



Mixed-severity natural disturbance regime dominates in an old-growth Norway spruce forest of northwest Russia

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Keywords

Boreal forest; Canopy gaps; Dendroecology; European spruce bark beetle; Forest continuity; Insect outbreaks; Natural disturbances; Northern Europe

Nomenclature

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Introduction

Canopy disturbance is a major factor driving natural forest dynamics (Runkle 1985; Gromtsev 2002). The disturbance regime, which represents a set of disturbance characteristics such as type, frequency and severity of disturbance, directly affects species regeneration, biomass accumulation rates and mortality patterns (Pickett & White 1985; Runkle 1985; Fraver & White 2005a; Nagel & Diaci 2006). Understanding disturbance regimes advances our knowledge of

Abstract

Questions: What were the long-term disturbance rates (including variability) and agents in pristine Norway spruce-dominated (*Picea abies* (L.) Karst.) forests? Have soil moisture conditions influenced disturbance rates across this boreal spruce-dominated forest? Were the temporal recruitment patterns of canopy dominants associated with past disturbance periods?

Location: Interfluvial region of Northern Dvina and Pinega rivers, Arkhangelsk, northwest Russia.

Methods: We linked dendrochronological data with tree spatial data (n trees = 1659) to reconstruct the temporal and spatial patterns of canopy gaps in a 1.8-ha area from 1831–2008, and to develop a growth-release chronology from 1775–2008.

Results: No evidence of stand-replacing disturbances was found within selected forest stands over the studied period. Forest dynamics were driven by small- to moderate-scale canopy disturbances, which maintained a multi-cohort age structure. Disturbance peaks were observed in the 1820s, 1920s, 1970s and 2000s, with decadal rates reaching 32% of the stand area disturbed.

Conclusions: The overall mean decadal rate was 8.3% canopy area disturbed, which suggests a canopy turnover time of 122 yr, with a 95% confidence envelop of 91–186 yr. Bark beetle outbreaks (possibly exacerbated by droughts) and wind-storms emerged as the principal disturbance agents. Recruitment of both Norway spruce and downy birch was associated with periods of increased canopy disturbance. Moisture conditions (moist vs mesic stands) were not significantly related to long-term disturbance rates. The studied spruce-dominated boreal forests of this region apparently exhibited long-term forest continuity under this mixed-severity disturbance regime. These disturbances caused considerable structural alterations to forest canopies, but apparently did not result in a pronounced successional shifts in tree species composition, rather occasional minor enrichments of birch in these heavily spruce-dominated stands.

natural processes in forest ecosystems and supports development of sustainable forest management practices aimed to maintain species and habitat diversity (Bergeron & Harvey 1997; Kuuluvainen 2002). Specifically, quantifying the frequency, severity and spatial characteristics of natural disturbances is critical to the development of 'ecologically-based' forest management prescriptions. For example, natural disturbance characteristics have been used to determine harvest patch sizes and cutting cycles (Seymour et al. 2002), design variable density thinning

prescriptions (Carey 2003), devise prescribed burning regimes (Peterson & Reich 2001) and set targets for old-growth restoration efforts (Bergeron & Harvey 1997; Kuuluvainen 2002; Franklin et al. 2007).

Small-scale disturbance events (<100 m²), resulting from mortality of one or several canopy trees, are thought to prevail in dark coniferous forest of Northern Europe (Hytteborn et al. 1987; Hofgaard 1993; Drobyshev 1999), which in European Russia are typically dominated by *Picea abies* and *P. obovata* (Gromtsev 2002). The main natural disturbance agents in such ecosystem are windthrow (Liu & Hytteborn 1991; Drobyshev 1999, 2001) and insect outbreaks (Schroeder 2007; Aakala et al. 2011). Forest susceptibility to these agents is related to climatic variability, e.g. periods with extreme precipitation (Abrazko 1988) or summer droughts (Aakala & Kuuluvainen 2011). Although fires may occur in dark coniferous forests of this region, the return intervals appear to be quite long, possibly exceeding 1000 yr (Segerström et al. 1994; Wallenius 2002).

The vast majority of the Northern European boreal forest has been actively exploited in the past, and natural dynamics are increasingly being replaced by the dynamics initiated by timber harvesting (Kuuluvainen 2002; Achard et al. 2006), which has been commonly conducted through clear-cuts of various sizes at least since the beginning of the 20th century (Burnett et al. 2003). There are concerns that both the spatial scale and intensity of these harvests may be outside the historic range of variability of the natural disturbance regime, which may lead to declines in biodiversity, ecosystem function and structural complexity (Kuuluvainen 2002). A long history of forest exploitation in the Northern European boreal forest has left few sizeable areas of forests driven by natural dynamics. Presently, only a few large areas of intact dark coniferous forests outside mountainous regions exist in Northern Europe, the majority of them being located on the flat and poorly drained interfluves of the Russian northwest (Yaroshenko et al. 2002).

The Arkhangelsk region of northwest Russia, particularly the interfluves between Northern Dvina and Pinega rivers (Fig. 1), provides an ideal location to explore the historic range of variability in natural forest disturbance. The central part of this area represents one of the few examples of unfragmented and largely unmanaged forest landscapes (or *Intact Forest Landscapes*; Anonymous 2014) within the northern and middle boreal region (Aksenov et al. 2002), also known as Dvinsky forest (Anonymous 2014). It supports unbroken reaches of old-growth and multi-cohort Norway spruce-dominated (*Picea abies* (L.) Karst.) forests, with areas of continuous forest tracks reaching several thousand hectares. Previous reports indicate high value of these forests as reference ecosys-

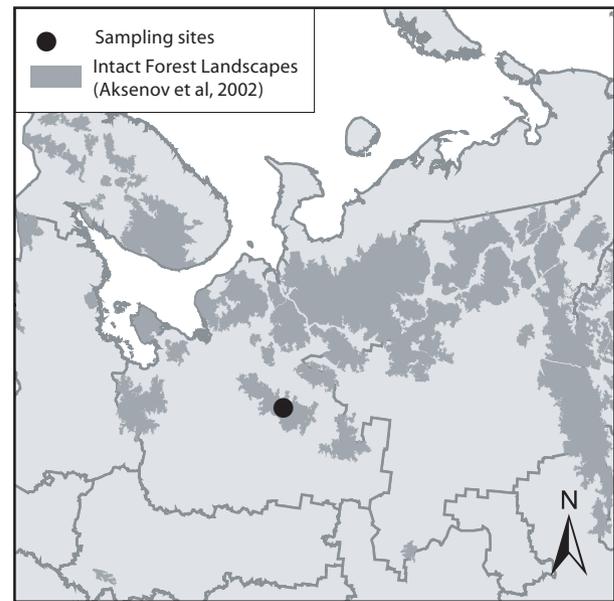


Fig. 1. Location of the study area and the sampled sites within Northern European Russia.

tems for biological conservation (Yaroshenko et al. 2002; Zhuravlyova et al. 2007).

The primary goals of this study were to characterize the historical variability in canopy disturbance of pristine spruce-dominated forests. Three particular focus points of the study were long-term dynamics of canopy disturbance rates, regeneration patterns of canopy dominants and the effect of local site conditions on disturbance rates. Understanding these aspects of ecosystem dynamics is of critical importance for developing sustainable management strategies of both commercial and protected forests (Bergeron & Harvey 1997; Kuuluvainen et al. 2014). Despite a large volume of research on these topics (Kuuluvainen et al. 2014 and references within), there is still a need for long-term and quantitative estimates of the ecosystem processes. Understanding the within-stand (10¹⁻² ha) spatial patterns created by natural disturbances and vegetation response to them is one such knowledge gap that the current study attempted to fill. Spatially explicit studies of canopy disturbances at this scale are uncommon (Drobyshev & Nihlgård 2000; Fraver & White 2005a), yet many management actions (e.g. thinning and final fellings) are carried out at this very scale. We therefore included detailed tree spatial data in our study to elucidate the potential fine-scale patterns of canopy dynamics. Finally, we were also interested in understanding the role of variability of site conditions and associated changes in vegetation cover within single tracts of forests in affecting long-term disturbance rates. The importance of such variability has been postulated in many Russian studies (Sukachev &

Zonn 1961; Jurkevich et al. 1971; Rysin & Saveljeva 2002), although spatially explicit data to support this assumption are largely missing. In this study we capitalized on the combination of dendrochronological and modern spatial data, realizing that tree-ring records provide quantitative and long-term (often multi-century) records of forest dynamics (e.g. Fraver & White 2005a; Aakala et al. 2011). We put forward three research questions: (1) what were the long-term disturbance rates (including variability) and agents; (2) were the temporal recruitment patterns of canopy dominants associated with past disturbance episodes; and (3) have soil moisture conditions influenced disturbance rates across this boreal spruce-dominated forest?

Methods

Study area

The study was conducted in an old-growth spruce-dominated forest located in the interfluvium between the Northern Dvina and Pinega rivers in the Arkhangelsk region, northwest Russia (63°15' N, 43°49' E; Fig. 1). The area pertains to the transitional vegetation zone between middle and northern European taiga. Regional climate is influenced by proximity to the White Sea. Throughout the 1900s, the mean annual temperature was 0.9 °C and mean annual precipitation was roughly 600 mm, with its minimum in March–April and maximum in July (Stolpovski 2013). The coldest month is January, with the mean temperature of –14.1 °C, and the warmest month is July, with a mean of 16.1 °C. A major portion of the watershed is rather flat with elevations up to 267 m a.s.l. The dominant soils are poorly drained loams and sandy loams of low fertility (Zagidullina 2009).

The large unfragmented forest area between the two rivers is designated as one of Russia's last Intact Forest Landscapes (Yaroshenko et al. 2002), i.e. a forest landscape without signs of significant human activity in the past, and large enough 'to maintain its natural biodiversity' (Aksenov et al. 2002). Over recent decades (late 1990s and 2000s) the area of intact forests has been rapidly shrinking due to extensive timber harvesting (Yaroshenko et al. 2002). Yet, the total area of roughly 1 million ha makes the studied landscape the largest of such forests in the European middle taiga. The data collected in this study, originating from the central part of the area undisturbed by humans, should therefore be considered as representing natural dynamics of spruce-dominated forests in this part of the European boreal zone.

The majority of pristine old-growth forests stands in this landscape were dominated by Norway spruce (about 82.3% of total area). Stands of Scots pine (*Pinus sylvestris* L.) and downy birch (*Betula pubescens* Ehrh.) contributed

10.1% and 7.6% of the area, respectively (Zhuravlyova et al. 2007). Ground vegetation in spruce stands examined in the study was dominated by *Vaccinium myrtillus* L., *Dryopteris* spp. and *Gymnocarpium dryopteris* (L.) Newman. *Sphagnum girgensohnii* Russow and *Polytrichum commune* Hedw. were two major moss species, while *Hylocomium splendens* (Hedw.) W.P. Schimp, *Pleurozium shreberi* Mitten and *Dicranum* spp. were common on elevated and drier microsites (i.e. decomposed logs). The understorey layer was represented by sparse patches of *Sorbus aucuparia* L., which were common in canopy gaps.

Wind and insect disturbances have been reported earlier in the forest of the studied area. A windstorm occurred in winter 2001 and resulted in breakage of canopy trees (Ogibin & Demidova 2009). A wave of tree mortality, induced by European spruce bark beetle (*Ips typographus* L.) has been recorded in the area since 1999 (Nevolin et al. 2005; Ogibin & Demidova 2009; Aakala & Kuuluvainen 2011). An earlier outbreak of *I. typographus* occurred in the study area at the turn of the 20th century (Kuznetsov 1912).

Site selection and sampling design

To preliminarily locate the study area, we used false colour images from Landsat 5 TM and Landsat 7 ETM+ data sets, with spatial resolution of 28.5 m and band combination 5-4-3 covering 1990 to 2006, and the map of Intact Forest Landscapes (Zhuravlyova et al. 2007). In the field, we searched for homogenous tracks of forest that met the following requirements: (1) located at least 120 m from the nearest forest road to avoid edge effects; (2) not disturbed by any harvesting operations, as evidenced by cut stumps; and (3) represented regionally common moist spruce-dominated forests. We established two belt transects (450 m × 20 m), each composed of a continuous array of 20 m × 20 m sample plots (with one terminal plot 20 m × 10 m), with the total sampling area of 1.8 ha. Transects were placed within the dominant topographic elements, i.e. upper parts of the flat slopes gently rolling towards small forest streams, at elevations of 180–210 m a.s.l. Transects were oriented south–north, perpendicular to the dominant westerly wind direction. Field sampling took place in June and July 2009.

Within each transect we mapped (with accuracy of 0.1 m) all living trees and deadwood above 6 cm DBH ($n = 2126$) and recorded species identity, life status (alive or dead), DBH, canopy position class (dominant, co-dominant, intermediate and overtopped) and type of deadwood. Deadwood types included snag (standing dead trees), uprooted tree or stump (a vertical stem <1.3 m). Deadwood was classified into five decay classes, with class I being least decayed and class V being most decayed (Shorohova & Shorohov 2001).

Increment cores were extracted from all living and recently dead trees (DBH \geq 6 cm) within transects, at a height of 40 cm above ground level ($n = 1678$, or 79% of all inventoried trees). Among the sampled trees, Norway spruce represented 90.9% ($n = 1525$), downy birch 8.0% ($n = 134$) and rowan (*S. aucuparia*) 1.1% ($n = 19$). Dead spruce represented 20.7% of all spruce trees sampled.

We measured tree heights on three spruces and one birch within each of the three dominant DBH classes (total n for spruce = 9). The same measurements were done for one birch tree within each of the three dominant birch DBH classes ($n = 3$).

We measured tree crown diameters in two perpendicular directions on trees representing the dominant DBH classes within transects ($n = 9$ for spruce and $n = 3$ for birch). We also recorded current total area of canopy gaps in each transect by mapping areas under the open sky that exceeded 15 m². This threshold was subjectively selected to avoid naturally occurring tree interstices smaller than a typical spruce canopy area.

Data processing

Cores were mounted on wooden planks, sanded with up to 400-grit sanding paper, and cross-dated using pointer years (Stokes & Smiley 1968). Samples were scanned with 2400 or 3200 ppi resolution, depending on sample length and ring visibility, and measured on-screen using *CooRecorder 7.2* and *CDendro 7.2* software (Cybis AB; <http://www.cybis.se/>). This method also yielded total ring counts at the coring height of 40 cm. For cores that did not directly hit the pith, the number of rings to pith was estimated using a pith locator (Applequist 1958). For age structure analyses, we used only samples where pith was estimated to be within 25 yr away from the earliest ring of the sample. All spruce trees were successfully cross-dated and used for subsequent analyses. For birch, we counted rings to estimate age at 40 cm above the forest floor but were able to use only 32% of the birches ($n = 60$) in subsequent analyses. The remaining birch samples had extensive internal rot, and could not be used to define birch recruitment years with confidence. We do not consider a low number of birch trees used for analyses as a limitation, since it was unlikely to produce a bias in estimation of birch regeneration waves. Calculation of stand volumes was based on DBH and tree height data, using forest inventory tables for the Arkhangelsk region (Anonymous 1952; Moiseev et al. 1987).

The first two deadwood decay classes were characterized by the presence of bark to various extents and a low amount (5–10%) of sapwood rot (Shorohova & Shorohov 2001). Deadwood classified in these two classes and bearing the damage marks of European bark beetle was consid-

ered to represent insect-induced mortality from the most recent outbreak. We therefore assumed that these trees were alive prior to the 1999–2009 insect outbreak, which allowed us to reconstruct canopy composition prior to the outbreak. In total, we inventoried 316 dead spruce trees associated with the recent mortality episode, out of which 34.5% ($n = 109$) were not cored due to partially decomposed wood.

Growth release detection

Using all correctly dated ring-width chronologies, we inspected past radial growth patterns for growth releases (rapid increases in growth following a period of suppression) as evidence of past canopy disturbance. For the release detection analyses, we worked exclusively with understorey trees (*overtopped* and *intermediate* canopy classes) or current dominant trees (*co-dominant* and *dominant* classes) during the period they had resided in the understorey. Understorey trees typically show an increase in growth under the improved light conditions that follow a canopy disturbance (Lorimer & Frelich 1989) and are thus a better proxy for past canopy disturbances in closed-canopy forests, as compared to the dominant trees. To retrospectively estimate the understorey period of current canopy dominants, we used the relationship between DBH and canopy class to estimate typical DBH of a tree reaching *co-dominant* class, following the methods of Lorimer & Frelich (1989). In particular, we used relationship between DBH and canopy class, recorded in the field, to reconstruct the period during which the tree had the DBH characteristic of the current understorey trees. Thus, we calculated the DBH corresponding to 90% probability of a tree residing in the canopy and then selected that portion of the tree-ring series corresponding to the previous understorey period. The DBH at which a tree reached *co-dominant* canopy class, and therefore entered the canopy, was estimated to be 17.3 cm.

To detect growth releases in ring-width chronologies, we used the absolute increase method (Fraver & White 2005b) with a 10-yr running mean window. The absolute increase threshold, derived from these data, was set at 0.50 mm following the methods outlined in Fraver & White (2005b). Additional evidence of past canopy disturbance can be derived from the rapid initial growth, as this indicates recruitment under open-canopy conditions (Lorimer & Frelich 1989). To identify such 'gap recruitment' events, we used a minimum annual growth rate of 1.5 mm over the first decade, when followed by a declining, parabolic or flat growth pattern (Frelich 2002), as evidence of former canopy disturbance. While applying growth release and gap recruitment methods, we visually inspected all samples to avoid 'false releases' due to the

presence of compression wood. Evidence of disturbance (both releases and gap recruitments) was expressed as a percentage of total trees alive in a given decade that showed one of these responses. We extended these chronologies, one for each transect, back in time until the number of trees dropped below 40.

Spatial reconstruction of canopy disturbance

To reconstruct the location and size of past canopy disturbances, we used growth release data from spruce trees, and gap recruitment dates from spruce and birch, as well as the x and y coordinates of these trees on the transects. From these data, for each decade, we compiled a map of trees that were classified as being within canopy gaps or under the closed canopies. Kriging methods (*Prediction map* method in *Universal kriging* in ESRI ArcGIS, ESRI 2009, Anonymous 2009) were subsequently used to spatially interpolate and delineate areas existing as gaps or closed canopies. During this procedure we filtered out tree interstices by calculating trees' crown projections using a regression between tree DBH and crown projection area, obtained on the reference trees. We extended the spatial reconstruction back in time until the number of trees available for analyses dropped below 150, which corresponded to the 1830s and 1840s for the first and second transects, respectively. A more stringent threshold employed for this spatial reconstruction, as compared to growth release chronology (see previous subsection), resulted in a shorter disturbance chronology. However, we considered it justified by the spatial nature of the analysis, i.e. higher data requirement for the kriging process, as compared to the construction of growth release chronology.

To verify preliminary results of the spatial reconstructions, we ground-truthed the output of spatial analysis for the 2001–2008 period. Both estimates of gap area were scaled to 11 of 20 m \times 40 m plots in each transect, providing means to assess the utility in converting growth release data (point-type data) into spatial estimates of area under gaps. Given the success of this approach (Appendix 3), we subsequently considered these canopy area estimates (not simply proportion of trees exhibiting growth release) as proxies for stand-wide disturbance rates. This approach to quantifying disturbance rates is a spatially explicit outgrowth of the canopy area-based approach introduced by Lorimer & Frelich (1989) and elaborated by Fraver & White (2005a).

Finally, to evaluate variability in disturbance rates in relation to soil moisture regimes, we classified plots into one of three groups based on the cover of *Sphagnum* species, which represented the general site quality (Chertov 1981): low soil moisture plots (<5% *Sphagnum*), moderate moisture plots (5–40%) and high moisture plots (>40%).

We used repeated measures ANOVA, using decadal estimates of the areas under gaps as the dependent variable and three classes of soil moisture variability as the second independent variable (with time as the first independent variable).

Results

Stand characteristics

As of 2009, Norway spruce and downy birch were the only tree species present in the forest canopy of the examined stands (Table 1). Spruce contributed 73% of the mean stand volume, 75% of the basal area and 93.6% of tree density. Average stand volume was 211 m³·ha⁻¹, the absolute basal area was 21.5 m²·ha⁻¹ and average stem density was 781 trees·ha⁻¹. Stand characteristics varied somewhat between the two transects; the second transect exhibiting higher volume, basal area and tree density. The mean stand DBH was lower at the second transect, because of a higher number of suppressed trees under the canopy (Appendix 1).

Age structure

The oldest tree reached the sampling height of 40 cm in 1726 and the youngest tree in 1981 (Appendices 2 and 3). Generally, the mean age at 40 cm increased from under-

Table 1. Characteristics of studied stands in 1999 and 2009, demonstrating the effect of the recent bark beetle outbreak that began in 1999. Column *Change* refers to changes in the variables following the bark beetle outbreak. Data for 1999 was back-calculated by considering recently dead trees as being alive in 1999 and combining them with currently living trees, whose DBHs were reconstructed back to 1999. Values in parentheses are percentages for respective absolute values. Data are averaged across two transects.

Variables	Inventories		Change
	1999	2009	
Number of Trees (n·ha⁻¹)			
Spruce	893	723	-170 (19.0)
Birch	84	58	-26 (31.0)
Total	977	781	-196 (20.1)
Absolute Basal Area (m²·ha⁻¹)			
Spruce	27	16	-11 (40.7)
Birch	7	5.5	-1.5 (21.4)
Total	34	21.5	-12.5 (36.8)
Standing Volume (m³·ha⁻¹)			
Spruce	267	154	-113 (42.3)
Birch	74	57	-17 (23.0)
Total	341	211	-130 (38.1)
Mean Diameter (cm)			
Spruce	16.5	14.6	-1.9 (11.5)
Birch	31.6	33.3	1.7 (5.4)

storey to dominate canopy position classes, but with large variability of ages observed within each class (Appendix 2). Age and DBH were moderately correlated ($R^2 = 0.46$). Spruce trees in the dominant and co-dominant canopy positions were between 60 and 270 yr old at the sampled height. The largest variability was found for trees of intermediate position, with estimated ages ranging from 31 to 285 yr. Almost half (46%, $n = 612$) of the spruce trees in the data set did not exceed 10 cm DBH, and more than half of these (57%, $n = 347$) were older than 80 yr.

Evaluation of tree ages on cores with missing pith might introduce a bias due to errors associated with estimation of the rings-to-the-pith, which were missed during coring, especially while working with shade-tolerant trees (Baker 2003). Despite the fact that the age estimation for 24% of the spruce trees required adding more than 10 yr to the date of the oldest ring on the sample, it did not introduce a bias in resulting age structure. The comparison of age structures obtained on (1) the complete data set and (2) a reduced data set composed of trees where the pith was estimated as missed by not more than 10 yr, showed no statistically significant differences (Appendix 4).

Tree recruitment patterns

Spruce recruitment age structure (including gap-recruited and non-gap-recruited trees) on both transects indicated nearly continuous recruitment of trees since the 1700s, with recruitment peaks centred around 1850 and the 1900s (Fig. 2a). The second transect had a larger number of younger spruce trees (30 to 110 yr old), implying more intensive tree recruitment after the 1900s. Birch age structure suggested an intensive regeneration period from the 1800s to 1860s, peaking around the 1830s, and rather high birch recruitment at the first transect around the 1890s (Fig. 2b). In general, spruce and birch age structures were coherent with each other, pointing to synchronized disturbance events.

Canopy gaps

The mean canopy gap size reconstructed over the 180-yr period was 92 m², with its maximum at 2047 m². The mean size of recent gaps delineated in 2009 was 166 m², ranging from 15 to 963 m². Together, these recent gaps represented 40.5% and 28.0% of the total stand area on the first and second transects, respectively. Due to a reduction in data available for spatial reconstructions with time, our ability to detect small gaps deteriorated as we progressed further back in time, which likely resulted in their underrepresentation in the reconstruction. As a consequence, the historical gap size distribution likely included even more small gaps, creating an even larger

difference between modern and historical disturbance rates.

Roughly half of recent canopy gaps (51.5% of the total) resulted from the synchronous death of five or more dominant and co-dominant canopy trees. Only 16% of the recent canopy gaps were formed by the death of a single tree. This low percentage was apparently the result of extensive outbreak-related mortality and was likely higher in the past.

Reconstruction of canopy disturbance rates

A total of 554 growth release and 64 gap recruitment events were identified. Most of the trees released (98%) required only one release to reach the canopy; 25 trees (2% of dated spruces) required two or more releases. Reconstructions of the location and size of past canopy gaps revealed the dynamic nature of the forest canopy, with peaks of disturbance and intervening periods of quiescence, as well as portions of the sites experiencing disturbance and portions relatively free from disturbance (Figs 3c and 4). The overall mean decadal disturbance rate was 8.3% of the area. Our results identified decades with increased rates: 1840s, 1870–80s, 1920s, 1970s and 2000s. Corresponding decadal disturbance rates, identified in spatial analyses, were 20.9, 11.9, 6.6, 11.5 and 32.2% of the area. Because we used the same data set for spatial reconstructions and growth release analysis, these peak decades mirrored those with peaks in releases and gap recruitment events (Fig. 2c,d). A prolonged disturbance episode occurred on the second transect from the 1950s to the 1970s; cumulatively, 34% of the area was disturbed during these three decades.

A decline in the number of trees available for spatial reconstruction might contribute to uncertainties in estimating disturbance rates in the earlier period. An indication of systematic bias associated with decreasing sample size would be an increase in the canopy gap size in the earlier period. However, the reconstruction (Fig. 3) did not indicate such a pattern, suggesting that the chosen threshold of the minimum sample size (40 trees) was reasonable.

Even though the spatial and temporal characteristics of disturbances differed somewhat between two transects, the mean decadal disturbance rates over 1830–2009 were very similar (8.24% and 8.37% of area disturbed, at first and second transects, respectively). The mean decadal disturbance rates over that period correspond to a canopy turnover time of 122 yr, 95% confidence envelope being 91 to 184 yr. Soil moisture did not significantly affect disturbance rates over 1861–2008 (Table 2), although disturbance rates in moist stands appeared higher than in drier stands during the middle of the 20th century (Fig. 4).

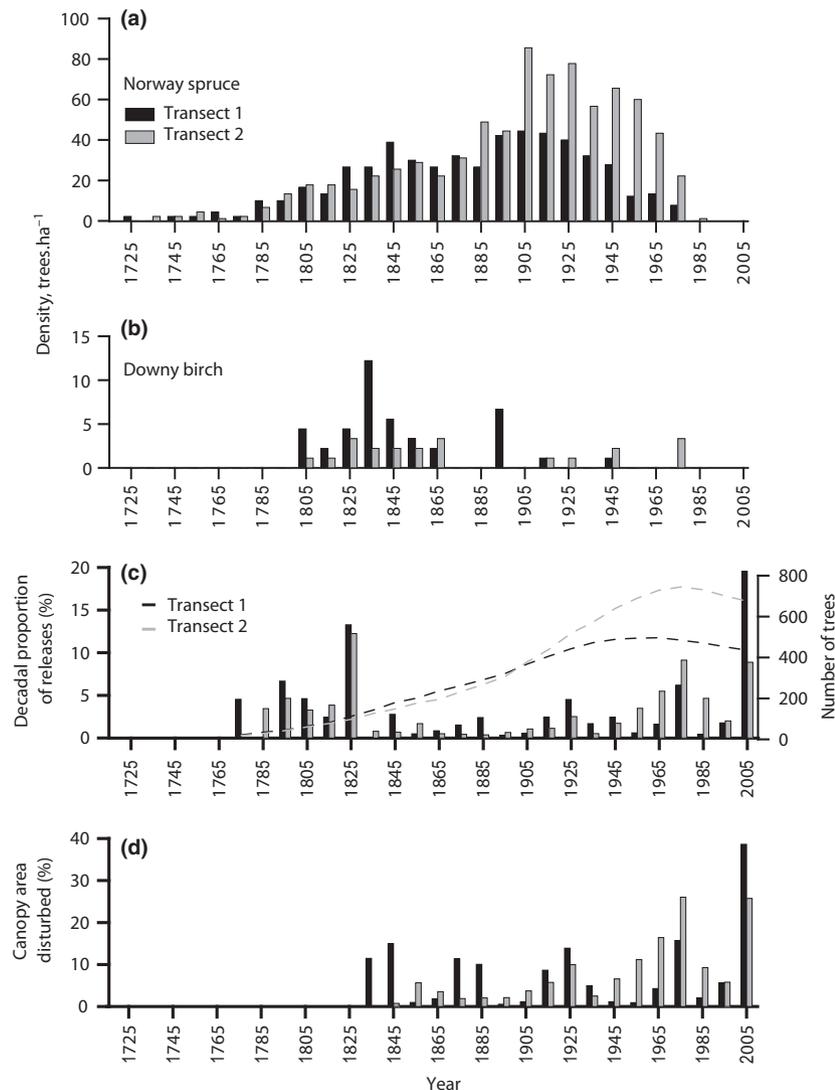


Fig. 2. Canopy age structure and historical disturbance rates in the studied spruce-dominated forests. **(a, b)** show age structure of spruce and birch populations at a height of 40 cm in two transects. Data represent current tree densities grouped into 10-yr classes. **(c, d)** show canopy disturbance rates based on spatially explicit reconstructions separately for two transects (**c**, period 1840–2008) and tallies of releases and gap-recruitment events (**d**, 1790–2008). Disturbance rates were obtained from the spatially explicit reconstruction of canopy gaps and represent percentage of stand area occupied by canopy gaps (see Fig. 3). Proportion of releases is a ratio between trees showing release and total number of trees covering a respective time period. Dashed lines and the right-hand axis represent number of trees covering a particular decade.

Recent spruce mortality episode

The most recent (since 1999) mortality episode, mainly associated with an outbreak of European spruce bark beetle, killed 42.3% of trees and reduced spruce stand volume by $113 \text{ m}^3 \cdot \text{ha}^{-1}$ (Table 1). The spruce mortality occurred in all size classes; however, it was especially prevalent among dominant trees. The outermost rings on dead trees indicated a period of high spruce mortality from 2004 to 2008, culminating in 2006 (Fig. 5). Mortality of sub-canopy trees reached a maximum dur-

ing 2007 and 2008. The period of intensive canopy tree mortality lasted approximately 7 yr. Between 2006 and 2008 the density of large trees decreased from ca. 14 to ca. 3 trees·ha⁻¹ (Table 1). Decline in canopy tree density was in line with a dramatic increase in growth releases and areas in canopy gaps (Fig. 3c,d). The rapid increase in mortality of dominant trees in the early 2000s might be attributed, in part, to a sampling artefact, because the trees that died before 1999 were not sampled due to difficulties in extracting sound increment cores.

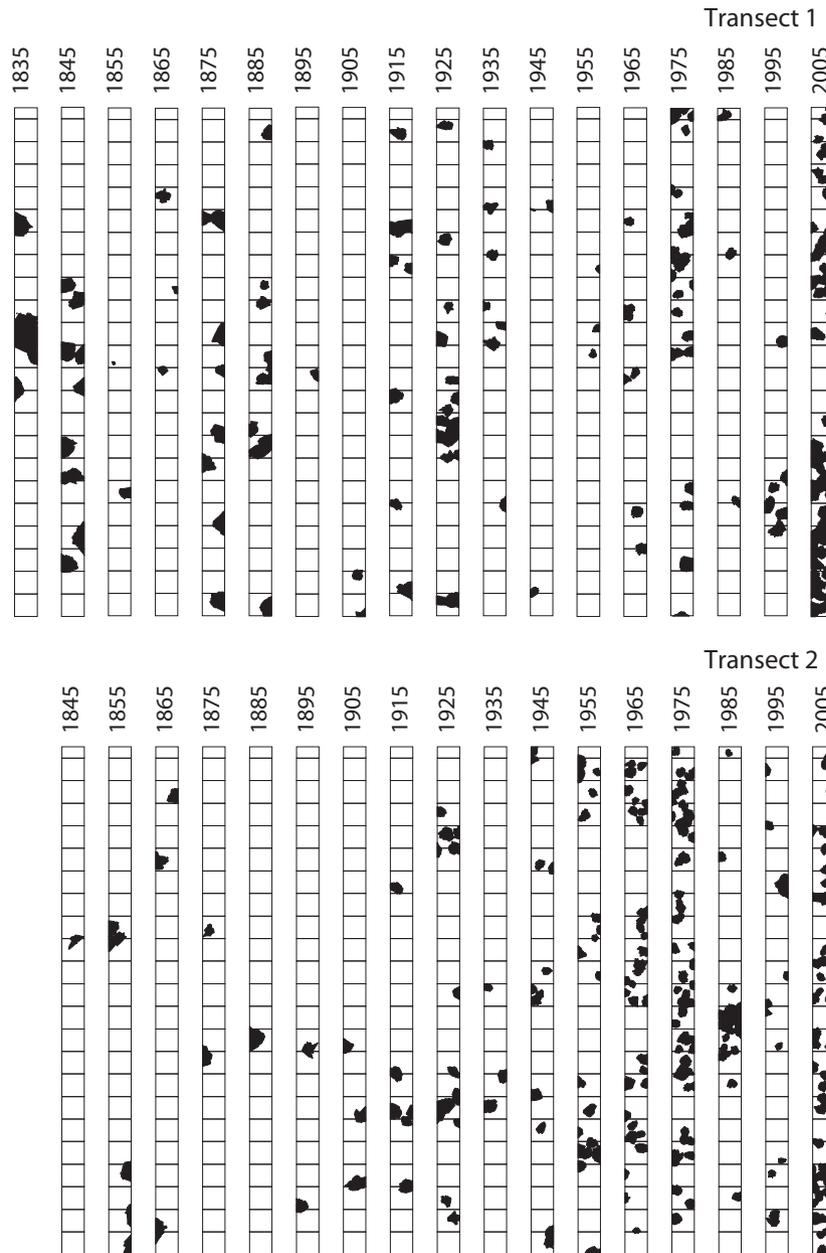


Fig. 3. Spatial location of gaps formed (black polygons) for each transect from 1830–40 to 2008, emphasizing the temporal variability and spatial patchiness of canopy disturbances in this system. Dates on the figure refer to the midpoint of the respective decade.

Discussion

Disturbance rates and spatial patterns

The reconstructed disturbance history since AD 1790 revealed mixed severity events, with a background of small-scale canopy gaps and periodic pulses of moderate-scale disturbances. Further, because a considerable proportion of spruce trees sampled at 40-cm height were initially slow-growing (annual radial increment <1.5 mm), it is

likely that the period without stand-replacing disturbance approached 280 yr, the projected age of the oldest trees in our data set. Similar patterns of mixed-severity disturbances have been recently reported in spruce forests of Northern Europe (Drobyshev 2001; Fraver et al. 2008; Caron et al. 2009; Aakala et al. 2011; Kuuluvainen et al. 2014), suggesting that this disturbance regime may be more common than had been previously assumed. Taken together, these recent findings further support the growing

Table 2. Repeated-measures ANOVA results depicting the effect of soil drainage conditions on the canopy area disturbed through time (dependent variable). Drainage conditions were placed into three classes: poor, intermediate or well drained. Significant factors are indicated in bold. Repeated-measures factor (R1) was decadal disturbance rates over the period 1840–2008.

Factors	SS	df	MS	F	P
Drainage	701	2	351	0.18	0.838
Transect	1599	1	1599	0.81	0.374
Drainage x Transect	4537	2	2268	1.15	0.329
R1	3.86E+05	15	2.57E+04	10.31	0.000
R1 x Drainage	4.72E+04	30	1573	0.63	0.938
R1 x Transect	1.01E+05	15	6738	2.7	0.001
R1 x Drainage x Transect	9.97E+04	30	3322	1.33	0.113

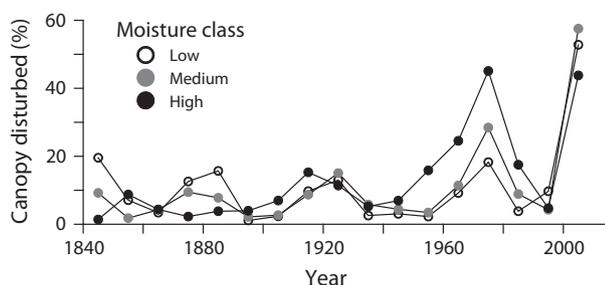


Fig. 4. Decadal disturbance rates in stands of three soil moisture classes, revealing marked similarity across classes. Statistical details of the analysis are presented in Table 2.

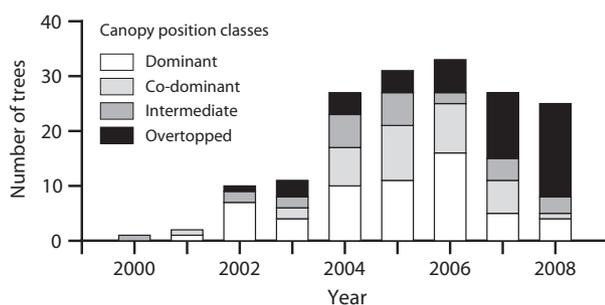


Fig. 5. Spruce mortality over the 2000–2008 period, which was assumed to be a result of the recent bark beetle outbreak, as estimated with dendrochronological dating of dead trees.

recognition that disturbance regimes in boreal spruce forests of Europe do not necessarily fit neatly into one of two traditional categories, namely gap dynamics or catastrophic disturbance, as had been previously thought (see also McCarthy 2001; Kuuluvainen & Aakala 2011). Instead, disturbances may span rather complex temporal and spatial gradients. Our findings classify this disturbance

regime as *patch dynamics*, following the classification of Kuuluvainen & Aakala (2011), which is defined by pulsed disturbances that create aggregated patches occasionally exceeding 200 m² and resulting in primarily multi-cohort stands.

The mean decadal disturbance rate for the entire reconstructed period (transects pooled) was 8.3%, with pulses of moderate-severity disturbance occurring roughly every 40 yr. Three out of five disturbance-prone periods (1880s, 1920s and 1970s) coincided with peaks reported from spruce forests approximately 25 km southeast of our study area (Aakala & Kuuluvainen 2011), suggesting the region-wide synchrony of these events (see Disturbance agents, below). Disturbance chronologies suggested that the recent outbreak was the most severe disturbance event in the studied stands over 1831–2008. Although historical accounts documented the outbreak at the beginning of the 20th century as severe (Kuznetsov 1912), our reconstruction data suggested much a milder event in the studied stands.

Despite the coincidence of peak disturbances (above) and the general coherence in the disturbance histories between our two transects (Figs 3 and 4), several differences existed between transects (Table 2). A protracted increase in disturbance rates between 1940 and 1970 was evident on transect 2, as well as on the study sites to the south (Aakala & Kuuluvainen 2011), yet was not evident in transect 1. Differences in disturbance rates between these two transects were also evident in the 1870–80s, as well as during the recent bark beetle outbreak.

Our linking of dendrochronological data with tree spatial locations allowed us to reconstruct the size and location of past canopy disturbances, confirming that the disturbance regime of spruce-dominated forests consists of small- to moderate-scale canopy disturbances, and revealing a mean gap size occurring over the 180-yr period of 92 m² (maximum 2047 m²). Importantly, these analyses point to the patchy nature of canopy disturbance, with portions of the sites experiencing disturbance and portions relatively free from disturbance (Fig. 3), a finding quite notable on both transects, and similar to results from red spruce (*Picea rubens* Sarg.) forests of temperate North America (Fraver & White 2005a) and Norway spruce forests of central Sweden (Hytteborn & Verwijst 2014). The data from the most recent decade provide a rare glimpse of the spatial pattern resulting from a bark beetle outbreak, which is also known to be spatially patchy (Aakala et al. 2011).

Disturbance agents

Although our data did not allow us to positively identify the agents responsible for past disturbances, the temporal

association of these disturbance events with previously published accounts suggests that bark beetle outbreaks play an important role in dynamics of this system. In this same region, disturbances in ca. 1900 and 2000 were attributed to outbreaks of European spruce bark beetle (Kuznetsov 1912; Nevolin et al. 2005). Lesser forest damage by bark beetles in this region has also been documented during the 1940–50s (Nevolin & Torkhov 2007). The fact that some evidence for all of these outbreaks can be seen in our reconstructed disturbance histories (Fig. 2c, d) confirms the role of bark beetles in the dynamics of spruce forests in this region.

When considered the entire length of the study, canopy disturbance rates were not affected by soil moisture conditions (Table 2, Fig. 4); however, this finding may not apply to particular time periods and disturbance agents. Although wetter sites had higher disturbance rates during most of the 20th century, the recent bark beetle outbreak may show a reversal of that pattern: following this outbreak (early 2000s), the disturbance rates at drier sites were higher than those in wetter sites. We speculate that drier soil conditions might subject trees to higher water deficit during drought periods, subsequently leading to higher susceptibility to insect attacks. Indeed, climatic anomalies such as droughts have been previously suggested as triggers for insect outbreaks and possibly associated with declines in tree vigour (Rolland & Lemperiere 2004; McDowell et al. 2008). Drought stress has been shown to precede the recent bark beetle outbreak in this landscape (Nevolin et al. 2005; Aakala & Kuuluvainen 2011). It follows that the edges of the modern clear-cuts may be more susceptible to insect attacks due to higher evapotranspiration of trees in these habitats, as compared to undisturbed forest matrix, predisposing forest edges to insect attacks (Kautz et al. 2013). In addition, trees on edges may be more affected by wind-related stress, causing loss of fine roots, as compared to the trees in the forest matrix. Since fine roots are the primary suppliers of water, the wind effect may lead to a further increase in water stress in edge trees (Abrazko 1988). The onset of forest exploitation, associated with an increase in the amount of forest edges, could therefore indirectly increase spruce forests' susceptibility to bark beetle infestation (Kuznetsov 1912; Nevolin & Torkhov 2007). A stronger impact of the outbreak on the dominant trees, as observed here, mirrored a pattern previously reported for bark beetle outbreaks (Wermelinger 2004; Maslov 2010) and may reflect increased susceptibility of larger canopy dominants to the summer drought (D'Amato et al. 2013).

Wind storms also likely play a significant role in forest dynamics in this system, as suggested by abundant recent (10–20 yr-old) windthrows in several spruce stands within 10 km of our study area. Earlier, wind has been reported

as a principal disturbance agent in the Northern European boreal forests, especially for spruce-dominated stands on moist soils (Hytteborn et al. 1987; Drobyshch 1999). However, in the current study, we found that a small proportion (7.6%) of dead trees were uprooted, suggesting that wind was not an important *primary* tree mortality agent, at least in recent decades. Further, windthrow followed by favourable climate conditions could trigger bark beetle outbreaks at the landscape scale, as has been shown in other spruce forests of Europe (Wichmann & Ravn 2001; Jonsson et al. 2007). Wood-decay fungi likely increased the vulnerability of individual trees to windthrow, given the proportion of rotten stems (26%) among living spruces. Previous work has shown fungi to be an important contributing disturbance agent in Scandinavian spruce forests (Lannenpaa et al. 2008).

Although fire is often considered as the primary disturbance agent in European boreal spruce forests, a number of recent studies have called this assumption into question (Wallenius et al. 2005; Fraver et al. 2008; Aakala et al. 2011; Kuuluvainen & Aakala 2011). Although our sampling strategy was not specifically designed to recover fire history of the area, our field observations revealed no evidence of past fires, such as fire scars, charred stumps or fire-associated Scots pine, within at least 4 km of our study area. Thus, the fire return interval of the studied portion of the landscape exceeded 280 yr and likely extended over much longer periods.

Tree recruitment patterns

Norway spruce and downy birch differed in their recruitment histories, apparently due to the differences in shade tolerance, with spruce being very shade tolerant and birch intolerant. Spruce recruited continuously over the 285-yr period, with pulses following disturbance (Fig. 3a,b). Due to spruce's shade tolerance, old individuals were common in the understorey. On average, the age of understorey spruces was 105 yr, compared to 175 yr for canopy trees. It follows that spruce trees remained in the canopy for an average of 70 yr.

In contrast to spruce, birch showed several minor recruitment pulses in the 1800s, with sporadic recruitment thereafter (Fig. 2b). However, since ages were estimated for only 32% of sampled birch trees, considerable uncertainty remains concerning birch regeneration history. Birch recruitment pulses were associated with the disturbance peaks evident in our disturbance reconstructions, as well as historical accounts. For example, a moderate-severity disturbance during the 1820–30s fostered abundant birch recruitment in the following decade (Fig. 2). The size of disturbed patches was apparently large enough to admit birch (Fig. 3), thereby enriching the otherwise pure stands

of spruce. Although birch recruitment was much lower than that of spruce, the pulses in recruitment were generally coherent between the two species (Fig. 2). However, birch recruitment waves predated those of spruce, perhaps due to higher initial growth rates of birch or as a result of its earlier establishment dates. The synchronicity in recruitment patterns between transects suggests the recruitment pattern was probably representative of a larger part of the studied landscape, highlighting the importance of canopy disturbance in regulating landscape-level forest composition. Thus, despite causing dramatic structural alterations to the forest canopies, these disturbances – and associated recruitment patterns – did not result in a pronounced successional shift in tree species composition, rather occasional minor enrichments of birch in these heavily spruce-dominated stands. We acknowledge that the use of a pith locator (Applequist 1958; see Methods) introduces uncertainty in our recruitment ages, such that recruitment dates may have occasionally been placed in an incorrect decade. This uncertainty, however, was unlikely to obscure the general patterns evident in our results.

Conclusion

Our reconstruction of canopy dynamics since AD 1790 revealed a disturbance regime characterized by patchy small- to moderate-severity disturbances. The severity evident here is comparable to that of other natural closed-canopy dark coniferous forests of Northern Europe, where the annual canopy disturbance rates vary between 0.45% and 1.12% (Hytteborn et al. 1991; Linder et al. 1997; Fra-ver et al. 2008). The disturbance pulses in the studied spruce-dominated forests (up to 32% of forest canopy loss per decade, since 1831) were severe enough to cause minor enrichments of light-demanding birch.

The mixed-severity disturbance regime characterized by our findings may provide a benchmark for comparison against current harvesting practices. The common harvesting practices in the Russian north (large-scale clear-cuts) represent disturbance sizes and frequencies outside the natural range of variability for this forest type. These practices result in simplification of forest structure and a shift in species composition (Anonymous 2014), which may present a biodiversity risk (Seymour & Hunter 1999). Our results, together with earlier studies (Drobyshev 1999), call for a re-evaluation of these harvesting practices. To maintain the historical range of structure and species composition, while also ensuring adequate spruce regeneration, harvesting practices in such forests should leave or create patchy forest structure after harvesting, similar to natural forest structures revealed in the study. It is however important to note that our disturbance reconstruction was based on dendrochronological proxies that captured only recent

centuries; our methods do not address forest dynamics at longer, e.g. millennial, scales.

Further, the spatial variability in the modern forest, often highlighted through forest cover classification into phytosociological units (Jurkevich et al. 1971; Rysin & Saveljeva 2002), may not necessarily represent significant historical differences in natural disturbance regimes. For practical management, this observation would highlight the importance of landscape-level management and would warrant development of landscape-specific thresholds in intensity/severity of disturbances resulting from forest operations. Large areas covered by old-growth forests are scarce in Northern Europe. Due to their high conservation and scientific values, the widespread conservation of these forests, e.g. through establishment of protected areas and setting limits on commercial forestry activities in such areas, should receive careful consideration.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix 1. Characteristics of studied stands.

Appendix 2. Age structure of the spruce population.

Appendix 3. Age structure of the spruce population in four canopy position classes.

Appendix 4. Verification of the gap area reconstruction quality.