Stand Structure and Spatial Pattern of Regeneration of *Pinus sylvestris* in a Natural Treed Mire in Latvia

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We examined the regeneration patterns of *Pinus sylvestris* L. in a natural treed mire in the hemiboreal zone in Latvia. Data on tree stem age and size was collected in 207 fine-scale plots (10 m^2) and 4 medium-scale plots (400 m^2). Size structure of living and dead trees was also estimated on transects 180-m and 250-m length and 10-m width. In addition, the vegetation was described in 1-m^2 plots to determine preferred microsites for *P. sylvestris* establishment. *Pinus sylvestris* showed continuous regeneration by an inverse J-shaped age and size structure. Pulses of mortality induced by fire were also evident. Regeneration of *P. sylvestris* was mostly on *Sphagnum magellanicam* Brid. hummocks free of competition from *Ledum palustre* L. and graminoids, which were found in small interspersed patches throughout the mire. The spatial pattern of tree cohorts differed, probably due to changing moisture conditions altering seedbed conditions and by fire-induced mortality in specific areas. Recent rapid invasion by *Betula pubescens* Ehrh. and *Picea abies* (L.) Karst. in a post-fire period since 1971 is probably associated with drier conditions.

1 Introduction

Central aspects of the concept of a natural forest are structure and dynamics that have not been significantly changed by humans (Rouvinen and Kouki 2008). Understanding of disturbance patterns in forests led to a need to abandon the climax equilibrium view of forest succession (Clements 1916) in favour of an individualistic concept, whereby "on every spot of ground, the environment varies in time, and consequently the vegetation varies in time" (Gleason 1939). The idea of "climax" forests has been overshadowed by knowledge of the natural patterns and processes shaped by disturbance at multi-scale landscape levels (Kuuluvainen 2002), but there is still insufficient understanding of the links between the heterogeneity of natural disturbance processes at stand and landscape levels and biodiversity (Angelstam 1998). The long history of conventional forest management in northern Europe has caused a loss of pristine forests undisturbed by humans, and thus there is a need to identify reference forests that can serve as models of natural disturbance processes (Kuuluvainen 2002).

Fire is the main disturbance controlling forest dynamics in the boreal region (Zackrisson 1977). In *Picea abies*-dominated landscape fires are rare and usually stand-replacing (Wallenius 2002), while some trees usually survive fire in *Pinus sylvestris* stands on dry site types (Kuuluvainen et al. 2002, Brumelis et al. 2005). Under a developed canopy of *P. sylvestris* a feather moss layer retards establishment of seedlings (Steijlen et al. 1995, Nilsson et al. 1996, Zackrisson et al. 1997). Waves of regeneration are initiated after fire by creation of microsites for establishment (Engelmark et al. 1998, Gromtsev 2002, Brumelis et al. 2005), or they may be related to periods of climatic optimum for good seed production and seedling development (Zackrisson et al. 1995). Less is known of the patterns of disturbance, regeneration and mortality on treed mires. In a study of the age and size structure of *P. sylvestris* on eight mires in Sweden, there were no signs of fire disturbance, and waves of regeneration were suggested to be related to a fluctuating climate (Ågren and Zackrisson 1990). In three of the eight mires, the age structure suggested a continuous pattern of recruitment, or recent improved conditions. Sarkkola (2006) described *P. sylvestris* age and DBH structure on pristine peatlands in northern Finland as usually reverse J-shaped, but bell-shaped in southern Finland where there is an increased forcing effect of climatic and other factors (Sarkkola 2006). Continuous presence of a favourable seedbed for germination on *Sphagnum* hummocks can result in continuous regeneration of *P. sylvestris* (Ohlson et al. 2001). *Sphagnum* can quickly overgrow *P. sylvestris* seedlings, but if seedlings reach a diameter (above root collar) of 10 mm then they interfere with *Sphagnum* growth (Ohlson et al. 2001). A sparse canopy might limit competition-induced mortality (Sarkkola 2006), allowing continuous entry of seedlings into the sapling layer and further into the canopy.

In Latvia there are no forests that have escaped disturbance by man, but there are many stands in which natural structures indicate a considerable period of domination by natural disturbance processes, evident by large volumes of dead wood and other features of naturalness (MCPFE 2007). A large part of wetland forests in Latvia have been drained, particularly in the 1970s and 1980s (Prieditis 1999). However, today many of the drainage systems are old, overgrown and not functioning (Ministry of Agriculture 2009), thus still supporting natural vegetation and biodiversity.

A treed mire in Seržu Tīrelis Nature Reserve was recently found to support the oldest *P. sylvestris* trees in Latvia. The stands have a mixed size structure suggestive of a long history of minimal disturbance by humans. The aim of the study was to determine the past history of regeneration of tree species in the mire by determining the age and size structure at different spatial scales, as well as to identify the preferred vegetation for establishment of *P. sylvestris*.

2 Material and Methods

2.1 Site Description

Latvia is located in the boreo-nemoral region zone (Hytteborn et al. 2005). The climate is characterised by mild winters (January mean temperature –4.3 °C) and cool summers (mean July temperature 18.1 °C) with annual precipitation 615 mm
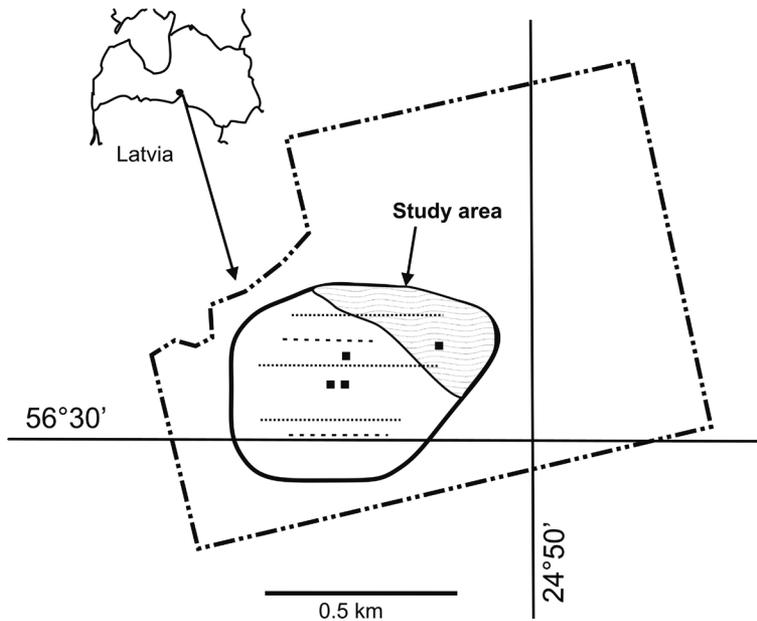
Fig. 1. Location of study area within the Seržu Tīrelis Restricted Area. The ombrotrophic part of the mire to the northeast is shown as a stippled pattern. Squares show locations of 400-m² plots: three in the minerotrophic part, and one on the ombrotrophic peat. Lines show transects for 1-m² plots (dotted line) used in vegetation description, and for estimation of living and dead wood density (dashed line).

(Riga Hydrometeorological Station).

The study area is part of the Seržu Tirelis Restricted Area (151 ha), protected since 1977 and now part of the Natura 2000 network. The forests are mostly bog woodland, a priority EU habitat (European Commission DG Environment 2003). There is no evidence of drainage ditches in the area. However, forest maps from 1929 (produced by the Military Geodesic/Topography Section) show a stream draining from the mire, which today has almost completely overgrown, and can be considered to have insignificant impact on the hydrology. Presently, little evidence of logging can be seen, but scattered cut stumps are evident around the periphery of the study area.

The Serzu Tirelis restricted territory is an important habitat for several bird species protected by the EU Habitat and Species Directive, for example, capercaillie, black grouse, black stork, black woodpecker, and Tengmalm's owl. The study area encompassed the central part of

the restricted area (Fig. 1), which has little evidence of human disturbance, and is a capercaillie lekking ground. The larger part of the studied peatland is a minerotrophic *P. sylvestris* mire (<30 cm peat) with *Picea abies* and *Betula pubescens* in the understory. The shrub layer is dominated by sparse to dense *Vaccinium myrtillus* L. The moss layer is patchy, with feather mosses *Hylocomium splendens* (Hedw.) Br.Eur. and *Pleurozium schreberi* Mitten interspersed with *Sphagnum magellanicum* Brid., and also *Sphagnum girgensohnii* Russow. in uprooting depressions. The northeastern part (Fig. 1) of the peatland is ombrotrophic with a peat horizon >30 cm, dense *Ledum palustre* L. and without *P. abies*.

2.2 Sampling Design

Age and size structure of trees was determined at three spatial scales. Firstly, in 2003 at a fine spa-

tial scale, 207 circular plots with size 10 m^2 (1.78 m radius) were located randomly by previously chosen coordinates. Plot centre was taken as the closest tree to located coordinates. Secondly, in 2005–2006, on a medium scale four 20 m × 20 m plots (one plot 20 m × 40 m) were established in locations (Fig. 1) chosen subjectively by size structure to be representative of a larger area. Of the four medium scale plots, three were placed in the minerotrophic part of the mire, and one on the deeper peat. Thirdly, size structure (not age structure) of living trees and dead wood was determined in two transects (180 m and 250 m × 10 m) in 2008 (Fig. 1). The transects were located randomly, transversing only the minerotrophic part of the bog where the oldest trees were located, in a East-West direction.

Ground level vegetation was described in 1 m × 1 m plots located at 10-m regular intervals along three transects (Fig. 1) running E-W across the mire, about 200 m from each other. In addition, a search was made for *P. sylvestris* seedlings in 10-m wide sections on each side of the transects, and when found additional plots were also established fitting the seedling(s) in the plot centre. Seedlings were defined as individuals <0.5 m in height.

Coordinates of all plots and transects were recorded with a GPS (Global Positioning System) satellite navigation devise using the LKS-92 Latvian coordinate system.

2.3 Analysis of Age- and Size Structure

In the fine- and medium-scale plots heights and diameter at 1.3 m height (DBH) of *Pinus sylvestris* L., *Picea abies* (L.) H. Karst. and *Betula pubescens* Ehrh. trees were measured. Record was made of all trees with fire scars. Cores were taken from tree stems >3 cm DBH as close as possible to stem base to determine age. If the core did not reach the pith then the number of missing rings was estimated. For smaller *P. sylvestris* and *P. abies* age was determined by counting branch nodes.

On the two transects, for determining size structure on a larger scale, DBH was measured for all trees >1.3 m height, but the trees were not cored.

Trees less than 1.3 m height were counted in a 2-m wide section running along the centre of the transect. DBH of all standing snags and dead trees as well as fallen dead trees was also measured.

Age of trees was determined by counting tree rings of cores under a microscope after cutting with a razor blade or after sanding with up to 200 grade sand paper. If the core did not reach the pith then the number of missing rings was estimated by considering the curvature and width of tree rings. Additionally, a number of years was added based on the height of the removed core. For determination of age structure of *P. abies*, only trees with cores reaching pith or with well visible branching nodes were used, as the species can grow very slowly in suppressed conditions (Steijlen and Zackrisson 1987) resulting in a large number of rings within a small DBH range. As the field work was conducted in different years, the tree ages were adjusted to those in 2003.

Time of fire was also determined in five pine trees (in 2009 winter) by cutting wedges with hand saw up to the scar. The wedges were sanded with up to 200 grade sandpaper to distinguish tree rings. In one case the wedge sample was soaked in alcohol to remove resin.

2.4 Analysis of Ground Vegetation Plots

In the ground vegetation plots, (Fig. 1) percent cover of all moss and herbaceous/shrub species was estimated in 10% intervals. Sedges were treated together as an ecological group. Seedlings were counted by species.

The plots (n = 122) were divided into two groups, depending on the presence or absence of *P. sylvestris, P. abies* or *B. pubescens* seedlings. Multiple Response Permutation Procedure (MRPP) on a calculated Euclidian distance matrix was used to test for differences in vegetation composition between the groups (McCune and Mefford 1999). In short, MRPP is a nonparametric multivariate technique based on a distance matrix that does not require distributional assumptions. Significance is determined by calculating the probability of obtaining a weighted mean within-group distance (expected) that is smaller or just as small as that observed. Equal chance of groupings is assumed when calculating the expected distance. The sta-

tistic A estimates within-group homogeneity, compared to that expected by chance (McCune and Mefford 1999). If significant differences were shown by MRPP, then moss, herbaceous and shrub species showing significant differences in cover in relation to presence or absence of tree species were identified using Indicator species analysis (Dufrêne and Legendre 1997). These analyses were conducted using PC-ORD Version 5.0 software (McCune and Mefford 1999).

A logistic regression model was derived using the Canoco for Windows Version 4.53 (ter Braak and Šmilauer 2002) GLM procedure (binomial distribution, logit link function) to predict presence of *P. sylvestris* seedlings as a response variable from cover of indicator species as predictor variables.

3 Results

3.1 Age and Size Structure

The size structure of *P. sylvestris* in the 10 m^2 plots showed a peak in the smallest DBH class (Fig. 2a). As no age class was missed, continuous recruitment is suggested, confirmed also by the age structure (Fig. 2b). There was a large number of trees <10 years of age, with peaks also in the 30–40- and possibly 61–70-year age class. The oldest pine tree found was 459 years of age, but this tree was actually just outside of a plot, and was not included in age and DBH structure plots.

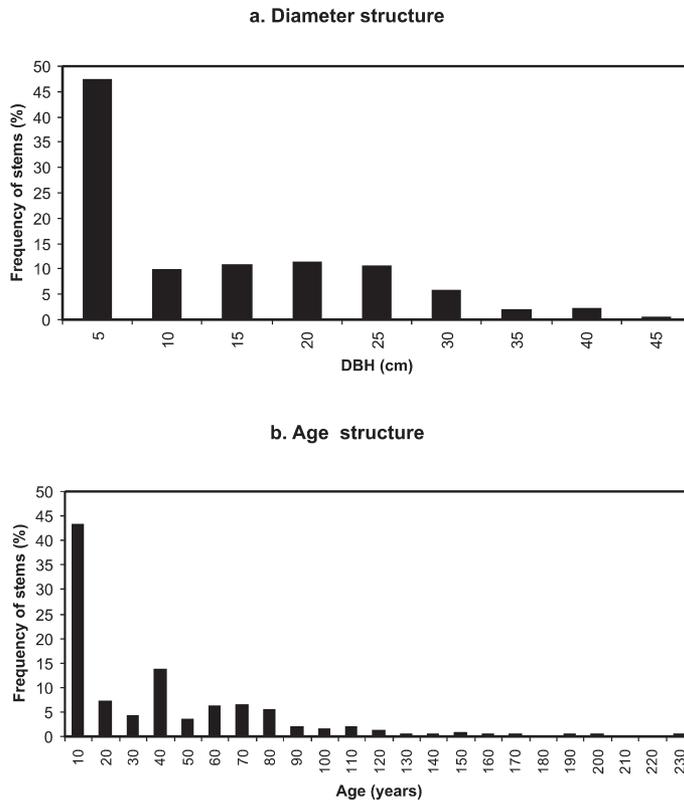On a spatial scale, the number of plots with *P. sylvestris* stems did not show a peak in the younger

a. Diameter structure

b. Age structure

Fig. 2. Diameter and age structure of *Pinus sylvestris* estimated in 10-m^2 plots. Frequency of stems (%) in 5-cm DBH classes (a) and 10-year age classes (b) is given.
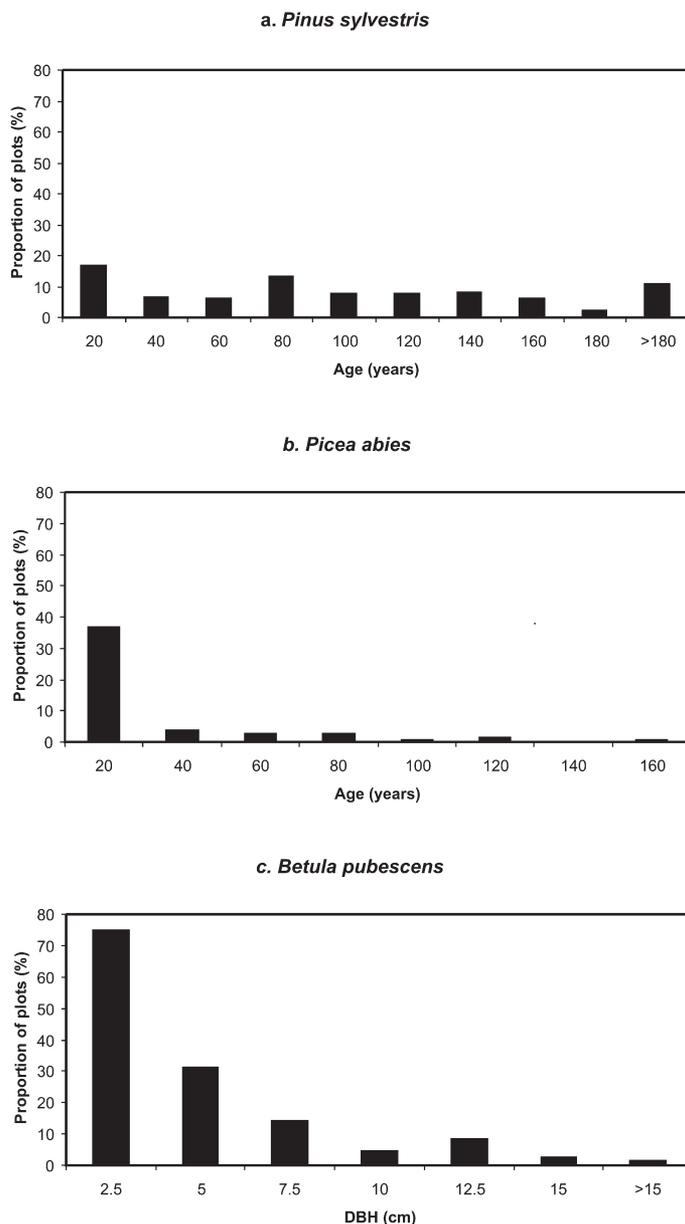
a. *Pinus sylvestris*

b. *Picea abies*

c. *Betula pubescens*

Fig. 3. Proportion of 10-m^2 plots containing 20-year age classes of *Pinus sylvestris* (a) and *Picea abies* (b) and 2.5-cm DBH classes of *Betula pubescens*.

class (<20 years), clearly indicating aggregation in a low number of plots (Fig 3a). There were almost as many plots with 61–80-year-old trees as with <20-year-old stems. While *P. sylvestris* regeneration was patchy with scattered groups of individuals (1–18 individuals/10 m^2), *B. pubescens* and *P. abies* were abundant in the understorey throughout (Fig. 3b–c). *B. pubescens* was found in 75% of plots and *P. abies* in 37%, reaching densities of 53 stems/10 m^2 and 17 stems/10 m^2,

Table 1. Stand structural characteristics. Mean values were per hectare for three 20 m × 20 m (40 m) plots in the minerotrophic part of the Serži peatland, for one 20 m × 20 m plot in the ombrotrophic part, and for both living and dead tree on the transects in the minerotrophic part. Values are calculated for individuals >1 cm DBH. Density of individuals <1 cm DBH are given in parentheses. Age is not given for *B. pubescens* as it was not determined for trees <3 cm DBH.

20 m × 20 m plots

	Minerotrophic			Ombrotrophic
	P. sylvestris	*P. abies*	*B. pubescens*	*P. sylvestris*
Tree density (number of stems ha^{-1})	544 (0)	688 (88)	219 (8794)	1575 (0)
Basal area (m^2 ha^{-1})	24.3	2.7	2.5	23.3
Mean DBH (cm)	22.3	6.5	1.3	13
Mean age (years)	168	29	-	80

Transects (living/dead trees)

	Minerotrophic					
	Living trees			Dead trees		
	P. sylvestris	*P. abies*	*B. pubescens*	*P. sylvestris*	*P. abies*	*B. pubescens*
Tree density (number of stems ha^{-1})	644 (303)	270 (1192)	649 (4141)	112	2	44
Basal area (m^2 ha^{-1})	23.7	3.0	2.1	3.2	0.1	0.2
Mean DBH (cm)	19.4	9.3	5.2	15.5	16	6.7

respectively. The age structure of *B. pubescens* and *P. abies* when estimated as frequency of trees was even more skewed (not shown) towards large numbers of young trees than when presented as frequency of plots. In contrast with *P. sylvestris*, most *P. abies* stems were in age classes under 20 years. The oldest *P. abies* was 152 years. Almost all *B. pubescens* were less than 3 cm DBH and were not cored for age determination. A total of 23 larger *B. pubescens* stems were found in the 10 m^2 plots and cored, and the ages ranged between 22 and 145 years.

In the three 20 m × 20 m plots *P. sylvestris* density was lower, and mean DBH and age higher, in the minerotrophic part of the bog (Table 1). Individuals of *P. sylvestris* stems less than 40-years old (Fig. 4) were not found in these plots, which was not surprising considering the patchy regeneration seen in the fine-scale 10 m^2 plots. The age structure of *P. sylvestris* in the plot on ombrotropic peat is skewed with a peak in the 50–70-year age class. Strong peaks of regeneration are seen in the 60–70-, 130–150- and 190–220-year age classes of *P. sylvestris*, and in the 10–30-year class of *P. abies*. The layer of trees <1 cm DBH was domi-

nated by *P. abies* and particularly *B. pubescens* in the minerotrophic part of the mire (Table 1), where the latter tended to form dense but sparsely-leaved clumps of suppressed individuals.

Seven 10 m^2 plots (Fig. 6) had trees with fire scars (in addition 5 trees outside the plots were mapped and scars were dated). Only scattered trees had fire scars, and large spruce reaching 100 years could often be found within 10 m of pines with scars. Time of fire in 5 trees was dated to 1971, and in one additionally to about (difficulty in discerning tree rings) 1915.

The DBH structure of living and dead *P. sylvestris* in the transects (Fig. 5) suggests a similar level of mortality in the DBH classes, with no evidence of a peak cohort. The total number of dead *P. sylvestris* stumps and standing trees with DBH >1 cm was 112 stems ha^{-1}, with a basal area of 3.2 m^2. Almost no dead spruce were found (Table 1), and birch only in the smallest DBH classes (Fig. 5b–c).

a. *Pinus sylvestris* on minerotrophic soil

b. *Picea abies* on minerotrophic soil

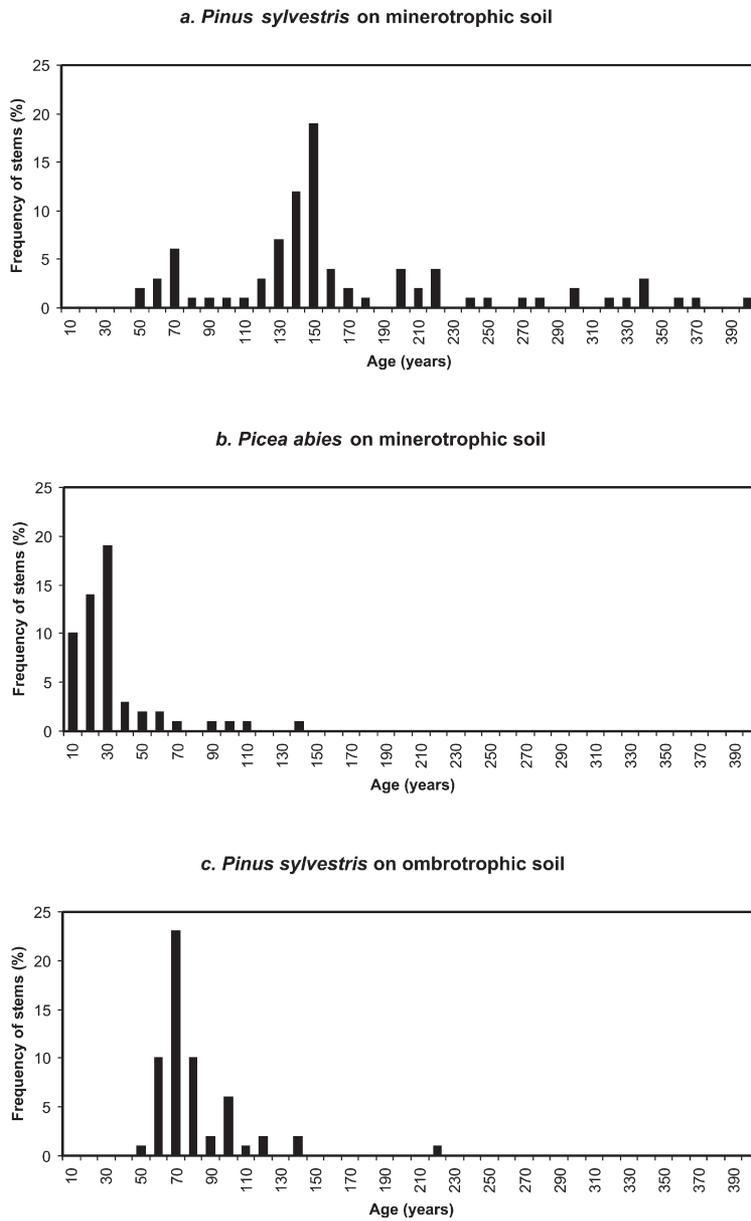**c. *Pinus sylvestris* on ombrotrophic soil**

Fig. 4. Age structure of trees in 400-m² plots: *Pinus sylvestris* (a) and *Picea abies* (b) on minerotrophic soil, and *Pinus sylvestris* (c) on ombrotrophic soil. Bars represent frequency of stems in 10-year age classes. Three plots on minerotrophic soil are grouped.
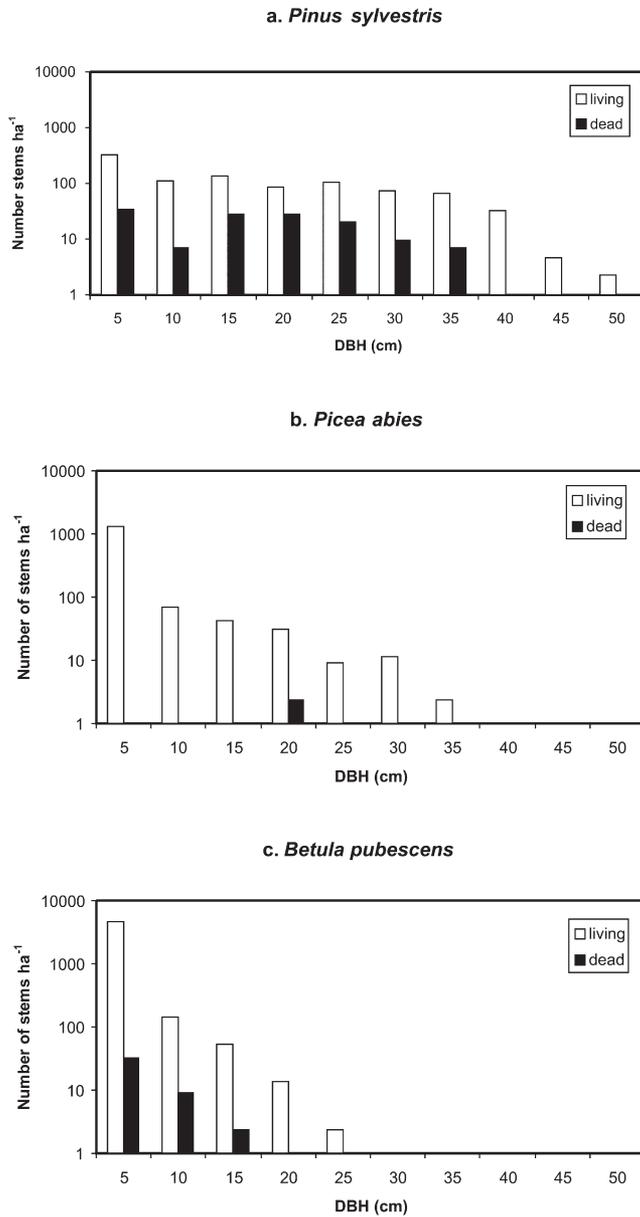
a. *Pinus sylvestris*

b. *Picea abies*

c. *Betula pubescens*

Fig. 5. Diameter structure of living and dead stems of *Pinus sylvestris* (a), *Picea abies* (b) and *Betula pubescens* (c) in two transects (pooled) with a total area of 4300 m². Bars represent number of stems ha⁻¹ in 5-cm DBH classes. A logarithmic scale is used.
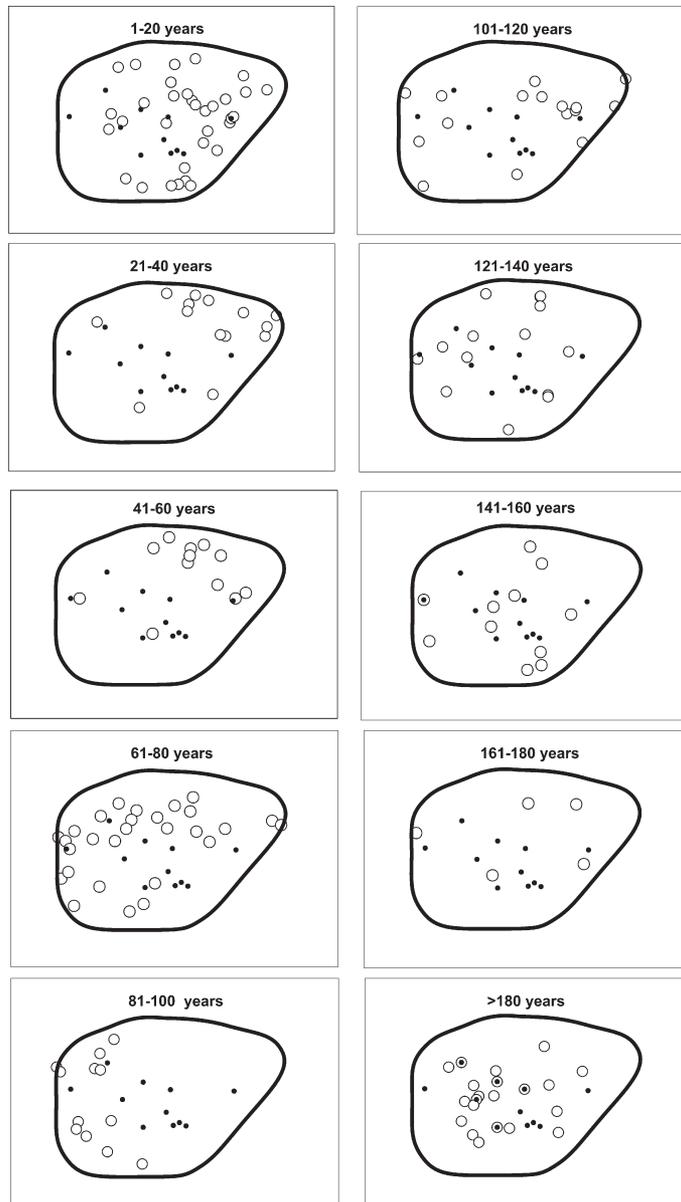
Fig. 6. Locations of 10-m² plots containing stems of 20-year age classes of *Pinus sylvestris*. Open circles represent plots, and black points show locations of trees with fire scars.

Table 2. Generalised linear model for predicting presence of *Pinus sylvestris* from cover of *Sphagnum magellanicum, Ledum palustre* and grasses/sedges in ground vegetation plots. A binomial distribution with logit link function (logistic regression model) was used.

Predictor variable(s)	F-ratio	p-level
S. magellanicum	5.16	0.026
S. magellanicum × *L. palustre*	7.69	0.0007
S. magellanicum × grass/sedge	5.09	0.003

3.2 Spatial Structure of Age Classes

Mapping of the stems in the 10 m² plots shows differences in spatial patterns for the *P. sylvestris* age classes, and in relation to the area of trees with fire scars (Fig. 6). The youngest age class 1–20 years was found throughout the study area, except for the far western part. By visual inspection, age classes 20–120 years were generally not found or were infrequent in the area of fire scars (Fig. 6). The 20–60-year old trees regenerated/survived mostly on the north-eastern part where peat is deeper than 30 cm, and the 80–100-year old *P. sylvestris* cohort on the opposite south-western part. The more abundant 60–80 age class was found throughout, but less in the burnt area. Older classes were spread throughout the mire, with increasingly (with age) less segregation from the burnt area, and the oldest class >180 years appeared restricted to the area with fire scars. All age classes of *P. abies* and DBH classes of *B. pubescens* were missing in the north-eastern part on the deeper mire, but otherwise were found throughout (not shown).

3.3 Pine Regeneration Microsites

MRPP indicated no relationship between vegetation and presence of birch and spruce seedlings. Visually *P. abies* regeneration was associated with decayed logs and uprooting zones, but this was not recorded in the vegetation plots. The vegetation composition significantly differed (p < 0.001) in plots (1 m²) with *P. sylvestris* seedlings, compared to plots without seedlings. However, the A value

(A = 0.01) calculated was extremely low, indicating at best a minor turnover in species. Indicator species analysis showed that only three species significantly differed between the groups of plots: *Sphagnum magellanicum* was a preferred site for pine establishment, while sedge/grass and *Ledum palustre* cover were avoided. Logistic regression models (GLM with binomial distribution and logit link function) of probability of pine occurrence predicted by S. magellanicum, as well as by *S. magellanicum* × sedge/grass cover, and *S. magellanicum* × *L. palustre* cover were significant (Table 2). GLM analysis showed that probability of *P. sylvestris* being present increased with cover of *Sphagnum* and decreased with cover of *Ledum* or sedges/grasses.

4 Discussion

The age and DBH structure of *P. sylvestris* in the treed mire clearly shows continuous regeneration, as all age and DBH classes were represented (Fig. 2b). This indicates the continuous presence of suitable microsites for germination and seedling establishment. In Finland, all-age structure for *P. sylvestris* on mires has previously been shown (Sarkkola et al. 2008), which may have an inverse J-or bell-shaped, or may be flatter. However, in that study trees <4.5 cm DBH were not inventoried, and a J-structure may be more common. In Canada, continuous regeneration of *Picea mariana* on *Sphagnum*-dominanted mires with *Ledum* and *Alnus* also has been reported, which is in sharp contrast with the post-fire even-aged structures that are the prevailing successional type in North American boreal forests (Groot and Horton 1994).

On dry sites non-stand-replacing fire exposes mineral soil resulting in initiation of cohorts (Kuuluvainen et al. 2002, Rouvinen and Kuuluvainen 2005), which are otherwise suppressed by a cover of feather moss (Steijlen et al. 1995, Nilsson et al. 1999, Zackrisson et al. 1997). In forests on mineral soil *P. sylvestris* can also utilise windthrow pits and mounds for regeneration, exploiting lack of competition from understorey vegetation (Kuuluvainen and Juntunen 1998, Kuuluvainen and Rouvinen 2000) and the larger part of *P. abies* regeneration is on decaying logs (Hörnberg et al.

1997). In the studied mire, the regeneration of pine was generally restricted to *Sphagnum magellanicum* hummocks free of competition from *Ledum palustre* and graminoids. The favourable seedbed properties of *Sphagnum* have been reported previously (Ohlson et al. 2001, Saarinen 2002). These microsites are presently available throughout the mire, and probably have been for a period of at least 300 years. However, considering the low number of 10 m^2 plots (Fig. 3a) with *P. sylvestris* seedlings, the regeneration is spatially restricted, at least in comparison to *P. abies* and *B. pubescens*. The plot size is comparable to the space required for one mature tree on the mire, as the plots mostly contained one large-DBH stem. Based on the presence of *P. sylvestris* individuals with DBH < 20 cm in the 10 m^2 plots (Fig. 3a), it can thereby be estimated that about 18% of fine-scale patches contain microsites suitable for seedling establishment, from which entry into the canopy might occur. Thus, although the DBH and age structure (Fig. 2) suggest a copious number of seedlings and saplings, the density of regeneration patches at the scale of 10 m^2 is limited (Fig. 3). This is also confirmed by the age structure of *P. sylvestris* in the larger 400-m2 plots, which totally lacked < 20-year-old stems.

The structural heterogeneity of the forest stand on the mire is forced by the spatial template of regeneration sites. However, competitive interactions and disturbance will determine the subsequent survival dynamics (Kuuluvainen et al. 1998). Clearly, the presence of a seedling cohort does not imply that it will over time reach the canopy, as aggregation of seedlings in small patches will result in severe future competition, particularly in patches under dominant large individuals (Sarkkola 2008). This likely explains the steep J-shape of the age distribution (Fig. 2). Also, *Sphagnum* can rapidly overgrow *P. sylvestris* seedlings, but the seedlings can suppress *Sphagnum* (Ohlson et al. 2001). We lack information on the dynamics of *Sphagnum*, but new hummocks might develop over time in wet uprooting depressions, providing a constant input of new microsites. The 20–60-year-old age classes of *P. sylvestris* were generally restricted to the north-eastern part of the mire on deeper peat (Fig. 6) presently dominated in the understory by *Ledum palustre*. This dense low shrub layer was shown

to limit pine regeneration, but obviously some regeneration was previously possible on shrub free patches of *Sphagnum*. Considering the higher stem densities in this area (Table 1), compared to the minerotrophic part, competition-induced mortality (Sarkkola 2008) is expected in the future.

There was no evidence of a flush of *P. sylvestris* regeneration in the area of the fire of 1971, i.e. there was no peak seen in the 10–30 age classes. As the 40–120-year age classes are rather unrepresented in the burnt area, we suppose that a part of these cohorts were likely destroyed by the fire, while older larger trees survived. Another fire was suggested also about 1915, which also may have caused mortality depending on tree size. The suggested peak in *P. sylvestris* recruitment in the 61–80-year (Fig. 2b) and 130–150-year (Fig. 4a) age classes might be an artefact due to survival of older trees and groups of trees in more humid refugia. The strong cohort peaks in the 400-m^2 plots, compared to weaker in the pooled fine-scale plots certainly suggests that survival of cohorts occurred in spatially distinct groups. We suspect that the age structure has an inverse J-shaped structure with overlain pulses of mortality dependent on tree size and local moisture conditions.

The age structure of *P. abies* (Figs. 3b, 4b) and size structure of *B. pubescens* estimated in fine- and medium-scale plots suggest a recent pulse in regeneration. While *B. pubescens* saplings less than 5 cm DBH were not cored, the determined ages of larger trees (minimum 22 years) clearly indicate that the overwhelming majority of the stems have post-1971 fire origin. Also, birch dead wood is more abundant in the smaller DBH classes, implying recent competition-induced mortality after colonisation. Spruce and birch are largely destroyed by fire (Linder et al. 1997, Lehtonen 1998, Parviainen 1996), but the few scattered spruce and birch reaching over 100 years suggest that the fire was patchy and not intense. As there was an almost complete absence of spruce dead wood, relative to the abundant *P. sylvestris* dead wood, we suggest that the pre-fire forest had a smaller proportion of spruce than today. In swamps, *P. abies* can efficiently utilise raised microrelief (logs, uprooting mounds) for successful establishment (Hörnberg et al. 1997), and perhaps, successful regeneration sites were created by the fire.

We consider that the post-1971-fire period was

associated with drier conditions in the mire. Mire drainage can promote invasion by *B. pubescens* (Korpela 2004) and *P. abies*, and lead to increase of cover of *Pleurozium schreberi* at the expense of *Sphagnum* (Laine et al. 1995). An increased cover of *P. schreberi* might explain the poor post-fire establishment of *P. sylvestris* in the fire area. Also, drier conditions in the ombrotrophic part of the study area might have resulted in denser *Ledum palustre* shrub growth, limiting regeneration to safe patches. Dramatic shifts between dry and wet climatic phases over a short period of time can produce major changes in bog woodland structure (Leuschner and Bauerochse 2007), and probably the conditions today reflect a drier period in the studied mire.

We can explain the continuous regeneration of *P. sylvestris* by presence of *Sphagnum* hummocks. In late post-fire successional stages of upland forest communities in eastern Canada *Sphagnum* species can be the dominant species for long periods of time (Foster 1984). However, we lack information on the dynamics of *Sphagnum* patches and the past growth conditions in the studied mire. Perhaps during previous prolonged wetter periods *Sphagnum* hummocks were more available, and the present conditions represent a shift to *P. abies* and *B. pubescens* at the expense of a *P. sylvestris* recession. In view of value of the mire for biological diversity, succession to *P. abies* and *B. pubescens* will result in deteriorating conditions for the capercaillie lekking area.

The different size plots in the study provide contrasting interpretation. Obviously, medium-sized plots 400 m², if only a few are used, can give misleading results if regeneration patches are small and with low coverage, i.e. they can be easily missed or over-exaggerated. However, it seems likely that they estimate a post-fire disturbance patch, as the estimated age structures show strong distinct regeneration pulses. The many fine-scale plots provide information in a spatial context, for example, on regeneration microsites, but cannot provide information on disturbance patch size if the disturbance is larger than plot size. In our case plot size was approximately individual tree patch size, but perhaps, *Sphagnum* regeneration sites were clumped in larger patches. On the other hand, the 1m² plots describe vegetation from a seedling perspective. Long transects sample larger areas

crossing heterogenous patches, and can be used to provide estimates of structures, in our case, living and dead wood DBH and density, on a stand level. However, if stems are not mapped, the spatial structure is not recorded in transect data. We consider that the different methods used in combination complemented each other to provide a detailed portrait of stand structure in a spatial setting.

We cannot exclude past human disturbance in the studied mire, particularly considering that it is easily accessible to humans. However, the proportions (calculated from Table 1) of number of stems ha^{-1} and basal DBH ha^{-1} of dead trees among all trees (27% and 12%, respectively for *P. sylvestris* >1 cm DBH)) are in the range of those reported for old growth forests (Siitonen et al. 2000, Nilsson et al. 2003), and dead trees were found in all but the larger size classes (Fig. 5). Also, the lack of cut stumps, at least in the study area, and the multi-age structure of living trees suggest a long history of natural development, and a better reference area for study of minerotrophic wetland pine forests cannot be found in Latvia.

5   Conclusions

The age and size structure of a natural treed mire in a spatial context showed natural regeneration dynamics over a period of 450 years with little disturbance by humans. Age structure indicates continuous regeneration of *Pinus sylvestris*, which is supported by selective recruitment on *Sphagnum magellanicum* hummocks. Size-specific mortality due to fire results in waves of cohort peaks in age structures, which are spatially segregated in the study area. *Picea* abies and *Betula pubescens* has successfully invaded the understorey in a post-fire period after 1971, which is likely associated with drier conditions.

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