Historical Variability of Deciduous Trees and Deciduous Forests in Northern Sweden

Effects of forest fires, land-use and climate

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Doctoral thesis
Swedish University of Agricultural Sciences
Umeå 2004

Acta Universitatis Agriculturae Sueciae
Silvestria 308

ISSN 1401-6230
ISBN 91-576-6542-7

Tryck: SLU Grafiska enheten, Umeå 2004

Abstract

Hellberg, E. 2004. Historical variability of deciduous trees and deciduous forests in northern Sweden. Effects of forest fires, land-use and climate. Doctor's dissertation. ISSN 1401-6230, ISBN 91-576-6542-7.

The aim of the work underlying this thesis was to study the historical variability of deciduous trees and deciduous forests in northern Sweden. To ascertain the effects of forest fires and human activities on the historical variability of deciduous trees, retrospective studies were carried out at different. These studies were designed to: improve our understanding of the genesis of deciduous forests in the present boreal landscape; the role of forest fires and effects of forest management on the structure and composition of spruce-dominated ecosystems; develop methods to separate charcoal fragments of birch based on wood anatomy, to be able to; study the effects of past human activities on forest-limit ecosystems in northern Sweden. Different sets of retrospective methods (i.e. dendroecology, pollen analysis, anthracology and analyses of written historical sources) were used to achieve these aims.

The first study revealed that the effects of aggregated disturbances (forest grazing, human interference with fire regimes and logging) were responsible for the formation of deciduous forests in the present landscape. In the study of spruce-dominated ecosystems, forest fire cycles were found to be long, but had profound effects on the structure and composition of the landscapes until the beginning of the 20th century; *i.e.* deciduous forests were dominating in areas previously affected by fires. Furthermore, forestry had strong negative effects on the coverage of old coniferous forests and deciduous forests. In the third study, the methodology developed showed that dwarf birch and mountain birch can be distinguished from one another and from silver birch and hairy birch based on wood anatomy, while silver birch and hairy birch could not be distinguished from one another. In the forest limit-ecosystem studied, human impact was found to be strong. Due to the exploitation of trees for fuel wood the area was cleared during the Viking-ages, and in combination, with climate the forest has not recovered since then.

A general conclusion was that the scale and effects of human impact were ecosystem- and region- specific depending on the prior role of natural disturbances and the nature of the anthropogenic modification.

Keywords: *Betula*, boreal forest, ecosystem management, forest history, *Populus*

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Hellberg, E., Hörnberg, G., Östlund, L. & Zackrisson, O. 2003. Vegetation dynamics and disturbance history in three deciduous forests in boreal Sweden. *Journal of Vegetation Science* 14(2), 267-276.

II. Hellberg, E. Pre-industrial forest conditions and effects of industrial exploitation in spruce-dominated forest ecosystems of northern Sweden. (Manuscript)

III Hellberg, E. & Carcaillet, C. 2003. Wood anatomy of West-European Betula L.: quantitative descriptions and applications for routine identification in paleoecological studies. *Écoscience* 10(3), 370-379.

IV. Erik Hellberg, Greger Hörnberg, Lars Liedgren, Hanna Karlsson, Ingela Bergman, Olle Zackrisson & Lars Östlund. Human impact on forest-limit ecosystems - palaeoecological indications of deforestation and prolonged ecological effects of land-use at a site in the Swedish Scandes. (Manuscript).

Introduction

Deciduous tree species constitute an important component of the forest landscape in northern Sweden (Ahti *et al*. 1968; Påhlson 1998). The deciduous trees – birches (*Betula pendula* Roth. and *B. pubescens* Ehrh.), aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.), goat willow (*Salix caprea* L.) and alders (*Alnus incana* (L.) Moench and *A. glutinosa* (L.) Gaertner) – occur as scattered trees or patches of deciduous forest in the boreal landscape. In addition, large areas of mountain birch (*Betula pubescens* ssp. *tortuosa* Ledeb., also called *B. pubescens* ssp. *cerepanovii* (N. I. Orlova) Hämet-Ahti), forests are found in the Swedish Scandes where they form the altitudinal forest-line (Ahti *et al*. 1968; Påhlson 1998). Knowledge of the historical variability of deciduous trees is important to understand ecosystem function, the evolution of boreal forest characteristics and peoples long-term impact on the boreal forest. Insights to the historical distribution and dynamics of deciduous trees are important for developing sound ecosystem management strategies (see, for instance, Kuuluvainen 2002). Knowledge of these factors, together with reconstructed fluctuations of altitudinal forest-limits, is also important for studies of past climatic conditions (see, for instance, Barnekow & Sandgren 2001).

Most deciduous trees in boreal Sweden are pioneer species, and spatial and temporal dynamics of deciduous trees and deciduous forests in the landscape are strongly affected by physical factors, for example elevation, soil type, and disturbances (Zackrisson 1985). However, the structure and function of forest ecosystems cannot be understood without accounting for the strong influence of people (Vitousek *et al*. 1997). The northern parts of Sweden have been sparsely populated, and pre-industrial land use can be characterised as of low intensity but spatially broad. Here the end of the pre-industrial period is considered to be the time when industrial forest exploitation started. The start of industrial forest exploitation varies from the southern parts (*ca.* 200 years ago) to the northern parts (*ca.* 100-150 years ago) of the boreal forest, and within regions. Even though pre-industrial land use could be considered as of low intensity, such land-use systems required large areas. Consequently, they could have caused large-scale shifts in vegetation, and this possibility has to be considered in studies of the historical variability of the ecosystems. Spatial and temporal variability of past disturbances, and especially the magnitude of human effects on vegetation composition, can be studied by detailed analysis of biological and historical archives.

According to the Swedish National Forest Inventory (SNFI) (Anon. 2003), deciduous trees constitute 15% of the total standing volume in the boreal forest today. Birches are most abundant (12.5%), while aspen and all other species occur at low frequencies (0.9% and 1.3%, respectively). Many forest-dwelling species that depend on deciduous trees are found on the Swedish red list of threatened species (Gärdenfors 2000), and in recent decades concerns related to the conservation of boreal forest have grown. In Fennoscandia, the idea of using natural forests as models for ecosystem management has been widely accepted (Fries *et al*. 1998; Kuluuvainen 2002). The use of natural variability concepts demands recognition of processes that cause spatial and temporal variation, such as disturbances, and their role in sustaining ecological systems and the species that depend on them (Landres *et al*. 1999). Consequently, a historical perspective on ecosystem components (such as deciduous trees) and how disturbances have affected them is needed.

During the last few centuries, profound changes have taken place in forest ecosystems in boreal Sweden, mainly due to large scale industrial exploitation of the forest. Before industrial use of the boreal forest, forest fire was the primary driving force shaping and affecting successional development in the Fennoscandian boreal forest (Zackrisson 1977; Lehtonen 1998; Niklasson & Granström 2000; Hellberg *et al*. 2004) and pre-industrial human effects have traditionally been regarded as being of minor importance (Linder 1998; Axelsson 2000). In the 19th century (earlier in the southern boreal zone) industrial exploitation of the boreal forest started (Östlund 1993) and fires were suppressed (Niklasson & Granström 2000; Hellberg *et al*. 2004). Initially, forest exploitation was mainly based on high-grading and selective loggings (Östlund 1993). The cut-over landscapes in the early 1900s were still largely forested, although the stands were sparser and contained fewer large trees than prior to the exploitation (Holmgren 1959; Östlund *et al*. 1997). In the 1950s, clear-cut systems were introduced, resulting in major changes in forest structure (Ebeling 1959; Östlund *et al*. 1997; Linder & Östlund 1998) and configuration of landscape elements (Axelson & Östlund 2001).

Forest management in the 20th century has been mainly based on promoting monocultures of coniferous species. Deciduous trees had low commercial value and were regarded as obstacles to successive management of the more valuable coniferous tree species. However, the cleared areas provided opportunities for the natural regeneration of deciduous trees. Thus, cleaning, selective thinning and herbicide treatments were carried out to “extinguish” the deciduous trees from the forest (Bergman 1991). The introduction of clear-cut systems as the main silvicultural regimes also increased the food resource, *e.g.* young pines, birches and aspens, for large browsers. Consequently, a sharp increase in the moose population occurred from the 1960s (Edenius *et al*. 2002), with negative effects on the abundance of young deciduous trees (Hörnberg 1995; Angelstam *et al*. 2000). The effects of browsing, forest management (including active measures taken against deciduous trees) and effective suppression of forest fires, prompted the common perception that deciduous trees are less abundant in the present landscape than in the past (as held, for example, by Esseen *et al*. 1997). However, this view is contradicted by historical data on the patterns and abundance of deciduous trees in boreal Sweden. Even though forestry has been documented to have had strong negative effects on the abundance of deciduous trees at a local scale (Axelsson *et al*. 2002), data from the SNFI (Official statistics of Sweden) show that the total volume of deciduous trees has increased since the 1920s (Fig 1). Furthermore, reconstructions of pre-industrial forest conditions based on inventories of forests conducted just before the exploitation started in the boreal part of Fennoscandia reveal that deciduous trees only constituted a minor component in the 19th century forests, and deciduous trees were mainly scattered in coniferous-dominated forest types (Östlund *et al*. 1997; Linder & Östlund 1998; Axelsson & Östlund 2001).

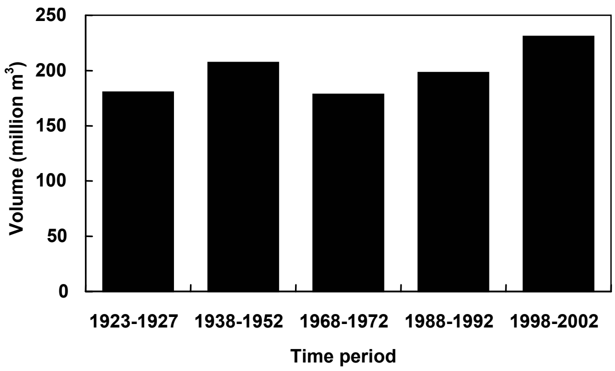

Fig. 1. Total volume of deciduous species in boreal Sweden, 1923-2002. Data from the Swedish National Forest Inventory.

It has been suggested that the 19th century pre-industrial forest conditions could be used as baseline conditions for ecosystem restoration and management (Linder 1998; Axelsson 2001). In such an approach, characteristics of the forest ecosystem at a single, targeted point in time are reconstructed. However, since the boreal forest is dynamic, it is important to realise that the observed characteristics of the forest landscape are created and maintained by processes that are in a continuous state of flux (Smith *et al.* 1993). Consequently, reconstruction of past disturbance regimes, preceding the baseline time, is crucial in order to understand the temporal and spatial dynamics of deciduous trees in the boreal landscape. The role of pre-industrial human activities must be emphasised since there is evidence that human interference caused large-scale changes to fire regimes (Lehtonen 1998; Pitkänen 1999; Niklasson & Granström 2000), and pre-industrial forest use profoundly affected tree species composition (Lehtonen 1998; Segerström & Emanuelsson 2001). Nevertheless, reconstructions of forest conditions just prior to industrialisation, based on forest survey data, are essential tools for defining the historical variability of forest ecosystems. They provide more detailed information on historical landscapes than any other retrospective method (*e.g.* pollen analysis and dendroecology), revealing patterns resulting from former disturbance regimes and the effects of industrial forest management. However, to include a wider range of ecosystems it is important to consider the historical dynamics of deciduous trees, as most studies to date of pre-industrial forest conditions and effects of industrial exploitation have mainly focused on pine-dominated ecosystems.

A completely different setting, in terms of ecosystem characteristics and nature of human impact, is the mountain birch forests found along the Swedish Scandes. Altitudinal forest- and tree-limits in the Swedish Scandes have been studied for at least a century (Gavelin 1909; Smith 1920), and during the last few decades the research has intensified due to the interest in global climate change. Most Scandinavian studies of past and present forest- and tree-limit altitudes have emphasised the influence of climate (Karlén & Kuylenstierna 1996; Barnekow 2000; Kullman & Kjällgren 2000; Barnekow & Sandgren 2001), and tree- and forest-limit altitudes are considered to be valid proxies for climate reconstructions (Karlén 1976; Barnekow 1999; Barnett *et al.* 2001). In the southern parts of the Scandes, human impact has been recognised as a factor affecting the forest-limit

(Ve 1940, 1968; Kullman 1976; Bryn & Daugstad 2001). Further north, in the northern Scandes, recent human effects (*i.e.* < 300 years) have been acknowledged in some areas (Emanuelsson 1987), but earlier effects have been largely neglected. Recent archaeological inventories of the mountain regions (Mulk 1997; Olofsson 2000; Edbom 2001; Olofsson & Olsson 2001) have revealed that people have lived in these areas for thousands of years, suggesting that human interference with past and present vegetation patterns might have been substantial. This stresses the importance of incorporating people as an important factor in studies of past and present sub-alpine ecosystems in order to understand the processes affecting past and present forest- and tree-limits.

Objectives

In the work underlying this thesis I focused on the historical variability of deciduous trees and deciduous forests in the mid-boreal, northern-boreal and sub-alpine regions in northern Sweden (Fig. 2). The overall goal was to acquire a long-term perspective (*ca.* 1000 years) of the effects of natural and anthropogenic disturbances on the deciduous tree component at local and regional scales. Specific objectives were to investigate:

(i) The role of fire, human impact and interactions of disturbances in the genesis of old deciduous forests found at present in mid-boreal Sweden (Paper I).
(ii) Historical patterns of fire and deciduous trees in spruce-dominated ecosystems (Paper II).
(iii) Effects of past human activities on sub-alpine birch forest ecosystems (Paper IV).
(iv) Methods to improve the identification of charcoal fragments of *Betula* species based on quantitative wood anatomy (Paper III).

Methods

All retrospective methods have specific advantages and limitations, therefore methods often need to be combined, and carefully selected according to the aim of each study. Special attention has to be paid to the chosen methods' potential to provide information relevant to the questions posed; *e.g.* the ability of palaeoecological methods and historical inventories to separate species adequately.

In the studies described in Paper I, dendroecological methods were used to reconstruct fire regimes and loggings with high spatial and temporal precision. Pollen analysis was used to determine trends in vegetation development and extensive agricultural use. In addition, charred particles were analysed to assess their potential use in long term reconstructions of fire history. In Paper II, a combination of dendroecology and archival sources were used to describe the influence of fire in spruce-dominated ecosystems and written historical sources were used to study pre-industrial forest conditions and industrial transformation. In the studies reported in Paper IV, fragments of charcoal from archaeological dwellings were identified to gather information on the wood selected for fuel in sub-alpine birch forests. In order to do this, the methodology for separating tree and shrub species of *Betula* had to be improved (Paper III). The exploitation of trees for firewood was related to trends in vegetation development at the site detected by pollen analysis.

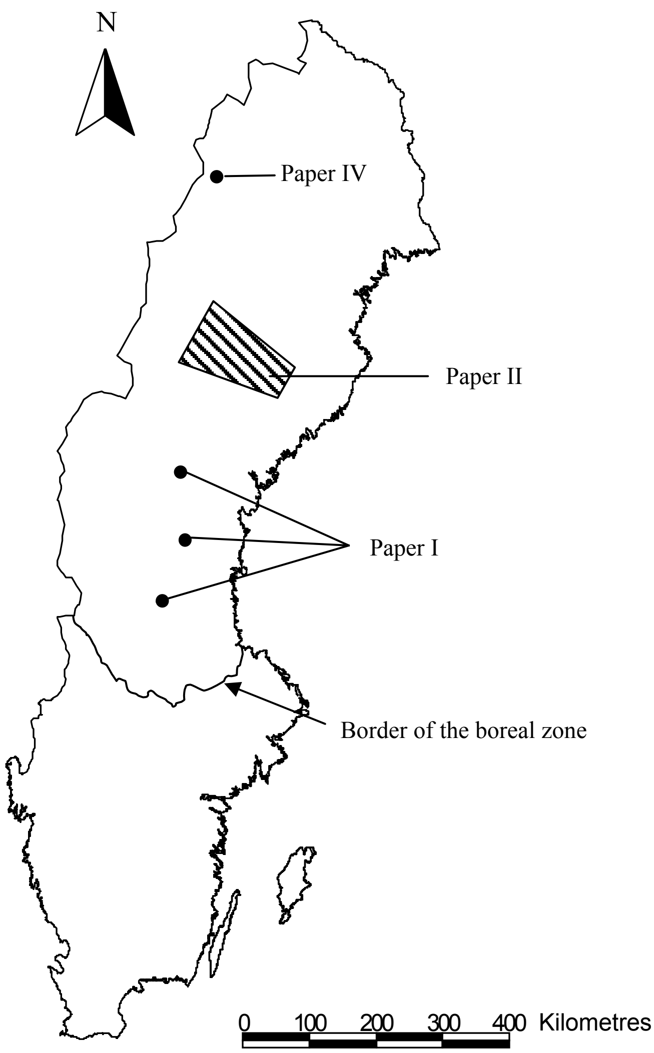

Fig. 2. Map indicating the locations of the studied areas. The border of the boreal forest, as shown in the map, is set to the southern boundaries of the counties Dalarna and Gävleborg. This border approximately follows the classifications according to Ahti *et al.* (1968) and Påhlsson (1998). This approximation was adopted since data from the Swedish National Forest Inventory used in this thesis, are presented for each county.

Outline and summary of papers

Paper I:
To improve our understanding of the genesis of deciduous forests in the present landscape, we studied past disturbance regimes and vegetation dynamics in three deciduous forests in boreal Sweden. All three stands were found to have been highly modified by human activities in the past. We identified three stages in the development of the studied stands. Firstly, the coniferous period (pre-1800), a prolonged period characterized by frequent fires, livestock grazing and extensive agriculture during which *Pinus sylvestris* was dominant. Secondly, the transformation period (1800-1900), when all or almost all of the pines were removed from the sites by logging, while fire and grazing continued. At the time of the last fire, the sites lacked a local seed source of pines, resulting in a post-fire succession dominated by deciduous species. Thirdly, the deciduous period (1900-2000), with little or no disturbance from fire, grazing or logging. Thus, the present deciduous stands have their origins in a complex interaction between changes in fire regime, extensive land-use patterns and logging, contrary to earlier simplified explanations. We conclude that the complexity of historical patterns of land use, vegetation dynamics and disturbance should be acknowledged in the future when selecting areas for nature conservation and developing models for ecologically-oriented forestry.

Paper II:
Studies of pre-industrial forest conditions and effects of industrial forestry involving the analysis of written historical sources in northern Sweden have hitherto focused on pine-dominated ecosystems. This paper presents a regional study of pre-industrial (early 20th century) forest conditions and effects of industrial exploitation in a spruce-dominated ecosystem of northern Sweden. Historical records (1917-1927) were used to obtain quantitative data on fire influence, forest composition, forest age and stand structure. Historical data were compared with a modern data set on forest age and composition to detect changes due to industrial transformation. Special emphasis was paid to the deciduous tree component. The early 20th century landscape was dominated by old, multi-cohort spruce forests and mixed coniferous forests. Although fire cycles seem to have been long, fires had profound effects on the structure and composition of the forest landscape. On burnt areas even aged deciduous-dominated forests were the dominant types of forest. From 1917-1927 to 2003, profound changes in species composition and age structure due to industrial forest management were documented. There were major increases in pine-dominated forest types and the total volume of pine. A substantial increase in total volume of deciduous species was also documented, but the coverage of deciduous-dominated forests decreased. I conclude that the industrial transformation of the forest landscapes studied had profound effects on stand age and stand structure of spruce forests, while its effects on the stand age and stand structure of deciduous forests were minor.

Paper III:

Separation of *Betula* species based on wood anatomy, for example in analyses of charcoal, is problematic. The main reference texts currently used for identification of *Betula* at species level are qualitative descriptions of wood anatomy. These provide ambiguous guidelines for identification, and exclude anatomical features of the wood of the subspecies *B. pubescens* ssp. *tortuosa*. The aim of the studies described in Paper III was to characterise the wood anatomy of *Betula* species more fully, and quantitatively. For this, the size, abundance and organisation of vessels and rays were quantitatively estimated in carbonised wood samples of four *Betula* taxa: *B. pendula* Roth., *B. pubescens* Ehrh., *B. pubescens* ssp. *tortuosa* Ledeb. and *B. nana* L.. Principal component analyses were then used to detect statistical differences between the species and to identify useful characters for distinguishing species. An anatomical gradient between *B. pendula* and *B. nana* was found, in which *B. nana* was clearly distinct from the three tree species. Differences were also observed between the tree species, but with less statistical significance. Our quantitative results support earlier, qualitative descriptions in some respects and conflict with them in others. We highlight the occurrence of narrow vessels in the wood that have not been described previously. We suggest that *B. nana* and *B. pubescens* ssp. *tortuosa* can be distinguished from one another and from *B. pendula* and *B. pubescens*. However, our results do not allow *B. pendula* and *B. pubescens* to be distinguished, at least not in the routine identification of wood charcoal.

Paper IV:

Most Scandinavian studies of changes in past and present tree- and forest-limit altitudes have emphasised the influence of climate. However, archaeological surveys in the alpine and sub-alpine zones in the Swedish Scandes have revealed that people have lived in the area for thousands of years, indicating that these ecosystems are cultural landscapes. It seems likely that this human presence could have had a substantial impact on the function, productivity and biodiversity of mountain ecosystems and hence, tree- and forest-limit altitudes. To study the effects of human activities in the forest-alpine ecotone, a palaeoecological study was carried out in an area with a high density of ancient monuments in the northern part of the Swedish Scandes. The forest-limit in the study area is lower than in surrounding areas. This could be an effect of earlier human activities at the site. The study included identification of charcoal from archaeological excavations, analysis of pollen and charred particles in peat and loss-on-ignition analysis. AMS ^{14}C-datings revealed that many of the settlements were restricted to the period AD 700 – 1180. Charcoal assemblages in these monuments were almost entirely composed of *Betula* remains. A decrease in *Betula* pollen at the same time indicated that tree cutting was intense and that trees were cut in the surroundings. This period of intense use was followed by a period with a colder climate, and the forest did not recover. During the last century the climate has been warmer, but the site has still not been reforested, suggesting that the human activities might have had long-term effects on the functioning of the ecosystem. We stress the fact that earlier human effects have to be acknowledged when evaluating the present position of tree- and forest-limits and when using fluctuations of these limits as proxies for climate.

Discussion

Although northern Sweden has been sparsely populated historically, effects of human activities on the distribution and abundance of deciduous trees have been profound, highlighting the importance of considering the human dimension in ecosystem studies. Effects of multiple disturbances and timing of one disturbance event in relation to another, and to climate, are crucial factors to consider in such investigations.

Disturbance history – interactive effects and timing of events

Interactive effects of disturbances, human activities and climate all influence vegetation composition at any given point in time. The deciduous forests described in Paper I have their origin in effects of fire, forest grazing and industrial exploitation (Fig. 3). Over centuries, the structure of the stands has been affected by frequent, low intensity fires and livestock grazing, preventing the recruitment of younger cohorts. Cumulatively, these disturbances profoundly influenced the patterns of industrial logging that took place in the 19th century. During this period high grading was a common practice (Holmgren 1959; Östlund 1993) and only pine trees with diameters exceeding a certain measure were logged. Since previous disturbances had caused the tree size distribution to be skewed towards large and old trees, almost all of the pine trees were removed from the affected sites. Consequently, there was a close connection between the preceding disturbance regime and the resulting patterns of industrial logging.

Fig. 3. A stump remaining from a large pine tree cut in the mid-1800s in one of the deciduous forests, Gåsberget, studied in Paper I. The stump contains multiple fire scars and the surface of the stump is charred by the fire that burned in the stand 1888. Photo: Erik Hellberg

Often the history of an area is described in general terms, *e.g.* as being affected by pre-industrial agricultural land-use and logging, but such generalities encompass a wide range of variations. Hence, detailed descriptions of both the magnitude and relative timing of each factor are essential for a full understanding of the interactive effects of multiple disturbances. However, acquiring relevant data for large-scale investigations is a demanding task, especially in areas lacking suitable study material, *e.g.* wood for detailed dendroecological analysis, relevant historical sources and good sites for pollen analysis.

In more marginal areas, such as the sub-alpine birch forest in the Scandes, climate has a more significant role in vegetation development. Here, timing of disturbance events in relation to climate dynamics is of great importance (Paper IV). If forest clearings, *e.g.* due to cutting of trees for fuel and constructions, are created during periods with a favourable climate, trees can successfully regenerate on the cleared areas (*e.g.* Holmgren 1912). However, if the deforestation is followed by continuous land-use and/or a cold period, regeneration of trees may fail and an ecosystem shift may occur as cleared areas may turn into alpine heath. Alpine environments can also have a high level of inertia (Wookey & Robinson 1997), which may be reinforced by human activities that make it difficult for trees to regenerate. Consequently, the expansion of the forest, during warmer periods, into formerly cleared areas may fail and the effects of human activities can be prolonged (Paper IV). In studies of the effects of land-use in marginal areas, *e.g.* the forest-alpine ecotone, the importance of factors such as ecological resilience (Scheffer *et al*. 2001) and ecosystem productivity must be accounted for to a greater extent than in more robust ecosystems situated in more favourable climate zones (*e.g.* boreal forests).

Spatial patterns of pre-industrial land-use

Studies I and IV documented strong local effects on vegetation patterns caused by human activities. However, an important issue to address was whether the documented human effects were limited in scale or part of a large-scale transformation of these forest ecosystems. In the boreal forest, large scale changes due to pre-industrial human activities are likely to have occurred since peasant farmers colonising areas had strong influence on fire regimes (Niklasson & Granström 2000). Manipulation of fire regimes can include changes in fire frequency (Lehtonen & Huttunen 1997; Lehtonen 1998), size (Niklasson & Granström 2000), seasonality (Niklasson & Drakenberg 2001), and intensity (Pitkänen 1999). As both interference with fire regimes and the use of forests for grazing took place on large scales, human activities probably caused regional shifts in species composition and forest structure. However, local effects on vegetation have been greatest around habitations, for example villages and summer farms (Ericsson 2001). Hence, there were gradients of impact from heavily affected habitats close to the settlements, due to farming and cutting trees, to forests situated further away that were affected by changes in fire regimes and extensive grazing at regional scales. In sub-alpine ecosystems, fire is not a major disturbance factor. Hence, manipulation of large scale disturbance regimes were not a part of the human induced changes in vegetation patterns in the sub-alpine site studied in Paper IV. Consequently, land use here could probably be characterised as forming islands of affected environments. In sub-alpine areas, human induced changes in vegetation at regional scales would require higher densities of population and livestock than in regions where large scale disturbance regimes could be altered (*i.e.* the boreal forest). However, as sub-alpine environments are marginal, even low degrees of human impact could potentially have strong and long lasting effects.

Effects of pre-industrial land-use on deciduous trees in the boreal forest

The greatest effects of pre-industrial land-use on the distribution and abundance of deciduous trees were probably associated with the anthropogenic changes in fire regimes. Before human interference with fire regimes in the boreal forest occurred, large fires (> 10 000 ha) accounted for the main proportion of the area burnt (Niklasson & Granström 2000). Considering the size of these fires, they were probably of high intensity, at least in some parts (Granström & Niklasson 2001). Based on palaeoecological data, Pitkänen (1999) estimated that in N. Karelia in Finland, prior to significant human impact, approximately half of the fires may have been stand-replacing. Such fire regimes would have promoted deciduous-dominated forest types. It has been suggested that in areas where humans burn to improve grazing conditions fires tends to be less severe, but more frequent, and the intensity of the fires may have been reduced by human effects on the ignition patterns (Granström & Niklasson 2001). Consequently, the pre-industrial state of the forests discussed in Paper I and the pre-industrial state of pine-dominated ecosystems, which almost exclusively consisted of open, multi-layered pine forests as documented by Östlund *et al.* (1997) and Linder & Östlund (1998), could therefore be legacies of past land-use patterns, including human interference with the fire regimes during the preceding centuries. In contrast, fire influence in the spruce-dominated landscapes discussed in Paper II may have had a positive effect on the abundance of deciduous trees and deciduous-dominated forests. Even though the degree of human intervention with disturbance regimes was not ascertained, due to the lack of datable fire scars, there are reasons to believe that human activities affected vegetation patterns at a regional scale since many of the fires were stated by foresters conducting forest surveys to have had human origins, and grazing was a common practice in the studied areas (Paper II).

In addition to fire, grazing and trampling by livestock can have marked effects on the regeneration patterns of trees (Ronge 1940; Frödin 1952; Bjor & Graffer 1963; Ericsson 2001). Palaeoecological studies from the mid-boreal region in Sweden show that deciduous trees declined during periods when grazing occurred (Segerström 1997; Segerström & Emanuelsson 2002). However, the direct impact of grazing is not easily determined, since changes in fire regime nearly always occurred in periods with grazing. However, direct observations of the effects of livestock grazing have shown that it could have substantial negative effects on deciduous species (Tirén 1948). Furthermore, in the areas studied in Paper II grazing was stated by foresters as a problem for successful regeneration practices in the early 20th century, suggesting that early foresters considered grazing as having a profound effect on the recruitment of both conifers and deciduous trees.

The use of fires for purposes other than to improve grazing, *e.g.* for slash-and-burn cultivation (Larsson 1995), might have had different effects on the deciduous trees than burning to improve grazing conditions. In Finland, deciduous forests in the present landscape are found mainly in areas previously used for slash-and-burn cultivation (Lehtonen 1998). Consequently, this practice could have led to an increase in deciduous-dominated forests. However, as this practice tended to increase fire frequency at a regional scale it resulted in a decrease of deciduous trees in the areas surrounding the slash and burn sites (Lehtonen 1998).

In addition to the effects of fire and grazing, harvesting of leaf-fodder could have had considerable effects on the abundance of deciduous trees in the boreal forest. This practice was common throughout the boreal forest at times and places where an agrarian population was present (Slotte 2000). Leaf-fodder was collected either by stripping leaves from young trees or by collecting branches, predominantly from trees that were felled. Findings by Slotte (2000) indicate that in the boreal forest almost all areas with deciduous trees were subjected to leaf-fodder harvesting, and that a considerable amount of leaf-fodder was collected each year. However, the magnitude of the effects of such activities is not known.

One type of pre-industrial exploitation, which could have had strong local effects on deciduous trees was potash production, which started in northern Sweden in the early 19th century, reached considerable proportions within a few decades, and then completely ceased in the 1860s (Tirén 1937; Östlund *et al.* 1998). For potash production, old or dead deciduous trees were considered the best raw material (Tirén 1937). Consequently, this practice reduced the amounts of old and dead deciduous trees. The geographical distribution of potash production in the boreal forest has not been investigated in detail. However, it seems that the production was concentrated to the northern parts of boreal Sweden (Tirén 1937). Tirén (1937) suggested that the cessation of potash production was primarily due to shortage of raw material, and that the effects of potash production on the landscape were great. However, this interpretation is contradicted by Östlund *et al.* (1998), who argue that the cessation was due to the declining economic importance of potash production as a subsidiary occupation for farmers, and substitution of potash with soda ash. However, local deficits of raw material have been documented for coastal areas in northern Sweden (Zackrisson 1976).

Effects of industrial forest management

The driving forces of forest landscape change from the late 19th century and onwards are the cutting systems used (Östlund *et al.* 1997; Papers I and II), regeneration practices (Östlund *et al.* 1997; Bürgi & Schuler 2003) and silvicultural stand treatments (Östlund & Lindersson 1995). The underlying driving force has been an attempt to transform “natural” and disorderly forest ecosystems into orderly, manageable and high-yielding forests (Langston 1995). At the start of the industrial exploitation of the boreal forest, from the mid-1800s, large diameter pines were cut to supply the growing sawmill industry (Östlund

1993). As only a selection of trees was removed, the forest was thinned rather than cleared (Östlund *et al*. 1997; Linder & Östlund 1998). However, cuttings could have been intense locally (Paper I), creating opportunities for deciduous-dominated successions. Further, early in the exploitation period fire was still present in the landscape and fire in partially cut stands could have induced post-fire successions dominated by deciduous tree species (Axelsson *et al*. 2002). In spruce stands, logging techniques were somewhat different. In addition to selective loggings (similar to high-grading), strip cutting ("kulisshuggning" in Swedish) was used (Holmgren 1959). Regeneration of deciduous trees on such areas could be abundant, especially in high altitude areas (>400 m above sea level) (Ebeling 1959). Consequently, clear-cut areas were present in the landscape from the start of the exploitation of spruce-dominated areas (Paper II).

The amount of cleared areas has increased since the 1940-50s when clear-cut systems were introduced as the standard management scheme for forestry in boreal Sweden (Ebeling 1959). Consequently, opportunities for the expansion of deciduous trees were created on a broad scale. Measures were taken to reduce the increasing amounts of young deciduous trees and older deciduous trees that could act as seed sources, but the expansion seems only to have been retarded by these steps, rather than stopped, as the SNFI data indicate that the abundance of deciduous trees continued to increase (Fig 1). However, at a local scale, the reduction of deciduous trees was effective (Axelsson *et al*. 2002). During the industrial transformation of boreal forests the total volume of deciduous trees has been shown, at different sites, to have decreased (Östlund *et al*. 1997), increased (Paper II) or to have varied at low levels (Linder & Östlund 1998). The coverage of deciduous-dominated forest types has been documented to have declined (Paper II), or to have first decreased and then increased (Axelsson & Östlund 2001). Strong regional differences in the coverage of deciduous-dominated forests have also been recorded (Axelsson 2001; Paper II).

Hitherto, I have only discussed effects of forest management on the amounts and proportions of deciduous trees. However, as many forest-dwelling species, *e.g.* insects, lichens and bryophytes, specifically depend on certain tree species and often require large, old or dead trees as substrate (Berg *et al*. 1994; Esseen *et al*. 1997), quality aspects are important elements to consider. Based on SNFI data, Andersson & Östlund (2004) documented an increase in old deciduous trees (> 99 years) at a regional scale (*ca.* 50 000 km^2) for the northernmost boreal part of Sweden. Changes in the abundance of large diameter trees in the areas discussed in Paper II seemed to be minor, and SNFI data show increases in the abundance of both large diameter birches (Fig. 4) and aspens (Fig. 5). In terms of the stand structure of deciduous-dominated forests, stands were found to be even aged and quite dense during both pre-industrial conditions and in 2003 (Paper II). However, changes may have occurred as both the historical archives and the modern forest data have limitations in describing stand structure. The changes in stand structure of deciduous forests are in marked contrast to the effects of industrialisation on coniferous-dominated forest types, where a transition from semi-open multi-layered stands with high proportions of old trees to even-aged stands with low structural heterogeneity has been documented (Östlund *et al*. 1997; Linder & Östlund 1998; Paper II). However, negative effects on deciduous trees in moist

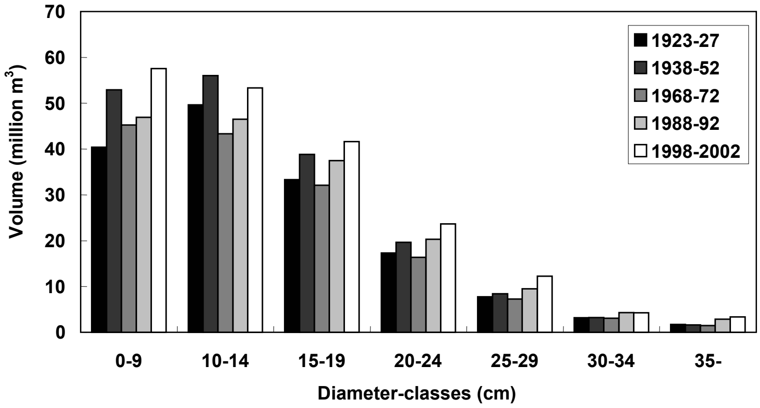

Fig. 4. Total volume of birch in boreal Sweden, 1923-2002, divided into diameter (breast height) classes. Data from the Swedish National Forest Inventory (http://www-nfi.slu.se; 16-feb-2004).

spruce forests have likely occurred, due to structural changes in spruce forests, since deciduous trees in such habitats are maintained by their exploitation of gaps (Kuluuvainen 1994). Effects of forest management on the amounts of coarse woody debris (CWD) of deciduous species have not been evaluated. However, in the years 1994 and 1995 the amounts of CWD of deciduous species were found to be very low, *ca.* 1 m^3/ha, in northern Sweden (Fridman & Walheim 1997), suggesting that effects of forest management have been strong on this type of substrate. An indirect effect of industrialisation of the forest landscape is that browsing pressure has increased sharply, due to the extremely high populations of large ungulates that have developed (Edenius *et al.* 2002), causing especially pronounced effects on the recruitment of aspen, goat willow and rowan (Hörnberg 1995; Angelstam *et al.* 2000). Furthermore, severe effects on the regeneration of these species have probably been caused by the suppression of fires since their establishment is strongly favoured in burnt areas (Ericsson 1992).

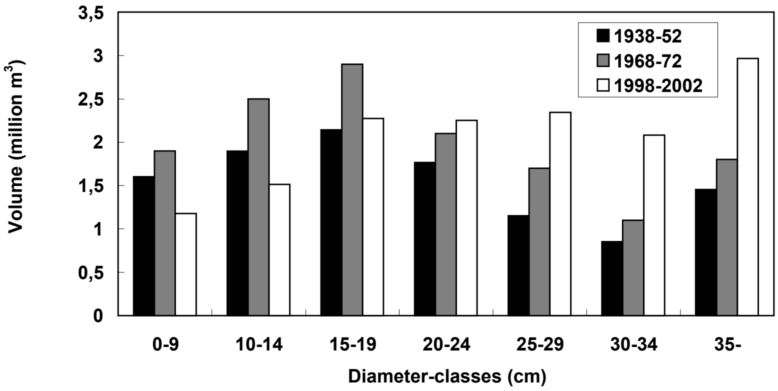

Fig. 5. Total volume of aspen in boreal Sweden, 1938-2002, divided into diameter (breast height) classes. Data from the Swedish National Forest Inventory (http://www-nfi.slu.se; 16-feb-2004).

Limitations in interpreting historical variability

To understand ecosystem patterns, data that match the spatial and temporal scales of the processes affecting them have to be obtained and evaluated (Ricklefs 1987; Levin 1992). In Paper I, effects of disturbances on species composition and stand structure were addressed at the local scale, but the processes involved, *i.e.* fire and grazing, act at large spatial scales. Consequently, spatial and temporal patterns of these processes at regional scales have to be evaluated to obtain a full understanding of the effects of pre-industrial land-use of the boreal forest. Many studies of the effects of land-use, including grazing, have focused on the southern part of the boreal zone, at sites around summer farms ("fäbodar" in Swedish) (*e.g.* Emanuelsson *et al*. 2001; Segerström & Emanuelsson 2002; Karlsson & Emanuelsson 2002). Consequently, the spatial scale of such activities at regional levels has not been fully addressed. However, since indications of grazing at sites located relatively far from summer farms can be found in the southern boreal zone (see, for instance, Nordström 2003), human activities seem to have affected large areas in these regions.

In the northern parts of the boreal zone, the use of forests for grazing, including burning to improve pasture, has been described by Campbell (1948), and grazing was shown to have taken place in all the areas examined in Paper II. The temporal scales of grazing also need to be considered, not only to determine long-term effects of grazing, but also because land-use activities including grazing can have substantial effects on fire regimes. Niklasson & Granström (2000) addressed the historical variability of fire regimes at appropriate spatial and temporal scales to reveal the magnitude of human interference during the period 1650-1870. However, as the duration of the human interference varied, effects on spatial and temporal patterns of fires and successional patterns may differ between regions (as shown, for instance, in Paper II). Therefore, generalisations about human effects on fire regimes must be treated cautiously. Analyses of dendroecological material from other regions to evaluate the effects of human interference are often hampered by, for example, limitations of temporal (Hellberg *et al*. 2004; Paper II) or spatial scale (Hellberg *et al*. 2004). This stresses the importance of acquiring historical knowledge that is specific to the area of interest and highlights the risks of extrapolating mechanisms of ecosystem change from one area to another (*cf.* Swetnam *et al*. 1999).

When discussing effects of industrial exploitation, similar concerns must be addressed. Even though studies of pre-industrial forest conditions and effects of industrial exploitation in the Swedish boreal forest have covered large areas (Östlund *et al*. 1997; Linder & Östlund 1998; Axelsson & Östlund 2001; Paper II), they are not fully representative of the boreal forest as a whole. Studies to date have been limited to state-owned forests and forest commons, the location of which often differ from private estates. Furthermore, including areas with different types of ownership would be desirable, since management schemes may differ (see Bürgi & Schuler 2003, for an example from Switzerland). Furthermore, forest history is often limited to areas that are forested today, especially in the boreal zone. In eastern North America, approaches including the whole landscape in studies of forest history have been used (*e.g.* Foster *et al*. 1998; Bürgi *et al*. 2000).

Similar studies would make an important contribution to our understanding of the historical variability of deciduous trees in boreal Sweden, since areas used for agricultural purposes are strongly biased towards nutrient-rich sites with fine textured soils: conditions that strongly favour deciduous trees. Due to the recent abandonment of former agricultural land, expansion of deciduous-dominated forest types has been noted (Mikusinski & Angelstam 1999). Gradients with higher amounts of deciduous trees close to villages and lower amounts in the forests far from villages have been found in hemi-boreal and southern boreal regions, as well as in coastal areas in northern Sweden, but in northern and interior parts of Sweden the pattern was reversed (Mikusinski *et al*. 2003). Such processes influence the SNFI data, since agricultural land reverts to forestland when it is abandoned. However, deciduous forests on former agricultural land may not provide the same habitat conditions as deciduous forests in the forest landscape (Hedenås & Ericsson 2002). Furthermore, expansion of hydroelectric plants along major rivers has profoundly changed the water and ice disturbance regimes along the river banks (Nilsson & Ekblad 1990). This could also have led to a substantial loss of sites with a natural dominance of deciduous trees.

Accounting for historical variability in management of the boreal forest

Ecosystem management of the boreal forest in Sweden is usually focused on the preservation of biodiversity. Historical variations in ecosystems may indicate conditions that have allowed different species to survive in the past. However, even though species that are found today have managed to survive, landscapes at specific points in time may have provided conditions that were far from optimal for specific species. Consequently, both natural conditions and anthropogenic influences may have favoured some and disfavoured other species.

In general, the greatest negative effects on biodiversity in the boreal forest have been due to the industrial transformation of the forest ecosystems. Pre-industrial human activities may also have had profound negative effects on biodiversity, at least at local scales. However, although pre-industrial human effects were profound, fire was still the main factor shaping the pre-industrial landscape. Compared to the effects of industrial transformation, pre-industrial use of the boreal forest caused changes in the proportions of forest types and structural elements rather than a complete transformation of the forest landscape. As few trees were generally removed, critical habitat components for forest-dwelling species, *e.g.* old and large trees and dead wood, were still abundant in the landscape. However, pre-industrial human activities may have had negative effects on the abundance of suitable habitats for species that depend on deciduous trees, due to the effects of changes in fire regimes, grazing in forests and the exploitation of rich mesic sites for agriculture. Consequently, at least at local scales, pre-industrial land-use could have had stronger negative effects on species that depend on deciduous trees than large-scale forestry.

However, since the spatial and temporal extent of pre-industrial land-use activities is not well known, the effects of such activities on forest ecosystems at regional scales are not easily interpreted. Furthermore, the appropriate scale to interpret effects on species that depend on deciduous trees is not easily defined. Processes involved in the creation of deciduous forests have highly variable spatial and temporal scales, under both natural and anthopogenically-influenced conditions. This implies that species connected to such habitats would probably have high dispersal ability. Consequently, regional scales might be appropriate to interpret habitat availability for species that depend on deciduous trees or deciduous forests. However, attention also has to be paid to whether species depend on single trees (living or dead) as substrates, or habitats formed by patches of deciduous forest (see, for instance, Ås 1993). Such differences in demand among species have to be considered in analyses of habitat availability during different time periods, since the differences in distance between single trees vs. patches may be great. Furthermore, different species depend on different types of substrates or habitats; *e.g.* some insect species are favoured by the presence of snags of deciduous trees exposed to the sun (Kaila *et al.* 1997; Martikainen 2000; Sverdrup-Thygesson & Ims 2002), while others are found on similar substrates in shady environments (Kaila *et al.* 1997); epiphytic lichens depend on living aspen trees (Hedenås 2002) and goat willow, while bird species may depend on patches of old deciduous forests (Jansson & Angelstam 1999). However, studying the historical variability of habitat components in sufficient detail is usually difficult or even impossible.

Even if the historical variability of the boreal forest was fully understood, we would not automatically obtain clear and easy answers about how the boreal landscape should be managed today and in the future. Although natural disturbance-based forest management regimes theoretically respect the inherent variability of natural disturbance regimes, in practice the aim is to achieve economically, socially and environmentally acceptable compromises that remain within the limits of historical variability and reduce the risk of negatively affecting biodiversity to prescribed levels. To optimise the financial returns of forest management regimes that include preservation of biodiversity as a goal, levels of habitat retention and restoration should aim to create (or preserve) amounts of habitat close to threshold levels for the persistence of targeted species. Consequently, with such an approach there is little leeway for variability in the amounts of available habitat. Furthermore, this approach requires forecasts to be made of future habitat availability to ensure that sufficient levels will be sustained in the long-term. The scale of spatial variability that should be allowed is not easy to define. If a limited amount of habitat is present in the landscape, the strength of potential sources of propagules (*i.e.* localities in which the species is present) that could be dispersed to new areas may be low. Hence, spatial clustering of restoration measures and preservation areas may benefit the target species (Hanski 2000). Consequently, historical variability might not provide definitive clues about the spatial scales that should be applied in ecosystem management.

The conclusion from the above considerations is that historical insights are important for our understanding of the structure and dynamics of forest ecosystems. However, as only a limited amount of ecosystem variability and heterogeneity can be incorporated in economical forest management strategies, a functional aspect including species ecology has to be considered to ensure the persistence of biodiversity. In practice this means that clustering of specific nature conservation measures would be a beneficial strategy for preservation of forest dwelling species. For example, in one area the focus could be to promote habitats and structures of deciduous trees and in another area focus could be on maintaining and restoring coniferous habitats. Areas to be selected for promoting deciduous habitats do not have to be those that have been deciduous rich in the past. More appropriately areas that contain high qualities of deciduous habitats and where focal species are present should be selected.

Methodological considerations

The methods used in retrospective studies of ecosystems all have limitations. Furthermore, the availability of study material is often restricted. For example, the analysis of the fire regime in Paper II was hampered by the lack of wood containing fire scars. Consequently, it was not possible to use such material to study the long-term mechanisms affecting the structure and composition of the studied landscapes in the early 20th century. Alternative methods, *e.g.* analysis of charcoal in peat and lake sediments, do not provide enough spatial and temporal precision for studies of fire history (Paper I). Thus, there is a lack of spatially explicit and temporally precise fire history studies in spruce-dominated areas. Such gaps in knowledge are often over-looked, and generalisations about disturbance regimes in the boreal forest landscape will be based solely on data from areas where such reconstructions are possible. The availability of material for palynological analysis may also be problematic, for example in calcareous areas (Paper I).

In analyses of pollen and macrofossils (including identification of charcoal) attention has to be paid to the possibility of separating the different species of birch. For birch pollen, data on morphology and size distribution are available (Mäkelä 1996) that have increased the precision in the study of mountain birch forests (Paper IV). However, birch pollen sizes are variable. Therefore, a complementary study of the characteristics of the local birch pollen sources is important to obtain even more precise results (Mäkelä 1998). Separation of birch species in charcoal fragments, based on wood anatomy, has also been problematic. Previously, all descriptions available for identification were qualitative, and contradictory in several respects (see Paper III for discussion). However, a reliable identification scheme was developed based on the quantitative approach presented in paper III. This was especially important for studies of sites where mountain birch is present in charcoal assemblages since this subspecies of hairy birch has been suggested to have originated from hybridisation with dwarf birch (Vaarama & Valanne 1973). The results from Paper III also highlighted the occurrence of small-diameter vessels not previously described in descriptions of the anatomy of birch wood (Fig. 6). We believe that these small-diameter vessels were not previously recognised as vessels, but were thought to be fibres due to their narrowness.

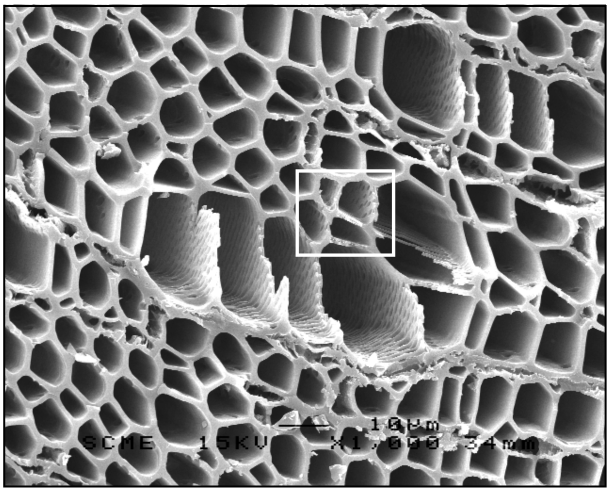

Fig 6. Scanning electronic microscope photo of dwarf birch (transverse section). The small window indicates four small diameter vessels (note the perforated cell walls).

The study of charcoal remains, anthracology, is often limited by poor temporal resolution in the available biological archives. In Paper IV, archaeological charcoal assemblages were analysed to identify species used for firewood. This material was quite well defined in temporal respects. However, the representativeness of the charcoal found in old dwellings may be questionable. As charcoal is repeatedly combusted when new fires are set in the fireplace, only charcoal that is found outside the perimeter of the fireplace or buried in the soil underneath it will represent older use than the most recent fires. For application of anthracology to large-scale vegetation reconstructions, it is difficult to find biological archives with good, or even any, temporal resolution. In forest humus and soil, charcoal is generally found in a single layer, which may contain charcoal from all fires that occurred during the Holocene, in unknown ratios. Consequently, there is no temporal resolution (Rosengren 2000). However, areas with several preserved and buried charcoal layers, *e.g.* areas subject to solifluction, or sand dunes, may provide better temporal resolution.

The above considerations high-lights the importance of focusing on the specific research question to be answered first and then apply the most appropriate methodology to answer the question posed. Some questions might not be possible to answer appropriately with available methodology and application of inappropriate methodology might provide unclear or even wrong answers.

Acknowledgements

Thanks to Greger Hörnberg, Henrik von Stedingk and Lars Östlund for providing comments on earlier versions of this thesis. Thanks also to John Blackwell for linguistic improvements. The work of this thesis has been funded by grants from The Bank of Sweden Tercentenary Foundation, The Structural Funds of the

European Union, Stiftelsen fonden för skogsvetenskaplig forskning and Stiftelsen Mauritz Carlgrens Fond.

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Postscript

Without the help, criticism, knowledge, company and support provided by a lot of people, these last five years would definitely not have been the same rewarding experience that they have been.

First and foremost, I thank my supervisors that has encouraged and helped me during the work with this thesis: Greger for always being there, having time to discuss, and for your never ending patience. You're a good guy!; Olle for giving me the possibility to start a PhD-education, introducing me to the vast field of vegetation ecology and for interesting discussions; and Christopher for sharing your great knowledge in palaeoecology, charcoal analysis and wood anatomy; and for your great hospitality during my visit in France.

Many thanks also to: Ingela and Lars L. at the Silvermuseum for co-operation, arranging great field-trips, and introducing me to the field of archaeology; Lars Ö. for co-authorship, comments on manuscripts and rewarding discussions on forest history.; Henrik, for rewarding discussions on science and teaching and for your invaluable scrutiny and criticism of various manuscripts; Anders G. for sharing your great knowledge of science in general, and ecology, in particular; Mats N. for dendrochronological advices; Sören Holm, Anders Jäderlund and Anna Shevtsova for statistical support; Ronny Löfstrand, Björn Enbom and Staffan Härdelin at Sveaskog for help with forest data; Anna-Lena for advices on the use of historical sources; John-Erik Hansson at the Provincial archives in Härnösand for help with archival sources; and Jim and Abbe for assistance when preparing the thesis for printing.

Back at the department there are many people that need a special thank: Malin for being the best of room-mates; Linda and other "kvälls- och helgjobbare" for company during evenings and weekends during the last months; Rikard for answering all my questions about GIS software; the magnificent lab-duo Hanna and Eva-Maria for making the "palaeo-lab" an enjoyable place to work with your jokes and your will to discuss any subject at any time, and to Helena and all other PhD-students over the years for company, stimulating seminars and discussions; and the staff at the Department of Forest Vegetation Ecology – present and past (some of you already mentioned, the rest not at all forgotten) for making the department an enjoyable place to work.

My sincere thanks go also to my family (Bo, Agneta, Johan and Lisa) for believing in my abilities and for encouraging my interest for nature.

Last but not least, my thanks go to Jenny, my beloved life companion, for your support during the ups and downs of the work with this thesis.