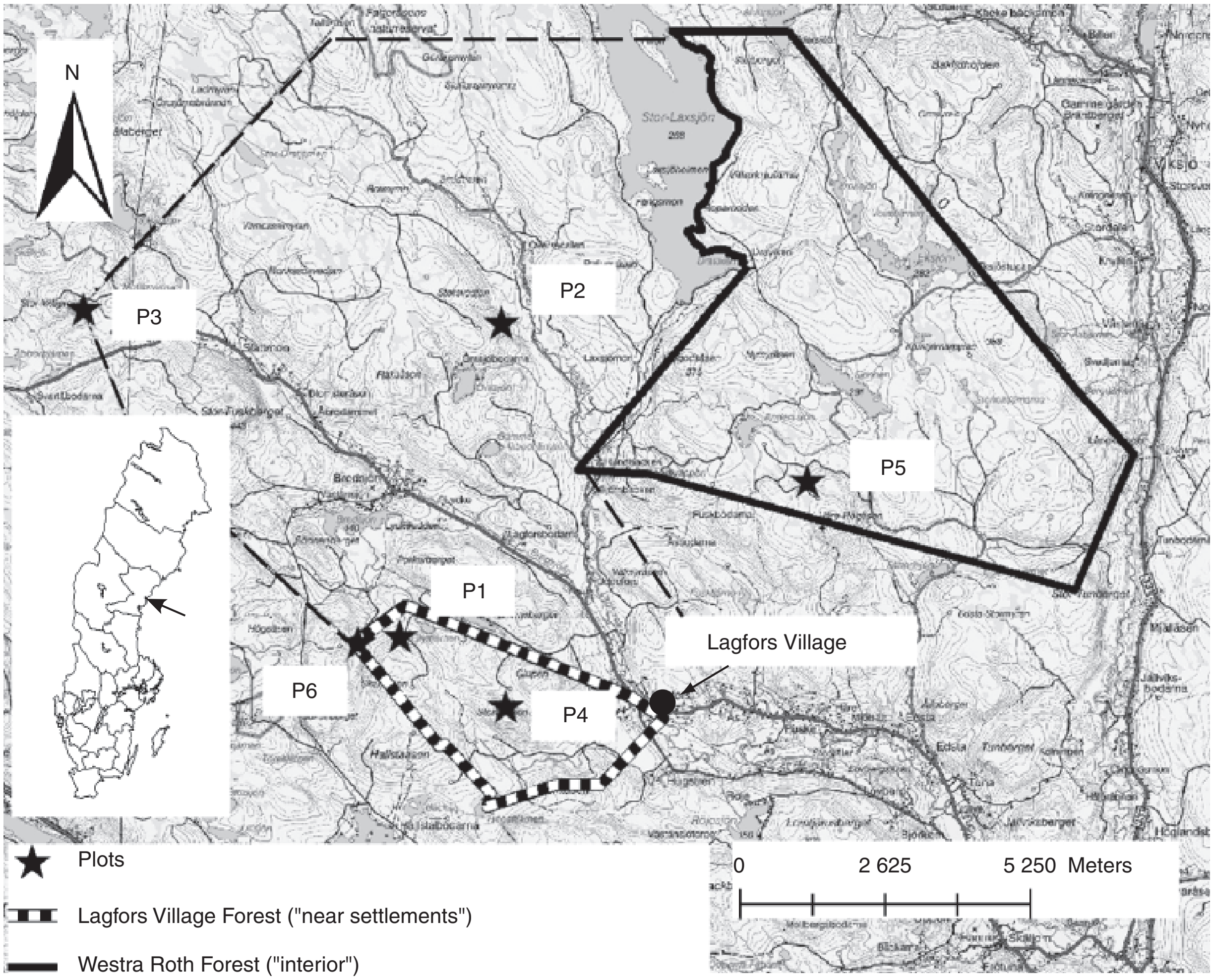

Fig. 1. Location of the study area in Västernorrland County, southern boreal zone of central Sweden. The forestland located within the lines belonged to Lagfors Iron Foundry and was surveyed and mapped in 1864. Detailed stand-level retrospective reconstructions were performed within six woodland key habitats (P1-P6, shown by stars). Thicker lines delineate two regions for which we conducted landscape-level analyses based on historical records. We refer to these as Westra Roth (the interior forest) and Lagfors Village (the near-settlement forest).

in Ljustorp Parish (area 481 km^2; Hässjö Lions Club 1981), which is included in the study area. Settlement occurred mainly on arable land along rivers. Domestic exploitation of forest resources (i.e. firewood and building material) was probably significant in close proximity to Lagfors Village and nearby Ljustorp Village but had limited influence on the overall forest landscape. The forested interior probably remained relatively unaffected until the arrival in the 1620s of Finnish immigrants who practiced small-scale slash-and-burn agriculture (Ljustorps Hembygdsförening 1997). In 1741, the Lagfors Iron Foundry was established, making use of the nearby rivers for water power and the vast forests for charcoal production (SPF Höstsols 1990). The foundry produced fairly large amounts of iron (some 306 tons annually) until the 1860s, when production decreased, and the foundry was finally closed after a fire in 1877 (Carlander 1992). During the iron works era, the human population increased, and additional lands were cleared for small-scale agriculture and animal husbandry (Hässjö Lions Club 1981; SPF Höstsols 1990). Given the growing demand for timber at that time, exports of saw timber, square-cut beams, and balks became important for Swedish commerce. Commercial timber harvesting greatly accelerated in the 1860s, creating a level of forest exploitation the region had not previously experienced.

If the effect of the first phase of exploitation was significant, the impact of the gradual introduction of intensive forestry in the 1900s onward was even greater. The previously selectively cut forests were gradually transformed into well-defined and uniform stands that were clear-cut and planted with single-age monocultures. The large majority of the forests today are effectively managed for timber and pulp with increased standing volumes and forest yields. The remaining old-growth stands occur isolated in a matrix of managed forests.

Sampling for WKH stand reconstruction

We established one 50 m × 50 m plot in each of the six WKHs (P1–P6, Table 1). To avoid subjectivity in plot placement, we simply placed plots in the geographical center of each WKH. Within each plot, we recorded X and Y coordinates for all living and dead trees (stems ≥ 10 cm diameter at breast height, i.e. dbh, 1.3 m), as well as saplings (individuals > 1.3 m high, < 10 cm dbh). For each tree, we also recorded species, dbh, and crown class (canopy versus undergrown). For a random subset of the living trees, we also measured diameters at stump height (0.5 m) to be able to predict former dbh of harvested trees. We inventoried downed woody debris (pieces ≥ 10 cm diameter at large end), recording X and Y coordinates, species (when possible), diameters at large and small ends, length, and decay class (using an eight class system with class 1 being least decayed and class 8 most decayed; Hofgaard 1993). For stumps, we recorded X and Y coordinates, diameter, species (when possible), and decay class.

On one plot (P2), we extracted an increment core from each living tree; the remaining five plots were sub-sampled as follows. While mapping stem locations, plots were divided into 10 5 m × 50 m transects, and trees were uniquely numbered and tagged consecutively from south to north in each transect. Subsampling was conducted simply by coring every other numbered tree. On one particularly dense plot (P1), we cored every third tree. This sampling scheme ensures representative sampling throughout the plot and across size classes, while eliminating bias in tree selection.

Because *Picea* saplings can persist for decades beneath a closed canopy, we consider an individual to be recruited into the stand only when it surpassed breast height. For this reason, we extracted cores at breast height, and all ages are expressed as *recruitment ages*. Sampling was conducted between 2004 and 2006.

Sampling for WKH fire history

We carried out a comprehensive search of each WKH looking for fire scars in living and dead pine trees. Wood containing fire scars from living trees, snags, downed logs, and stumps was sampled with a chain saw. Complete cross-sections of fire scars were taken from logs and stumps, while only partial sections were collected from living trees and snags in order to minimize tree damage. Surface-charred dead wood was recorded but not sampled due to the infeasibility of dating fires on dead wood surfaces. A total of 27 fire-scarred wood samples were collected from the six WKHs. Nine samples contained scars from repeated fires. For the purpose of dating fire scars, we extracted increment cores from 50 older pine trees to create a local chronology, extending back in time as far as possible without any hiatus, against which the scarred samples could be cross-dated.

Dendrochronology and cross-dating

Cores were mounted and sanded to a fine polish using standard methods. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted following the marker-year method of Yamaguchi

Table 1. Stand characteristics and abundance of cut stumps, as recorded in six *Picea abies* dominated WKHs in Västernorrland county, central Sweden. [a] = standing (snags and broken stems) and downed dead wood with dbh ≥ 10 cm and heights or lengths ≥ 1.3 m. Volumes do not include stumps. [b] = cut stumps of *Picea abies* and *Pinus sylvestris* with a diameter ≥ 10 cm at 0.5 m. [c] = former WKH that was given Nature Reserve status in December 2006.

Name	Plot abbr	Size (ha)	Productivity ($m^3\,ha^{-1}\,year^{-1}$)	Slope	Basal area of living trees ($m^2\,ha^{-1}$)			Saplings (no./ha)		Dead wood volume ($m^3\,ha^{-1}$)[a]		Cut stumps[b]	
					Picea	Pinus	Betula	Picea	Deciduous	Standing	Downed	no./ha	Basal area ($m^2\,ha^{-1}$)
Mjösjöområdet	P1	10	5.5	6-10°	18.1	12.4	11.1	348	0	17.0	31.0	168	16.2
Storsvedjan[c]	P2	25	6.9	11-17°	39.8	0.0	2.2	648	0	30.5	70.8	300	11.8
Stor-Vitberget	P3	9	4.8	11-17°	22.6	1.7	4.1	432	20	9.3	26.4	52	2.9
Storbacken	P4	19	6.8	11-17°	33.4	0.0	1.7	608	4	10.2	24.0	564	19.3
Häre-Högåsen	P5	15	4.2	0-5°	25.9	1.0	0.3	1108	0	25.7	47.2	360	20.5
Moaknylen	P6	3	4.0	11-17°	16.3	0.0	4.9	768	54	19.2	50.5	132	8.3

(1991), with verification by COFECHA (Holmes 1983). For cores that missed the pith, the number of rings to pith was estimated using Applequist's (1958) pith locator.

We evaluated each tree ring series for abrupt increases in radial growth (i.e. *growth release*) and rapid growth at the time the tree reached breast height (i.e. *gap-recruited* trees), both taken as evidence of past disturbance (Lorimer 1985). Gap-recruited trees were considered as such if the mean width for the first 10 rings in the series exceeded 1.0 mm (Lorimer 1980, pers. experience), and the subsequent growth pattern was declining, parabolic, or flat (Frelich 2002). Growth releases were detected following the absolute increase method (Fraver & White 2005), based on comparisons of consecutive 10-year periods of growth. The absolute increase threshold (0.55 mm, equivalent to a 97% increase if averaged across all rates of prior growth) was derived from Näslund's (1942) data, which presents *Picea* radial growth increases resulting from various levels of partial harvesting in central and northern Sweden. To estimate the dates of disturbance, we subtracted 3 years from the dated growth release to account for the known lag period between canopy removal and radial growth response in surviving trees (Näslund 1942). Release and gap recruitment events were tallied by decade. For each decade, we expressed the number of releases and gap recruited trees as a percentage of the total number of sampled trees known to be living during that decade. We refer to this percentage as the *disturbance rate*. Disturbance chronologies were truncated when the sample depth dropped below 20.

To further investigate stand-wide disturbance events, we produced standardized chronologies for *Picea* for each plot using the ARSTAN program (Cook & Krusic 2005). Tree ring series with questionable dating were eliminated prior to standardization. Each tree ring series was standardized by first fitting a horizontal line through the mean ring width, then dividing ring widths by the fitted values, producing a unit-less index for each year in the series (Fritts 1978). Indexed series were then averaged to produce the standardized chronologies. Using the horizontal line, as opposed to a flexible spline, does not detrend the series, and thus maintains the stand-wide growth trends resulting from major disturbance events (Veblen et al. 1991). Standardized chronologies were truncated when the sample depth dropped below 10.

All fire-scarred wood samples were dried, mounted on boards (when needed) and sanded to a fine polish. Ring width measurements and cross-dating was conducted using the same methods as used for the cores. After dating of wood samples, the year of the fire scar was determined under a stereo-microscope using a scalpel and zinc oxide paste, when needed (to enhance anatomical features).

Reconstructions of past forest characteristics in WKHs

Because not all trees were cored, we used the average species- and plot-specific tree ring widths to reconstruct diameter growth, and hence basal area back in time, including dead and harvested trees. Bark thickness for each reconstructed diameter was estimated using the species-specific bark versus dbh functions provided by Jonson & Östlin (1962). The linear relationship between diameter at stump height and dbh was used to predict pre-harvest diameters of former trees now evident as cut stumps. The advanced state of decay for cut stumps precluded the use of dendrochronological dating of harvests. Hence, we used decay classes and disturbance rates (determined from growth releases and gap recruitment) to assign cut stumps to the correct logging year. The vast majority of stumps within all stands were from roughly the same time period (represented by decay classes 6 and 7). The majority of the stumps were felled by handsaw or chainsaw (evident by a straight cut surface). However, a few older *Pinus* stumps (decay class 7) in P6 were felled by axe, indicating that they were felled earlier than the other stumps (e.g. Josefsson et al. 2005). Stumps of decay class 8 were omitted from the analyses because of difficulties in identification and size determination associated with advanced decay.

We calculated the volume of logs and broken snags using the conic-paraboloid formula (Fraver et al. 2007), which has greater precision and lower bias than more commonly used formulae. We estimated volumes (V_{sn}, in dm^3) of intact standing dead wood (snags) using the following formula:

$$V_{sn} = 0.12 \cdot d^{2.5}$$

where d is diameter at breast height (in cm). This rough approximation, used by the Swedish National Forest Inventories (NFI), provides reasonable volume estimates for various species of snags (J. Fridman, pers. comm.).

The criterion for identifying a logging event was met when $>20\%$ of the trees showed a growth release or gap recruitment, which we considered to be a stringent criterion to distinguish the major harvesting events (see also Groven et al. 2002). Dead

Picea trees (decay classes 1-6) were assigned a year of death according to the mean times since death for snags and logs of each decay class. The means were obtained from 84 logs and 87 snags (from these same WKHs) dated by dendrochronological methods in a related study (unpubl. data). These means fall within the range of decomposition times found for *Picea* in other studies (Storaunet & Rolstad 2002, 2004). *Pinus* snags and logs were assumed to have the same average time since death as *Picea*. Using the mean time since death introduced uncertainty into basal area reconstructions; however, we considered this to be of minor importance as dead wood generally comprised a very small portion of the total basal area within stands.

We then estimated tree diameters and stand basal areas at the beginning of each 5-year period. We were unable to reconstruct diameters and basal area of logs of advanced decay classes (class >6) or deciduous species due to the poor sample quality and unknown decomposition time, respectively.

Historical records

The earliest historical sources to which we had access were unpublished forest surveys and maps of Lagfors Iron Foundry from 1864 (Fig. 1, Oscarsmerling 1864–1865, in Merlo Archives of Svenska Cellulosa Aktiebolaget, SCA, unpublished records). These historical records contain maps, stand descriptions, timber surveys (tabulated counts and volumes), and proposed harvesting schedules. These surveys were performed to evaluate the forest resources at the time and, to some extent, to manage future forest resources. Typical of the time, very large trees used for square-cut balks and saw timbers were prioritized for harvesting. The maps show the spatial configuration of four forest categories: already harvested (for charcoal production or timber), young forest, spruce- and pine-dominated forest (including both middle-aged and old-growth stands). In the late 19th century, forest stands <50 years old were usually considered as young forest, stand ages between 50 and 150 years as middle-aged, and stands older than 150 years as old-growth (A.-L. Axelsson, pers. comm.).

We used the timber surveys to reconstruct the approximate landscape-level abundance of large and intermediate diameter trees of *Pinus* and *Picea*. The corresponding tree size classes of square-cut balks and saw timber were based on estimates from Östlund & Lindersson (1995). Maps (scale approximately 1:40 000) and accompanying stand descriptions could be used to assess the overall forest composition and human influence of the forestland at the time. These landscape-level analyses were limited to two parts of the study area (Lagfors and Westra Roth), mainly because these had complete surveys and maps that were in good condition (Fig. 1). The forests located closest to Lagfors Iron Foundry and Lagfors Village are henceforth referred to as *near-settlement forests* (1610 ha forestland and 81 ha farmland) and the forests of Westra Roth are henceforth referred to as *interior forests* (5370 ha forestland and <74 ha farmland). In the present study, we attempt contrast the approximate forest composition and configuration of these two historical landscapes with the landscape of today. The historic harvesting schedules provided valuable knowledge of the escalating industrial forest exploitation in the region, and served as a known reference against which the long-term trends of forest dynamics and development within WKHs could be contrasted. More generally, the results derived from our interpretations of the historical records should be seen as approximations of the actual state of the historical forestland (see e.g. Östlund 1993).

Results

WKH stand histories

Disturbance rates and standardized chronologies revealed that all WKHs had been subjected to one or two major disturbance events within the last 150 years (Fig. 2). The high abundance of cut stumps within plots (dominated by decay classes 6 and 7, Table 1), together with the historical records confirmed disturbances were caused by extensive harvesting in the late 1800s and early 1900s. Windstorm records from the region provide no evidence that storms caused these disturbance peaks (Holmberg 2005). Time elapsed since the last harvest ranged from approximately 100 to 150 years, although P4 and P6 had also been subjected to low-intensity harvests (presumably thinning) in the 1930s and 1920s, respectively (Fig. 2). Harvesting decades of P1, P2, P4, and P5 (stands distinguishable in historical records) agreed with the scheduled timing of harvests in historical records. Recruitment age distributions revealed pulses in tree recruitment following harvests, providing further support to the correct identification of logging events (Fig. 3).

The average density of cut stumps was 263 stumps ha^{-1}, corresponding to an average harvested basal area of 13.2 m^2 ha^{-1} (see Table 1 for plot-level

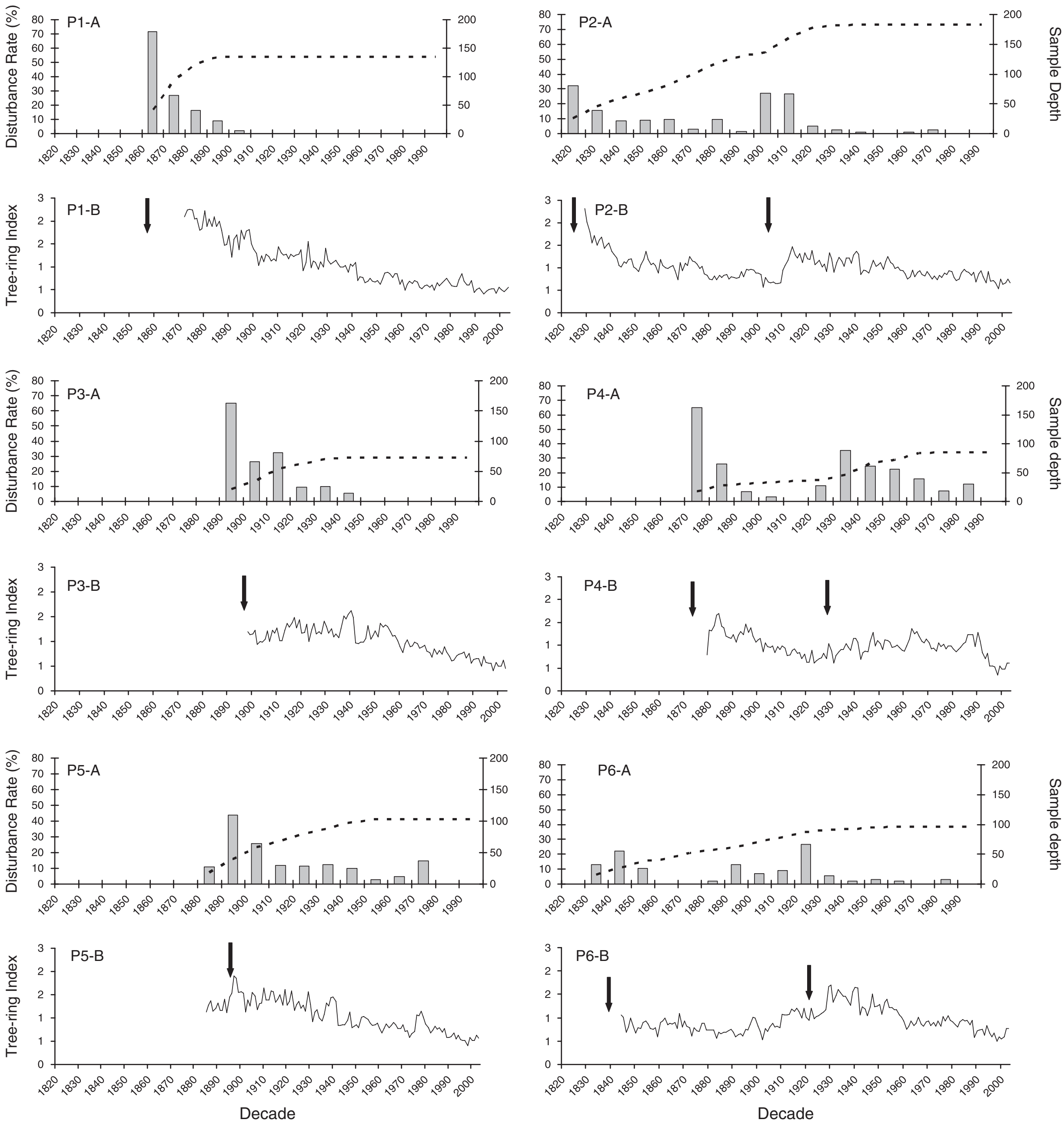

Fig. 2. Disturbance rates (percent of trees showing growth release) including sample depth (number of trees) (a) and standardized chronologies for *Picea* (b) for the six WKHs. Arrows indicate inferred logging events.

details). The harvested basal area within stands constituted 28–75% of the present-day basal area. Stump diameters indicated that harvested trees had an average dbh of 23 cm (range 10–65 cm), approximately the same as the present-day average of 20 cm dbh (range 10–52 cm). Stand reconstructions indicated that most stands had relatively low basal areas and tree densities prior to the harvests in the late 1800s and early 1900s (Figs 4 and 5). A combination of selective harvests prior to the 1860s (as indicated from historical records and our reconstructions) and fire histories were the most probable causes for these findings. For example, three WKHs were affected by fire < 20 years prior to harvesting. In total, we identified 13 separate fires within the WKHs occurring between 1462 and 1889 (Fig. 6). Of the 27 fire-scarred specimens that were collected, we failed to cross-date eight because of advanced decay and/or short tree ring series. Most undated samples were presumably older than the

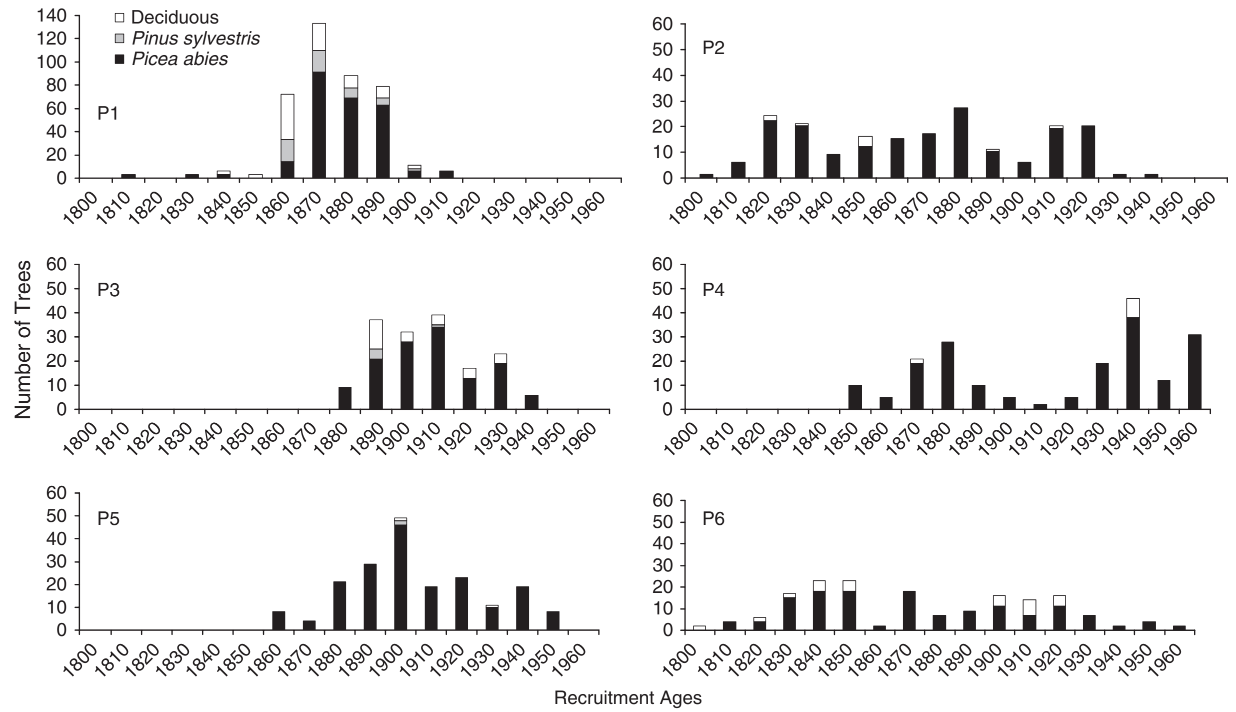

Fig. 3. Tree recruitment age distributions tallied by decades, plots P1–P6. The lack of recruitment after 1960 is due to the fact that only trees with dbh $\geq$ 10 cm were sampled. Note the difference in vertical scale of P1.

period of analysis obtained from the respective WKH. Half of the stands had also been affected by repeated fires; with a mean fire interval of 92 years (range 49–148 years, only counting fire intervals of dated samples).

P2 and P6 had not been affected by fire for several hundred years (Fig. 6). Disturbance chronologies of these two stands did, however, provide evidence of early harvests in the 1820s and 1840s, respectively (Fig. 2). In the most productive site P2, stumps from the 1820s were completely decomposed. This constrained the confirmation of a harvest, although the absence of fire and lack of documented windstorms (historical documents; Holmberg 2005) suggest that the stand had been harvested. Not surprisingly, *Pinus* stumps from the 1840s in P6 were much better preserved and had been visibly felled by axe.

WKH stand development in relation to disturbance history

Stand reconstructions revealed that all post-harvest plots were completely devoid of large trees (dbh $\geq$ 30 cm, Fig. 5) in the late 1800s. However, stands had not been completely clear-cut, retaining on average 156 trees ha^{-1} post-harvest (range 44–348) with a dbh $\geq$ 10 cm. Prolonged fire-free periods and greater levels of post-harvest tree retention in P2 and P6 (Fig. 5) had resulted in wider recruitment age distributions, with little evidence for distinct cohorts (Fig. 3). Age structures of stands that had been recently affected by fire prior to the harvests in the late 1800s (P1, P3 and P5) suggest single cohorts that had regenerated within 50 years after the harvest. These stands included very few trees that had been recruited before the 1850s. P4 had two distinct cohorts, due to the partial harvest in the 1930s (Fig. 3). All stands had living deciduous trees, where the vast majority of trees were recruited as a result of the selective harvests.

The average current tree density within WKH plots was 797 trees ha^{-1} (range 540–1196) and the average current total basal area was 32.6 m^2 ha^{-1} (range 21.2–42.0). This corresponds to an average standing volume of approximately 293 m^3 ha^{-1} (range 182–359; provided by the landowner, SCA). Viewed over the last 100 years, the total basal area of living trees has continued to rise within all WKH plots (Fig. 4), despite stand-wide gradually declining radial growth rates of *Picea* (Fig. 2). Basal area reconstructions did not include dead deciduous trees, suggesting that the actual basal area was somewhat larger. *Picea* has become the dominant tree species in all plots (43–95% of the present basal area), with *Pinus* (0–30%) and *Betula* (1–27%) as subordinate

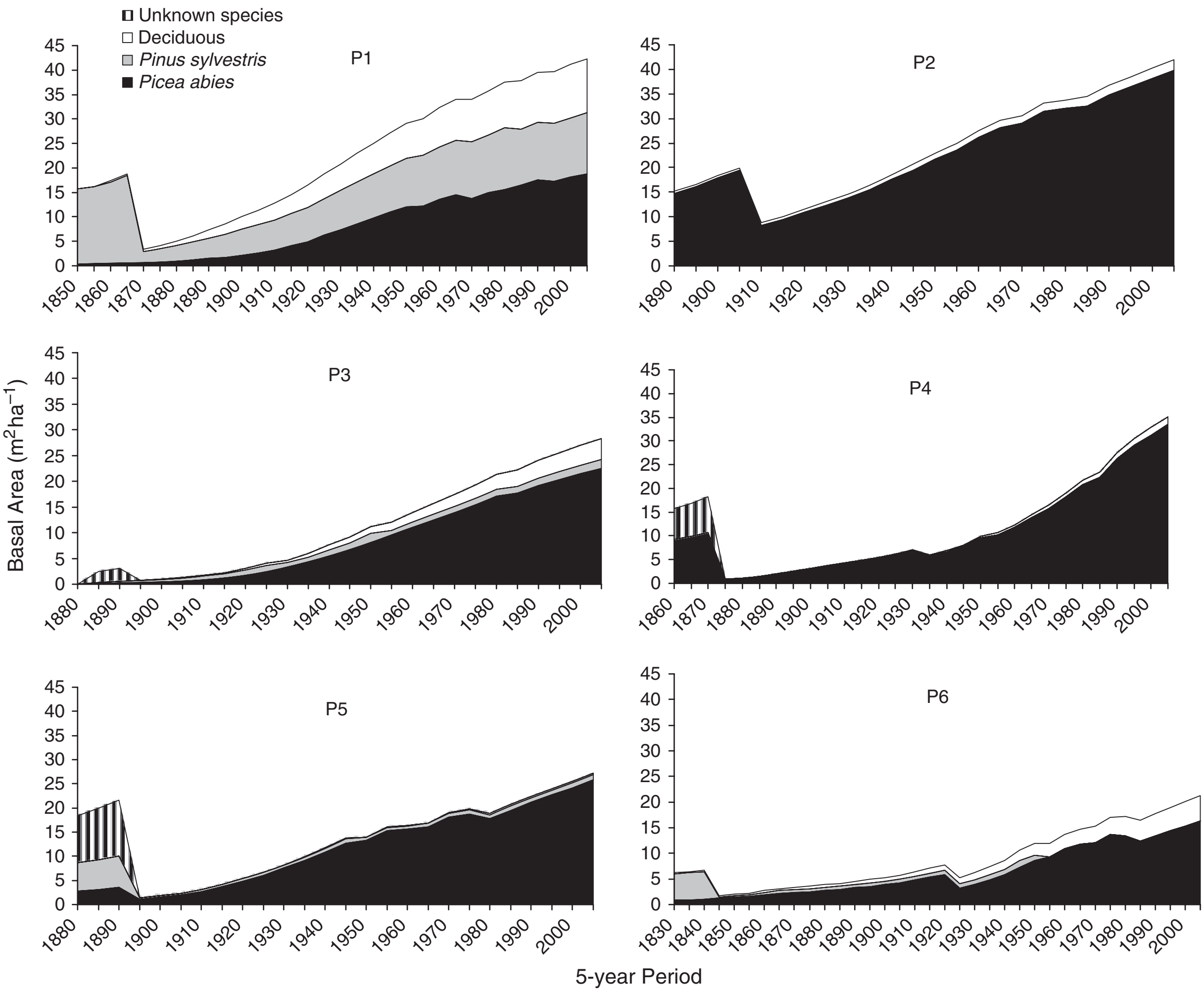

Fig. 4. Basal area reconstructions of trees (dbh $\geq$ 10 cm) in the WKH study plots P1–P6. Unknown species are most likely *Picea abies*, as preservation of *Pinus sylvestris* stumps usually allows easy identification at this stage of decomposition.

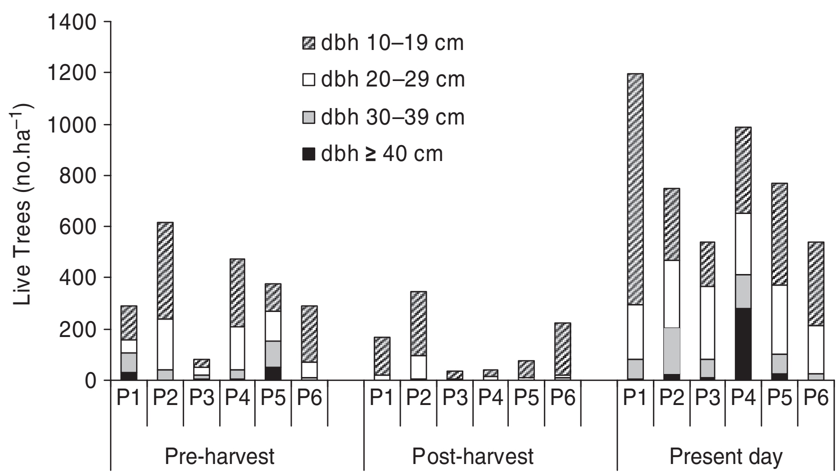

Fig. 5. The total number of living trees of *Picea abies* and *Pinus sylvestris* by diameter class within the WKH study plots (P1–P6) prior to the last major harvest (pre-harvest), immediately after harvest (post-harvest) and present day (2004).

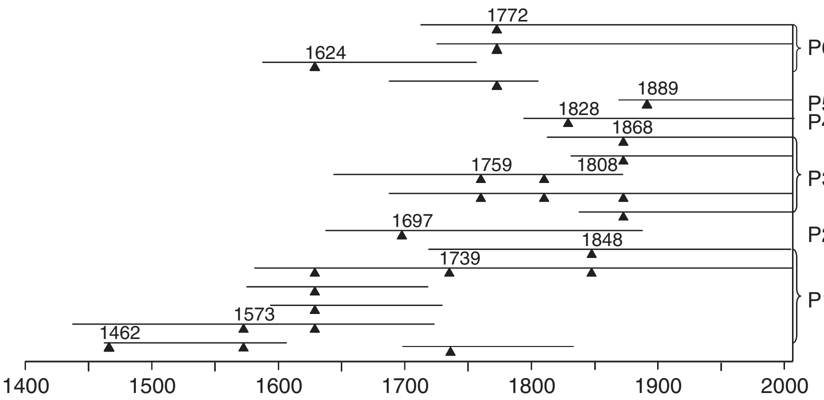

Fig. 6. Fire chronologies of the six WKHs, illustrated by the 19 fire-scarred samples of living and dead *Pinus sylvestris* that were dated with confidence. The triangles mark the year of fire of the individual specimens.

species. *Pinus* dominated the basal area of P1 up to 80 years after the harvest, after which *Pinus* was replaced with *Picea*. Diameter distributions of living trees diversified substantially over the 100 years that had elapsed since harvest and now include most diameter classes (Fig. 5). However, very large trees (dbh $\geq$ 40 cm) remained uncommon within all plots except P4, where thinning in the 1930s accelerated and maintained higher tree growth rates until the 1990s (Fig. 2).

The mean volume of dead wood (standing and downed combined) within WKH plots was 60.3 m^3 ha^{-1} (range 34.2–101.3), of which *Picea* comprised 56%, *Pinus* 20%, and deciduous species 24%. Dead wood volume and characteristics varied considerably between plots (Table 1). From the total log volume, small-diameter logs (10–19 cm) accounted for 16%, intermediate-diameter logs (20–29 cm) 33%, and large logs ($\geq$ 30 cm) for 51%. Logs of advanced decay classes $\geq$ 6 were generally most abundant, accounting for as much as 54% of the total log volume within plots and as much as 70% of the total volume of large logs ($\geq$ 30 cm). A substantial proportion (43%) of the total volume of large logs ($\geq$ 30 cm) was uprootings or cut tops of *Pinus*, the latter presumably the result of logging residue. Snag densities within stands ranged from 56 to 148 ha^{-1}, with a mean of 103 ha^{-1}. Small-diameter snags (dbh 10–19 cm) accounted for 46% of the total snag volume and 80% of the total number of snags. Large snags (dbh $\geq$ 30 cm) occurred within half of the stands, at densities of 4 or 8 ha^{-1}.

The landscape-level transformation

The historical records revealed that forestland in the studied area in the 1860s was dominated by multi-aged forests at various successional stages. The forest was predominantly described to have a multi-storied canopy dominated by large, old *Pinus* trees with an understory of saplings, young and middle-aged cohorts of *Pinus*, *Picea*, and deciduous species. Historical maps and descriptions revealed that the near-settlement forests closest to Lagfors Iron Foundry and Lagfors Village differed from the interior forests of Westra Roth. For example, harvested areas comprised approximately 30% of near-settlements forest areas and 12% of the interior forests. Middle-aged or older forests of *Pinus* comprised around 16% of near-settlements forests and 22% of interior forests. Similarly, middle-aged or older *Picea* forests comprised 16% and 25%, respectively. Young forests were abundant, comprising 38% of the near-settlement forests and 41% of the interior forests.

The historical harvesting schedules provided valuable information on the industrial exploitation of forests during the late 1800s to the early 1900s. In the 1870s, selective harvests were focused on the remaining very large old-growth pine and spruce timber. In the 1880-1890s, the focus had generally shifted to intermediate-sized trees used for saw timber. According to the timber surveys, interior forests held on average six square-cut balk timbers ha^{-1} (97% *Pinus*, 3% *Picea*), corresponding to very large trees with a dbh 50–100 cm, and 13 trees ha^{-1} suitable for saw timber with a dbh 40–70 cm (82% *Pinus*, 18% *Picea*). Thus, large trees with a dbh $\geq$ 40 cm on average occurred at densities of 19 ha^{-1}. Trees considered suitable for saw timber within 50 years, with an approximate dbh of 30–40 cm, occurred at mean densities of 15 ha^{-1}. In striking contrast, near-settlement forests held on average one square-cut balk timber and three saw timbers ha^{-1} of *Pinus* and no timber of *Picea*. The historical records revealed that around 220 and

1172 m^3 of wood suitable for charcoal production (primarily undergrown spruce, windfelled and deciduous trees) could be cut annually in near-settlement and interior forests, respectively. This illustrates a 'charcoal wood frontier' where forests close to the ironworks and human settlement had been more affected than forests in the periphery. However, the production of iron was ceasing at this time, presumably because of a shortage of charcoal wood and the increased value of timber trees. Later, a shortage of charcoal wood in the 1860s was to become a shortage of timber wood in the 1920s.

What separates the present-day WKHs from the surrounding managed forest matrix is that these forests were left to regenerate naturally after the first phase of forest exploitation, whilst intensive forestry escalated in the rest of the study landscape. Since the 1860s, the study landscape had changed from a matrix of multi-age, fire-influenced and selectively cut forest stands to a landscape dominated by clear-cuts and young forests (all tree species, stand age <50 years). At the present time, young forest spatially comprises approximately 68% of the two studied landscapes (the near-settlement forest and interior forest combined). Remnant high-conservation value forests (stand age ≥ 120 years) comprise around 10%, where *Picea* forests (6%) are somewhat more common than Pinus (4%). Lodgepole pine (*Pinus contorta*) from North America was planted extensively in the 1970–1980s, presently comprising large proportions (17%) of the forestland.

Discussion

Development of old-growth forest characteristics in relation to disturbance history

Our results suggest that 100 to 150 years of allogenic succession after an intensive selective harvest is sufficient to develop many important structural characteristics of spruce-dominated old-growth forests, such as substantial amounts of diverse dead wood structures, a range of tree ages and sizes, and dominance by shade-tolerant spruce. To our knowledge, there are only two other studies that have reconstructed the development of old-growth forest structures in selectively cut Norway spruce-dominated forests (Storaunet et al. 2000; Groven et al. 2002). These studies found that forests not selectively logged for 40–70 years started to develop old-growth forest structures (e.g. large trees, dead wood) although not at the levels and diversities characteristic of old-growth forests. They projected that old-growth stand characteristics (uneven age distributions, large dead wood volumes, snags, logs in advanced decay) and small-scale gap dynamics would develop within 100–150 years after intensive selective logging. Further, Storaunet (2006) modeled the time required for *Picea* forests to recover old-growth conditions after selective logging, showing that the estimated time varied between 125 and 200 years, depending on site productivity. Our results confirm that many of these old-growth components do develop within this specified time window. However, our results suggest that 100–150 years of succession may not be enough to obtain a clearly uneven tree age structure or important structural features such as very large living and dead trees. In comparison, Lilja et al. (2006) showed that *Picea* forests undergo significant structural and compositional changes over 110–300 years following a stand-replacing fire, and that it may take up to 300 years to develop a clearly uneven tree age structure. Similarly, old-growth conditions in *Picea* swamp forests in boreal Sweden have been shown to develop within some 300 years after a major disturbance (Ohlson et al. 1997).

Stand reconstructions generally become less accurate the further back in time they are projected (Storaunet et al. 2000; Groven et al. 2002). For example, our basal area reconstructions back to the 1840s in P6 should be viewed conservatively. Stumps and dead wood of *Picea* may be completely decomposed from this time, possibly underestimating the basal area. Also, the overall lower past and present basal area in P6 can be explained in part by the presence of large stone blocks and boulders in the western half of the study plot, which would have inhibited tree establishment. The very low pre-harvest basal area and tree density in P3 were more difficult to explain. It is possible that *Pinus* stumps had been removed from the site and used in tar production, a relatively common practice in northern Sweden during the 19th century (Östlund 1993). The fact the WKHs studied had only been harvested once or twice may be unique for this landscape and its corporate landowner (Lagfors Iron Foundry, today SCA). Reconstructive studies from Norway illustrate how stands generally have been selectively harvested at much shorter time intervals (Storaunet et al. 2000; Groven et al. 2002).

Fire dynamics clearly had a major influence on the structural characteristics of the stands until the late 1800s. The cessation of fires at this time was probably influenced by the increased value of timber, thereby leading to increased interest in fire suppression methods to conserve timber resources.

The relatively long fire intervals recorded within the WKHs were within the natural range for this region, which suggest that these fires were natural wildfires (Niklasson & Granström 2000). This conclusion was also supported by historical records, where none of the stands were recorded as areas deliberately burned to improve the conditions for grazing or slash-and-burn cultivation. Forest fires within the WKHs were probably patchy and not stand replacing. For example, it is unlikely that trees recorded multiple fire scars from stand-replacing fires. Additionally, if stands had been continuously dominated by *Picea*, even low-intensity fires would have killed many or most trees. Evidently, fire suppression and human interventions over the last 100-150 years had improved habitat conditions for the *Picea* undergrowth in all plots, presumably at the expense of *Pinus*. Similarly, in a study of protected areas in northern Sweden, Linder et al. (1997) recorded increasing stand densities of *Picea* at the expense of pioneer species such as *Pinus*, aspen (*Populus tremula*), and *Betula*.

WKHs were not true representatives of old-growth or natural forests, but exhibited many important structural components that make them valuable semi-natural forests (Rouvinen & Kuuluvainen 2001; Uotila et al. 2001; Rouvinen et al. 2002; Rouvinen et al. 2005; Storaunet et al. 2005; Jönsson & Jonsson 2007). For example, the diameter distribution of logs within WKHs did resemble that of old-growth spruce-dominated forests, where intermediate- and large-diameter logs generally account for the majority of the total dead wood volume (Jonsson 2000; Siitonen et al. 2000; Siitonen 2001). In contrast, the decay class distribution of logs showed that intermediate stages of decay (classes 3-5) were generally underrepresented when compared to old-growth forests (Jonsson 2000; Siitonen et al. 2000). This imbalance was particularly evident for large-diameter logs, where 70% of the total log volume had already passed on to later decay stages (classes ≥ 6), which generally support fewer wood-living species than intermediate stages (Bader et al. 1995; Lindblad 1998; Dahlberg & Stokland 2004). Only P2 had started to accumulate new large logs, presumably the result of older recruitment age structure and the greater levels of post-harvest tree retention in the stand. Evidently, once pre-harvest logs have decomposed, selectively cut stands may experience bottleneck periods with very low abundances of large logs for as longs as 100–150 years. Similarly, Storaunet (2006) used simulation models to illustrate that logs in advanced stages of decay were the most protracted old-growth component to recover after an intensive selective harvest, possibly requiring up to 150–175 years. Snag densities within WKHs were approximately two to four times greater than that reported from old-growth spruce forests (Jonsson 2000). This was presumably the result of the high basal area within stands, causing increased competition and tree mortality (in accordance with self-thinning processes). Snags offer important food and breeding substrates for many threatened saproxylic insects (e.g. Jonsell et al. 1998) and woodpeckers (e.g. Bütler et al. 2004). However, the majority of these snags were of small diameter, which may limit their use and longevity. Historical selective harvests had improved conditions for deciduous species such as *Betula*, *Populus*, and *Salix* in the stands (see also Hedenås & Ericson 2000). These species constitute particularly important substrates for wildlife and have declined dramatically in boreal Fennoscandia. This is evident from the marked population declines in a large number of deciduous specialist species, several of which are included on Fennoscandian red lists (Tønsberg et al. 1996; Rassi et al. 2001; Gärdenfors 2005).

The landscape level

Our retrospective analyses clearly illustrated how the historical spatial extent, distribution, and boundaries of old-growth forests have shifted and contracted over the last 150 years, with present forestlands containing a greater proportion of young forests and non-native species. In the context of these major landscape-level changes, the stands that escaped clear-cutting and conversion to plantations now represent the remaining core localities that may potentially help counteract negative effects from the homogenized managed forests. However, fragmentation and isolation may already have contributed to local extinctions of the most rare species (Aune et al. 2005; Berglund & Jonsson 2005; Junninen & Kouki 2006) or species populations may have declined to such a degree that they represent a future extinction debt (Gu et al. 2002; Berglund & Jonsson 2005).

Furthermore, historical selective harvests and modern forest management had reduced the landscape-level frequency of many key features of old-growth forests in our study area. For example, the historical documents revealed extended landscape-level bottleneck periods with very few large living trees, initiated by selective harvests in the late 1800s and thereafter maintained through modern forestry practices The timing, magnitude, and character of the accelerating industrial forest exploitation portrayed in the historical documents are supported by timber floating records from the rivers of Ljustorpsån and nearby Mjällån (years on record: 1866–1915). Floating of large square-cut timber beams and balks peaked in the 1870s, continued annually until 1886, then decreased substantially. The sudden decrease suggests that almost all large timber trees were removed from the area by the 1890s. Meanwhile, the number of saw timbers floated from the area continued to increase from around 70 000 in 1866 to 430 000 in 1915 (Ljustorps Hembygdsförening 2002), clearly becoming more in demand as larger-sized timber diminished. This is further supported by the first National Forest Inventory in Västernorrland County undertaken in the 1920s, which revealed that trees with a dbh $\geq$ 30 cm comprised only 6% of the total timber volume, compared with 10% of today's volumes (Anon 2005b). Thus, the accelerated industrial exploitation of the late 1800s caused a significant impact on forests of the study area, which were already substantially affected by earlier harvests of charcoal wood. The remaining high-quality forests were intensively (and extensively) harvested for large- and intermediate-size timber trees, but never clear-cut (the general recommendation was to retain ca. 80-100 seed trees of 60-80 years old for *Pinus* ha $^{-1}$). Today's frequency of very large trees with a dbh $\geq$ 45 cm in Västernorrland County is on average only one per hectare (NFI data, Anon 2005b). In comparison, the historical densities of interior forests were around 19 trees ha $^{-1}$. Remaining large and old trees are very important for maintaining biodiversity and they may also preserve a record of natural disturbances or cultural heritage from preindustrial times (Linder & Östlund 1992; Andersson & Östlund 2004).

Conclusions

The structural development of semi-natural forest stands is complex and generally best explained as a combination of anthropogenic and natural disturbances. Our results show that selectively harvested stands undergo substantial structural and compositional reorganization during the 100–150 years following harvest. This time is sufficient to recover considerable amounts of standing and downed dead wood, a range of tree ages and sizes, and dominance by shade-tolerant spruce. Uneven tree age structures, sizable woody debris, and large snags have even longer delivery times. Thus, these forests contain some, but not all, important compositional and structural attributes of old-growth forests. Nonetheless, as time progresses, these forests will likely develop larger dead-wood substrates that are more spread out over diameters and states of decay. Also, small-scale gap dynamics and blowdowns may become important disturbances in the absence of fire, possibly maintaining a deciduous component in these forests through removing canopy trees of *Picea* and freeing up available growing space and creating microsites for establishment of early successional trees. The time required to obtain these components and functions is likely to vary depending on the magnitude of past disturbances. Although not true representatives of the pre-industrial landscapes, selectively harvested stands often represent the last vestige of forests that have regenerated naturally and maintained a continuous tree cover. These traits, coupled with the capacity of such stands to recover attributes typical of old-growth forests, make them valuable focal areas for conservation. However, because WKHs are not, and will probably never be, large enough and regionally representative, they should be seen as a complementary conservation measure to biodiversity-oriented forest management and traditional protected areas.

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