BOREAL ENVIRONMENT RESEARCH 23: 209–219
ISSN 1797-2469 (online)

Helsinki 17 August 2018

Forest fire histories and tree age structures in Värriö and Maltio Strict Nature Reserves, northern Finland

Tuomas Aakala

Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland (tuomas.aakala@helsinki.fi)

Received 31 May 2017, final version received 8 Dec. 2017, accepted 8 Dec. 2017

Aakala T. 2018: Forest fire histories and tree age structures in Värriö and Maltio Strict Nature Reserves, northern Finland. *Boreal Env. Res.* 23: 209–219.

Wildfires virtually disappeared from the Fennoscandian forests in the 20th century, but have left persistent legacies in forest structure. Here, I reconstructed past fires in three northern boreal landscapes (each 2 km × 2 km) from fire scars, and described the fire regime for the past 300 years. The average fire cycles (1700–1999) were 72 and 156 years in *Pinus sylvestris*-dominated landscapes, and 579 years in a *Picea abies*-dominated landscape. At the site level, the number of fires was clearly related to soil hydraulic properties. Age structures from 1800 live and dead trees showed strong cohorts associated with large fires in two of the landscapes. Although tree growth and regeneration in sub-arctic regions are considered highly climate-sensitive, fires have been a major driver of forest dynamics in these areas. Continued absence of fires will lead to considerable changes in the forest structure and species composition in the future.

Introduction

Forest fires were historically the most important disturbance agent in the northern European boreal forest (Wallenius 2011, Drobyshev *et al.* 2014). Forest fires have been a strong determinant for the structure and species composition of the landscape mosaic (Niklasson and Granström 2000, Frelich 2017), as well as for the age and size structure within individual forest stands (Kuuluvainen and Aakala 2011, Wallenius 2011).

In eastern Fennoscandia, several studies have addressed local-to-landscape scale fire histories at high temporal resolution, using tree rings and tree age structures to determine fire years. In these studies, fire occurrence has shown wide variation in both time and space (Wallenius *et al.* 2010). Over large spatial scales, this variability is driven by climate (so-called top-down control; Aakala *et al.* 2018), but at individual stands or landscapes, bottom-up controls dominate, making landscape fire histories unique by reflecting particular features of specific landscapes. The main factors influencing the local characteristics of the fire regime are humans (particularly in igniting fires; Haapanen and Siitonen 1978, Lehtonen and Huttunen 1997, Pitkänen *et al.* 1999, Wallenius 2011), and the landscape characteristics such as topography and fire breaks that influence the spread of fires (e.g., Niklasson and Granström 2000). Spatial variability in fires is also related to site properties: fuel characteristics (amount of fuels and its moisture content) vary, which affects how often fires occur, and how severe they are (Zackrisson 1977). In general, xeric sites are likely to burn

Editor in charge of this article: Jukka Pumpanen

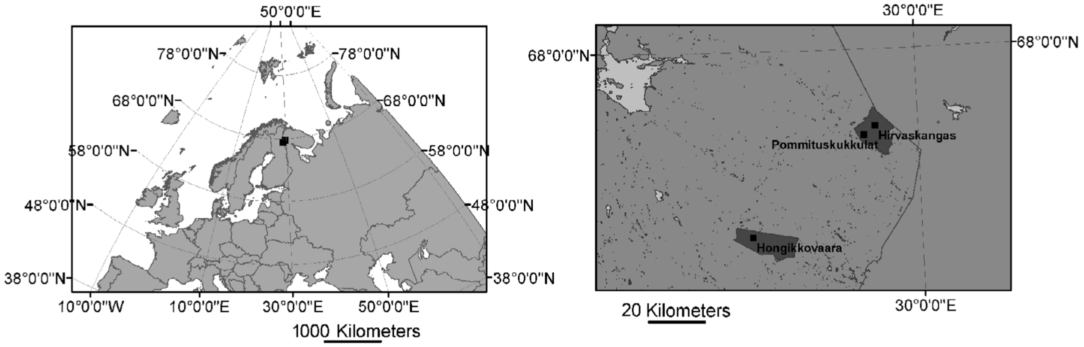

Fig. 1. Locations of the study landscapes in Värriö and Maltio strict nature reserves.

less intensively but more often, compared to mesic sites which are less flammable and thus burn rarely, but carry higher biomass and burn more severely (Agee and Skinner 2005).

One key finding from the local fire histories has been the virtual cessation of forest fires in the last two centuries (Wallenius 2011, Rolstad *et al.* 2017). This has led to concerns that fire-dependent species are losing their habitat, and has prompted considerable restoration efforts (e.g., Kuuluvainen *et al.* 2002, Junninen *et al.* 2008). However, the cessation of fires has other, more subtle implications as fires leave long-term legacies for instance to species compositions and stand age structures (Zackrisson 1977). As an example, in areas with recurrent low-intensity surface fires, fire occurrence is often visible as age cohorts (Kuuluvainen and Aakala 2011). As tree growth and mortality are related to the age of the trees, the legacy influences from disturbances may persist for centuries and continue influencing the dynamics of forests (Coomes and Allen 2007). Hence, understanding how past fires have shaped the structure of the remnant unlogged forests is imperative for understanding current forest dynamics and for predicting their future development.

Here, I reconstructed the forest fire history in three areas in northeastern Fennoscandia in the strict nature reserves in Värriö and Maltio. Forest dynamics in these northern ecosystems are often considered highly sensitive to climatic variability, and any changes in forest structure and dynamics are easily associated with changing climate, disregarding the legacies from changing disturbance regimes. The aims of this work were to (1) document the forest fire history in the past several centuries and its spatial variability, and to (2) assess the role of fire as a determinant of past forest dynamics, visible as legacy age structures observable today.

Material and methods

Study area

The study was conducted in Värriö and Maltio Strict Nature Reserves (Fig. 1). The area belongs to the northern boreal vegetation zone (Ahti *et al*. 1968). Mean annual temperature in the region is –0.9 °C (mean of years 1970–2000; Fick and Hijmans 2017). Mean temperature of the coldest month (January) is –12.7 °C, and 13.1 °C of the warmest month (July). Average annual precipitation sum is 570 mm.

The region is topographically variable, with elevations commonly ranging between 200 and 500 m a.s.l. The gently rolling low treeless mountains (or fells) are the dominant feature in the landscape. At lower elevations the landscape is a mosaic of open mires, paludified forests and forests on mineral soil. Forests on mineral soils are dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and in the early successional stages also by pubescent birch (*Betula pubescens*). Tree species dominance generally reflects soil properties, with Scots pine dominating the xeric to mesic sites (*sensu* Cajander 1949), and Norway spruce the mesic to the more fertile herb-rich sites. In sub-xeric and mesic sites suitable for both spruce and pine, the disturbance history determines the tree species composition so that frequent surface fires tend to favor the fire-adapted pine, and the absence of fire favors spruce.

Sampling and sample preparation

Three 2 km × 2 km landscapes were sampled in the summer 2012 (for details *see* Aakala *et al.* 2016): Hirvaskangas and Pommituskukkulat in the Värriö strict nature reserve, and Hongikkovaara in the Maltio strict nature reserve (Fig. 1). Sample sites were located so that each of the three areas was first divided into four 1 km × 1 km quadrants. Each quadrant was further divided into contiguous 0.1 ha cells, and four cells randomly selected for sampling (16 cells per area in Hirvaskangas, Pommituskukkulat, and Hongikkovaara each). Within each randomly located cell, all trees > 9.9 cm diameter at 1.3 m height were mapped, and their species, diameter and height recorded. Increment cores were extracted from all trees between 1 and 1.3 m height. Stoniness was determined using a metal probe at 16 locations around the cell center (Viro 1952), into each cardinal direction, one meter apart. Four soil samples were extracted from the cell center, 2 m apart, from the parent material a few cm below the B horizon.

Fire scars were searched from the vicinity of each site (approx. 50 m radius). When encountered from fallen dead trees, sample discs or partial discs containing the tip of the fire scar was extracted. Due to the strict protection status of the reserves, standing dead trees and live trees could not be cut in these areas and instead, a standard 5.15 mm increment borer was used for sampling. Increment cores were extracted from the scarred trees attempting to hit the tip of the fire scar. If the tip of the scar was not hit after three attempts, the approximate dates for the fire scars were determined from the growth patterns in the increment cores. In most cases these were assigned exact dates based on nearby fallen trees for which fire years were assigned unambiguously.

Standard dendrochronological methods were used to date the exact years of fire scars from the samples, as well as in constructing the stand age structures. The increment cores were glued to wooden mounts and sanded to fine grit (600). Sample disks or partial disks were similarly sanded. Tree rings were crossdated visually, based on marker rings from Wallenius *et al.* (2010). For uncertain samples, the tree rings were measured, using the WinDendro software (Regents Instruments Inc.) connected to an Epson V750 scanner. Visual crossdating was then verified against a master chronology from Aakala *et al.* (2014), using the COFECHA software (Holmes 1983).

For the age structures, both live and dead trees were included in the sampling. Samples were in most cases taken between 1 and 1.3 m height. The samples from the fallen dead trees were occasionally extracted higher up the stem due to the lower parts of the stem being too decayed for crossdating. When compiling the stand age structure, samples from dead trees that were taken higher than 2 m along the bole were omitted to have a comparable ages for all trees.

Fire history

For each site, fire history was computed over the time interval in which there were recorder trees (i.e. the sites were "active" for that period of time; Kilgore and Taylor 1979). Pines become active after first scarring: the thick-barked pines may well experience a surface fire without a fire scar, but once scarred, the scarred part exposes the tree to further scarring. For sites without fire scars, fire history was determined so that the age of the oldest fire-sensitive tree (spruce or birch) cored in determining the age structure was used as the minimum time since fire. In other words, a particular site was actively recording the absence of fires since the recruitment of fire-sensitive tree species.

For each area, I computed the average annually burnt proportion and the fire cycle (i.e., the time needed for the combined area of fires to burn an area equal in size to the study area; Johnson and Gutsell 1994). I estimated the average annually burnt proportion for a period from year t_0 to year t_1 as the mean proportion of burnt plots to total plots over the time period

$$a_{t_0,t_1} = \frac{1}{t_1 - t_0 + 1} \sum\nolimits_{t=t_0}^{t_1} \frac{b_t}{c_t}$$

where b_t is the number of burnt plots and c_t is the number of active plots in year t. From this, I estimated the fire cycle as

$$f_{t_0,t_1} = \frac{1}{a_{t_0,t_1}}$$

To compare the landscapes, I computed the fire cycle between years 1700 and 2000, for which there was good data coverage for all three areas. In addition, to assess the temporal change, and take full advantage of the varying temporal coverage of the fire record, I computed fire cycles for consecutive 100 year periods, beginning from 1535 in Hirvaskangas, 1682 in Pommituskukkulat, and 1524 in Hongikkovaara. All computations were done in the R environment for statistical computing (ver. 3.3.2; R Core Team 2016).

Fire occurrence and soil properties

Both soil stoniness measurements, and the collected field samples were used to examine the influence of differences in soil hydraulic properties on fire occurrence. Vegetation is shown to be related to the fire occurrence as it is a determinant of both the fuels and ignitions. However, because vegetation is partly a reflection of the time since fire (Zackrisson 1977), using soil hydraulic properties is more appropriate. In particular the field capacity of the soil is considered a useful measure of soil hydraulic properties in forest soils (Viro 1962). For this, the four soil samples extracted in the field were pooled, and the particle size distribution was determined from the oven-dried < 2 mm soil fraction using laser diffraction (Coulter LS 230, Beckman Coulter Inc.). The stoniness that was estimated at 16 points systematically spread over the site, was converted to a stoniness percentage following Viro (1952). From the particle size and stoniness, the field capacity for the soils were estimated at each site, using the functions of Saxton *et al.* (1986). Although the soil properties were determined only from the center point of each sample site and fire scars were obtained within 50 m distance from this point, I believe this serves as a rough approximation of the soil characteristics around the site.

Results

Fire occurrence and soil characteristics

Out of the 48 sampled sites, 36 sites had evidence of fire either as fire scars, or the stand age structure corresponded to a fire-year dated nearby (Fig. 2). Within study areas, fire occurrence varied. In Hirvaskangas, major fires were detected in 1751, 1800, and 1831 that burnt throughout most of the study area. In addition, in 1917, slightly less than half of the study area recorded a fire. Other fires (1882, 1888, 1923, and 1961) were sporadic. Prior to 1751, only three sites were active (Fig. 3), and hence the earlier fires are were not considered further.

In Pommituskukkulat, two fires were recorded, in 1700 and 1831. These fires had occurred in the northern part of the study area (Fig. 2). For the southern parts, no fires were detected either directly from fire scars, or in the age distributions.

In Hongikkovaara, most of the fires had scarred only one or two sites (1917, 1864, 1808, 1772, 1764, 1734, 1696, 1671). During a wide data coverage, only the fire in 1777 burnt widely throughout the area. Only sites in the northern part of the area predate the fire 1671, so the spatial coverage of those earlier fires is poor. As the species composition is fairly similar throughout the area (i.e., the lack of fire evidence is not the result of short-lived species), it seems plausible that the southern parts may have experienced a stand-replacing fire (or other disturbance) therefore lacking fire scars. Of the seven northernmost plots that were still recording in 1600, six had burnt, making this a candidate year for a larger burn.

During the past 300 years, fire occurrence was related to the soil type (Fig. 2) so that drier sites were more likely to have recorded more than one fire (multiple comparisons after Kruskall-Wallis, $p < 0.05$; as implemented in the pgirmess-package in R; Giraudoux 2012), between sites that had not burnt in the last 300 years, and those that had burnt at least twice (Fig. 4).

Fire cycle

I computed the fire cycle for the period 1700 to 1999, for which data was available for all three

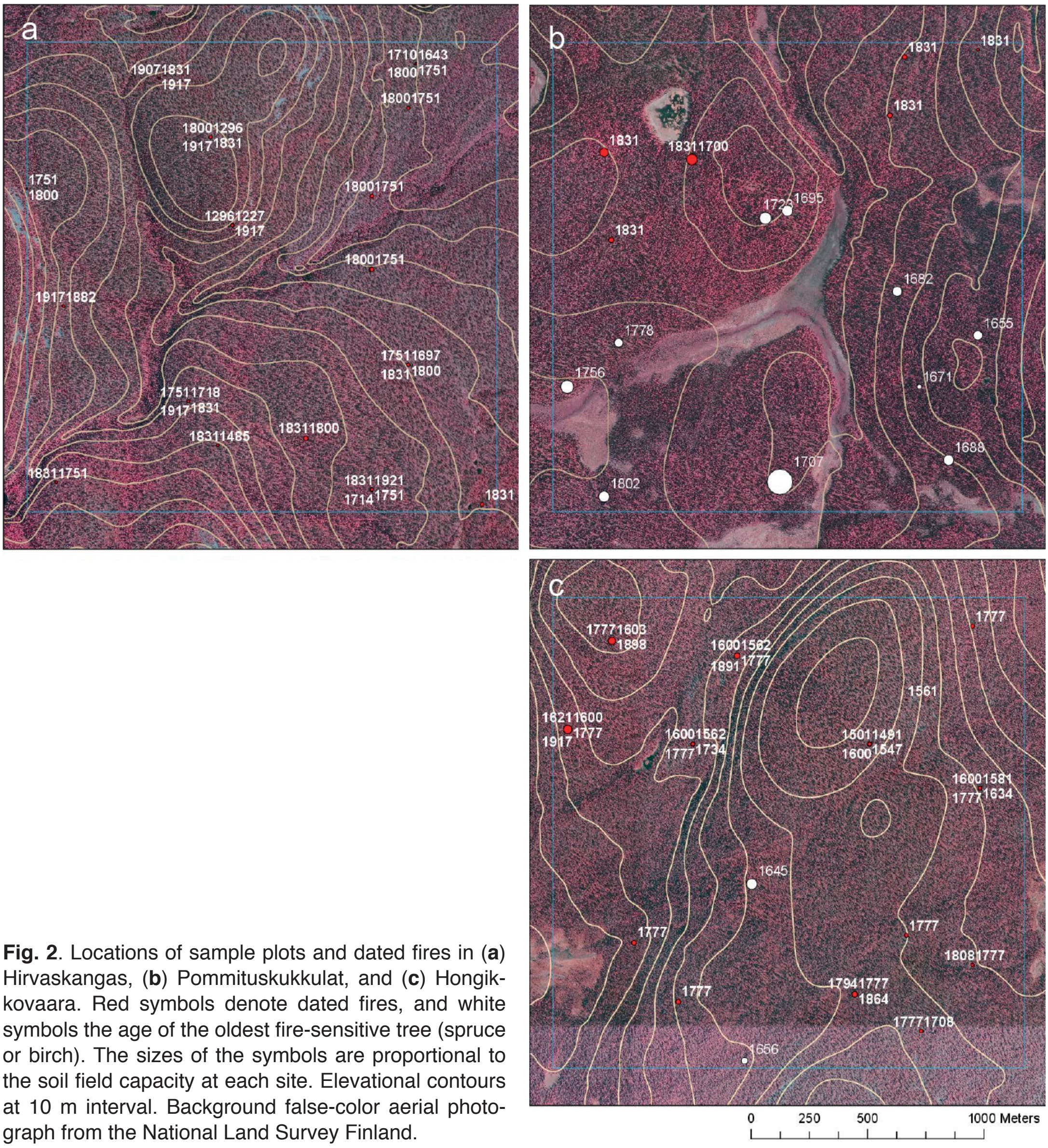

Fig. 2. Locations of sample plots and dated fires in (**a**) Hirvaskangas, (**b**) Pommituskukkulat, and (**c**) Hongikkovaara. Red symbols denote dated fires, and white symbols the age of the oldest fire-sensitive tree (spruce or birch). The sizes of the symbols are proportional to the soil field capacity at each site. Elevational contours at 10 m interval. Background false-color aerial photograph from the National Land Survey Finland.

landscapes (Fig. 2). During this period 11 years with fires had occurred in the Hirvaskangas and Hongikkovaara study areas, an average of one fire every 30 years. In the Pommituskukkulat landscape, only two years with fire were recorded, so a fire occurred once every 165 years. The fire cycle, taking into account the proportion of study sites burnt during each year for that 300 year period was 72 years in Hirvaskangas, 579 years in Pommituskukkulat, and 156 years in Hongikkovaara study area.

When comparing the temporal variation within a study area (Fig. 5, not limited to the common period of 1700–1999), in Hirvaskangas and Hongikkovaara, there was little temporal variation early in the study period. In Hirvaskangas, the fire cycle reached its minimum of 41 years at the end of the 18th century (computed for 100-year periods), and gradually increased thereafter. In Hongikkovaara, reconstructed fire activity was similarly high earlier in the period, with an approximately 48 year fire cycle from

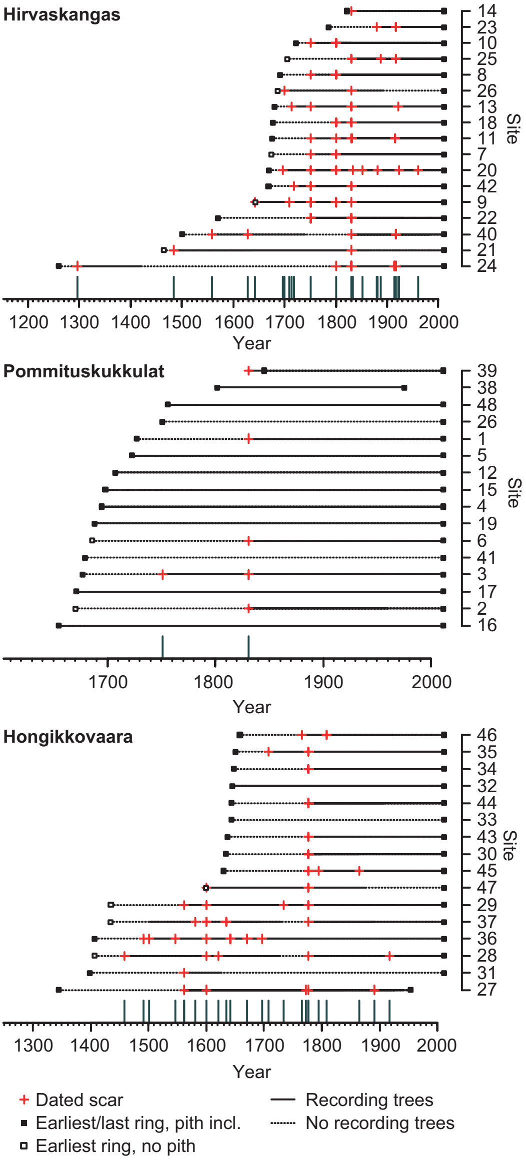

Fig. 3. Fire chronologies in the three study areas, each horizontal line representing one site. The bottom part of each panel is the composite chronology, showing all years when a fire was recorded in that area. Modified from Aakala *et al.* 2018.

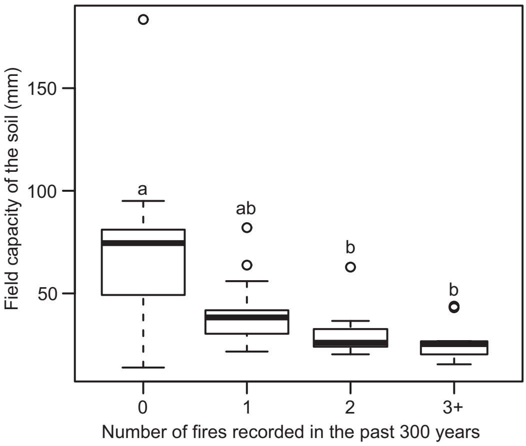

Fig. 4. Number of fires recorded, and the soil field capacity shown as boxplos indicating median (horizontal line) 50% (box), 1.5 times the interquartile range (whiskers), and outliers (points). Letters on top denote statistically significant differences.

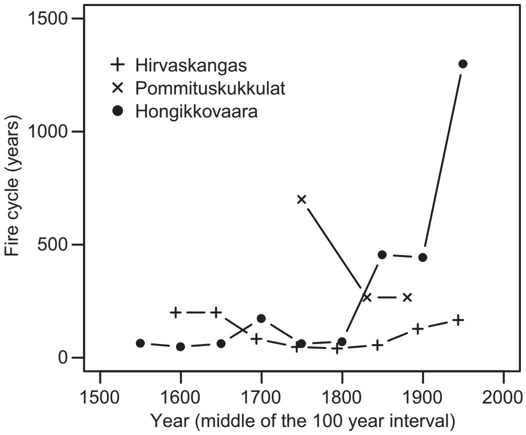

Fig. 5. Fire cycles for each study area. Fire cycle was computed for 100 year periods, and is visualized here at 50 year intervals. For the Pommituskukkulat area the fire cycle computation was possible only for a short time window, as only two fire years were recorded in that study area.

the 1600–1610. In Hongikkovaara, fire activity declined earlier than Hirvaskangas, from the early 19th century onwards. In the Pommituskukkulat study area, fires were rare during most of the period. The two fires that occurred in 1700 and 1831 reduced the 100-year fire cycle for that area to 267 years in the late 18th century. The last fire recorded in the tree rings in that area was in 1831.

Age structures

The landscape-scale age structures were compiled from 1800 live and dead trees sampled and cross-dated in the 48 sample plots (Fig. 6). The

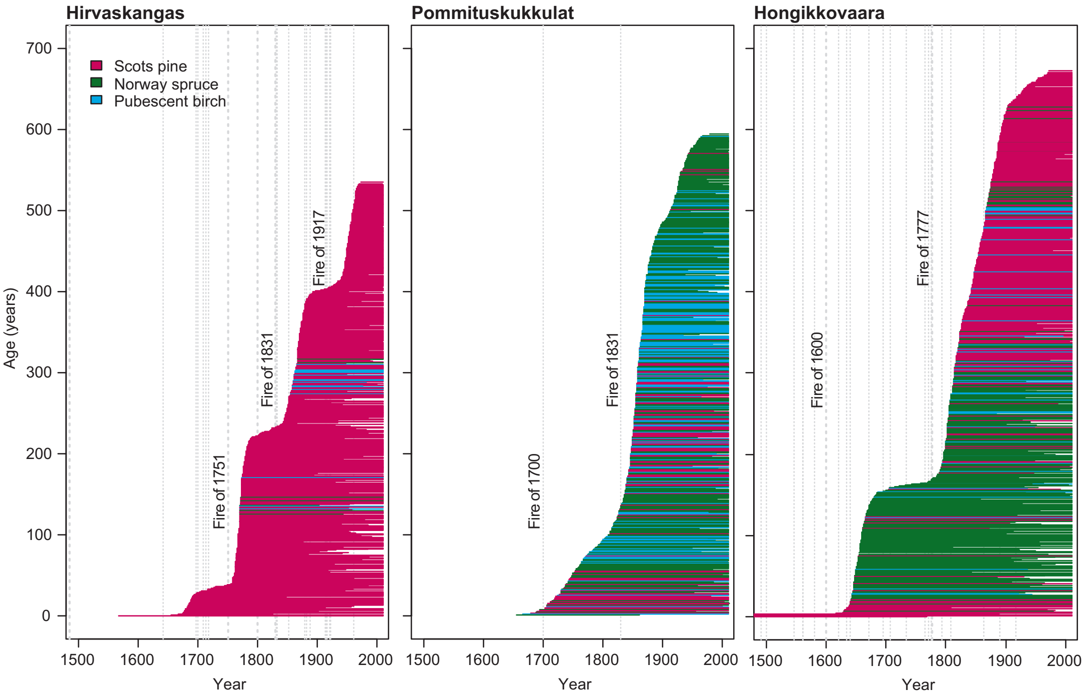

Fig. 6. Landscape age structure shown as tree life spans, and dated forest fires (vertical dotted lines). Fires that appear as major determinants for the age structure are shown as years.

fire-influenced Hirvaskangas and Hongikkovaara were characterized by strong age cohorts. Looking at the years in which fires were common, years 1751 and 1831 in Hirvaskangas are followed by prolific recruitment of pine trees. The fairly widespread fire of 1917 is followed by several smaller fires in subsequent years, followed by regeneration with some delay. In Hongikkovaara there are two strong cohorts. The first follows a period that was characterized by multiple fires (late 16th and early 17th centuries), and the second follows the fairly widespread fire of 1777. A characteristic feature of these two age cohorts is that they consist primarily of Norway spruce. After the 1777 fire tree recruitment has been more or less continuous.

In the Norway spruce-dominated Pommituskukkulat area the age structure is more or less continuous. The fire of 1831 that influenced the northern part of the area is followed by an increase in recruiting trees, but the cohort-like age structures are lacking.

Discussion

Fire occurrence, the fire cycle, and spatial patterns

Fires were common throughout the period recorded in the Scots pine dominated Hirvaskangas and Hongikkovaara study areas. The fire cycles, computed over the analysis period from 1700–1999 were 72 and 156 years. In the Norway spruce dominated Pommituskukkulat study area fires were rare and the fire cycle was much longer (579 years). The computed fire cycles for the pine-dominated areas are somewhat shorter compared to other northern Fennoscandian fire cycles, over longer time frames. For instance, some 100–150 km north from our study area, Wallenius *et al.* (2010) reported a fire cycle of 350 years for the last 1000 year period in Scots pine-dominated landscapes. However, they found a somewhat shorter fire cycle for the 17th and 18th centuries, which was more in line with our results. The finding that the spruce-dominated mesic sites (with a higher soil field capacity) had longer fire cycles is well in line with earlier studies (e.g., Zackrisson 1977, Haapanen and Siitonen 1978, Wallenius *et al.* 2002).

Most of the fires detected were small and only influenced a small proportion of the study area. However, large fires also occurred. A large proportion of the study landscape burnt in Hirvaskangas in years 1751, 1831, and 1917, and in Hongikkovaara in 1777 and possibly also in 1600. To some extent, the timing of major fires in our data coincides with those reported earlier from northern Fennoscandia. In particular, the last larger fire in our data was the fire that influenced almost all the Hirvaskangas landscape and part of the Pommituskukkulat area in 1831, coincides with the fire years of Zackrisson (1977) who reported that in northern Sweden fires were prominent especially in the 1830s. These type of "large fire years", in which fires occur over larger geographic regions are associated with climatically anomalous conditions (Drobyshev *et al.* 2014), particularly dry years (Aakala *et al.* 2018).

In addition to the fires occurring at different years between the Hongikkovaara and the other study areas, also the cessation of fires that has been demonstrated throughout Fennoscandia (Wallenius 2011, Rolstad *et al.* 2017) occurred at different times: in Hongikkovaara the last fire was recorded in 1917, but all the fires that occurred after the larger fire in 1777 scarred only individual sites and were hence limited in size. On the contrary in the Hirvaskangas area pines still recorded several fires still in the 20th century, and the lengthening of the fire cycle started later.

In addition to the area burnt and variation between the landscapes, spatial patterns also varied greatly within the landscapes; fires are known to be patchy and to burn unevenly (Wallenius *et al.* 2002). In the Hirvaskangas study area, the most widespread fire occurred in 1831, and this fire was also detected in the northern part of the Pommituskukkulat area, located approx. 1.5 km away. Otherwise in the Pommituskukkulat area only the northern part showed signs of fire. The Norway spruce dominated southern parts of the area showed no signs of fire and has been unburnt since at least the past 350 years (as inferred from the age of the oldest spruce trees). This difference between the northern and the southern parts of the landscape may be explained by the open mire in the middle of that area (Fig. 2), that has acted as a fire break, thus demonstrating the role that landscape structure may play in determining fire history at the landscape-scale (Niklasson and Granström 2000). In the Hongikkovaara study area it was noteworthy that the central part of the study area remained unburnt for over 200 years, after the widespread fire of 1777. The other larger fire (year 1600) in that study area was recorded in a time when only seven of the northernmost study plots were recording fires, and that particular fire was recorded in six out of the seven active sites. It seems well possible that this fire may have burnt throughout the entire study area, being intense enough to be lethal to the pines in the southern parts of the study area so that no recording trees were left alive to form scars.

Both the fire cycle differences between landscapes, and the spatial variation within landscapes were linked to soil hydraulic properties: the lower the field capacity of the soil, the more likely it was that the site experienced several fires. It is well known that xeric sites burn more frequently than mesic sites (Gauthier *et al.* 1993, Syrjänen *et al.* 1994) in general, and in northern Fennoscandia in particular the pine-dominated forests burn more frequently than spruce forests (Zackrisson 1977, Engelmark 1987, Wallenius 2002). However, as demonstrated in the North American boreal forests, when the fire regime is characterized by a higher frequency of stand-replacing fires the role of soil characteristics may be negligible (Bergeron 1991).

In addition to the soil hydraulic properties, the proximity to human ignition sources plays a role for forest fires (Syrjänen *et al.* 1994, Pitkänen and Huttunen 1999, Granström and Niklasson 2008). In the remote uninhabited areas, landscape features such as the presence of water bodies, and hunting trails have played a role (Josefsson *et al.* 2010). This has potentially been a contributing factor for the shorter fire cycle in the Hirvaskangas area, which is located next to a small lake that may have served as a campsite, and is the current location of the Värriö Subarctic Research Station. This is further suggested by the fact that the pine trees near the lake carry as many as six fire scars (P. Hari pers. comm.).

There are also remnants of old bear traps in the study area, as evidence of long-term human presence in the forests.

Ecological implications

An important finding in this study was that despite the stands growing in harsh climate and close to the tree line, tree population dynamics in the xeric sites were primarily controlled by the occurrence of fire prior to the 20th century. Fire-driven cohorts have been well described in the more southern locations (e.g., Wallenius *et al.* 2002), but the role has been less straightforward in the northern forests, growing close to the edge of their distribution range (Hofgaard 1993a, 1993b, Zackrisson *et al.* 1995).

In our data, two lines of evidence attest to the role of fires as an important determinant of forest dynamics. First, at landscape-scales there were clear cohort-like age structures in the Hirvaskangas and Hongikkovaara landscapes in which fires were frequent. These cohorts followed fires that were recorded widely over the landscape. Second, these cohorts were not synchronized between the landscapes (Hirvaskangas and Hongikkovaara were located approx. 50 km apart), as would be expected if the top-down influence of climate was the main determinant. Third, the cohorts vanish along with the cessation of forest fires, after which the age structure development resembles the fairly continuous recruitment characteristic of a gap dynamic forest, in which randomly occurring tree mortality and consequent regeneration at the scales of tree individuals are the dominant drivers (Kuuluvainen and Aakala 2011).

This third finding has important consequences. It signals a major shift in the dynamics of forests that are still under the natural dynamics, in which the pine-dominated landscapes switch from fire-driven cohort dynamics to a “gap dynamic” forest (Kuuluvainen and Aakala 2011). Hence, in addition to the influence of age (and consequently size) structure of the forests, the cessation of fires (similar to other changes in disturbances; Coomes and Allen 2007) can be expected to have a major influence on the species composition of the stands. In the Pommituskukkulat landscape dominated by mesic sites and in which the forests that have rarely burnt will become increasingly spruce-dominated in the course of the tree species succession (Sirén 1955). There is some evidence of sporadic windthrow in these study areas (N. Kulha unpubl. data), which would benefit the early successional species at the expense of *P. abies*, but their influence appears minor in comparison with the widespread influence of fires had in the past, in particular the large fires in 1777 (in Hongikkovaara) and 1751 and 1831 in the Hirvaskangas area.

Conclusions

Understanding the influence of fire is particularly important for high-latitude and high-elevation areas close to the timberline. This is because the influence of fires and cessation of fire occurrence may lead to differences in age structures and stand densification that could carelessly be attributed to other environmental drivers, especially climatic variability. Overall, the almost complete cessation of forest fire in much of the northern boreal forests of Europe has been one of the most dramatic changes influencing forest dynamics in the past several centuries. In our study areas, this shift from a cohort-dynamic to gap dynamic forests will lead to major changes in the age structures of the trees, as well as in the tree species composition on sites in which spruce and pine compete, to the benefit of spruce.

Acknowledgements: I thank Tapio Kara, Annukka Valkeapää, Paavo Ojanen, and Timo Kuuluvainen for their assistance in the field. This work was funded by the Academy of Finland (proj. no. 252629 and 276255), and the manuscript was finalized with a grant from the Kone foundation. Fire scar and site data are available at https://doi.org/10.6084/m9.figshare.5683711.

References

Aakala, T., Pasanen, L., Helama, S., Vakkari, V., Drobyshev, I., Seppä, H., Kuuluvainen, T., Stivrins, N., Wallenius, T., Vasander, H., & Holmström, L. 2018. Multiscale variation in drought controlled historical forest fire activity in the boreal forests of eastern Fennoscandia. *Ecological Monographs* 88: 74–91.

Aakala T., Shimatani K., Abe T., Kubota Y. & Kuuluvainen T. 2016. Crown asymmetry in high latitude forests: disentangling the directional effects of tree competition and solar radiation. *Oikos* 125: 1035–1043.

Aakala T., Hari P., Dengel S., Newberry S.L., Mizunuma T. & Grace J. 2014. A prominent stepwise advance of the tree line in north-east Finland. *Journal of Ecology* 102: 1582–1591.

Agee J.K. & Skinner C.N. 2005. Basic principles of forest fuel reduction treatments. *Forest Ecology and Management* 211: 83–96.

Ahti T., Hämet-Ahti L. & Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5: 169–211.

Bergeron, Y. 1991. The Influence of Island and Mainland Lakeshore Landscapes on Boreal Forest Fire Regimes. *Ecology* 72: 1980–1992.

Cajander A.K. 1949. Forest types and their significance. *Acta Forestalia Fennica* 56: 1–71.

Coomes D.A. & Allen R.B. 2007. Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology* 95: 27–40.

Drobyshev I., Granström A., Linderholm H.W., Hellberg E., Bergeron Y. & Niklasson M. 2014. Multi-century reconstruction of fire activity in Northern European boreal forest suggests differences in regional fire regimes and their sensitivity to climate. *Journal of Ecology* 102: 738–748.

Engelmark O. 1987. Fire history correlations to forest type and topography in northern Sweden. *Annales Botanici Fennici*: 317–324.

Fick S.E. & Hijmans R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315.

Frelich L.E. 2017. Wildland Fire: Understanding and Maintaining an Ecological Baseline. *Current Forestry Reports*: 1–14.

Gauthier S., Gagnon J. & Bergeron Y. 1993. Population age structure of *Pinus banksiana* at the southern edge of the Canadian boreal forest. *Journal of Vegetation Science* 4: 783–790.

Giraudoux P. 2012. *pgirmess: Data analysis in ecology*. R package version 1: 617. [Available at https://cran.r-project.org/web/packages/pgirmess/index.html].

Granström A. & Niklasson M. 2008. Potentials and limitations for human control over historic fire regimes in the boreal forest. *Philosophical Transactions of the Royal Society of London B* 363: 2351–2356.

Haapanen A. & Siitonen P. 1978. Kulojen esiintyminen Ulvinsalon luonnonpuistossa. *Silva Fennica* 12: 187–200.

Hofgaard A. 1993a. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science* 4: 601–608.

Hofgaard A. 1993b. 50 years of change in a Swedish boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* 4: 773–782.

Holmes R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring bulletin* 43: 69–78.

Johnson E.A. & Gutsell S.L. 1994. Fire frequency models, methods and interpretations. *Advances in Ecological Research* 25: 239–287.

Josefsson T., Gunnarson B., Liedgren L., Bergman I. & Östlund L. 2010. Historical human influence on forest composition and structure in boreal Fennoscandia. *Canadian Journal of Forest Research* 40: 872–884.

Junninen K., Kouki J. & Renvall P. 2008. Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. *Canadian Journal of Forest Research* 38: 202–215.

Kilgore B.M. & Taylor D. 1979. Fire history of a sequoia-mixed conifer forest. *Ecology* 60: 129–142.

Kuuluvainen T. & Aakala T. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica* 45: 823–841.

Kuuluvainen T., Aapala K., Ahlroth P., Kuusinen M., Lindholm T., Sallantaus T., Siitonen J. & Tukia H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. *Silva Fennica* 36: 409–422.

Lehtonen H. & Huttunen P. 1997. History of forest fires in eastern Finland from the fifteenth century AD-the possible effects of slash-and-burn cultivation. *The Holocene* 7: 223–228.

Niklasson M. & Granström A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81: 1484–1499.

Pitkänen A. & Huttunen P. 1999. A 1300-year forest-fire history at a site in eastern Finland based on charcoal and pollen records in laminated lake sediment. *The Holocene* 9: 311–320.

Pitkänen A., Lehtonen H. & Huttunen P. 1999. Comparison of sedimentary microscopic charcoal particle records in a small lake with dendrochronological data: evidence for the local origin of microscopic charcoal produced by forest fires of low intensity in eastern Finland. *The Holocene* 9: 559–567.

R Core Team 2016. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rolstad J., Blanck Y.l. & Storaunet K.O. 2017. Fire history in a western Fennoscandian boreal forest as influenced by human land use and climate. *Ecological Monographs* 87: 219–245.

Saxton K., Rawls W.J., Romberger J. & Papendick R. 1986. Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal* 50: 1031–1036.

Sirén G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. *Acta Forestalia Fennica* 62: 1–363.

Syrjänen K., Kalliola R., Puolasmaa A. & Mattsson J. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. *Annales Zoologici Fennici*: 19–34.

Viro P. 1952. Kivisyyden määrittämisestä. *Communicationes Instituti Forestalis Fenniae* 40: 8.

Viro P. 1962. Forest site evaluation in Lapland. *Communicationes Instituti Forestalis Fenniae* 55: 1–14.

Wallenius T. 2002. Forest age distribution and traces of past fires in a natural boreal landscape dominated by *Picea* *abies*. *Silva Fennica* 36: 201–211.

Wallenius T. 2011. Major decline in fires in coniferous forests-reconstructing the phenomenon and seeking for the cause. *Silva Fennica* 45: 139–155.

Wallenius T., Kuuluvainen T., Heikkila R. & Lindholm T. 2002. Spatial tree age structure and fire history in two old-growth forests in eastern Fennoscandia. *Silva Fennica* 36: 185–199.

Wallenius T., Kauhanen H., Herva H. & Pennanen J. 2010. Long fire cycle in northern boreal Pinus forests in Finnish Lapland. *Canadian Journal of Forest Research* 40: 2027–2035.

Zackrisson O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29: 22–32.

Zackrisson O., Nilsson M.-C., Steijlen I. & Hornberg G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. *Journal of Ecology* 83: 469–483.