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1 Mixed-severity natural disturbance regime dominates in an old-  
2 growth Norway spruce forest of North-Western Russia

3

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15

16 *Keywords:* Boreal forest, canopy gaps, dendroecology, European spruce bark beetle, forest continuity,  
17 insect outbreaks, natural disturbances, Northern Europe.

18

## 19 Abstract

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

24 *Location.* Interfluvial region of the Northern Dvina and Pinega rivers, Arkhangelsk region, north-western  
25 Russia.

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

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

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

43

## 44 Introduction

45 Canopy disturbance is a major factor driving natural forest dynamics (Runkle 1985; Gromtsev 2002). The  
46 disturbance regime, which represents a set of disturbance characteristics such as type, frequency and  
47 severity of disturbance, directly affects species regeneration, biomass accumulation rates, and mortality  
48 patterns (Pickett et al. 1985; Runkle 1985; Fraver & White 2005a; Nagel & Diaci 2006). Understanding  
49 disturbance regimes advances our knowledge of natural processes in forest ecosystems and supports  
50 development of sustainable forest management practices aimed to maintain species and habitat diversity  
51 (Bergeron & Harvey 1997; Kuuluvainen 2002). Specifically, quantifying the frequency, severity, and  
52 spatial characteristics of natural disturbances is critical to the development of ‘ecologically-based’ forest  
53 management prescriptions. For example, natural disturbance characteristics have been used to determine  
54 harvest patch sizes and cutting cycles (Seymour et al. 2002), design variable density thinning prescriptions  
55 (Carey 2003), devise prescribed burning regimes (Peterson and Reich 2001), and set targets for old-growth  
56 restoration efforts (Bergeron & Harvey 1997; Kuuluvainen 2002, Franklin et al. 2007).

57 Small-scale disturbance events ( $< 100 \text{ m}^2$ ), resulting from mortality of one or several canopy trees, are  
58 thought to prevail in dark coniferous forest of Northern Europe (Hytteborn et al. 1987; Hofgaard 1993;  
59 Drobyshev 1999), which in European Russia are typically dominated by *Picea abies* and *P. obovata*  
60 (Gromtsev, 2002). The main natural disturbance agents in such ecosystem are windthrow (Liu & Hytteborn  
61 1991; Drobyshev 1999; Drobyshev 2001) and insect outbreaks (Schroeder 2007; Aakala et al. 2011). Forest  
62 susceptibility to these agents is related to climatic variability, e.g. periods with extreme precipitation  
63 (Abrazko 1988) or summer droughts (Aakala & Kuuluvainen 2011). Although fires may occur in dark  
64 coniferous forests of this region, the return intervals appear to be quite long, possibly exceeding 1000 years  
65 (Segerström et al. 1994; Wallenius 2002).

66 The vast majority of the Northern European boreal forest has been actively exploited in the past, and  
67 natural dynamics are increasingly being replaced by the dynamics initiated by timber harvesting  
68 (Kuuluvainen 2002; Achard et al. 2006), which has been commonly conducted through clearcuts of various  
69 sizes at least since the beginning of 20<sup>th</sup> century (Burnett et al. 2003). There are concerns that both the  
70 spatial scale and intensity of these harvests may be outside the historic range of variability of the natural

71 disturbance regime, which may lead to declines in biodiversity, ecosystem function, and structural  
72 complexity (Kuuluvainen 2002). A long history of forest exploitation in the Northern European boreal  
73 forest has left few sizeable areas of forests driven by natural dynamics. Presently, only few large areas of  
74 intact dark coniferous forests outside mountainous regions exist in Northern Europe, the majority of them  
75 being located on the flat and poorly drained interfluves of the Russian North-West (Yaroshenko et al. 2002;  
76 Potapov et al. 2008).

77 The Arkhangelsk region of North-West Russia, particularly the interfluves between Northern Dvina and  
78 Pinega rivers (Fig. 1), provides an ideal location to explore the historic range of variability in natural forest  
79 disturbance. The central part of this area represents one of the few examples of unfragmented and largely  
80 unmanaged forest landscapes (or *Intact Forest Landscapes*, Anonymous 2014) within the northern and  
81 middle boreal region (Aksenov et al. 2002), also known as Dvinsky forest (Anonymous 2014). It supports  
82 unbroken reaches of old-growth and multi-cohort Norway spruce (*Picea abies* (L.) Karst.) -dominated  
83 forests, with areas of continuous forest tracks reaching several thousand hectares. Previous reports indicate  
84 high value of these forests as reference ecosystems for biological conservation (Yaroshenko et al. 2002;  
85 Zhuravlyova et al. 2007).

86 The primary goals of this study were to characterize the historical variability in canopy disturbance of  
87 pristine spruce-dominated forests. Three particular focus points of the study were long-term dynamics of  
88 canopy disturbance rates, regeneration patterns of canopy dominants, and the effect of local site conditions  
89 on disturbance rates. Understanding these aspects of ecosystem dynamics is of critical importance for  
90 developing sustainable management strategies of both commercial and protected forests (Bergeron &  
91 Harvey 1997; Kuuluvainen et al. 2014). Despite a large volume of research on these topics (Kuuluvainen et  
92 al. 2014 and references within), there is still a need for long-term and quantitative estimates of the  
93 ecosystem processes. Understanding the within-stand (101-2 ha) spatial patterns created by natural  
94 disturbances and vegetation response to them is one such knowledge gap that the current study attempted to  
95 fill. Spatially-explicit studies of canopy disturbances at this scale are uncommon (Drobyshev & Nihlgård  
96 2000; Fraver & White 2005a), yet many management actions (e.g. thinning and final fellings) are carried  
97 out at this very scale. We therefore included detailed tree spatial data in our study to elucidate the potential  
98 fine-scale patterns of canopy dynamics. Finally, we were also interested in understanding the role of

99 variability of site conditions and associated changes in vegetation cover within single tracks of forests in  
100 affecting long-term disturbance rates. The importance of such variability has been postulated in many  
101 Russian studies (Sukachev & Zonn 1961; Jurkevich et al. 1971; Rysin & Saveljeva 2002), though spatially-  
102 explicit data to support this assumption are largely missing. In this study we capitalized on the combination  
103 of dendrochronological and modern spatial data, realizing that tree-ring records provide quantitative and  
104 long-term (often multi-century) records of forest dynamics (e.g. Fraver and White 2005a, Aakala et al.  
105 2011). We put forward three research questions: (1) What were the long-term disturbance rates (including  
106 variability) and agents?, (2) Were the temporal recruitment patterns of canopy dominants associated with  
107 past disturbance episodes?, and (3) Have soil moisture conditions influenced disturbance rates across this  
108 boreal spruce-dominated forest?

109

## 110 Material and methods

### 111 *Study area*

112 The study was conducted in an old-growth spruce-dominated forest located in the interfluvium between the  
113 Northern Dvina and Pinega rivers in the Arkhangelsk region, North-Western Russia (N 63° 15', E 43° 49',  
114 Fig 1). The area pertains to the transitional vegetation zone between middle and northern European taiga.  
115 Regional climate is influenced by proximity to the White Sea. Throughout the 1900s, the mean annual  
116 temperature was 0.9 °C and mean annual precipitation was roughly 600 mm, with its minimum in March-  
117 April and maximum in July (Stolpovski 2013). The coldest month is January, with the mean temperature of  
118 -14.1°C, and the warmest month is July, with a mean of 16.1°C. A major portion of the watershed is rather  
119 flat with elevations up to 267 m a.s.l. The dominant soils are poorly drained loams and sandy loams of low  
120 fertility (Zagidullina 2009).

121 The large unfragmented forest area between the two rivers is designated as one of Russia's last Intact  
122 Forest Landscapes (Yaroshenko et al. 2002), that is, a forest landscape without signs of significant human  
123 activity in the past, and large enough "to maintain its natural biodiversity" (Aksenov et al. 2002). Over  
124 recent decades (late 1990s and 2000s) the area of intact forests has been rapidly shrinking due to extensive

125 timber harvesting (Yaroshenko et al. 2002). Yet, the total area of roughly 1 million ha makes the studied  
126 landscape the largest of such forests in the European middle taiga. The data collected in this study,  
127 originating from the central part of the area undisturbed by humans, should therefore be considered as  
128 representing natural dynamics of spruce-dominated forests in this part of the European boreal zone.

129 The majority of pristine old-growth forests stands in this landscape were dominated by Norway spruce  
130 (about 82.3% of the total area). Stands of Scots pine (*Pinus sylvestris* L.) and downy birch (*Betula*  
131 *pubescens* Ehrh.) contributed, with 10.1% and 7.6% of the area, respectively (Zhuravlyova et al. 2007).  
132 Ground vegetation in spruce stands examined in the study was dominated by *Vaccinium myrtillus* L.,  
133 *Dryopteris* spp., and *Gymnocarpium dryopteris* (L.) Newman. *Sphagnum girgensohnii* Russow and  
134 *Polytrichum commune* Hedw. were two major moss species, while *Hylocomium splendens* (Hedw.) W.P.  
135 Schimp, *Pleurozium shreberi* Mitten and *Dicranum* spp. were common on elevated and drier micro-sites  
136 (i.e. decomposed logs). The understory layer was represented by sparse patches of *Sorbus aucuparia* L.,  
137 which were common in canopy gaps.

138 Wind and insect disturbances have been reported earlier in the forest of the studied area. A windstorm  
139 occurred in the winter of 2001 and resulted in breakage of canopy trees (Ogibin & Demidova 2009). A  
140 wave of tree mortality, induced by European spruce bark beetle (*Ips typographus* L.) has been recorded in  
141 the area since 1999 (Nevolin et al. 2005; Ogibin & Demidova 2009; Aakala & Kuuluvainen 2011). An  
142 earlier outbreak of *I. typographus* occurred in the study area at the turn of the 20<sup>th</sup> century (Kuznetsov  
143 1912).

#### 144 *Site selection and sampling design*

145 To preliminarily locate the study area we used false color images from Landsat 5 TM and Landsat 7 ETM+  
146 datasets with spatial resolution of 28.5 m and band combination 5-4-3 covering 1990 to 2006, and the map  
147 of Intact Forest Landscapes (Zhuravlyova et al. 2007). In the field we searched for homogenous tracks of  
148 forest that met the following requirements: (a) located at least 120 m from the nearest forest road to avoid  
149 edge effects, (b) not disturbed by any harvesting operations, as evidenced by cut stumps, and (c)  
150 represented regionally common moist spruce-dominated forests). We established two belt transects (450 m  
151 × 20 m), each composed of a continuous array of 20 m × 20 m sample plots (with one terminal plot 20 m

152 ×10 m), with the total sampling area of 1.8 ha. Transects were placed within the dominant topographical  
153 elements, that is, upper parts of the flat slopes gently rolling towards small forest streams, at elevations of  
154 180-210 m a.s.l. Transects were oriented south-north, perpendicular to the dominant westerly wind  
155 direction. Field sampling took place in June and July 2009.

156 Within each transect we mapped (with accuracy of 0.1 m) all living trees and deadwood above 6 cm  
157 diameter at breast height (DBH,  $n = 2126$ ) and recorded species identity, life status (alive or dead), DBH,  
158 canopy position class (dominant, co-dominant, intermediate, and overtopped), and type of deadwood.  
159 Deadwood types included snag (standing dead trees), uprooted tree or stump (a vertical stem shorter than  
160 1.3 m). Deadwood was classified into five decay classes, with class I being least decayed and class V being  
161 most decayed (Shorohova & Shorohov 2001).

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

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

169 We measured tree crown diameter in two perpendicular directions on trees representing the dominant DBH  
170 classes within transects ( $n = 9$  for spruce and  $n = 3$  for birch). We also recorded current total area of canopy  
171 gaps in each transect by mapping areas under the open sky that exceeded 15 m<sup>2</sup>. This threshold was  
172 subjectively selected to avoid naturally occurring tree interstices smaller than a typical spruce canopy area.

### 173 *Data processing*

174 Cores were mounted on wooden planks, sanded with up to 400-grit sanding paper, and cross-dated using  
175 pointer years (Stokes & Smiley 1968). Samples were scanned with 2400 or 3200 ppi resolution, depending  
176 on sample length and ring visibility, and measured onscreen using *CooRecorder 7.2* and *CDendro 7.2*  
177 software (Cybis AB, <http://www.cybis.se/>). This method also yielded total ring counts at the coring height  
178 of 40 cm. For cores that did not directly hit the pith, the number of rings to pith was estimated using a pith



179 locator (Applequist 1958). For age structure analyses we used only samples where pith was estimated to be  
180 within 25 years away from the earliest ring of the sample. All spruce trees were successfully cross-dated  
181 and used for subsequent analyses. For birch we counted rings to estimate age at 40 cm above the forest  
182 floor but were able to use only 32% of the birches ( $n = 60$ ) in subsequent analyses. The remaining birch  
183 samples had extensive internal rot, and could not be used to define birch recruitment years with confidence.  
184 We do not consider a low number of birch trees used for analyses as a limitation since it unlikely produced  
185 a bias in estimation of birch regeneration waves. Calculation of stand volumes was based on DBH and tree  
186 height data, using forest inventory tables for the Arkhangelsk region (Anonymous 1952; Moiseev et al.  
187 1987).

188 The first two deadwood decay classes were characterized by the presence of bark to various extents and  
189 low amount (5 to 10%) of sapwood rot (Shorohova & Shorohov 2001). Deadwood classified in these two  
190 classes and bearing the damage marks of European bark beetle was considered to represent insect-induced  
191 mortality from the most recent outbreak. We therefore assumed that these trees were alive prior to the  
192 1999-2009 insect outbreak, which allowed us to reconstruct canopy composition prior to the outbreak. In  
193 total we inventoried 316 dead spruce trees, associated with the recent mortality episode, out of which  
194 34.5% ( $n = 109$ ) were not cored due to partially decomposed wood.

#### 195 *Growth release detection*

196 Using all properly dated ring-width chronologies, we inspected past radial growth patterns for growth  
197 releases (rapid increases in growth following a period of suppression) as evidence of past canopy  
198 disturbance. For the release-detection analyses, we worked exclusively with understory trees (*overtopped*  
199 and *intermediate* canopy classes) or current dominant trees (*co-dominant* and *dominant* classes) during the  
200 period they had resided in the understory. Understory trees typically show an increase in growth under the  
201 improved light conditions that follow a canopy disturbance (Lorimer & Frelich 1989) and are thus a better  
202 proxy for past canopy disturbances in closed-canopy forests, as compared to the dominant trees. To  
203 retrospectively estimate the understory period of current canopy dominants, we used the relationship  
204 between DBH and canopy class to estimate typical DBH of a tree reaching *co-dominant* class, following  
205 the methods of Lorimer and Frelich (1989). In particular, we used relationship between DBH and canopy

206 class, recorded in the field, to reconstruct the period during which the tree had the DBH characteristic of the  
207 current understory trees. Thus, we calculated the DBH corresponding to 90% probability of a tree residing  
208 in the canopy and then selected that portion of the tree-ring series corresponding to the previous understory  
209 period. The DBH at which a tree reached *co-dominant* canopy class and therefore entered the canopy, was  
210 estimated to be 17.3 cm.

211 To detect growth releases in ring-width chronologies we used the absolute-increase method (Fraver &  
212 White 2005b) with a 10-year running mean window. The absolute-increase threshold, derived from these  
213 data, was set at 0.50 mm following the methods outlined in (Fraver & White 2005b). Additional evidence  
214 of past canopy disturbance can be derived from the rapid initial growth, as this indicates recruitment under  
215 open-canopy conditions (Lorimer & Frelich 1989). To identify such ‘gap-recruitment’ events, we used a  
216 minimal annual growth rate of 1.5 mm over the first decade, when followed by a declining, parabolic or flat  
217 growth pattern (Frelich 2002), as evidence of former canopy disturbance. While applying growth-release  
218 and gap-recruitment methods, we visually inspected all samples to avoid “false releases” due to the  
219 presence of compression wood. Evidence of disturbance (both releases and gap-recruitments) was  
220 expressed as a percent of total trees alive in a given decade that showed one of these responses. We  
221 extended these chronologies, one for each transect, back in time until the number of trees dropped below  
222 40.

### 223 *Spatial reconstruction of canopy disturbance*

224 To reconstruct the location and size of past canopy disturbances, we used growth-release data from spruce  
225 trees, and gap-recruitment dates from spruce and birch, as well as the *X* and *Y* coordinates of these trees on  
226 the transects. From these data, for each decade we compiled a map of trees that were classified as being  
227 within canopy gaps or under the closed canopies. Kriging methods (*Prediction map* method in *Universal*  
228 *kriging* in ESRI ArcGIS, ESRI 2009) were subsequently used to spatially interpolate and delineate areas  
229 existing as gaps or closed canopies. During this procedure we filtered out tree interstices by calculating  
230 trees’ crown projections using a regression between tree DBH and crown projection area, obtained on the  
231 reference trees. We extended the spatial reconstruction back in time until the number of trees available for  
232 analyses dropped below 150, which corresponded to 1830s and 1840s for the first and the second transects,

233 respectively. A more stringent threshold employed for this spatial reconstruction, as compared to growth-  
234 release chronology (see previous sub-section), resulted in a shorter disturbance chronology. However, we  
235 considered it justified by the spatial nature of the analysis, i.e. higher data requirement for the kriging  
236 process, as compared to the construction of growth-release chronology.

237 To verify preliminary results of the spatial reconstructions, we ground-truthed the output of spatial analysis  
238 for the 2001-2008 period. Both estimates of gap area were scaled to 11 of 20 m × 40 m plots in each  
239 transect, providing means to assess the utility in converting growth-release data (point-type data) into  
240 spatial estimates of area under gaps. Given the success of this approach (Supplementary Information Fig.  
241 S2), we subsequently considered these canopy-area estimates (not simply proportion of trees exhibiting  
242 growth release) as proxies for stand-wide disturbance rates. This approach to quantifying disturbance rates  
243 is a spatially-explicit outgrowth of the canopy-area-based approach introduced by Lorimer and Frelich  
244 (1989) and elaborated by Fraver and White (2005a).

245 Finally, to evaluate variability in disturbance rates in relation to soil moisture regimes, we classified plots  
246 into one of three groups based on the cover of *Sphagnum* species, which represented the general site quality  
247 (Chertov, 1981): low soil moisture plots (<5% of *Sphagnum*), moderate moisture plots (5 to 40%), and high  
248 moisture plots (>40%). We used repeated measures ANOVA, using decadal estimates of the areas under  
249 gaps as the dependent variable and three classes of soil moisture variability as the second independent  
250 variable (with time as the first independent variable).

251

## 252 Results

### 253 *Stand characteristics*

254 As of 2009 Norway spruce and downy birch were the only tree species present in the forest canopy of the  
255 examined stands (Table 1). Spruce contributed with 73% of the mean stand volume, 75% of the basal area,  
256 and 93.6% of tree density. Average stand volume was 211 m<sup>3</sup> ha<sup>-1</sup>, the absolute basal area was 21.5 m<sup>2</sup> ha<sup>-1</sup>,  
257 and average stem density was 781 trees ha<sup>-1</sup>. Stand characteristics varied somewhat between the two  
258 transects, the second transect exhibiting higher volume, basal area, and tree density. The mean stand DBH

259 was lower at the second transect, owing to higher number of suppressed trees under the canopy  
260 (Supplementary Information Table S1).

### 261 *Age structure*

262 The oldest tree reached the sampling height of 40 cm in 1726 and the youngest tree in 1981 (Supplementary  
263 Information Figs. 1 and 2). Generally, the mean age at 40 cm increased from understory to dominate  
264 canopy position classes, but with large variability of ages observed within each class (Supplementary  
265 Information Fig. 1). Age and DBH were moderately correlated ( $R^2 = 0.46$ ). Spruce trees in the dominant  
266 and co-dominant canopy positions were between 60 and 270 years old at the sampled height. The largest  
267 variability was found for trees of intermediate position with estimated ages ranging from 31 to 285 years.  
268 Almost half (46 %,  $n = 612$ ) of the spruce trees in the dataset did not exceed 10 cm in DBH, and more than  
269 half of these (57%,  $n = 347$ ) were older than 80 years.

270 Evaluation of tree ages on cores with missing pith might introduce a bias due to errors associated with  
271 estimation of the rings-to-the-pith, which were missed during coring, especially while working with shade  
272 tolerant trees (Barker 2003). Despite the fact that the age estimation for 24% of the spruce trees required  
273 adding more than 10 years to the date of the oldest ring on the sample, it did not introduce a bias in resulting  
274 age structure. The comparison of age structures obtained on (a) the complete dataset and (b) a reduced  
275 dataset composed of trees where the pith was estimated to be missed by not more than ten years, showed no  
276 statistically significant differences (Supplementary Information Fig. 3).

### 277 *Tree recruitment patterns*

278 Spruce recruitment age structure (including gap-recruited and non-gap-recruited trees) on both transects  
279 indicated nearly continuous recruitment of trees since the 1700s, with recruitment peaks centered around  
280 1850 and 1900s (Fig. 2A). The second transect had a larger number of younger spruce trees (30 to 110  
281 years old) implying more intensive tree recruitment after 1900s. Birch age structure suggested an intensive  
282 regeneration period from 1800s to 1860s, peaking around 1830s, and rather high birch recruitment at the  
283 first transect around 1890s (Fig. 2B). In general, spruce and birch age structures were coherent with each  
284 other, pointing to synchronized disturbance events.

### 285 *Canopy gaps*

286 The mean canopy gap size reconstructed over the 180 year period was 92 m<sup>2</sup>, with its maximum at 2047  
287 m<sup>2</sup>. The mean size of recent gaps delineated in 2009 was 166 m<sup>2</sup>, ranging from 15 to 963 m<sup>2</sup>. Together,  
288 these recent gaps represented 40.5 % and 28.0 % of the total stand area on the first and the second transects,  
289 respectively. Due to reduction in data available for spatial reconstructions with time, our ability to detect  
290 small gaps deteriorated as we progressed further back in time, which likely resulted in their  
291 underrepresentation in the reconstruction. As a consequence, the historical gap size distribution likely  
292 included even more small gaps, creating an even greater difference between modern and historical  
293 disturbance rates.

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

#### 298 *Reconstruction of canopy disturbance rates*

299 A total of 554 growth release and 64 gap-recruitment events were identified. Most of the trees released  
300 (98%) required only one release to reach the canopy; 25 trees (2% of dated spruces) required two or more  
301 releases. Reconstructions of the location and size of past canopy gaps revealed the dynamic nature of the  
302 forest canopy, with peaks of disturbance and intervening periods of quiescence, as well as portions of the  
303 sites experiencing disturbance and portions relatively free from disturbance (Figs. 3C and 4). The overall  
304 mean decadal disturbance rate was 8.3% of the area. Our results identified decades with increased rates:  
305 1840s, 1870-80s, 1920s, 1970s, and 2000s. Corresponding decadal disturbance rates, identified in spatial  
306 analyses, were 20.9, 11.9, 6.6, 11.5, and 32.2% of the area. Because we used the same dataset for spatial  
307 reconstructions and growth-release analysis, these peak decades mirrored those with peaks in releases and  
308 gap-recruitment events (Fig. 2C and 2D). A prolonged disturbance episode occurred on the second transect  
309 from 1950s to 1970s; cumulatively, 34% of the area was disturbed during these three decades.

310 A decline in the number of trees available for spatial reconstruction might contribute to uncertainties in  
311 estimating disturbance rates in the earlier period. An indication of systematic bias associated with  
312 decreasing sample size would be an increase in the canopy gap size in the earlier period. However, the

313 reconstruction (Fig. 3) did not indicate such a pattern, suggesting that the chosen threshold of the minimum  
314 sample size (40 trees) was reasonable.

315 Even though the spatial and temporal characteristics of disturbances differed somewhat between two  
316 transects, the mean decadal disturbance rates over 1830-2009 were very similar (8.24 % and 8.17% of area  
317 disturbed, at the first and the second transects, respectively). The mean decadal disturbance rates over that  
318 period corresponds to a canopy turnover time of 122 years, 95% confidence envelop being 91 to 184 years.  
319 Soil moisture did not significantly affect disturbance rates over 1861-2008 (Table 2), although disturbance  
320 rates in moist stands appeared higher than in dryer stands during the middle of the 20th century (Fig. 4).

### 321 *Recent spruce mortality episode*

322 The most recent (since 1999) mortality episode, mainly associated with an outbreak of European spruce  
323 bark beetle, killed 42.3% of trees and reduced spruce stand volume by 113 m<sup>3</sup> ha<sup>-1</sup> (Table 1). The spruce  
324 mortality occurred in all size classes; however, it was especially prevalent among dominant trees. The  
325 outermost rings on dead trees indicated a period of high spruce mortality from 2004 to 2008, culminating in  
326 2006 (Fig. 5). Mortality of sub-canopy trees reached its maximum during 2007 and 2008. The period of  
327 intensive canopy tree mortality lasted approximately seven years. Between 2006 and 2008 the density of  
328 large trees decreased from approx. 14 to approx. 3 trees ha<sup>-1</sup> (Table 1). Decline in canopy tree density was  
329 in line with dramatic increase in growth releases and areas in canopy gaps (Figs. 3C and 3D). The rapid  
330 increase in mortality of dominant trees in the early 2000s might be attributed, in part, to a sampling artifact,  
331 because the trees died before 1999 were not sampled due to the difficulties in extracting sound increment  
332 cores.

## 333 Discussion

### 334 *Disturbance rates and spatial patterns*

335 The reconstructed disturbance history since 1790 AD revealed mixed severity events, with a background of  
336 small-scale canopy gaps and periodic pulses of moderate-scale disturbances. Further, because a  
337 considerable proportion of spruce trees sampled at 40 cm height were initially slow-growing (annual radial  
338 increment below 1.5 mm), it is likely that the period without stand-replacing disturbance approached 280

339 years, the projected age of the oldest trees in our dataset. Similar patterns of mixed-severity disturbances  
340 have been recently reported in spruce forests of northern Europe (Drobyshev 2001; Fraver et al. 2008;  
341 Caron et al. 2009; Aakala et al. 2011; Kuuluvainen et al. 2014), suggesting that this disturbance regime  
342 may be more common than had been previously assumed. Taken together, these recent findings further  
343 support the growing recognition that disturbance regimes in boreal spruce forests of Europe do not  
344 necessarily fit neatly into one of two traditional categories, namely gap-dynamics or catastrophic  
345 disturbance, as had been previously thought (see also Kuuluvainen & Aakala 2011; McCarthy 2001).  
346 Instead, disturbances may span rather complex temporal and spatial gradients. Our findings classify this  
347 disturbance regime as *patch dynamics*, following the classification of Kuuluvainen & Aakala (2011), which  
348 is defined by pulsed disturbances that create aggregated patches occasionally exceeding 200 m<sup>2</sup> and  
349 resulting in primarily multi-cohort stands.

350 The mean decadal disturbance rate for the entire reconstructed period (transects pooled) was 8.3%, with  
351 pulses of moderate-severity disturbance occurring roughly every 40 years. Three out of five disturbance-  
352 prone periods (1880s, 1920s and 1970s) coincided with peaks reported from spruce forests approximately  
353 25 km south-east of our study area (Aakala & Kuuluvainen 2011), suggesting the region-wide synchrony of  
354 these events (see *Disturbance agents*, below). Disturbance chronologies suggested that the recent outbreak  
355 was the most severe disturbance event in the studied stands over 1831–2008. Although historical accounts  
356 documented the outbreak at the beginning of the 20th century as severe (Kuznetsov 1912), our  
357 reconstruction data suggested much milder event in the studied stands.

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

364 Our linking of dendrochronological data with tree spatial locations allowed us to reconstruct the size and  
365 location of past canopy disturbances, confirming that the disturbance regime of spruce dominated forests  
366 consists of small- to moderate-scale canopy disturbances, and revealing a mean gap size occurring over the  
367 180-year period of 92 m<sup>2</sup> (maximum 2047 m<sup>2</sup>). Importantly, these analyses point to the patchy nature of  
368 canopy disturbance, with portions of the sites experiencing disturbance and portions relatively free from  
369 disturbance (Fig. 3), a finding quite notable on both transects, and similar to results from red spruce (*Picea*  
370 *rubens* Sarg.) forests of temperate North America (Fraver & White 2005a) and Norway spruce forests of  
371 central Sweden (Hytteborn & Verwijst 2014). The data from the most recent decade provide a rare glimpse  
372 of the spatial pattern resulting from a bark beetle outbreak, which is also known to be spatially patchy  
373 (Aakala et al. 2011).

#### 374 *Disturbance agents*

375 Although our data did not allow us to positively identify the agents responsible for past disturbances, the  
376 temporal association of these disturbance events with previously published accounts suggests that bark  
377 beetle outbreaks play an important role in dynamics in this system. In this same region, disturbances ca.  
378 1900 and 2000 were attributed to outbreaks of European spruce bark beetle (Kuznetsov 1912; Nevolin et al.  
379 2005). Lesser forest damage by bark beetles in this region has also been documented during the 1940-50s  
380 (Nevolin & Torkhov 2007). The fact that some degree of evidence for all of these outbreaks can be seen in  
381 our reconstructed disturbance histories (Fig. 2C and 2D) confirms the role of bark beetles in the dynamics  
382 of spruce forests in this region.

383 When considered over the entire length of the study, canopy disturbance rates were not affected by soil  
384 moisture conditions (Table 2, Fig. 4); however, this finding may not apply to particular time periods and  
385 disturbance agents. Although wetter sites had higher disturbance rates during most of the 20th century, the  
386 recent bark beetle outbreak may show a reversal of that pattern: following this outbreak (early 2000s), the  
387 disturbance rates at drier sites were higher than those in wetter sites. We speculate that drier soil conditions  
388 might subject trees to higher water deficit during drought periods, subsequently leading to higher  
389 susceptibility to insect attacks. Indeed, climatic anomalies such as droughts have been previously suggested



390 as triggers for insect outbreaks and possibly associated with declines in tree vigor (Rolland & Lemperiere  
391 2004; McDowell et al. 2008). Drought stress has been shown to precede the recent bark beetle outbreak in  
392 this landscape (Nevolin et al. 2005; Aakala & Kuuluvainen 2011). It follows that the edges of the modern  
393 clear-cuts may be more susceptible to insect attacks due to higher evapotranspiration of trees in these  
394 habitats, as compared to undisturbed forest matrix, predisposing forest edges to insect attacks (Kautz et al.  
395 2013). In addition, trees on edges may be more affected by wind-related stress, causing loss of fine roots, as  
396 compared to the trees in the forest matrix. Since fine roots are the primary suppliers of water, the wind  
397 effect may lead to further increase in water stress in edge trees (Abrazhko 1988). The onset of forest  
398 exploitation, associated with an increase in the amount of forest edges, could therefore indirectly increase  
399 spruce forests' susceptibility to bark beetle infestation (Kuznetsov 1912; Nevolin & Torkhov 2007). A  
400 stronger impact of the outbreak on the dominant trees, as observed here, mirrored a pattern previously  
401 reported for bark beetle outbreaks (Wermelinger 2004, Maslov 2010) and may reflect increased  
402 susceptibility of larger canopy dominants to the summer drought (D'Amato et al. 2013).

403 Wind storms also likely play a significant role in forest dynamics in this system, as suggested by abundant  
404 recent (10-20 year-old) windthrows in several spruce stands within 10 km of our study area. Earlier, wind  
405 has been reported as a principal disturbance agent in the northern European boreal forests, especially for  
406 spruce dominated stands on moist soils (Hytteborn et al. 1987; Drobyshev 1999). However, in the current  
407 study, we found that a small proportion (7.6%) of dead trees were uprooted, suggesting that wind was not  
408 an important *primary* tree mortality agent, at least in the recent decades. Further, windthrow followed by  
409 favourable climate conditions could trigger bark beetle outbreaks at the landscape scale, as has been shown  
410 in other spruce forests of Europe (Wichmann & Ravn 2001; Jonsson et al. 2007). Wood-decay fungi likely  
411 increased the vulnerability of individual trees to windthrow, given the proportion of rotten stems (26%)  
412 among living spruces. Previous work has shown fungi to be an important contributing disturbance agent in  
413 Scandinavian spruce forests (Lannenpaa et al. 2008).

414 Although fire is often considered as the primary disturbance agent in European boreal spruce forests, a  
415 number of recent studies have called this assumption into question (Wallenius et al. 2005, Fraver et al.  
416 2008, Aakala et al. 2011, Kuuluvainen & Aakala 2011). Although our sampling strategy was not

417 specifically designed to recover fire history of the area, our field observations revealed no evidence of past  
418 fires, such as fire scars, charred stumps, or fire-associated Scots pine, within at least 4 km of our study area.  
419 Thus, the fire return interval of the studied portion of the landscape exceeded 280 years and likely extended  
420 over much longer periods.

#### 421 *Tree recruitment patterns*

422 Norway spruce and downy birch differed in their recruitment histories, apparently due to the differences in  
423 shade-tolerance, with spruce being very shade tolerant and birch intolerant. Spruce recruited continuously  
424 over the 285-year period, with pulses following disturbance (Figs. 3A and 3B). Due to spruce's shade  
425 tolerance, old individuals were common in the understory. On average, the age of understory spruces was  
426 105 years, compared to 175 years for canopy trees. It follows that spruce trees remained in the canopy for  
427 an average of 70 years.

428 In contrast to spruce, birch showed several minor recruitment pulses in the 1800s, with sporadic  
429 recruitment afterwards (Fig. 2B). However, since ages were estimated for only 32% of sampled birch trees,  
430 considerable uncertainty remains concerning birch regeneration history. Birch recruitment pulses were  
431 associated with the disturbance peaks evident in our disturbance reconstructions, as well as historical  
432 accounts. For example, a moderate-severity disturbance during the 1820-30s fostered abundant birch  
433 recruitment in the following decade (Fig. 2). The size of disturbed patches was apparently large enough to  
434 admit birch (Fig. 3), thereby enriching the otherwise pure stands of spruce. Though birch recruitment was  
435 much lower than that of spruce, the pulses in recruitment were generally coherent between the two species  
436 (Fig. 2). However, birch recruitment waves predated those of spruce, perhaps due to higher initial growth  
437 rates of birch or a result of its earlier establishment dates. The synchronicity in recruitment patterns  
438 between transects suggests the recruitment pattern was probably representative of a larger part of the  
439 studied landscape, highlighting the importance of canopy disturbance in regulating landscape-level forest  
440 composition. Thus, despite causing dramatic structural alterations to the forest canopies, these disturbances  
441 – and associated recruitment patterns – did not result in a pronounced successional shift in tree species  
442 composition, rather occasional minor enrichments of birch in these heavily spruce-dominated stands. We

443 acknowledge that the use of a pith locator (Applequist 1958, see Methods) introduces uncertainty in our  
444 recruitment ages, such that recruitment dates may have occasionally been placed in an incorrect decade.  
445 This uncertainty, however, unlikely obscures the general patterns evident in our results.

## 446 Conclusion

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

453 The mixed-severity disturbance regime characterized by our findings may provide a benchmark for  
454 comparison against current harvesting practices. The common harvesting practices in the Russian North  
455 (large scale clearcuts) represent disturbance sizes and frequencies outside the natural range of variability for  
456 this forest type. These practices result in simplification of forest structures and a shift in species  
457 composition (Anonymous 2014), which may present a biodiversity risk (Seymour & Hunter 1999). Our  
458 results, together with earlier studies (Drobyshev 1999) call for a re-evaluation of these harvesting practices  
459 To maintain the historical range of structure and species composition, while also ensuring adequate spruce  
460 regeneration, harvesting practices in such forests should leave or create patchy forest structure after  
461 harvesting, similar to natural forest structures revealed in the study. It is however important to note that our  
462 disturbance reconstruction was based on dendrochronological proxies that captured only recent centuries;  
463 our methods do not address forest dynamics at longer, e.g. millennial, scales.

464 Further, the spatial variability in the modern forest, often highlighted through forest cover classification  
465 into phytosociological units (Jurkevich et al. 1971; Rysin & Saveljeva 2002), may not necessarily represent  
466 significant historical differences in natural disturbance regimes. For practical management, this observation  
467 would highlight the importance of landscape-level management and would warrant development of  
468 landscape-specific thresholds in intensity/severity of disturbances resulting from forest operations. Large  
469 areas covered by old-growth forests are scarce in Northern Europe. Due to their high conservation and

470 scientific values, the widespread conservation of these forests, e.g. through establishment of protected areas  
471 and setting the limits on commercial forestry activities in such areas, should receive careful consideration.

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641 List of appendices

642 Supplementary Information Table S1. Characteristics of studied stands.

643 Supplementary Information Figure S1. Age structure of the spruce population.

644 Supplementary Information Figure S2. Age structure of the spruce population in four canopy position  
645 classes.

646 Supplementary Information Figure S3. Verification of the gap area reconstruction quality.

647

648 Table 1.  
 649 Characteristics of studied stands in 1999 and 2009, demonstrating the effect of the recent bark beetle  
 650 outbreak that began in 1999. Column *Change* refers to changes in the variables following the bark beetle  
 651 outbreak. Data for 1999 was back calculated by considering recently dead trees as being alive in 1999 and  
 652 combining them with currently living trees, whose DBHs were reconstructed back to 1999. Values in  
 653 parentheses are percentages for respective absolute values. Data are averaged across two transects.  
 654

Variables	Inventories		Change
	1999	2009	
<i>Number of trees(n/ha)</i>			
Spruce	893	723	-170 (19.0)
Birch	84	58	-26 (31.0)
<i>Total</i>	977	781	-196 (20.1)
<i>Absolute basal area (m<sup>2</sup>/ha)</i>			
Spruce	27	16	-11 (40.7)
Birch	7	5.5	-1.5 (21.4)
<i>Total</i>	34	21.5	-12.5 (36.8)
<i>Standing volume (m<sup>3</sup>/ha)</i>			
Spruce	267	154	-113 (42.3)
Birch	74	57	-17 (23.0)
<i>Total</i>	341	211	-130 (38.1)
<i>Mean diameter (cm)</i>			
Spruce	16.5	14.6	-1.9 (11.5)
Birch	31.6	33.3	1.7 (5.4)

655  
 656

657 Table 2.

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

662

Factors	SS	df	MS	F	<i>p</i>
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
<b>R1</b>	<b>3.86E+05</b>	<b>15</b>	<b>2.57E+04</b>	<b>10.31</b>	<b>0.000</b>
R1 x Drainage	4.72E+04	30	1573	0.63	0.938
<b>R1 x Transect</b>	<b>1.01E+05</b>	<b>15</b>	<b>6738</b>	<b>2.7</b>	<b>0.001</b>
R1 x Drainage x Transect	9.97E+04	30	3322	1.33	0.113

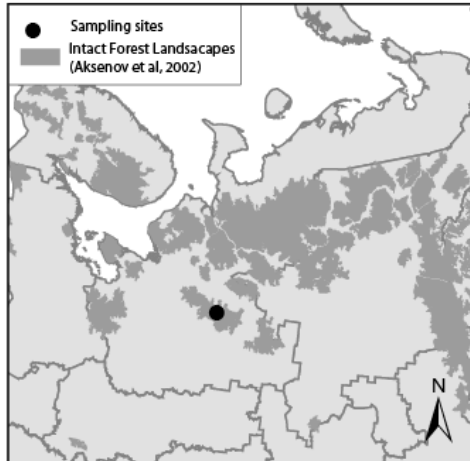
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665 Fig. 1

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

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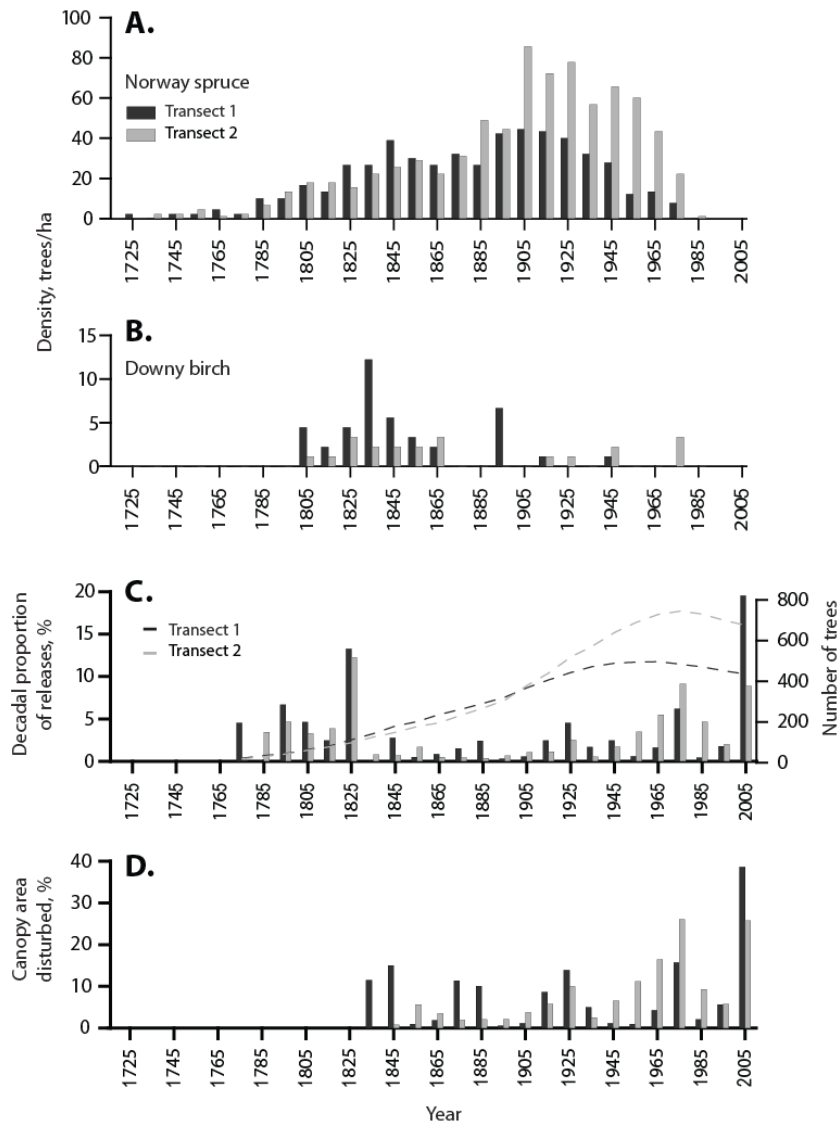
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670 Fig. 2.  
671 Canopy age structure and historical disturbance rates in the studied spruce-dominated forests. A & B show  
672 age structure of spruce and birch populations at the height of 40 cm in two transects. Data represent current  
673 trees densities grouped into 10 year classes. C & D show canopy disturbance rates based on spatially-  
674 explicit reconstructions separately for two transects (C, period 1840 - 2008) and tallies of releases and gap-  
675 recruitment events (D, 1790 - 2008). Disturbance rates were obtained from the spatially explicit  
676 reconstruction of canopy gaps and represent percent of stand area occupied by canopy gaps (see Fig. 3).  
677 Proportion of releases is a ratio between trees showing release and total number of trees covering a  
678 respective time period. Dashed lines and the right-hand axis represent number of trees covering a particular  
679 decade.

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Fig. 3

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Spatial location of gaps formed (black polygons) for each transect from 1830-40 to 2008, emphasizing the

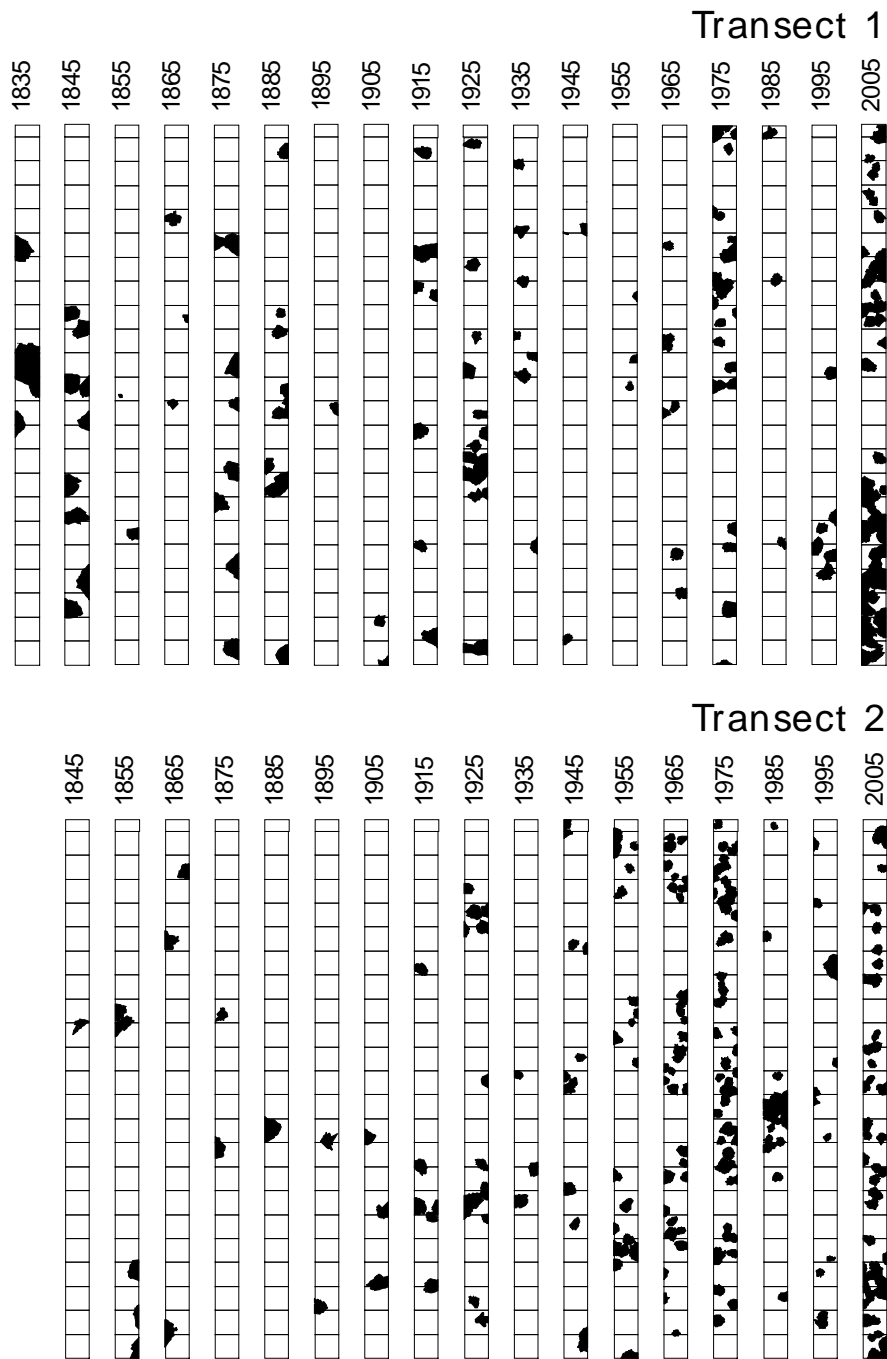
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temporal variability and spatial patchiness of canopy disturbances in this system. Dates on the figure refers

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to the midpoint of the respective decade.

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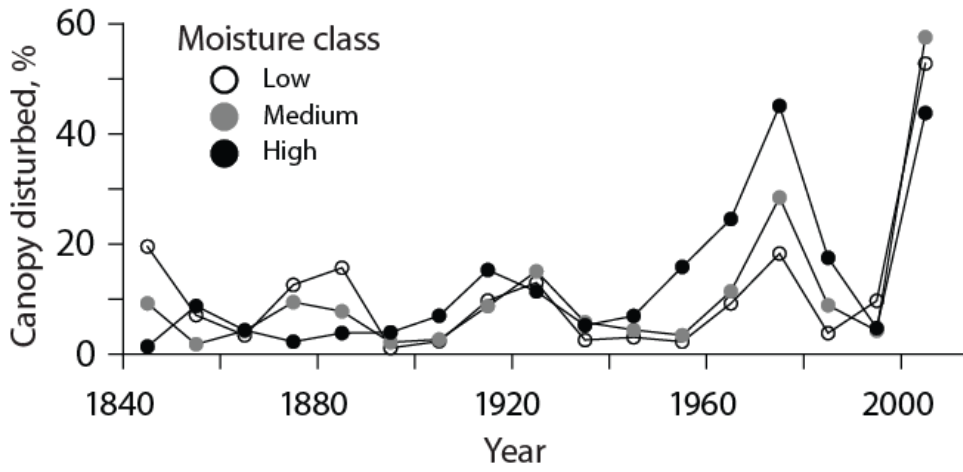
692 Fig. 4.

693 Decadal disturbance rates in stands of three soil moisture classes, revealing marked similarity across

694 classes. Statistical details of the analysis are presented in Table 2.

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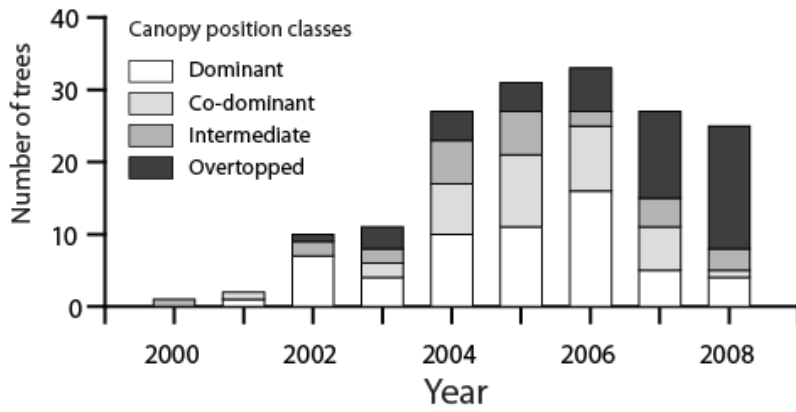
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698 Fig. 5.

699 Spruce mortality over the 2000-2008 period, which was assumed to be a result of the recent bark beetle  
 700 outbreak, as estimated by dendrochronological dating of dead trees.

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