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Influence of habitat history on the distribution of *Usnea longissima* in boreal Scandinavia: a methodological case study

T. JOSEFSSON, E. HELLBERG and L. ÖSTLUND

Abstract: Changes in habitat affect the distribution of species at different spatial and temporal scales. Our aim was to assess the use of several retrospective methods when determining habitat history and its influence on species distribution, using the pendent lichen *Usnea longissima* Ach. as a model organism. The study was carried out in a Norway spruce dominated forest, located in the middle boreal zone of northern Sweden. Historical sources (including forest inventories and maps) and dendrochronology were combined with field surveys to determine past stand characteristics with a high spatial precision. Also, present stand characteristics were thoroughly surveyed and the relationship between distribution of *U. longissima* and past and present habitat characteristics were evaluated. Our results showed that, despite the fact that historical logging was unevenly distributed within the study area, similarities in stand structure exist today. Several essential factors affecting the distribution of *U. longissima* could be related to changes in past stand structure, especially the extent and intensity of previous logging operations and the subsequent stand development during the last *c.* 150 years. Our results also showed that *U. longissima* was favoured by a continuous old age structure with canopy openness preserved. The importance of detailed reconstructions of specific habitat components is highlighted when relating species presence to habitat change. It is suggested that the use of retrospective methods presented in this study can be helpful in clarifying possible causes for the complex distribution of certain organisms.

Key words: canopy continuity, epiphytic lichens, forest history, late-successional species, stand reconstruction

Introduction

Habitats change at different rates over time, thus influencing the distribution of species with specific habitat requirements. In northern Scandinavia rapid changes in forest ecosystems, affecting large areas, have occurred as a result of forest exploitation and forest management during the last 100 years (Esseen *et al.* 1997; Östlund *et al.* 1997; Kuuluvainen 2002). In conservation biology it is important to understand how these changes in habitat have affected the distribution of species at different spatial and temporal scales. However, the relationship between habitat history and the occurrence of threatened species is complex (*cf.* Ericsson *et al.* 2005). For late successional species, the concept of 'ecological continuity' has been identified as a determining factor (Rose 1976). However, all species depend on the continuous presence of a suitable habitat within their dispersal range. Consequently, detailed studies of historical habitat conditions are needed to clarify the degree to which ecological continuity is important for specific species. In such studies the choice of methodology is critical in determining whether reliable information about connections between species presence and habitat change can be made. By using dendrochronological and palaeoecological methods, Ohlson *et al.* (1997) related the presence of particular species to the history of disturbance (i.e. fire) and current habitat quality. They found present habitat quality to be the determining factor for the presence of all species studied except for vascular

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plants. However, few studies have provided information on changes to specific habitat components (e.g. coarse woody debris or canopy openness). Groven *et al.* (2002) used dendrochronological methods to relate the presence of a number of wood decaying fungi in Norwegian spruce forests to the dynamics of coarse woody debris over time. They found that the continuous presence of coarse woody debris at the landscape scale, not at the stand scale, is the determining factor for the occurrence of these organisms. Other organisms, including epiphytic lichens, may be dependent on the stability of certain habitat conditions at the stand scale. Holien & Tønsberg (1996) suggested that some epiphytic lichens may be adapted to long term stability in canopy cover. This, however, has not been thoroughly investigated, although some studies have shown that certain epiphytic lichens have an unpredictable pattern of occurrence in relation to habitat quality and may display a patchy distribution in apparently homogenous stands (Esseen & Ericson 1982; Gauslaa *et al.* 1998). Although no single current stand characteristic, or a combination of these, has provided a complete explanation of the complex occurrence patterns of epiphytic lichens, valuable information may be revealed by considering the local habitat history. In a study by Rolstad *et al.* (2001), the presence and abundance of epiphytic lichens was related to previous logging history, i.e. logging events and harvested volume were studied with the aid of dendrochronological techniques. However, this method provides only rough estimates of changes in canopy cover. We believe that a multi-disciplinary retrospective approach, including different methods, i.e. historical sources (forest inventories and maps), dendrochronology and field investigations, can provide more accurate spatial data for studies of small scale forest change in relation to the distribution of certain species. The objectives of the present study were (1) to assess the use of several retrospective methods for determining habitat history, with high spatial precision and with special emphasis on canopy characteristics, and (2) to evaluate the relationship between species distribution and habitat history, using the pendent lichen *Usnea longissima* Ach. as a model organism in a specific case study.

Material and Methods

Study area

The study area comprises 23 ha (Fig. 1) and is located in the middle boreal zone (Sjörs 1963), in the county of Västernorrland, north Sweden (62°52′N, 17°31′E). The site was selected on the basis of the following criteria: (1) the occurrence of *U. longissima* and (2) the availability of historical forest inventory data. The study area is situated on a small plateau surrounded by mires and clear cuts. Elevation ranges from 320 m to 380 m a.s.l. and the region has a cool temperate climate with mean annual precipitation of 725 mm and mean annual temperature of 2°C (Alexandersson 2001). The bedrock is primarily sedimentary gneiss of greywacke origin with granite and pegmatite intrusions (Lundqvist 1990) and the soils are mainly sandy till (Lundqvist 1987). Norway spruce [*Picea abies* (L.) Karst] in mesic dwarf shrub stands with *Vaccinium myrtillus* L. and *Deschampsia flexuosa* (L.) Trin. dominates the forest. In the central part of the study area, the forest is less dense and contains large trees of birch (*Betula* spp.) and Scots pine (*Pinus sylvestris* L.). These parts of the study area also display the highest abundance of epiphytic lichens (Fig. 2). Scattered deciduous trees, mainly birches and goat willow (*Salix caprea* L.) also occur, while aspen (*Populus tremula* L.) and rowan (*Sorbus aucuparia* L.) are present, but less abundant. The spruce forest structure is multi-layered and interspersed with frequent small glades.

Due to low human population density, until the 19th century the overall human influence on the forest in these parts of Scandinavia was restricted. The earliest known farm settlements near the study area were established by Finnish immigrants during the late 16th century (Gothe 1948). With agrarian development and an enhanced population growth, impact on the forest increased and changed (*cf.* Emanuelsson 2001). The main impacts were the result of slash and burn cultivation, grazing and cutting for building materials and firewood. However, within this region such agrarian forest utilization was mainly concentrated in the immediate surroundings of settlements and temporarily used summer farms (*cf.* Östlund 1993). More intensive use of the forests in this region began in the early 18th century, when demands for charcoal for the ironworks increased dramatically (Almquist 1909). In the mid 19th century, a new phase of forest use began; the increasing demand for sawn wood products on the European market triggered a notable increase in the exploitation of the forest (Almquist 1909; Östlund 1993). Furthermore, when large-scale logging was introduced in the late

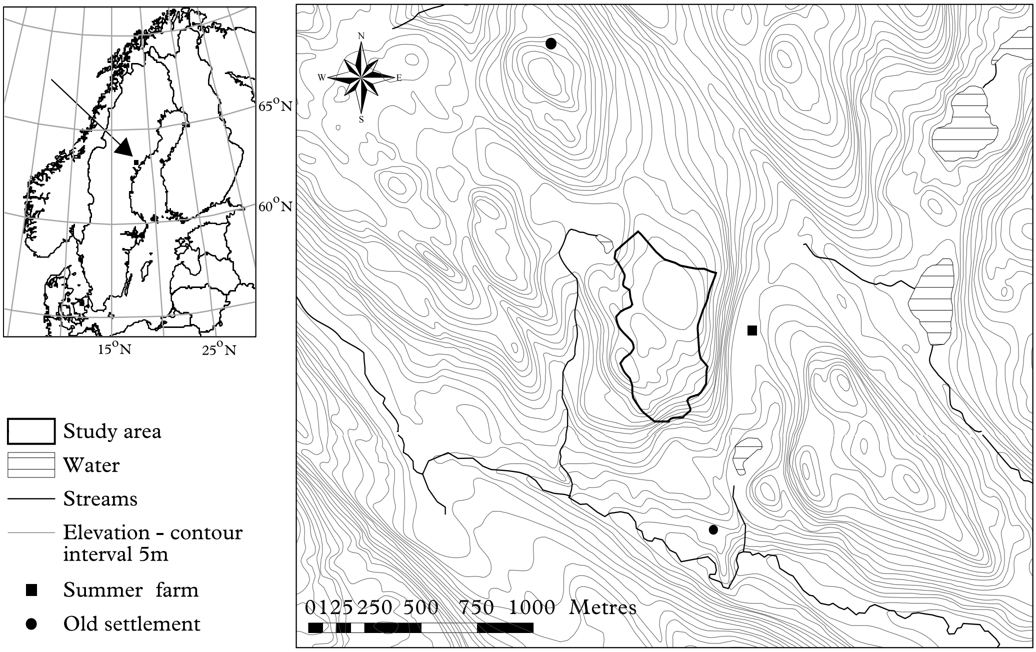

FIG. 1. Location and map of the study area, situated in the county of Västernorrland.

19th century, there was a sharp increase in the impact on the Scandinavian boreal forests (*cf*. Östlund 1993; Linder & Östlund 1998; Niklasson & Granström 2000; Axelsson & Östlund 2001). The logging operations in the late 19th century (primarily high grading) removed most of the large diameter trees, mainly Scots pine, which reduced the standing volume significantly (Östlund 1993). The structural effects on the forest after high grading operations were sometimes dramatic, leaving mainly small Norway spruce and deciduous trees. In the mid 20th century, further technical improvements and extensions to the existing road network made it possible to extend logging activities to previously un-logged stands (Embertsén 1976). The introduction of pulpwood manufacturing also meant that more slender trees and trees of lower quality could be economically logged. As a result, selective logging was mostly abandoned and clear cutting became the prevailing harvesting method (Östlund *et al.* 1997).

Study species

Usnea longissima is an epiphytic pendent lichen with an almost circumboreal distribution and is associated with a variety of tree species and forest ecosystems (Ahlner 1948; Ahti 1977). The ecology of this lichen has been comprehensively discussed by a number of authors, including Ahlner (1948), Esseen & Ericson (1982), Gauslaa (1997) and Thor & Arvidsson (1999). However, during the 20th century its abundance has decreased markedly throughout its range, for example in the boreal forest of Scandinavia (Esseen *et al.* 1981; Esseen & Ericson, 1982; Gärdenfors 2000; Nitare 2000). In Scandinavia and North America this epiphytic lichen is regarded as being particularly disadvantaged by modern forestry activities and has, therefore, been the subject of much scientific research (Esseen *et al.* 1981; Esseen & Ericson, 1982; Gauslaa 1997; Rolstad & Rolstad 1999; Peterson & McCune 2002; Keon & Muir 2002). Several variables have been suggested as affecting its distribution. Intensive industrial logging is considered to be the most important of these (Esseen & Ericson 1982), but air quality (Thor & Arvidsson 1999), tree age (Rolstad & Rolstad 1999), mineral composition of the substratum (Gauslaa *et al.* 1998), light (Gauslaa 1997), dispersal and stand age (Esseen 1985; Keon 2001) are also influential. Furthermore, it is believed that *U. longissima* and several other rare epiphytic lichens are dependent on spruce forests with long forest continuity (Esseen & Ericson 1982; Nitare 2000).

Study design and field sampling

The environmental data used in this study were collected from transect analyses and sample plots within the study area in the autumn of 2003. We used 50 × 50 m cells in a grid to form transects and sample plots.

Twenty-eight transects, running in an east–west direction, were defined with starting points along a base line running from south to north. Trees with *U. longissima* present at a height of up to 5 m, stumps produced as a result of forest exploitation and other

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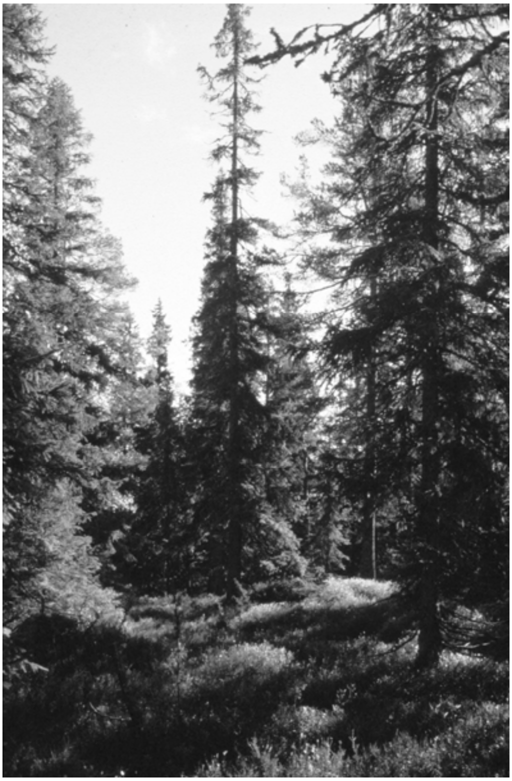

FIG. 2. Forest structure at the main location where *Usnea longissima* occurs. (Photo by Torbjörn Josefsson.)

signs of forestry (for example logging blazes) were recorded within the area up to 12·5 m on either side of the transect lines. Stumps were classified into three categories: class (1) stumps of Scots pine felled by axe >120 years ago; class (2) stumps of Scots pine felled by handsaw or chainsaw <120 years ago; and class (3) stumps of Norway spruce felled by handsaw or chainsaw <120 years ago. In addition, we sampled five potential fire scars using a chainsaw to determine possible fire events. Possible fire scars along with trees supporting *U. longissima*, logging stumps and other signs of previous forestry were numbered and described and their position and direction were determined using GPS (Swedish topographic system RT90) and a compass.

In eight sample plots (0·1 ha each) the distribution of tree species, the diameter at breast height (DBH) for all trees >5 cm, and the vitality of trees (divided into living or dead trees) were recorded. Four of the plots were randomly placed in an area where *U. longissima* was present and the other four plots were randomly chosen within the rest of the study area. Tree basal area and tree height in 24 additional sample plots placed randomly were also recorded, using a relascope and hypsometer. The tree basal area and tree height were used to estimate the current canopy openness, which was later compared with earlier data of canopy openness (calculated in the same way), extracted from old stand descriptions. Classifications of the forest-floor vegetation according to Ebeling (1978), and altitude, were also noted. When estimating the tree basal area of the 24 sample plots we randomly selected and cored 121 trees using increment borers (Ø4 and 5 mm). Samples were taken as near the germination point as possible. Tree age was later determined in the laboratory through year ring count, using a scalpel, zinc paste and stereo magnifier. The ages of 33 trees with *U. longissima* present (random samples were taken from the four selectively placed 0·1 ha sample plots) and six trees with logging blazes were determined in the same way. Trees with logging blazes were cored using an increment borer (Ø10 mm). The differences in tree age between trees with and without *U. longissima* present, were compared by means of a non-parametric statistical test (Wilcoxon Two-sample Test).

All samples were further analysed to detect possible growth responses that may indicate disturbance events. By comparing mean tree-ring width between two consecutive 10-year periods, we defined a 'growth response' as an increase in mean tree width, between two successive periods, of more than 100%. However, several factors (including logging events) may give rise to growth responses. The timing of logging events were determined by examining dated growth releases and relating these to the proportion of trees displaying such growth in the following 10 year period. In addition, this was related to other data, i.e. historical sources and occurrence of stumps and logging blazes. The method used for analysing logging events was similar to that used by Groven *et al.* (2002) in previous studies on tree age and logging history in Norway.

Historical maps and forest management plans

The primary sources used in this study were stand descriptions and forest inventory maps from the companies that have managed the forest within the study area since the 1870s. The historical documents and maps were provided by the Svenska Cellulosa Aktiebolags (SCAs) archive in Merlo and the local administration office in Ullånger, the Archive of Trade and Industry in Northern Sweden, the Regional Archive in Härnösand and the Swedish National Land Survey Office in Gävle (Table 1). To estimate the standing volume in the area in the late 19th century, we used data from 1890 and 1896 on DBH, tree species composition and number of trees. Changes in stand characteristics, including stand age and canopy openness, tree species composition and standing volume were estimated using forest inventory maps, stand descriptions, management plans and aerial photographs from 1920 to 1969. By using GIS (ArcView 3.2 program), digital maps showing the distribution of snags of different classes and trees with *U. longissima* present were produced. The oldest complete forest inventory maps (from 1938) were scanned and geo-referenced to fit the latest digital topographic maps. First, the

TABLE 1. *Unpublished sources used for data collection*

A. Landsarkivet, Härnösand [Regional archive]
Inskrivningsmyndigheten i Härnösands domsaga arkiv [Registration Authority of Härnösand judicial district archive]
Vol. DI:III Näverberget 1^2 i Gudmundrå socken (1876–1931)
Inskrivningsdomaren i Ångermanland Södra arkiv [Registration Authority of Ångermanland southern judicial district archive]
Vol. CII: a:1 and CI: a:2 (1933–1968)
Landskontoret i Västernorrlands läns arkiv [The County of Västernorrland archive]
Vol. EIII:89 Mantals och Skattskrifnings Längd för år 1850, Ångermanlands södra fögderi

B. Lantmäteriet, Gävle [Swedish National Land Survey Office]
Flygfoto 1:30000 18H 5g 1958 [Aerial photographs]

C. NIN—Näringslivsarkiv i Norrland, Härnösand [Archive of trade and industry in Northern Sweden]
Graningeverken AB
Skogsindelningar—kartor [Forest inventory maps and descriptions]
Tub 84 Näverberget 1866, 1866, 1939, 1939–40

D. SCA Centralarkiv Merlo, Timrå [SCA central archive]
Sunds AB
F: 3 Taxeringsinstrument 1895–1912 [Forest surveys]
Diverse brev, taxeringar mm. [Various letters, forest surveys]
14. Skogsräkning å hemmanen Westeråsen, Habbarn, Näverberg, Elgberget m.fl.
31. Transumt (20/5 1896) av E. Hessels taxeringsinstrument över Eriksdals Ångsågs Aktiebolags skogar år 1890
Fabian Gyllenhammar taxering av fastigheter och arrendeskogar 1897–1902 [Forest surveys]
15. 7/7 1896 Eriksdals Ångsågs AB's hemman och arrendeskogar i Gudmundrå, Ytterlännes och Wiksjö socknar

Svanö AB
2. Skogsbruk (Skogsvårdsstyrelsen, beståndsbeskrivningar, skogsindelningar, handlingar 1931–1952) [Forestry (Forestry Boards, stand descriptions, management plans)]
Arealuppgift: skogstillgång, avverkningsstatistik och kulturarbeten för Svanö, Dynäs & Wäija A/B:s egna skogar 1923–51. Ej insorterad. Sektion 26.11
261.53 Äldre skogsindelningshandlingar, sammandrag mm. 1931–46. Volym 15. Sektion 27:1
261.7 Arealuppgifter, skogstillgångar mm. 1923–1937. Volym 16. Sektion 27:2
266.301 Sammandrag över Svanö AB's skogsfastigheters arealer och kubikmassor 1933, 1942–46 och 1947–51, Volym 22. Sektion 27.2

E. SCA SKOG AB lokalkontor, Ullanger [SCA local administration office]
Graningeverken AB
Arkiv: skogsindelningar—kartor mm. [Archive: management plans and maps]
Karta över Block III omfattande reg.nr. 1^2 inom Näverbergets by uti Gudmundrå socken 1938, S.C. AB
Flygfoto 1:30000 18h 5g 1976+bestandsbeskrivningar

different forest stands were processed into polygons, then the stand development was analysed using the GIS overlay procedure.

Results

Present stand structure and occurrence of *Usnea longissima*

The forest displayed similar stand characteristics across the study area, with variations only in some small areas. The mean tree height within the 24 sample plots was 19 m (ranging from 12 m to 26 m) and the mean canopy openness was 0·6 (varying between 0·35 and 0·75). The main species of living trees within the study area was Norway spruce (83%), with subdominant deciduous species (15·5%) and solitary Scots pine trees (1·5%) scattered over the area. A comparison between areas with *U. longissima* and

TABLE 2. *Stand characteristics taken from eight sample plots (0·1 ha) with and without occurrence of* U. longissima. *All trees >5 cm DBH were counted*

	U. longissima present	*U. longissima* absent
Tree species (%)		
Betula sp.	16·7	13·8
Picea abies	81·1	83·6
Pinus sylvestris	2·0	1·6
Populus tremula	0·2	
Sorbus aucuparia		1·0
Tree size (mean DBH)		
Betula sp.	14·5	13·3
Picea abies	16·8	16·5
Pinus sylvestris	37·6	34·4
Populus tremula	44·0	
Sorbus aucuparia		9·0
Tree vitality (%)		
Living trees	83·8	83·3
Dead trees	16·2	16·7
Top breaks on trees		
Average height (m)	3·49	3·52
Proportion of trees (%)	9·7	8·2

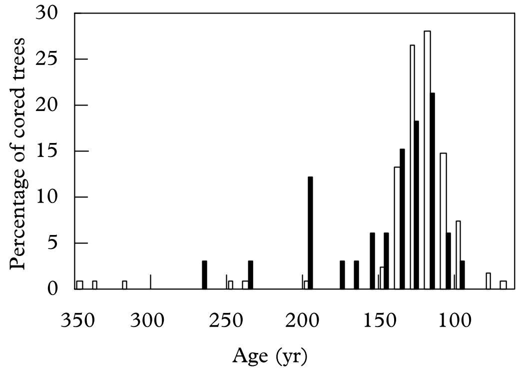

FIG. 3. Age structure of Norway spruce in 10-year intervals for trees >5 cm DBH, with (■) and without (□) *Usnea longissima*.

areas without *U. longissima* showed no distinct differences in the current stand characteristics, such as tree species composition, tree size and tree vitality including top breaks on trees (Table 2). The average tree age in the study area was 133 years ($n=154$). Although the age of the living Norway spruces with *U. longissima* varied between 102 and 265 years ($n=33$), most were 110 to 160 years old (Fig. 3). Trees without *U. longissima* displayed a similar age structure, although some trees were less than 100 years old and some were exceptionally old (>350 years). A significant difference in mean tree age was found between trees with *U. longissima* (149 years) and trees without this species (129 years) ($Z=3{\cdot}81$, $P<0{\cdot}05$).

Within the study area, we found *U. longissima* on 56 trees, of which 9% had a stem diameter less than 10 cm DBH. The number of trees with *U. longissima* was estimated to be 4·4 ha^{-1}. Furthermore, *U. longissima* was recorded on both dead and living trees and exclusively on Norway spruce. The species was unevenly distributed within the study area and was concentrated in the south-central part (Fig. 4). At this location, some trees were very lichen-rich and contained long-pendent specimens, while the forest was characterized by an open and multi-layered stand structure with slow growing trees. The topography was more hilly with drier conditions than the rest of the study area, with *Vaccinium vitis-idaea* L., *Cladonia rangiferina* (L.) F.H. Wigg. and *C. arbuscula* (Wallr.) Flot. present. Thalli of the lichen found in the northern and eastern parts of the study area were confined to small gaps, while specimens found in the north-central part showed no such pattern. Here the forest structure was still multi-layered but somewhat denser than the south-central section.

Reconstruction of stand characteristics 1860–2003

Stand structure within the study area has changed considerably during the last 150 years. Based on the information on stand descriptions extracted from Sunds AB and Svanö AB provided by the SCA Central Archive (Table 1), prior to the 1860s large trees of Scots pine and slow growing trees of Norway spruce dominated the forest, while deciduous trees are thought to have occurred less frequently. In the forest survey from 1896 (Sunds AB, SCA Central Archive), the forest within the study area was described as a dying and sparse spruce

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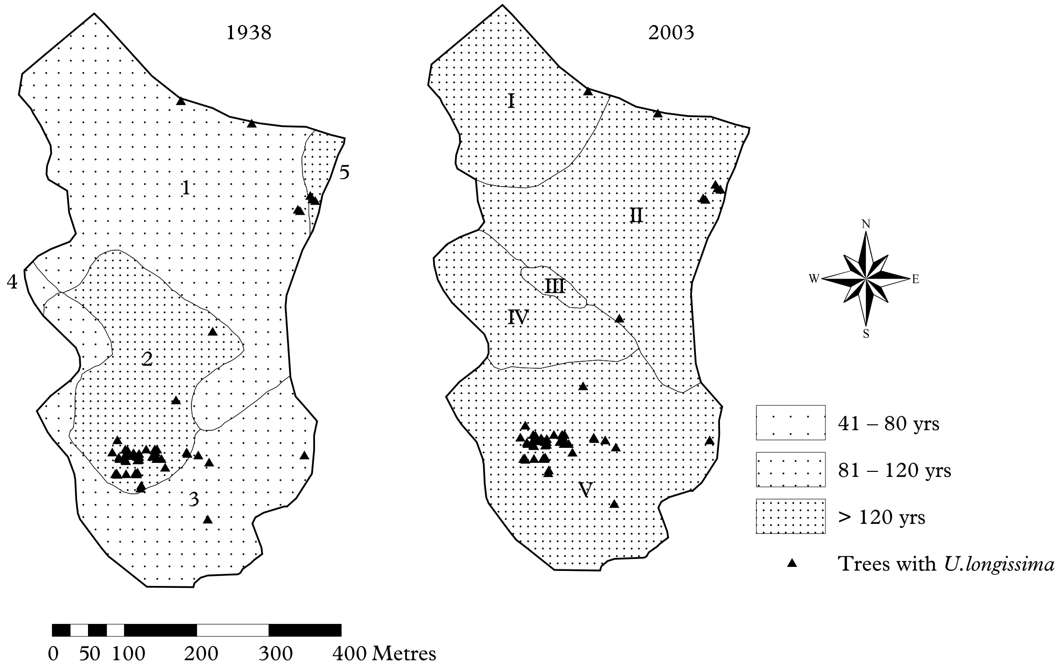

FIG. 4. Stand borders and age structure in 1938 and 2003. Stands are numbered 1–5 and I–V for 1938 and 2003, respectively. The current distribution of *Usnea longissima* is plotted on both maps. Data extracted from field sampling and maps provided by SCA Central Archive (Table 1): Graningeverken: Karta över Block II 1926 and Karta över block III 1938.

forest with limited re-growth. According to the logging data, most of the large Scots pine trees were felled before 1890, leaving a thinned stand of Scots pine, with restricted numbers of Norway spruce and deciduous trees. In 1890, the proportion of Scots pine had been substantially diminished but some of the trees still exceeded 45 cm in DBH. Through further selective logging operations in the first decades of the 20th century, additional Scots pine and large diameter Norway spruce as well as deciduous trees were felled. Consequently, the remaining forest was characterized by stands of Norway spruce exclusively or mixed Norway spruce and Scots pine. In the 1930s, a few deciduous trees were present, but subsequently there has been a substantial increase. In 1933, the standing volume of timber within the study area and its surroundings was 99 m^3 ha^{-1}. However, during the last century the standing volume has increased, except for a temporary decline in the late 1930s. In 1938, old forest (>120 years) covered less than 23% of the study area and was confined to stands 2 and 5 (Fig. 4). In stand 4, the forest was younger than 80 years. Today a multi-aged forest with an average stand age exceeding 120 years covers the entire study area and the standing volume of timber is approximately 200 m^3 ha^{-1}. Furthermore, at present the area contains twice as many trees in each diameter class up to 45 cm DBH, as in 1890. However, there were large trees (DBH >45 cm) present in 1890, but now there are none. A comparison of canopy openness in 1938 and 2003 identified changes in all areas except the central parts of the study area (stand 2), which today contains the highest concentration of trees with *U. longissima* (Table 3).

Dating of logging events

No evidence was found of clear-cutting operations within the study area. Scattered

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TABLE 3. *Canopy openness in 1938 and 2003 (within borders 1–5 corresponding to 1938 stand borders). Data extracted from field sampling and maps provided by SCA Central Archive (Table 1): Karta över block III 1938*

Stand number	Openness	
	1938	2003
1	0·7	0·55
2	0·6	0·6
3	0·5	0·6
4	0·7	0·55
5	0·9	0·65

stumps, however, of all three categories were observed (Fig. 5). Stumps of class 1 (Scots pine felled >120 years ago) were evenly distributed over the whole of the study area (9 ha^{-1}) and are thought to derive from the earliest logging period. Stumps of class 2 (Scots pine felled <120 years ago) were less common (4 ha^{-1}) and confined to the western parts. Many of the class 2 stumps had a straight cut surface and in some cases small pieces of bark left on the sides. Stumps of class 3 (Norway spruce felled <120 years ago) were found throughout the area (29 ha^{-1}) but concentrated in the north-west part. These stumps were often completely overgrown with bryophytes and ericaceous vegetation. Accordingly, the northern part of the study area displayed the highest concentration of stumps related to forestry activities, while the south-central part, which is the main location of *U. longissima*, contained few stumps of all three classes. Logging blazes were recorded on 47 trees (Norway spruce and birch) within the study area, although they were absent from the far north-west section and infrequent in the south-central area. Six of the logging blazes could be dated to 1929, 1936 (3), 1940 and 1941. However, logging operations were evident all over the study area, including areas where *U. longissima* is present.

Growth releases, indicating historical logging events, were detected in 22% (n=42) of the cored trees (Fig. 6). No difference in growth release was found between trees with and without *U. longissima*. Three possible periods of growth release were identified within the study area during the last 150 years: 1857–1868, 1913–1922 and 1937–1946. Since we did not detect any reliable fire-scars or other traces of larger fires within the study area, no forest fires seem to have occurred during at least the last two centuries. Nevertheless, one tree was discovered that had been struck by lightning, but this event does not seem to have affected the surrounding forest.

Discussion

In this study, we used retrospective methods with detailed spatial precision to assess the relationship between forest stand history and the present spatial distribution of the pendent lichen *U. longissima*. The results indicate that considerable changes in stand structure have had a major influence on this species' ability to survive periods of past forest utilization, intense logging and forest management in the last *c.* 150 years. These changes are in clear contrast to the seemingly uniform current stand structure. The area studied has been subjected to logging operations during at least three different periods, but no large scale forestry operations have been undertaken since the 1940s, which may explain the current homogenous forest structure. We found that several variables, including a continuous old age structure with canopy openness preserved, and moderate re-growth of trees after modest selective cuttings, may constitute prerequisites for the presence of *U. longissima* in areas affected by forestry.

Interpretation of forestry activities and logging history

The first major logging event in this area was high grading of Scots pine in the 1860s, which seems to have affected the forest structure over the entire study area (Figs 4 & 5). Logging operations from this period resulted in the loss of the largest trees but, more importantly, changed habitat conditions for the Norway spruce under-growth

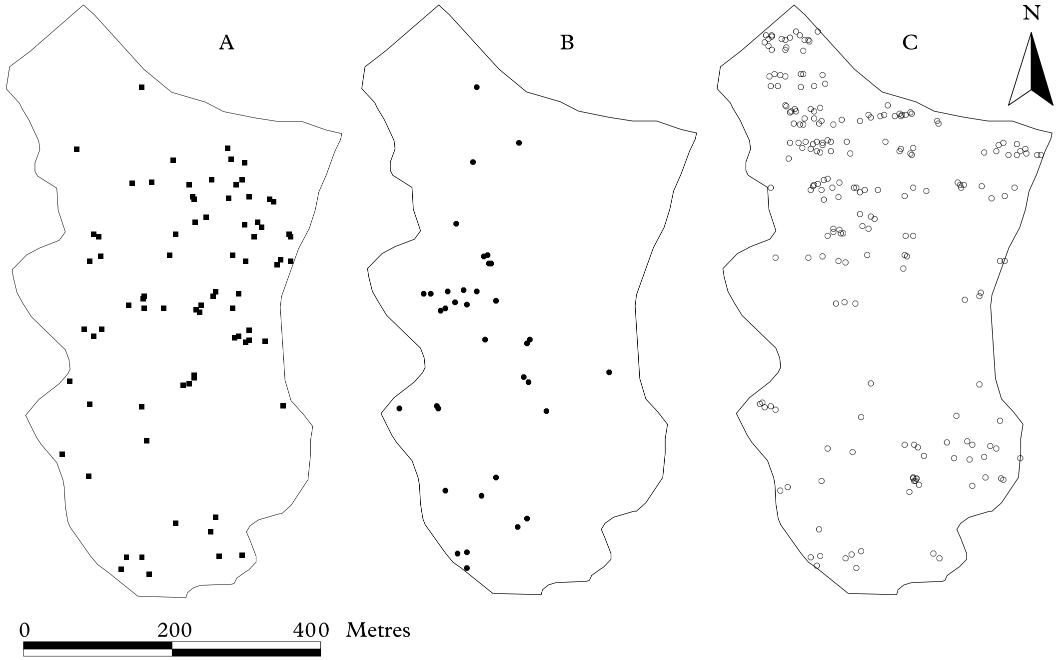

FIG. 5. Distribution of stumps within the study area in 2003. A, class 1 ■ (stumps of Scots pine felled by axe >120 years ago); B, class 2 ● (stumps of Scots pine felled by handsaw or chainsaw <120 years ago; C, class 3 ○ (stumps of Norway spruce felled by handsaw or chainsaw <120 years ago).

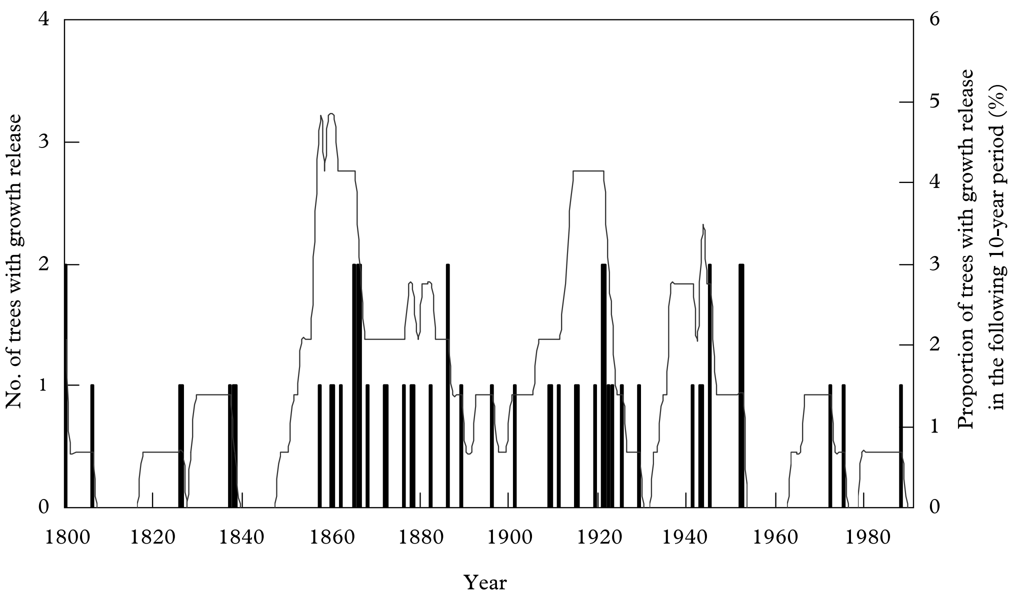

FIG. 6. Number of cored trees per year displaying growth release (■) and the percentage of cored trees displaying growth release in the following 10-year period (——).

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(Tirén 1937). In some stands, high grading resulted in slow re-growth and death of the remaining trees. In other stands, these logging operations resulted in noticeable growth responses and recruitment of new trees. This sudden change in habitat conditions may have influenced the distribution of *U. longissima*. In areas with an especially dense forest structure, the increase in canopy openness may have temporarily favoured populations of epiphytic lichens such as *U. longissima*. However, in areas where the trees displayed strong growth responses, this could have affected *U. longissima* and other epiphytic lichens negatively, since they are sensitive to abrupt changes in quality and availability of substratum (Johansson and Ehrlén, 2003) as well as changes in microclimate (Ahlner 1948; Esseen & Ericson 1982; Gaussla *et al*. 1998; Esseen *et al*. 1996). Even more intense effects on stand structure probably took place during the selective logging operations in the first half of the 20th century, particularly in the northern part of the study area (Figs 4 & 5). Consequently, during the period 1920–50, the standing volume seems to have been very low. The change in stand structure (including a severe reduction in available substratum and the almost certain removal of trees containing important sources of epiphytic lichens) evidently affected the distribution of old-growth forest. In areas where such felling was intense, this may be a decisive factor in explaining the absence of *U. longissima* today in seemingly suitable habitats. This is especially interesting since present forest structure (stand age and tree species composition) does not differ markedly across the whole study area (Fig. 4, Table 2). Notably, more than 86% of the trees supporting *U. longissima* today were found within areas corresponding to stands 2 and 5, which even in 1938 were covered by a forest more than 120 years old. This confirms earlier studies emphasizing the importance of stand age for several epiphytic lichens (Esseen & Ericson 1982; Hyvärinen *et al*. 1992; Dettki & Esseen 1998; Rolstad & Rolstad 1999; Price & Hochachka 2001; Juriado *et al*. 2003). In addition, the area within the borders of stand 2 displayed no significant changes in canopy openness between 1938 and 2003 (Table 3). This finding suggests that *U. longissima* is favoured by long-term stability in stand structure, including canopy continuity and absence of large-scale disturbances such as recent industrial forestry operations, including extensive thinning and clear cuts. The use of canopy continuity as a characteristic can be justified since changes in canopy openness reflect the actual number of standing trees and consequently are an indicator of stand structure. More precisely, *U. longissima* seems to require a specific level of canopy openness, i.e. not too open and not too closed. However, this depends on the species being studied. As noted by Rolstad *et al*. (2001), epiphytic lichens should be used with caution as indicators of canopy continuity. With respect to *U. longissima*, negative effects on its distribution within stands can be seen even 60 years after the last logging event.

Other factors influencing the distribution of Usnea longissima within stands

The reasoning above is based on the assumption that *U. longissima* was present in 1938 and before, and that it is limited by its poor dispersal ability, a characteristic which has also been suggested by Esseen & Ericson (1982) and Dettki *et al*. (2000). As an example, by transplanting thalli of *U. longissima* in different suitable habitats in the Oregon Coast Range in the US Pacific Northwest, Keon & Muir (2002) showed that dispersal limitations may play a more significant role than the availability of suitable habitats in determining the distribution of the lichen. However, since only one location is included in the present study, habitat changes may coincide with other factors, for example topography, tree species, stand age, tree age and/or the history of large-scale disturbances.

The topography of the south-central section of the study area, including an open and multi-layered stand structure, provides the habitat conditions for *U. longissima* described in Ahlner (1948), Esseen & Ericson (1982) and Thor & Arvidsson (1999). Topography may, therefore, be an important reason for the uneven distribution of *U. longissima* within the study area. However, we found no specimens in some other areas with habitat conditions resembling those in the south-central part. On the contrary, in areas without these typical habitat conditions we recorded several thalli, although these cases were confined to small canopy openings. These conflicting facts show that simple one-dimensioned explanations for the occurrence of this particular species are inappropriate. Furthermore, tree species and tree vitality (living or dead trees) are important variables determining the occurrence of several epiphytic lichens (Thor & Arvidsson 1999; Nitare 2000). In the present study, *U. longissima* was found solely on Norway spruce but showed no obvious preference for living or dead trees. These results are consistent with earlier studies (Esseen & Ericson 1982; Gaussla 1997; Rolstad & Rolstad 1999) and give support to the assumption that tree species but not tree vitality affects the distribution of this species and that the thallus fragments seen from the ground probably derive from populations higher up in the canopy. It has also been suggested that stand age is of greater importance in the distribution of *U. longissima* than the age of single trees (Esseen & Ericson 1982; Rolstad & Rolstad 1999). In the present study, trees containing *U. longissima* displayed only a slightly different age structure than trees without it (Fig. 3). For example, a number of the cored trees now supporting *U. longissima* germinated during 1800 to 1850, yet very few of the cored trees without the lichen originated in this period. In addition, we found a few exceptionally old specimens of Norway spruce without *U. longissima* but also some quite young individuals, while trees supporting *U. longissima* displayed no such pattern. However, regardless of the occurrence of the lichen, most trees germinated between 1850 and 1900, which points to the importance of disturbances during this period. Consequently, tree age seems to have relatively little impact on the occurrence of *U. longissima*. The small differences in age structure may also be the result of different sample sizes.

As described by Esseen & Ericson (1982) another important factor influencing *U. longissima*'s occurrence within an area is the long-term absence of forest fires, primarily because of its poor dispersal ability and rather slow growth rate. Accordingly, most *U. longissima* recorded in this region of Scandinavia is present in stands in a late successional stage (Esseen *et al.* 1981). In this study the absence of fire-scars on living trees, dead trees and stumps, as well as the presence of old spruces within the study area indicates a late post-fire successional forest stage and thus stable habitat conditions for *U. longissima*. However, one should be cautious when drawing conclusions concerning the role of forest fires from this small area. Furthermore, epiphytic lichens such as *U. longissima* may be prevented from colonizing sites because of unknown or subtle differences in habitat quality, for example unfavourable microclimate (Gauslaa 1997) or bark chemistry (Hyvärinen 1992; Gauslaa *et al.* 1998).

The importance of retrospective methods and their limitations

Studies that interpret stand history and long-term changes in habitat conditions not only provide information with a high spatial resolution, but they also identify critical variables. In this study, we highlight the importance of habitat history, emphasizing long-term stability in stand structure, including canopy continuity. One problem with the approach taken in the present study is that it might be difficult to produce a complete reconstruction of the different types of forest stands. The major limitation is the availability and quality of historical sources. Not all land-owners have archived their old forests surveys and maps and in many cases they are difficult to interpret. This can leave gaps in the historical reconstruction and subsequently gaps in the interpretation of the relevant factors (Östlund & Zackrisson 2000). Furthermore, retrospective methods involving dendrochronological analyses of stand history are very time consuming for larger areas. In our opinion, the best results are achieved when different complementary methods are used. However, a very clear focus on the decisive factor and the aim of the study are vital to ensure feasibility (Hellberg 2004). We suggest that the use of retrospective methods presented in this study can be helpful in clarifying possible causes for the complex distribution of certain forest-dwelling organisms. Furthermore, knowledge about previous stand structure and habitat history can play a significant role in future forest management and may provide guidance for ensuring the existence of threatened species such as *U. longissima* and other epiphytic lichens.

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