Fire History and Tree Population Dynamics in Białowieża Forest, Poland and Belarus

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Cover: Tree ring sample from a *Pinus sylvestris* stump, collected in one of the study sites in Białowieża Forest, Belarus (F6). The tree germinated a few years before 1645 and recorded the 1718 fire as a strong negative growth reaction. Visible fire scars in: 1655, 1667, 1692.

Photo: Ewa Zin, 2010, edited by Tomasz Kamiński, 2015.

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Abstract

Fire history and fire regime parameters in relation to the long-term tree population dynamics were studied with dendroecological methods across coniferous habitats of Białowieża Forest (E Poland and W Belarus), a semi-natural European temperate woodland ecosystem. In four different studies various aspects of fire dynamics were explored by using nearly 1500 tree ring samples of *Pinus sylvestris* and *Picea abies*. By applying tree diameter at the first fire scar and post-fire growth response as proxies for fire intensity, the fire regime of Białowieża Forest was proven to have been dominated by low-intensity surface fires. However, occasional occurrence of high-intensity stand-replacing fires that were causing substantial successional changes at the stand scale was also recorded (I). Using a multiple-site fire history reconstruction combined with historical maps, eye-witness accounts and information on the abundance of light-demanding flora the omnipresence of fire throughout the coniferous sections of Białowieża and its role in shaping landscape-scale Scots pine dominance was revealed (II), as well as massive spruce encroachment following the fire cessation across those habitats (III). By reconstructing the extent of historical fires in a 9 km^2 part of the study area, exploring the spatial dimension of fire disturbance in Białowieża Forest was proven to be possible and documented the occurrence of large-scale fires exceeding 500 ha (IV). The conclusion from these studies is that fire was the main driver of tree population dynamics across the coniferous portions of the Białowieża landscape until relatively recently, i.e. 100–150 yrs ago, with substantial influence on the tree species composition, habitat openness and the following biological diversity, especially of the light-demanding taxa. In that respect, the common opinion that fire is less important in shaping forest dynamics of both, Białowieża Forest, and temperate Europe, was challenged.

Keywords: age structure, Central Europe, disturbance, *Pinus sylvestris*, *Picea abies*, tree ring, fire scar, temperate forest

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To the memory of my grandmother, Olga Sakowicz,
who was never given the opportunity to graduate from any school
but who taught me to finish things. And that no reason is needed for loving.

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Zin, E., Drobyshev, I., Bernacki, D., Niklasson, M. (2015). Dendrochronological reconstruction reveals a mixed-intensity fire regime in *Pinus sylvestris*-dominated stands of Białowieża Forest, Belarus and Poland. *Journal of Vegetation Science* 26(5), 934–945.

II Zin, E. & Niklasson, M. Fire and pine dominance in Białowieża Forest, Poland and Belarus (manuscript).

III Zin, E., Kuberski, Ł., Pilch, K., Sańczyk, P., Bernacki, D., Drobyshev, I., Niklasson, M. Spruce population dynamics in Białowieża Forest (Poland, Belarus) in relation to fire disturbance (manuscript).

IV Zin, E., Kuberski, Ł., Drobyshev, I., Niklasson, M. Spatial aspects of historical fires in Białowieża Forest, Poland and Belarus (manuscript).

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The contribution of Ewa Zin (EZ) to the papers included in this thesis was as follows:

I EZ contributed 25% in the development of the idea and hypotheses, did 50% of the planning, 100% of the sampling, 90% of the crossdating, 45% of the analysis, 50% of the writing and 90% of the correspondence with the journal.

II EZ contributed 50% in the development of the idea and hypotheses, did 75% of the planning, 100% of the sampling, 75% of the crossdating, 50% of the analysis, and 65% of the writing.

III EZ contributed 75% in the development of the idea and hypotheses, did 50% of the planning, 100% of the sampling, 90% of the crossdating, 65% of the analysis, and 65% of the writing.

IV EZ contributed 50% in the development of the idea and hypotheses, did 80% of the planning, 100% of the sampling, 100% of the crossdating, 40% of the analysis, and 75% of the writing.

Abbreviations

BF	Białowieża Forest
BNP	Białowieża National Park, Poland
BPNP	Belovezhskaya Pushcha National Park, Belarus
D	Dormant
DBH	Diameter at breast height
EE	Early earlywood
FC	Fire Cycle
LE	Late earlywood
LW	Latewood
ME	Middle earlywood
I_r	Post-fire growth index defined for the fire in year *r*
r	Fire year
TWR	Tree ring width
$TWR_{10post\text{-}r}$	Tree ring width 10 years following the fire year *r*
$TWR_{10pre\text{-}r}$	Tree ring width 10 years preceding the fire year *r*
WWI	World War I
WWII	World War II
yrs	Years

Nomenclature:

Mirek et al. (2002) for vascular plants; Ochyra et al. (2003) for bryophytes

1 Introduction

1.1 Fire ecology *versus* tree population dynamics

Fire is generally acknowledged as an Earth system phenomenon of fundamental importance, shaping life histories of organisms, ecosystem processes and patterns, climate and biogeochemical cycles (e.g. Bond et al. 2005; Bowman et al. 2009; Pausas & Keeley 2009). It has been proven to play a key role in global vegetation distribution and structure (Bond & Keeley 2005; Bond et al. 2005) and in the origins of several evolutionary plant adaptations (Keeley & Zedler 1998; Pausas & Keeley 2009; Keeley 2012).

In forest dynamics, fire may be one of the main drivers of successional pathways and tree species composition by changing the respective share of fire resistant and fire susceptible taxa (Sannikov & Goldammer 1996; Fulé et al. 1997; Pausas et al. 2004; Wardle et al. 2004). Certain fire regime parameters, e.g. fire frequency, intensity and severity, are of fundamental importance for the resulting ecosystem structure. They shape tree survival and mortality, thus determining the canopy closure and light-availability for both ground flora and tree regeneration (e.g. Brown & Wu 2005; Marozas et al. 2007). Fire disturbance may also change seedbed conditions (e.g. Schimmel & Granström 1996; Hille & den Ouden 2004), modify deadwood amount (e.g. Linder et al. 1998), alter fuel quantity and structure (e.g. Kolström & Kellomäki 1993; Schimmel & Granström 1997; McRae et al. 2006) and influence tree recruitment patterns by promoting either sporadic (e.g. Wirth et al. 1999; Blanck et al. 2013) or cohort regeneration (e.g. Wallenius et al. 2002; Flatley et al. 2013). Furthermore, fire creates specific microhabitats and substrates for many organisms, hence playing an essential role for biodiversity (Granström 2001).

As mentioned above fire effects on forest ecosystems are diverse and complex since they depend on characteristics of both the fire itself (by means of fire behavior) and the respective ecosystem being subjected to this disturbance (by means of fuel abundance and features, canopy structure etc.). Hence, fire is eventually one of the most intricate factors shaping forest dynamics (e.g. Agee 1993). Recently a comprehensive conceptual model was introduced by Kuuluvainen (2009) based on three main modes of forest dynamics: even-aged, cohort and gap, driven by disturbances of three severity categories: high (stand-replacing), intermediate (partial) and scale-limited (fine scale). Fire is part of the first two (e.g. Kuuluvainen & Aakala 2011), whereas the third mode is characteristic to nonpyrogenic forest ecosystems (e.g. Aakala et al. 2009). The main difference between this new approach to the earlier models of forest dynamics, either directional or cyclical, is that it incorporates additionally the driving disturbance regime type (Kuuluvainen 2016 and literature therein).

Among tree taxa, the genus *Pinus* has been especially proven to be inseparably linked to fire in its life history and evolutionary traits. Certain fire regimes (i.e. high-, moderate- and low-severity fire regime *sensu* Agee 1993) have turned out to be one of the three main factors (besides geology and climate) that shaped evolution and spatial range of the pines, resulting in different ecological adaptations, such as grass stage, serotiny, sprouting, thick bark or self-pruning (Agee 1998; Keeley & Zedler 1998; Keeley 2012). Because of wide distribution of this fire-linked tree genus (Keeley 2012) and the rapid changes in fire regimes occurring globally throughout the last decades (e.g. Pausas & Keeley 2009), understanding of its life history and distribution patterns in relation to different fire regimes is essential for future conservation and resource management (including land, forest, fire management etc.) (Keeley 2012).

Detailed quantitative information on fire occurrence and fire regime parameters (including frequency, seasonality, severity etc.) may be achieved by applying dendrochronological reconstructions based on fire scars and forest demography data that document ecosystem dynamics with annual resolution over centuries or millennia (e.g. Zackrisson 1977; Swetnam et al. 2009). As crucial data source for ecologists and ecosystem managers (Falk et al. 2011) they are nowadays widely applied throughout the boreal (e.g. Niklasson & Granström 2000; Falk et al. 2011; Wallenius et al. 2011; Storaunet et al. 2013; Drobyshev et al. 2016), Mediterranean (e.g. Stephens et al. 2003; Fulé et al. 2008; Touchan et al. 2012; Christopoulou et al. 2013; Fournier et al. 2013), tropical (e.g. Cassell & Alvarado 2012; Harley et al. 2013) and temperate (e.g. Niklasson et al. 2010; Flatley et al. 2013; Grissino-Mayer 2016) regions across the globe.

Since fire regimes worldwide are currently experiencing remarkable alterations, but of diverse causes and directions, a regional approach when studying those disturbances has been suggested (Pausas & Keeley 2009; Whitlock & Tinner 2010) as an essential part of the holistic view on fire ecology and fire science (Bowman et al. 2009).

1.2 Dendrochronological fire evidence

A widely applied method of studying past fire occurrence in forest ecosystems are dendrochronological reconstructions. Fire scars are broadly acknowledged as reliable proxies for past fire events that yield quantitative information on low-severity fire regimes (e.g. Falk et al. 2011; *cf.* Lentile et al. 2005) at an annual resolution. However, when combined with additional tree ring analyzes, including age structures and post-fire growth responses, they also allow for reconstruction of high-intensity fires, typical for high-severity and/or mixed-severity fire regimes (Bergeron & Brisson 1990).

The foundation of these studies is the fire scar, which is formed when vascular cambium cells (i.e. the layer of actively dividing cells between wood and bark tissues responsible for the annual increase in tree diameter) are heated above their lethal temperature of approximately 55 °C (Hare 1965; Gill 1995). Usually the first scarring occurs on the leeward side of the tree bole due to longer flame residence time (Gutsell & Johnson 1996). If the cambium cells die on the part of the stem's circumference only, the remaining cells will continue their normal activity ensuring tree ring formation, resulting in survival of the tree. After some years the bark covering the area with killed cambium cells falls off, exposing a smooth wood surface. The wood growth from the scar sides may result in a complete over-healing of the wound, especially when no further fire occurs. However, a new fire will easily scar the already existing, not yet over-healed fire damage from previous event/-s due to high resin content in the exposed scar area and the relatively thin bark at the wood sections that overgrow the wound (McBride 1983). Repeated scarring results in formation of a characteristic, often triangular, open multiple fire scar area at the tree base, called 'catface' (e.g. Arno & Sneck 1977; Falk et al. 2011; Fig. 1). In Polish, two separate terms are used: 'blizna pożarowa' for fire scar and 'wyżar' (Karpiński 1948) for 'catface'. In Swedish, both fire scar and 'catface' are termed 'brandljud'. However, in old Swedish literature 'catface' is also called 'brandlyra' (M. Niklasson, pers. comm.).

Fire scars may be distinguished from wounds caused by other factors not only by the charcoal presence in the scar area (from the second fire on, i.e. only in multiple fire scars), but also by its specific shape and the characteristic heatinduced disturbances in tree ring morphology, visible under magnification (McBride 1983). Based on the scar position within the tree ring, reflecting cambial development at the time of damage, fire season may be reconstructed (Baisan & Swetnam 1990).

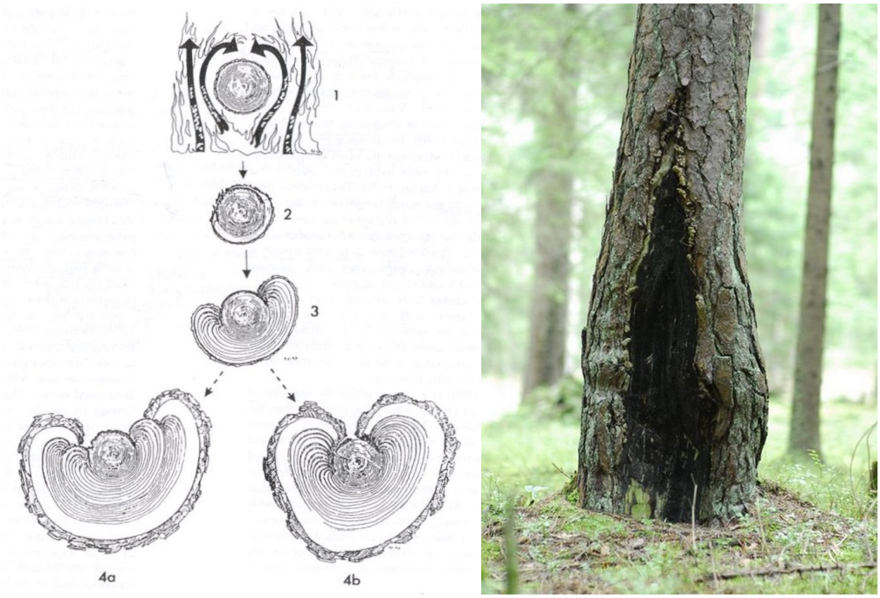

Figure 1. Left: Fire scar formation. Illustration by Tove Vollbrecht (reproduced from Niklasson 1998, p. 10). Right: Scots pine tree with an open, multiple fire scar ('catface') in one of the study sites in Białowieża Forest, Belarus. Photo: Dariusz Graszka-Petrykowski.

1.3 Fire in temperate Central Europe

When compared to the boreal and Mediterranean parts of Europe, the role of fire in shaping forest ecosystems of its temperate core has been little recognized (*cf.* Walter 1968; Ellenberg 1996; Bradshaw et al. 1997). One of the reasons behind this may be the fact that temperate regions are often associated with a diverse dendroflora of deciduous trees with less flammable fuels and a more humid climate (Ellenberg 1996), thus making the role of fire in driving forest dynamics of this biome less obvious. Still, many conifers, including several *Pinus* species, occur in temperate forests as an important component (Ellenberg 1996; Grissino-Mayer 2016) and an increasing number of studies is proving the significance of fire disturbance for tree population dynamics also in that climatic region (Abrams et al. 1999; Novák et al. 2012; Grissino-Mayer 2016 and literature therein).

In temperate Europe, studies of fire ecology and history are challenged by dense demographics and a long history of human economic activity, especially stationary agriculture and commercial forest management. In turn, these two factors became responsible for wide-scale fire suppression, which started earliest in the central part of this continent (Pyne 1997). Modern forest management, focusing on timber exploitation, effectively excludes fire as one of the main threats to the wood production (Granström & Niklasson 2008; Wallenius 2011). It is one of the reasons why Central Europe is now a 'no fire' region, where forest fires – though numerous – are efficiently controlled and, hence, usually very small (Szczygieł et al. 2009; Schmuck et al. 2011). In Poland, for example, the country with one of the highest annual number of fires in the region (9–10 000 individual fires per year), in that variable comparable even with the Mediterranean area, the mean forest fire size is only 0.5–0.95 ha. The annual burnt area in 1990–2013 equaled approximately 8 000 ha. The current fire cycle for the forested area of Poland is approximately 3 000 yrs reflecting the rather insignificant overall impact fires have from a spatial point of view (Szczygieł et al. 2009; Zajączkowski et al. 2014; Zin et al. 2014).

The general absence of fire across contemporary temperate Europe (*cf.* Pyne 1997) has likely influenced the basic ideas on forest ecology and tree population dynamics applied in this region. One of the dominant concepts is 'potential natural vegetation' (Tüxen 1956), assuming soil and climate as the main determinants of plant community composition (Matuszkiewicz 1984; Ellenberg 1996). This static approach is widely applied by phytosociology – the plant community science named with term coined by the Polish scientist Józef Paczoski in 1896 (Maycock 1967).

Another limiting factor for Central European fire history reconstructions, tightly connected to long-term land use, is a general lack of intact forest areas that could offer long tree ring sequences from old-growth trees and old dead wood (Hannah et al. 1995). Although palaeoecological records revealed fire as an important component of the forest dynamics in this region throughout the Holocene (e.g. Ralska-Jasiewiczowa & Van Geel 1992; Rösch 2000; Novák et al. 2012; Adámek et al. 2015; Latałowa et al. 2015), they still offer limited information on key fire regime parameters and their impact on forest ecosystems (Higuera et al. 2005; Ali et al. 2012) when compared to dendrochronological studies (Niklasson et al. 2010).

Given the high share of fire susceptible conifer woodlands, the observed increase in fire activity throughout temperate Europe, projected climate change and its possible influence on forest fire risk in the near future (Badeck et al.

2003; Schelhaas et al. 2003, 2010; Szczygieł et al. 2009; San-Miguel-Ayanz et al. 2011), expanding the knowledge on the role of fire in driving forest dynamics of the European temperate region seems valuable.

1.4 Białowieża Forest as a reference and/or model ecosystem

Białowieża Forest is widely acknowledged as one of the last remnants of natural old-growth woodlands in lowland Europe and as such it is often used as a reference and/or model ecosystem in forest ecology and dynamics (Faliński 1986; Koop 1989; Peterken 1996; Vera 2000; Angelstam & Kuuluvainen 2004). Białowieża Forest is also presented in several major textbooks of environmental history (Schama 1996; Rotherham 2013; Kirby & Watkins 2015) and Schama (1996) used exactly Białowieża woodland as a conceptual framework to extensively present and discuss both Polish (and Lithuanian) national history and perception of nature.

The survival and relatively well preserved status of Białowieża Forest result from the fact that it has been protected as a monarchial hunting ground by first Lithuanian dukes and Polish kings and later Russian tsars from as early as the 14th century until the beginning of the 20th century. The early beginning of its conservation safeguarded it from being transformed into arable land (Jędrzejewska & Jędrzejewski 1998; Samojlik 2005) like thousands of hectares of similar old-growth woodlands across the region (Schama 1996; Maruszczak 1999).

It is European bison – *Bison bonasus* (L.), the currently largest terrestrial mammal of the continent, that was the most important among the targeted royal game and that early became the flagship species of Białowieża (Schama 1996; Pucek 2004; Krasińska & Krasiński 2007). Historically it ranged across Western, Central and Southeastern Europe, spreading from eastern Iberian Peninsula to Caucasus Mountains (including also southernmost Scandinavia) but at the beginning of the 20th century Białowieża Forest was already the last bison refuge. Nevertheless, in 1919 it went extinct also in that area. Soon thereafter an intense restitution work began which in 1950s resulted in a successful reestablishment of a free ranging population (Pucek 2004; Krasińska & Krasiński 2007). At present, there are approximately 1 000 free living bison in Białowieża Forest (European Bison Pedigree Book 2015). Together with the rich fauna of large herbivores and carnivores (including wolf – *Canis lupus* L. and Eurasian lynx – *Lynx lynx* L.), not forgetting the old-growth forest characteristics itself, it makes Białowieża Forest to one of the most important wilderness areas in Europe (*cf.* Selva 2016).

When Białowieża Forest was protected as a royal property, the use of its resources was strictly regulated and limited to traditional land use forms like: scything of forest meadows, beekeeping, fishing, cattle pasturing and potash, tar and charcoal burning (Hedemann 1939; Samojlik 2005). More intense forest management, including timber exploitation, was introduced after 1795, when Poland disappeared from the map of Europe and Białowieża Forest was incorporated into Russian territory. However, already in 1803 the exceptional status of this forest was acknowledged and safeguarded by a special tsar's decree (Samojlik 2005). A few decades later, after the first tsar's hunt in 1860, when Białowieża Forest was declared an imperial hunting area, utilization of timber became strongly limited. Nevertheless, a very intensive game management was introduced instead, including massive supplementary feeding of target species and extermination of predators (Karcov 1903; Jędrzejewska et al. 1997).

The beginning of the industrial timber exploitation occurred in Białowieża Forest relatively late, during WWI. In 1915 massive fellings throughout the forest and timber processing industry in Hajnówka located at its border were initiated by German administration. The following timber exploitation by an English company "The Century European Timber Corporation" in 1920s, contracted by the Polish State Forest Administration, brought first clear-cut areas into Białowieża woods. In turn, during the first decades of the 20th century as much as nearly 8 mln m^3 timber was extracted. After WWII the area of Białowieża Forest was divided for the first time by the state border between two different countries – Poland and Soviet Union (at present Belarus). Since then both sections include areas of various management and conservation regimes, managed either by national park or state forest administration units (Więcko 1984; Jaroszewicz 2004; Krzyściak-Kosińska et al. 2012). Detailed description of land use history and the present forest management and nature conservation activities throughout the entire area of Białowieża Forest can be found in e.g. Hedemann (1939), Faliński (1986), Sokołowski (2004), Samojlik (2005), Krasińska & Krasiński (2007) and Okołów et al. (2009).

Although Białowieża Forest has been partly influenced by modern forest management, it still includes numerous stands and landscape sections that have never been clearfelled and replanted by man (also outside of strictly protected areas). Old-growth forest structures, like ancient, large size trees and deadwood continuity, make Białowieża Forest a valuable site for dendroecological studies, most likely unique for the whole region. A further feature, which determines the special status of this area, is its great biodiversity. Many species, which are common here, are threatened or already extinct in other

European locations (Jaroszewicz 2004; Sokołowski 2004; Gutowski & Jaroszewicz 2001, 2004; *cf.* e.g. ArtDatabanken 2015).

1.5 Fire in Białowieża Forest

Fires in Białowieża Forest occur today rather incidentally, alike in most of the region are effectively suppressed and thus affect very small areas, typically <0.5 ha (E. Zin and M. Niklasson, unpubl. data). Nevertheless, fire-scarred trees, stumps and snags, especially in the conifer dominated sections, are spread throughout the area (Karpiński 1948; Faliński 1986); indicating substantial fire presence in the past. Karpiński (1948) interpreted the occurrence of these structures as resulting from beekeepers' activity only; he explained that beekeepers were setting bonfires at the bases of Scots pine stems to cause injuries that would serve as a source of resinuous wood, which they could then chip and utilize as a sort of kindling or smoke fuel during their common practices while extracting honey (Karpiński 1948).

In the ongoing discussion of the long-term dynamics of this forest ecosystem (showing a.o. remarkable changes in the tree species composition across the recent decades) fire disturbance is only briefly included (Faliński 1986; Bernadzki et al. 1998; Sokołowski 2004; Kuijper et al. 2010; Brzeziecki et al. 2016). Quantitative information on historical fire occurrence in the area is also hardly present in written sources, besides the well documented 1811 fire, repeatedly described as a disastrous large-scale disturbance, lasting for several months (e.g. Ronke 1830; Genko 1902-1903; Faliński 1986). The only three other fire dates, mentioned in the less available historical sources, mainly Polish and Russian, are 1639, 1819 and 1834, with the last one characterized as a large event as well (Brincken 1826; Bobrovskii 1863; Genko 1902-1903).

However, some notions on fire occurrence in Białowieża Forest and its potential role in shaping forest dynamics of this area may be found in early descriptions, especially in relation to its conifer dominated sections. Brincken (1826) described the relation between fire disturbance and Scots pine stand structures and Paczoski (1930) discussed the possible significance of fire for the composition and dynamics of mixed coniferous stands. Similar statements about the potential fire influence on pine and spruce interrelations were also given by modern authors (Faliński 1986; Jędrzejewska & Jędrzejewski 1998), however with no broader discussion following. Recent studies in the environmental history of this area (Samojlik & Jędrzejewska 2004; Samojlik 2006) assume that some historical utilization forms, like for example beekeeping, grazing and charcoal and tar production, which existed in Białowieża Forest throughout the last centuries, were tightly related to anthropogenic fire disturbance eventually modifying the past and present forest structure.

Nevertheless, the amount of empirical data documenting and, in particular, quantifying historical fire occurrence in Białowieża Forest is strongly limited. Palaeoecological studies recorded sedimentary micro- and macrocharcoal, suggesting fire being present in that ecosystem throughout millennia (Dąbrowski 1959; Mitchell & Cole 1998; Zimny 2014; Latałowa et al. 2015). The first glimpse of the tree ring fire history of the area (Niklasson et al. 2010) indicated that fires were much more frequent than mirrored by written accounts (Genko 1902-1903; Faliński 1986) and suggested that they may have played a crucial role in shaping conifer forest dynamics at stand-scale. However, detailed information on the relation between key fire regime parameters and long-term tree population dynamics across different habitats in Białowieża Forest, including its spatial aspects, is still lacking.

2 Objectives of the thesis

The general objective of this thesis was to investigate the relation between fire disturbance and long-term tree population dynamics across coniferous habitats of Białowieża Forest, an example of one of the best preserved European temperate woodland ecosystems.

Specific objectives were:

(1) to describe the historical fire regime of Białowieża Forest over the last few hundred years, with particular focus on past fire intensities;

(2) to study long-term structural dynamics of Scots pine-dominated landscapes of Białowieża Forest in relation to fire disturbance;

(3) to explore the role of fire and fire regime changes in shaping the population dynamics of Norway spruce in Białowieża Forest;

(4) if possible, to shed some light on the spatial dimension of past fires in Białowieża Forest and to explore the potential for future studies within this field.

The focus on Białowieża Forest as a study area for the entire thesis was motivated by the fact that old-growth woodlands of comparable structure, conservation status and spatial extent are actually lacking across the region. However, the fundamental importance of the Białowieża Forest ecosystem in a European perspective allows for a wider discussion of the obtained results; the more that the geology and soil types of Białowieża do not differ from the neighbouring areas to the west and east, including large sections of Polish and German lowlands, which were transferred into arable land way ahead (*cf.* section 1.4). The results of this research will be discussed in broader context generally by referring to the existing data on long-term forest dynamics throughout Central Europe, with spotlight on the palaeoecological records of vegetation and/or fire history. Based on comparison of the results derived by this research with the results of palaeoecological studies from first Białowieża Forest and then other locations in the region more general conclusions on the role of fire in shaping temperate European forests may be drawn. Furthermore, by considering the North American data (both century- and millennia-long), a wider discussion of the long-term fire disturbance dynamics across temperate biome may be established.

3 Material and methods

3.1 Study area

Białowieża Forest (BF), recognized as one of the best preserved temperate forests in European lowland, is a continuous woodland area that spreads over approximately 1500 km^2 in the borderland between eastern Poland and western Belarus (52°30'–53° N, 23°30'–24°15' E). It is a continuous mixed forest characterized by a mosaic of different forest types aligned according to land relief, water availability and soil fertility gradients. The main forest communities are the following: rich deciduous forest (*Quercus robur* L. – pedunculate oak, *Tilia cordata* Mill. – small-leaved lime, *Acer platanoides* L. – Norway maple, *Carpinus betulus* L. – hornbeam); mixed deciduous and mixed coniferous forest (*Q. robur*, *Picea abies* (L.) H. Karst. – Norway spruce, *Pinus sylvestris* L. – Scots pine, *Betula pendula* Roth. – silver birch); coniferous forest (*P. sylvestris*, *P. abies*); and bog alderwood and streamside alder-ash forest (*Alnus glutinosa* (L.) Gaertn. – black alder, *Fraxinus excelsior* L. – ash, *Betula pubescens* Ehrh. – downy birch) (Faliński 1986; Jędrzejewska & Jędrzejewski 1998). Open habitats are sparse and account for approximately 8.6% (Kozulko 2003; Sokołowski 2004). The current stand composition of BF is a result of both the above mentioned environmental factors and the management history. Approximately 44% of the total forest area is covered by old-growth stands of natural origin (i.e. not planted by people) (Jędrzejewska & Jędrzejewski 1998). As a whole BF consists nowadays of strictly protected (approximately 53%) and managed (approximately 47%) forest stands with various nature conservation, forest management and land use regimes, some of which include commercial timber production (Sokołowski 2004; Krzyściak-Kosińska et al. 2012). The Polish section, covering approximately 635 km^2, consists of the Białowieża National Park (105 km^2) and the adjacent managed forest (500 km^2), including several scattered forest reserves (totaling 120 km^2).

The whole Belarusian part of BF (approximately 875 km^2) is Belovezhskaya Pushcha National Park, established in 1991 (Sokołowski 2004). The climate of BF is transitional between continental and Atlantic types, with a mean annual precipitation of 633 mm and a mean annual temperature of 6.8 °C, with January as the coldest (mean temperature of –4.2 °C) and July as the warmest (mean temperature of 17.7 °C) month (Pierzgalski et al. 2002). Land relief in BF is rather uniform. It is an old-morainic plateau with altitude range of 135–190 m a.s.l., built from glaciofluvial sands, clays and gravels. Some diversity in the local topography is assured by river valleys, melt-out hollows with accumulated peat cover and an elevated zone of glaciofluvial-kame origin that stretches throughout the middle part of the forest and ends at the study area's highest point – Kozia Góra (in Belarus), 202 m a.s.l. (Kwiatkowski 1994). The main soil types of BF include eutrophic and mesotrophic brown and lessive soils, oligotrophic rusty and podzol soils, and a range of gley and organic soil types, including peatbog and semi-bog soils (Kwiatkowski 1994).

3.2 Study sites

For this research six study sites were selected (further referred to as 'F1–F6') in conifer-dominated areas of both the Polish and Belarusian sections of BF (Fig. 2). The following criteria were used for the site selection: (1) presence of fire-scarred *P. sylvestris* trees and stumps; (2) stand structure reflecting relatively low human impact, evidenced by naturally regenerated uneven-aged Scots pine population, numerous old-growth individuals and deadwood continuity providing for long tree ring sequences (*cf.* Paper I). They were 8.5–16 ha multi-aged mixed coniferous (*P. sylvestris*-*P. abies*) stands with relatively low tree density (500–800 stems·ha^{-1}), dominated by over 200-year-old Scots pine populations mixed with younger generations of both pine (140–180 yrs old) and spruce (60–160 yrs old). In the canopy there was also admixture of silver birch (approximately 20 trees·ha^{-1}) and scattered oak individuals of smaller diameter (approximately 5 trees·ha^{-1}). Understorey was not particularly dense and clearly dominated by spruce regeneration. In none of the study sites was pine regeneration observed (i.e. no living trees below a DBH – diameter at 1.3 m above the ground – of 24.1 cm were found, Paper II). Ground vegetation of the study sites was composed of *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Trientalis europaea* L., *Dryopteris carthusiana* (Vill.) H.P. Fuchs and *Calamagrostis arundinacea* (L.) Roth, and the bottom layer by mosses: *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., *Hylocomium splendens* (Hedw.) Schimp. and *Dicranum undulatum* Schrad. ex Brid. The surrounding stands were mostly coniferous forests of parallel type or humid coniferous forests (with some share of *Sphagnum* spp. in the ground layer) and mixed forests (with higher share of deciduous tree species like oak, birch and hornbeam).

For the spatial analyses a 9.2 km^2 sub-study area was selected, representing a coherent section of coniferous habitat (similar to the one of the F1–F6 sites, described above) without potential fire breaks (streams, bogs, swampy areas etc.). A grid of 9 points aiming at a resolution of ca. 1 km^2 (100 ha) was designed. Two of the 9 points were the earlier studied stand-scale fire history sites, of 8 and 16 ha, with densely sampled wood (F4 and F6, Paper II). By including these two fire history sites studied in detail, it was reasoned that it would shed light on spatial aspects of fires at three magnitudes of scale: 10^1, 10^2 and 10^3 ha. Two additional satellite fire history sites – F1 and F3 (Paper II) – were located outside the study area, at the distance of 4 and 7 km, and could, at least in theory, give some indication on the potential spread of very large fires, on a scale of ca. 10^4 ha (Fig. 1). In the sub-study area further seven sites (yet totaling 16 sampling points altogether) were selected for fire history reconstruction.

3.3 Fieldwork

For long-term regeneration dynamics and fire history reconstruction *P. sylvestris* and *P. abies* tree ring material from six study sites located in Polish and Belarusian sections of BF (sites F1–F6, see Fig. 2) was sampled, following the sampling effort used by Niklasson et al. (2010). In each of these sites full or partial cross-sections from all Scots pine stumps, logs and snags with fire scars and increment cores from a sample of living trees over the area of 8.5–16 ha each were collected. Size of the sites was dependent on stand structure and tree ring material availability, final area was delimited from all the inventoried stumps and trees (even the ones finally unsampled due to high decomposition degree), as well as from GPS tracks within the given stand (reflecting the total inventoried area). The majority (approximately 95%) of the cross-sections was collected from stumps of anthropogenic origin. For most of them (approximately 80–90%) it was impossible to determine whether a living or dead tree had been cut due to the erosion of the sapwood part. Cross-sections were collected with chainsaw according to well-known fire history sampling procedures (Arno & Sneck 1977; McBride 1983). Living Scots pines were sampled subjectively with the aim to include the potentially youngest individuals assumed to be represented by trees with the lowest DBH and also the oldest generation with possibly the longest fire record, represented by old-growth trees with visible fire scars. All cores were collected with an Ø 12 mm-increment borer as close to the mineral soil level as possible (20–130 cm) with the aim of acquiring a field-estimated maximum of 10 years from the pith. In case of larger distance from the pith or presence of rot, more than one core per tree was extracted.

In the study sites additionally all standing trees, both living and dead, with diameter at breast height (i.e. at 1.3 m above the ground) of ≥5 cm on circular 200 m^2 sample plots (r=7.98 m) were cored. A few (usually 3–10 trees) potentially oldest pine and spruce individuals from outside the plots were also sampled. Increment cores were extracted with a Ø 12 mm-increment borer as close to the mineral soil level as possible (20–130 cm). In some cases (internal rot, too large distance from the pith etc.) more than one core per tree was extracted. In five of the study sites (F1, F3–F5) two sample plots where established, in the F2 site, because of the sampling permission limitation, one sample plot was used.

For spatial analyses Scots pine trees and stumps were sampled at nine major locations placed in a approximately 1 x 1 km grid over the selected sub-study area of ca. 9.2 km^2.

All together, during 2010–2015, 1137 wood samples (705 cross sections and 432 increment cores) from 798 Scots pine trees and stumps and 219 increment cores from 157 spruce trees were collected, totalling 1356 tree ring samples and 955 trees.

In addition the current stand density and diameter structure of all the fire history study sites (F1–F7, Fig. 2) was inventoried. This was done on circular sample plots of two sizes: 200 m^2 and 500 m^2 (r=7.98 m and r=12.62 m). From two to five sample plots of different size per study site were established (yielding on average the total sample area of 0.16 ha per study site, with range: 0.04–0.2 ha/site), located subjectively within the stand. While establishing the plots it was aimed at recording the stand structure least disturbed by forest management, i.e. with the lowest number of stumps or other tracks of human activity (e.g. timber extraction trails etc.). Different number of plots per site and two various plot sizes were motivated by respective stand structure of each site and – in one case – the granted sampling permission. Within each sample plot the species and DBH of all living and dead standing trees with DBH of ≥5 cm were inventoried. In order to get the more precise estimate of the past tree densities, in two of the study sites (F2 and F7), representing the best preserved old-growth structures due to the lowest human impact (one is a nature reserve and the other a permanent research plot), stumps and logs with diameter of ≥10 cm located inside the sample plots were also recorded.

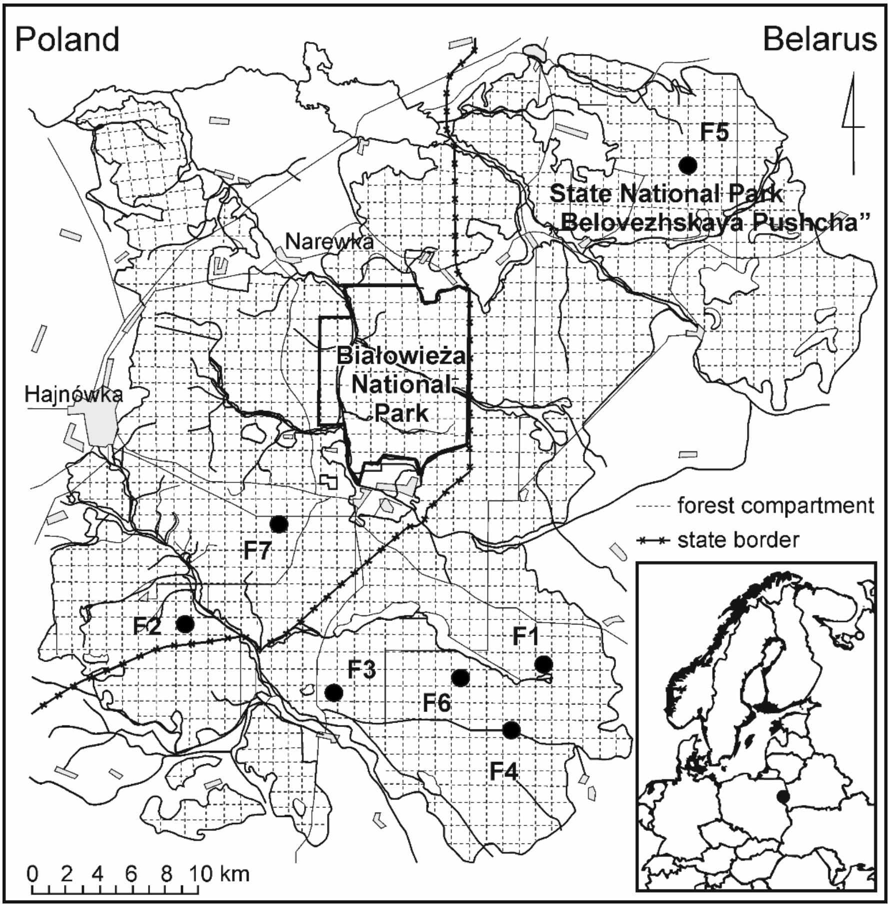

Figure 2. Location of the fire history reconstruction sites in Białowieża Forest. F1–F6: six 8.5–16 ha study sites located in the Polish and Belarusian sections of BF (this thesis), F7: a 13-ha study site in the Polish section (Niklasson et al. 2010). Map re-drawn after figures of Niklasson et al. (2010) and Zin et al. (2015, Paper I), modified.

Figure 3. Sampling of fire-scarred Scots pine stumps in one of the study sites in Białowieża Forest, Belarus. Left: collecting a cross-section with chainsaw. Right: Sample with at least two fire scars visible. Photo: Ewa Zin.

Figure 4. Sampling of *P. sylvestris* tree ring material in one of the study sites in Białowieża Forest, Belarus. Left: Final stage of the cross-section sampling. Middle: extracting an increment core at the tree base. Right: an increment core with pith visible. Photo: Izabela Sondej.

3.4 Dendrochronological procedures and analyses

All cross-sections and increment cores were gradually surfaced with a belt sander (down to grit 600) until wood cell structure within tree rings and fire scars was visible under a dissecting microscope with 6–40 × magnification. Calendar years were assigned to tree rings by visual crossdating according to standard dendrochronological techniques (Stokes & Smiley 1986; Yamaguchi 1991). This allowed identification of exact years of fire occurrence. A fire in a given year was recorded based on at least one fully developed fire scar among all sample trees in a particular site. In sample trees where there was no fire scar formed but the given date was recorded as fire event by at least one of the other individuals from the same site, also sudden short-term growth depressions, often accompanied by fire-induced disturbances in ring morphology (Niklasson

& Granström 2000), were used as positive fire indicators. Fire seasonality was determined according to scar position within the annual ring, with the following season categories: early earlywood (EE), middle earlywood (ME), late earlywood (LE), latewood (LW), and dormant (D) (Baisan & Swetnam 1990). In increment cores where the pith was slightly missed, a pith locator was used (Applequist 1958) to estimate the pith date. While recording tree germination dates the pith dates at sampling height were corrected by the early height increment estimate (Niklasson et al. 2010).

Based on the reconstructed fire dates, fire intervals at stand and point (single tree) scales were calculated. In the first case all fire years in a stand, even those represented by a single fire scar, were considered, thus not reflecting fire location or size. In the second case fire intervals between scars recorded by one tree were calculated, reflecting the potential minimum interval for fuel build-up.

Figure 5. P. sylvestris tree ring samples with fire scars. Left: Tree ring sample from a pine stump, collected in one of the study sites (F6). The tree germinated a few years before 1645 and recorded the 1718 fire as a strong negative growth reaction at the age of 73 yrs and the diameter of 24.3 cm. Visible fire scars in: 1655, 1667, 1692. Photo: Ewa Zin. Right: Fire scar with visible fire season – damage occurred in the middle of the earlywood portion of the tree ring (ME, middle earlywood), i.e. around mid-late July. Photo: Dariusz Graszka-Petrykowski.

3.5 Specific methods applied in different sub-studies

3.5.1 Paper I

In this study the historical fire regime of a *P. sylvestris*-dominated stand in the Belarusian part of Białowieża Forest (BF) was described, focusing specifically on the range of historical fire intensities. Tree diameter at the first fire scar and post-fire growth response were used as proxies for fire intensity. To evaluate the degree of generality in the results obtained within a single site and to address the question of climate influence on the historical fire regime in BF, the results from a previous study conducted in a structurally similar stand in the Polish section of BF (Niklasson et al. 2010) were employed.

3.5.2 Paper II

This study aimed to reconstruct fire history and long-term structural dynamics of conifer landscapes of Białowieża Forest, Poland and Belarus, spanning the last few centuries. Since the focal point of the analysis was the relation between fire disturbance and *Pinus* population dynamics, it focused on the situation before the period of thorough cultural and economic changes around the turn of the last century that resulted in effective fire suppression in the region (Więcko 1984; Pyne 1997). To test whether the stand-scale tree ring fire history data from two earlier studied locations in Białowieża Forest (Niklasson et al. 2010; Zin et al. 2015) represent a general pattern throughout the entire study area, corresponding reconstructions in further sites were conducted, expecting them to reveal analogous fire regime parameters (hypothesis 1). Furthermore, assuming that frequent fire disturbance in Białowieża Forest, which allowed for Scots pine establishment and dominance under certain habitat conditions, was not a point pattern but a landscape-scale pattern, it was expected to be visible in early forest inventory maps and to be reflected also by contemporary eye-witness accounts (hypothesis 2). Since light-demanding flora may be used as a proxy for habitat openness (Svenning 2002), the historical data on the abundance of photophilic species characteristic for Scots pine-dominated forests were reviewed and employed to test if they would mirror sparse canopy stand structure as typical under fire disturbance (hypothesis 3). For that purpose the current stand density and diameter structure of the studied sites were also inventoried.

3.5.3 Paper III

In this study tree ring data on stand demography across six sites in Białowieża Forest were objectively sampled with the aim to reveal long-term relation between Norway spruce population dynamics and fire disturbance. In total from the six study sites (F1–F6) 403 increment cores from 124 pines and 157 spruces were collected. In addition data on stand-scale fire history, Scots pine population dynamics, current stand density and diameter structure from the same study sites, collected within another study (Paper II) were used. *P. sylvestris* tree ring data derived from 802 cross-sections and increment cores collected from a total of 515 trees and stumps were applied. Supplementary data on stand density and diameter structure of the study sites came from a total of fourteen 500 m^2 sample plots (r=12.62 m), usually 2–3 plots per site.

3.5.4 Paper IV

In this study spatial extent of past fires using tree ring methods was reconstructed over a 9.2 km^2 area in a coherent conifer-dominated landscape of Białowieża Forest. Due to the pilot character and small size of the study area, only basic calculations relating to the spatial aspects of the fire regime were conducted by using two approaches: one using the proportion of points burned in each fire, yielding the Fire Cycle (FC) value, and the other using the reconstructed minimum fire areas.

4 Main results

4.1 Tree ring fire history and key parameters of the historical fire regime in Białowieża Forest throughout the last four centuries

From a total of over one thousand crossdated tree ring samples covering the period 1600–2015, a total of 145 individual fire years were detected, the earliest in 1621 and the last one in 1946. On average 28 fires were reconstructed from each of the six sites (25 to 31, Table 1, Paper II). The size of pines at the first fire they survived was generally small, on average 7.6 cm (1.4–31.4 cm). Tree age at the first fire was 18 yrs on average (variation from 2 to 59 yrs) (Paper II). Fire frequencies at stand scale varied little between sites, with an overall average of 9 yrs over the whole study period (variation 6.8–10.4 yrs, Table 1, Paper II). In this study we documented also point-scale (i.e. single tree) fire intervals as short as one and two yrs (Paper I and IV). Seasonal distribution of historical fires in BF proved dominance of dormant and early season events (likely reflecting burning in the period from March to mid June/July – Ermich 1959; Wodzicki & Zajączkowski 1983), that constituted more than half (50–70%) of all fires recorded in each site. Exact values for the respective sites were: F1 – 52%, F2 – 66.67%, F3 – 68.75%, F4 – 60.71%, F5 – 61.29% and F6 – 73.1%. A general decline in fire frequencies occurred during the mid-1800s with the last fire occurring in the early 1900s in most sites (Fig. 3, Paper II). As evidenced by post-fire growth reactions and the diameter of the surviving trees, the historical fire regime of Białowieża Forest was dominated by low-intensity surface fires. However, sporadic high-intensity stand-replacing fires occurred and led to successional changes at the stand scale (Paper I).

4.2 Role of fire in shaping landscape-scale Scots pine dominance in Białowieża Forest

Under the recorded frequent fire disturbance Scots pine regeneration occurred in pulses, resulting in multi-aged stands composed of two up to six cohorts, with some sporadic recruitment in between. At present, live tree ages range from 140 to 320 yrs. The youngest regeneration of pine thus dated back to 1869, no regeneration of pines could be detected after this year (Fig. 4, Paper II). Densities of Scots pines today averaged 205 trees·ha^{-1}. At two sites the additional number of old pine stumps and logs was 80·ha^{-1} on average (Table 4, Paper II). At present, all sites are dominated by dense Norway spruce populations (mean 526.5 ± 85.7 trees·ha^{-1}) of younger age (Paper III) and generally of smaller size than the pines, with mean DBH of 23.7 cm (Table 4, Paper II).

Old forest inventories in association with soil maps showed a strong association between sandy soil types (i.e. podzol and rusty soils) and the historical occurrence of Scots pine-dominated forests, documented by Bobrovskii (1863) and Karcov (1903). That picture was corroborated by eye-witness accounts which repeatedly pointed out the low tree density of Scots pine dominated stands. Also the analysis of the historical occurrence of light-demanding flora indicated substantially more open habitat conditions in the past (Paper II).

4.3 Long-term population dynamics of Norway spruce in relation to fire disturbance in Białowieża Forest

In all six sites the effective recruitment of Norway spruce occurred only during the relaxation in fire frequency, i.e. since ca. 1850; with massive regeneration following the last fire in the respective stand. In most cases the last fire dated to the first decades of 1900s. In turn all studied stands experienced a dramatic shift from Scots pine to spruce dominance in the course of a few decades. Tree densities increased dramatically from ca. 200 trees·ha^{-1} to 700–800 trees·ha^{-1} and stand structure went from open sparse into dense dark conditions. Although spruce is generally considered a fire sensitive species it was evident that in five of six studied stands single individuals of young spruces were able to survive fires of very low intensity (*cf.* Fig. 4, Paper III).

4.4 First insight into spatial aspects of historical fire occurrence in Białowieża Forest

The great majority of fires (76 out of 82) were not fully contained inside the 9.2 km^2 study area, i.e. they had one, or more, open border. Fires displayed large variation in size, from fires recorded in only one point to fires recorded in more than half of the nine sites sampled, thus exceeding 500 ha in size. Fire cycle was calculated to 11 yrs for the study period. In comparison with the present-day data on lightning ignition density for Poland, our recorded fire density of 3.2 fires·$(10^4$ ha$)^{-1}$·yr^{-1} exceeded lightning ignitions by two orders of magnitude. Due to the fact that many fires were not contained within the study area, a substantially larger area is needed to establish this finding with certainty. Furthermore, study on the role of possible fire breaks in this landscape is also required. The results reinforce earlier studies on the importance of fire in Białowieża Forest and show the potential for further spatial fire reconstruction for the studies of for example the drivers of the past fire regime. The only fire broadly known from historical sources, in 1811, was confirmed, burning half of the points in the studied area.

5 Discussion

5.1 Fire as the main driver of coniferous landscape in Białowieża Forest, an European temperate woodland

This thesis elucidated the crucial role of fires in shaping tree demography and structure of coniferous forest landscape throughout the last centuries in Białowieża Forest. In that respect, it shed new light on the general forest ecology concepts applied in that part of the European continent, which follow the rather static approach of phytosociology and the idea of the ‘potential natural vegetation’ (Tüxen 1956; Walter 1968; Faliński 1986; Matuszkiewicz 1984; Ellenberg 1996; Sokołowski 2004). One of the reasons why fire was never seriously incorporated into the discussions on forest and vegetation dynamics by phytosociology may be the fact that this scientific field has been developed relatively late (late 19th century), i.e. after the end of fires already. In Europe forest fire suppression was tightly connected with development of modern forest management, interested mainly in timber exploitation (Wallenius 2011). Nevertheless, it is worth mentioning, that in early publications by German silviculturalists (Conrad 1925; Recke 1928) the importance of fire for Scots pine regeneration was clearly stressed and even recommended to be included into common forest management practice.

This research, spanning the last four centuries, revealed frequent landscape-scale fire disturbance of both low- and high-intensity (Paper I) in Białowieża Forest until approximately 100–150 yrs ago. That result is in clear contrast to what was previously reported on the fire occurrence in this area, basically mentioning only the disastrous fire of 1811 (Genko 1902-1903; Faliński 1986). The collected tree ring data enabled reconstruction of key fire regime parameters (i.e. frequency, intensity, seasonality), as well as gave first insight into spatial aspects of historical fire activity in that ecosystem.

As documented by the tree ring record spanning from 1600 AD until today, historical forest inventories and maps and contemporary eye-witness accounts, large sections of the study area were covered by pure or strongly Scots pine-dominated forests in the past (Paper II) – a picture quite different from the one that can be observed today. At present several studies document lack of successful Scots pine regeneration (Kuijper et al. 2010; Sokołowski 1999; Drozdowski et al. 2012; Brzeziecki et al. 2016), hence challenging its long-term presence in Białowieża Forest. In this research it was proposed that under frequent fires not only the tree species composition of the coniferous landscape of Białowieża was different (Paper II and III). Stand density was much lower, creating a very different light environment from what can be seen at present. In turn, the dominating ground vegetation was likely composed of different elements than today. An increased share of grasses and heather (*Calluna vulgaris* (L.) Hull) besides the documented higher share of light-demanding plants (Paper II), was suggested as evolving in pinewoods of Białowieża under frequent fire disturbance (Paper I and II). Indeed, it was actually confirmed by some historical observations (Anonymous 1861; Bobrovskii 1863; Przybylski 1863; Paczoski 1930).

Since there is evidence of both fire and *Pinus* occurrence also in the other, more mesic habitats throughout Białowieża Forest (E. Zin and M. Niklasson, unpubl. data; Fig. 6), it may be suggested that this disturbance agent was likely operating at much broader spatial scale, crossing different stands and forest communities (*cf.* Błoński & Drymmer 1889; Flatley et al. 2013; Aldrich et al. 2014) and promoting long-term Scots pine existence over more extensive ranges.

As shown by this study, cessation of fires in Białowieża Forest was followed by massive spruce encroachment into previously Scots pine dominated stands. This process has been already observed in the late 19th-early 20th centuries (Błoński & Drymmer 1889; Genko 1902-1903; Krüdener 1909). The very interesting note by Paczoski (1930) shows actually that some of the Central European forest ecologists (and phytosociologists, including Paczoski himself – see Maycock 1967) did recognize the possible role of fire in driving forest dynamics of that region:

> (...) most likely, we have no mixed pine-spruce forest stands, which have not been affected, even a long time ago, by fire. And when exactly these fires happened – we don't know; so in most cases we are not able to evaluate whether spruce in the particular stand is lower than pine because of site conditions, or just because it is younger than pine there – as it belongs to a new generation and pine is represented by the generation that wasn't damaged by the fire. (Paczoski 1930, p. 256, translated by E. Zin).

The general conclusion on the long-term Norway spruce population dynamics, formulated in this research, was that the often-mentioned dominance and ubiquity of that tree species across Białowieża Forest (Faliński 1986; Sokołowski 2004) is a rather short-term phenomenon when compared in millennial time perspective.

This research gave also first insight (with quantitative information) into the spatial dimension of the past fire disturbance in this part of the world, showing that some fires in Białowieża Forest were of significant extent, with a large number of fires with a minimum size of 500 ha and probably several events that exceeded 1000 ha. These first results showed that exploring spatial features of the historical fire regime with tree ring methods in Białowieża Forest is possible, however requires larger, and preferably denser, networks of sampled wood material. Such further research could elucidate the role of potential fire breaks and define the minimum and maximum fire sizes as well as improve our understanding of drivers of this fire regime (humans and/or climate).

The existing palaeoecological data, both European (Huntley & Birks 1983; Novák et al. 2012; Adámek et al. 2015) and American (Fesenmyer & Christensen 2010), allow to propose that fire influence on temperate tree population dynamics – as depicted by this research – likely continued over millennia and therefore should be involved when interpreting long-term patterns in forest ecology and demography of this region.

My research was focused on the relation between fire and tree population patterns and not on the underlying causes of those disturbances. Hence the potential for future studies on fire regime of Białowieża Forest, exploring for example the fire-climate-humans relationships, is still large, though probably requiring more landscape-scale data.

Figure 6. Dead Scots pine tree with open multiple fire scar in a fertile oak-lime-hornbeam forest in Białowieża National Park, Poland, with at least 6 fire event records visible. In the best preserved sections of Białowieża Forest, fire-scarred pines are not uncommon and show that fires were also present in sites outside the conifer parts of the study area. Photo: Ewa Zin.

5.2 Methodological considerations

5.2.1 Fire record written in documents and in the wood

There are no detailed documentary records of fire occurrence from BF spanning over the whole reconstructed fire history period, with written fire reports only dating back to 1950s–70s (E. Zin and M. Niklasson, unpubl. data). From the four fire dates, known from written sources: 1639, 1811, 1819, 1834, with 1811 and 1834 being described as large-scale events (Brincken 1826; Ronke 1830; Bobrovskii 1863; Genko 1902-1903), only two were confirmed in the tree ring material (1811 and 1819). The famous 1811 fire was found in four of seven fire history sites throughout BF (Paper IV), so most likely it was indeed widespread. However, a fire that occurred only two years earlier, in 1809, was even more synchronous as it was recorded in almost all study sites (six out of seven) (Paper IV). A simple comparison of the number of individual fire dates, recorded in this study (145) with the number found in written sources shows the enormous discrepancy between the documentary and the tree ring fire record.

5.2.2 Sample availability in Białowieża Forest

One of the largest challenges of fire history studies is sample availability, strongly dependent on e.g. land use history, forest management, local topography and climate conditions. Wood decomposition is generally slower in colder and drier climates than in more humid and warmer regions (e.g. Stokland 2001). Białowieża Forest as a flat area lacking rocky outcrops covered by continuous mixed forest in the temperate zone has likely much shorter wood decomposition period when compared to boreal and Mediterranean locations, resulting in shorter tree ring chronologies (e.g. Niklasson & Granström 2000 *vs.* Niklasson et al. 2010). During sampling, the existence of substantial amounts of fire-scarred stumps, logs and standing trees with advanced wood decomposition in all parts other than the very 'catface' part (i.e. the fire scar section) was noted. Such material, despite multiple scars, proved very often to be lacking intact tree ring sequences, which excluded crossdating possibility and, hence, was not collected. Another factor decisive for sample availability is local management history, mainly forest management transferring old-growth tree stands into younger plantations. In Białowieża Forest another factor of importance was certainly the extraction of pine stumps for tar production, practiced in the 17th–19th centuries (Hedemann 1939; Samojlik 2007). Interestingly, Scots pine stumps are extracted by local inhabitants until today as source of resinous wood splints being used as a perfect material to ignite fire in the stove (Karpiński 1948; E. Zin, pers. obs.).

5.2.3 Crossdating

The core of dendrochronological crossdating is climate signal imprinted in tree rings of individuals of a certain species growing in the same region. It is widely accepted that climate signal is strongest in tree populations growing in extreme sites and/or at the border of their natural geographical distribution (e.g. Speer 2010).

Scots pine in most habitats of Białowieża Forest is not fulfilling any of those conditions since these habitats are not extreme sites and because Białowieża Forest is located in the very center of the natural range of Scots pine (Boratyński 1993). A separate factor is growth anomalies in form of the growth depressions and growth releases resulting from disturbances affecting individual trees and/or direct damages significantly influencing wood formation (which fire scars certainly are). If they are strong and frequent, the climate signal gets dissolved. Usually such ring sequences are omitted during the statistical crossdating and analysis.

In this study the crossdating 'on the wood' (Douglass 1941; Stokes & Smiley 1968; Pilcher 1990; Yamaguchi 1991) was applied, based on the chronology of local pointer years (Schweingruber et al. 1990). Examples of local pointer years used for crossdating of *P. sylvestris* tree ring material were: 1695 (narrow and/or pale), 1760 (narrow), 1762 (narrow), 1940 (narrow and/or pale), 1952 (narrow). Examples of very useful sequences of pointer years were: 1779/1780/1781 (wide/narrow/narrow) and 1900/1901/1902 (narrow/wide and/or dark/narrow and/or pale). In the Scots pine wood samples from Białowieża Forest the 19th century represented the most challenging period with basically only one strong pointer year – 1811, a narrow ring. In the tree ring fire history studies however, fire seasonality imprinted in fire scars provides additional support in crossdating at the stand scale.

The possible way to solve the problem of weak and/or disturbed climate signal is the high number of both sample trees and tree ring samples, enabling detection of very local (i.e. stand-scale) growth patterns. In this study we followed that approach; nevertheless, a small share of all the collected samples (approximately 0.9%) still remained undated.

Interestingly, Norway spruce in Białowieża Forest, most likely due to its drought sensitivity and geographical situation, seems to have much stronger climate signal, as documented by other dendrochronological studies from that area (Jaroszewicz 1993; Koprowski & Zielski 2008).

5.2.4 Scarring sensitivity

There are several concerns about scar-based fire history reconstructions and the accuracy and/or uncertainty of the reconstructed fire regime parameters, mainly because: not all trees within a burned area get scarred; not all fires form scars on trees; not all trees may have burned; and not all fire scars persist through time (Dieterich & Swetnam 1984; Swetnam & Baisan 1996). The process of scarring is highly dependent on features of both the disturbance agent, which is a certain fire event, and of the disturbance object, which is a given tree eventually surviving and recording this fire in its tree rings. Fire intensity and fire behavior (i.e. rate of spread, flame length etc.), tightly connected to the given habitat circumstances (mainly fuel, weather, topography), determine the heat that the tree and its parts are subjected to; tree age, size and condition decide its direct resistance to that factor. Generally older and larger trees with thick bark are less susceptible to scar damage since the bark insulating efficiency is a power function of bark thickness (Dickinson & Johnson 2001). However, the existence of previous scars, even on large trees, may increase the probability of further scarring (McBride 1983; Baker & Dugan 2013).

If a fire scar constitutes a certain fire evidence, the lack of it is much more challenging to interpret. There are several reasons why some trees within a given fire perimeter may not get scarred (Baker & Ehle 2001), resulting from the two main decisive factors described above. Existing empirical data show that the discrepancy between the scarred and unscarred trees in a given fire event may be large. In areas with repeated fire disturbance fire scars from previous events may be also simply consumed in subsequent fires. Therefore, it is generally acknowledged that fire frequencies reconstructed from fire scars are probably underestimating the real fire frequency, especially in areas where these disturbances were recurrent (Stephens et al. 2010).

Several authors have discussed the best ways of collecting and interpreting fire scar data, stressing the limitations of different sampling strategies and need of empirical studies to test key assumptions applied by fire historians (e.g. Swetnam & Baisan 1996; Baker & Ehle 2001; Fulé et al. 2003; Van Horne & Fulé 2006; Farris et al. 2010). One of the criticized aspects was subjective sampling with focus on multiple fire-scarred specimens only, being potentially ‘the best recorders’ (Swetnam & Baisan 1996; Van Horne & Fulé 2006).

Nonetheless, it has been postulated that spatially distributed fire scar samples (Farris et al. 2010) representing a certain sample size (of ca. 50 randomly sampled specimens, Van Horne & Fulé 2006) shall provide an accurate material allowing for representative landscape-scale fire history reconstructions. The issue of scarring sensitivity very much guided the sampling in this research, with very large local sample sizes (50–100) in much of the studies.

5.3 A broader perspective

The special conservation status of a royal hunting area (with main focus on bison as the most important royal game species) which Białowieża Forest possessed as early as in the 14th century clearly distinguished the area from the neighboring woodlands, which were gradually clearfelled as the development of stationary agriculture progressed throughout the region (Hedemann 1939; Schama 1996; Pyne 1997). No wonder, then, that already in the first half of the 19th century Białowieża Forest was described as an unique European woodland of primeval character (Brincken 1826). It intrigued and attracted naturalists and life scientists since centuries, resulting in plentiful descriptions and innumerable studies. In the course of the 20th century it became broadly accepted and used as a reference and/or model ecosystem for natural forest and vegetation dynamics (Faliński 1986; Koop 1989; Ellenberg 1996; Peterken 1996), wildlife & grazing ecology (Jędrzejewska & Jędrzejewski 1998; Vera 2000; Samojlik & Kuijper 2013) or cultural history (Schama 1996; Samojlik 2007).

Since virgin forests of comparable structure and extent are lacking in temperate Europe (Hannah et al. 1995; Peterken 1996) Białowieża Forest is the only available area of remarkable size where tree ring fire history reconstructions can be made. However, the existing palaeoecological data, both local (for Białowieża) and regional, allow for a wider discussion of the results obtained in this research.

Several palynological datasets from the study area confirm long-term interplay between fire disturbance and Scots pine dominance (Dąbrowski 1959; Mitchell & Cole 1998; Zimny 2014), hence challenging the contemporary recession of regeneration and recruitment of that species, recorded both in Białowieża Forest (e.g. Fig. 4, Paper II; Sokołowski 1999; Brzeziecki et al. 2016) and regionally (Vera 2000; Matuszkiewicz 2007). When compared to palaeoecological data from other Central European studies, documenting high (approximately 50%) pine pollen values in northeastern Poland throughout the last >10 000 yrs (Huntley & Birks 1983; Latałowa et al. 2004), Białowieża records turn out to be very similar: 40–70% (Dąbrowski 1959; Mitchell & Cole 1998; Zimny 2014). At the scale of the whole region of temperate Europe, charcoal and pollen evidence for the existence of Scots pine forests is now present for several thousand years back in time (e.g. Rösch 2000; Zimny 2014; Novák et al. 2012; Adámek et al. 2015). Some of these studies (Novák et al. 2012; Adámek et al. 2015) link that to continuous fire disturbance over millennia, thus questioning the common opinion that the landscape-scale pine dominance in that part of the continent is resulting from human management only (Walter 1968; Ellenberg 1996; Timbal et al. 2005).

Further comparison with North American data, both century- (Grissino-Mayer 2016 and literature therein) and millennia-long (Fesenmyer & Christensen 2010), reveals analogous patterns of fire history and population dynamics of other *Pinus* species. This allows to draw a more general conclusion that since thousands of years fire played a key role in shaping forest dynamics and pine dominance not only across the boreal and Mediterranean regions (Niklasson & Granström 2000; Falk et al. 2011; Christopoulou et al. 2013; Fournier et al. 2013; Drobyshev et al. 2016) but also in the temperate biome (Paper II).

Considering Norway spruce (Paper III), interpreting the results of this research from a palaeoecological perspective gives possibility of a wider discussion. In none of the pollen records from coniferous sites in Białowieża Forest (Dąbrowski 1959; Mitchell & Cole 1998; Latałowa et al. 2015) there was any evidence of a clear indication of an analogous increase in spruce share as the one documented in this research. In this context it is impossible to avoid the issue of the European spruce bark beetle (*Ips typographus* L.) outbreaks which over the last few decades have caused profound decrease in the share of this tree species across the area (Bernadzki et al. 1998; Bobiec et al. 2011; Brzeziecki et al. 2016). Empirical data derived by this research, which documented a relatively modern (i.e. during the last ca. 100–150 yrs) spruce expansion, supported by the lack of strong evidence of a similar dominance of this tree taxon in the more distant past allow to conclude that the former mass bark beetle outbreaks have likely had much smaller impact on the Norway spruce population in this area (Paper III).

Defining natural reference conditions (natural range of variation) has been widely acknowledged as crucial for sustainable ecosystem management, forest restoration and nature conservation (e.g. Heyerdahl & Card 2000; Halme et al. 2013). Detailed disturbance history and tree demography data derived from this research for the coniferous habitats of Białowieża may therefore serve as valuable aid supporting current management of the area; the more that the empirical tree ring data records of natural long-term forest dynamics for the whole variety of local forest types are still very limited (Zin et al., in prep.). Since Białowieża Forest is located in a 'no fire' region (see section 1.3), introducing prescribed burning into both forest management and nature conservation may be perceived as controversial although the results from this research point towards a need to include fire into the management discussion. Such discussion took place in the Scandinavian countries in the 1980s and 1990s and resulted in a broad scale introduction of prescribed fire in nature conservation (Granström 2001). However, prescribed fire use for nature conservation purposes has already found its way also into Poland with a recent workshop in 2015 (http://www.lasy.gov.pl/informacje/aktualnosci/ogien-w-gospodarce-lesnej-i-ochronie-przyrody).

The new findings of this research may broaden the ongoing discussion of long-term stand dynamics and management of the study area (e.g. Blicharska & Angelstam 2010; Kuijper et al. 2010; Bobiec 2012; Drozdowski et al. 2012; Brzeziecki et al. 2016; Jaroszewicz et al. 2016). Nevertheless, many questions related to the disturbance history and natural tree dynamics of Białowieża Forest are still open and call for future studies, in particular in richer and more deciduous dominated habitat types.

6 Conclusions

In this research, a century-long interplay between fire and tree population dynamics across coniferous habitats in Białowieża Forest was documented, evidencing landscape-scale fire influence on European temperate forest ecosystems. In that respect, the common opinion that fire is less important in shaping the forest dynamics of that biome was challenged.

Specific conclusions that were drawn from this study are the following:

(1) Fire was an important factor shaping structure and tree species composition of Białowieża Forest until approximately 100–150 yrs ago.

(2) In the historical fire regime of Białowieża Forest, similar to other Scots pine-dominated ecosystems, low-intensity fires prevailed. However, occasionally stand-replacing high-intensity events occurred that changed stand structure by initiating cohort regeneration in the midst of periods with only sporadic tree recruitment.

(3) Fire may be a factor assuring long-term landscape-scale Scots pine dominance by promoting its successful regeneration and by eliminating its fire sensitive competitors, such as Norway spruce, not only in the boreal, but also in the temperate Europe.

(4) The dominance of Norway spruce in Białowieża Forest, now abruptly truncated by massive spruce bark beetle outbreaks, have few, if any, parallels in the long-term history of this area.

(5) It is possible to reconstruct the spatial dimension of historical fire disturbance in Białowieża Forest, thus providing a promising foundation for future studies of fire-climate-human interactions.

References

Akala, T., Kuuluvainen, T., Wallenius, T. & Kauhanen, H. 2009. Contrasting patterns of tree mortality in late-successional *Picea abies* stands in two areas in northern Fennoscandia. *Journal of Vegetation Science* 20: 1016–1026.
Abrams, M.D., Copenheaver, C.A., Terazawa, K., Umeki, K., Takiya, M. & Akashi, N. 1999. A 370-year dendroecological history of an old-growth *Abies-Acer-Quercus* forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 29: 1891–1899.
Adámek, M., Bobek, P., Hadincová, V., Wild, J. & Kopecký, M. 2015. Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *Forest Ecology and Management* 336: 81–90.
Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, D.C.
Ali, A.A., Blarquez, O., Girardin, M.P., Hely, C., Tinquaut, F., El Guellab, A., Valsecchi, V., Terrier, A., Bremond, L., Genries, A., Gauthier, S. & Bergeron, Y. 2012. Control of the multimillennial wildfire size in boreal North America by spring climatic conditions. *Proceedings of the National Academy of Sciences of the United States of America* 109: 20966–20970.
Angelstam, P. & Kuuluvainen, T. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. *Ecological Bulletins* 51: 117–136.
Applequist, M.B. 1958. A simple pith locator for use with off-centre increment cores. *Journal of Forestry* 56: 141.
Arno, S.F. & Sneck, K.M. 1977. A method for determining fire history in coniferous forests of the mountain West USA. *USDA Forest Service General Technical Report, Intermountain Forest and Range Experiment Station*: 28 pp.
ArtDatabanken 2015. *Rödlistade arter i Sverige 2015*. ArtDatabanken SLU, Uppsala.
Badeck, F.-W., Lasch, P., Hauf, Y., Rock, J., Suckow, F. & Thonicke, K. 2003. Steigendes klimatisches Waldbrandrisiko. Eine Prognose bis 2050. *AFZ-Der Wald* 2003: 2–5.
Baisan, C.H. & Swetnam, T.W. 1990. Fire History on a Desert Mountain-Range - Rincon Mountain Wilderness, Arizona, USA. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 20: 1559–1569.
Baker, W.L. & Dugan, A.J. 2013. Fire-history implications of fire scarring. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 43: 951–962.
Baker, W.L. & Ehle, D. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 31: 1205–1226.
Bergeron, Y. & Brisson, J. 1990. Fire Regime in Red Pine Stands at the Northern Limit of the Species Range. *Ecology* 71: 1352–1364.
Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajączkowski, J. & Żybura, H. 1998. Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. *Journal of Vegetation Science* 9: 229–238.

Blanck, Y.L., Rolstad, J. & Storaunet, K.O. 2013. Low- to moderate-severity historical fires promoted high tree growth in a boreal Scots pine forest of Norway. *Scandinavian Journal of Forest Research* 28: 126–135.
Blicharska, M. & Angelstam, P. 2010. Conservation at risk: conflict analysis in the Białowieża Forest, a European biodiversity hotspot. *International Journal of Biodiversity Science, Ecosystem Services & Management* 6: 68–74.
Błoński, F. & Drymmer, K. 1889. Sprawozdanie z wycieczki botanicznéj, odbytéj do Puszczy Białowieskiéj, Ladzkiéj i Świsłockiéj w 1888 roku. *Pamiętnik Fizyjograficzny* 9: 55–62.
Bobiec, A. & Bobiec, M. 2012. Influence of spruce decline in stands of the Białowieża National Park on natural oak regeneration. *Sylwan* 156: 243–251.
Bobiec, A., Jaszcz, E. & Wojtunik, K. 2011. Oak (*Quercus robur* L.) regeneration as a response to natural dynamics of stands in European hemiboreal zone. *European Journal of Forest Research* 130: 785–797.
Bobrovskii, I. 1863. *Materialy dlya geografi i statistiki Rossii, sobraniye ofitserami generalnogo shtaba. Grodnenskaya Guberniya.* Tipografiya Departamenta Generalnogo Shtaba, Sankt Petersburg.
Bond, W.J. & Keeley, J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20: 387–394.
Bond, W.J., Woodward, F.I. & Midgley, G.F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–537.
Boratyński, A. 1993. Systematyka i geograficzne rozmieszczenie. In: Białobok, S., Boratyński, A. & Bugała, W. (eds.) *Biologia sosny zwyczajnej*, pp. 45–69. Wydawnictwo Sorus, Poznań – Kórnik.
Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R. & Pyne, S.J. 2009. Fire in the Earth System. *Science* 324: 481–484.
Bradshaw, R.H.W., Tolonen, K. & Tolonen, M. 1997. Holocene records of fire from the boreal and temperate zones of Europe. In: Clark, J.S., Cachier, H., Goldammer, J.G. & Stocks, B. (eds.) *Sediment Records of Biomass Burning and Global Change*, pp. 347–365. Springer Verlag, Berlin – Heidelberg.
Brincken, J. 1826. *Mémoire Descriptif sur la Forêt Impériale de Białowieża, en Lithuanie*. Glücksberg, Varsovie.
Brown, P.M. & Wu, R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86: 3030–3038.
Brzeziecki, B., Pommerening, A., Miścicki, S., Drozdowski, S. & Żybura, H. 2016. A common lack of demographic equilibrium among tree species in Białowieża National Park (NE Poland): evidence from long-term plots. *Journal of Vegetation Science*. DOI: 10.1111/jvs.12369.
Cassell, B.A. & Alvarado, E. 2012. Reconstruction of fire history in Mexican tropical pines using tree rings. *Forestry Chronicle* 88: 553–555.
Christopoulou, A., Fulé, P.Z., Andriopoulos, P., Sarris, D. & Arianoutsou, M. 2013. Dendrochronology-based fire history of *Pinus nigra* forests in Mount Taygetos, Southern Greece. *Forest Ecology and Management* 293: 132–139.
Conrad, A. 1925. Das Bodenfeuer als Freund des Forstmanns. *Forstliche Wochenschrift Silva* 13: 139–141.
Dąbrowski, M.J. 1959. Późnoglacjalna i holoceńska historia lasów Puszczy Białowieskiej. Część I. Białowieski Park Narodowy. *Acta Societatis Botanicorum Poloniae* 28: 197–248.
Dickinson, M.B. & Johnson, E.A. 2001. Fire effects on trees. In: Johnson, E.A. & Miyanishi, K. (eds.) *Forest fires: behavior and ecological effects*, pp. 477–525. Academic Press, New York.
Dieterich, J.H. & Swetnam, T.W. 1984. Dendrochronology of a Fire-Scarred Ponderosa Pine. *Forest Science* 30: 238–247.
Douglass, A.E. 1941. Crossdating in Dendrochronology. *Journal of Forestry* 39: 825–831.
Drobyshev, I., Bergeron, Y., de Vernal, A., Moberg, A., Ali, A.A. & Niklasson, M. 2016. Atlantic SSTs control regime shifts in forest fire activity of Northern Scandinavia. *Scientific Reports* 6. DOI: 10.1038/srep22532.
Drozdowski, S., Brzeziecki, B., Żybura, H., Żybura, B., Gawron, L., Buraczyk, W., Zajączkowski, J., Bolibok, L., Szeligowski, H., Bielak, K. & Widawska, Z. 2012. Long-term dynamics of old-

growth stands in the managed part of the Białowieża Forest: increasing and declining tree species. *Sylwan* 156: 663–671.
Ellenberg, H. 1996. *Vegetation Mitteleuropas mit den Alpen. 5. Auflage*. Ulmer, Stuttgart.
Ermich, K. 1959. Badania nad sezonowym przebiegiem przyrostu grubości pnia u *Pinus silvestris* L. i *Quercus robur* L. *Botanicorum Poloniae Acta Societatis* 28: 15–63.
European Bison Pedigree Book 2015. *European Bison Pedigree Book.* Białowieski Park Narodowy, Białowieża.
Faliński, J.B. 1986. *Vegetation Dynamics in Temperate Lowland Primeval Forest. Ecological Studies in Białowieża Forest*. Dr W. Junk Publishers, Dordrecht.
Falk, D.A., Heyerdahl, E.K., Brown, P.M., Farris, C., Fule, P.Z., McKenzie, D., Swetnam, T.W., Taylor, A.H. & Van Horne, M.L. 2011. Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9: 446–454.
Farris, C.A., Baisan, C.H., Falk, D.A., Yool, S.R. & Swetnam, T.W. 2010. Spatial and temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. *Ecological Applications* 20: 1598–1614.
Fesenmyer, K.A. & Christensen, N.L., Jr. 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. *Ecology* 91: 662–670.
Flatley, W.T., Lafon, C.W., Grissino-Mayer, H.D. & LaForest, L.B. 2013. Fire history, related to climate and land use in three southern Appalachian landscapes in the eastern United States. *Ecological Applications* 23: 1250–1266.
Fournier, T.P., Battipaglia, G., Brossier, B. & Carcaillet, C. 2013. Fire-scars and polymodal age-structure provide evidence of fire-events in an Aleppo pine population in southern France. *Dendrochronologia* 31: 159–164.
Fulé, P.Z., Covington, W.W. & Moore, M.M. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7: 895–908.
Fulé, P.Z., Heinlein, T.A., Covington, W.W. & Moore, M.M. 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *International Journal of Wildland Fire* 12: 129–145.
Fulé, P.Z., Ribas, M., Gutierrez, E., Vallejo, R. & Kaye, M.W. 2008. Forest structure and fire history in an old *Pinus nigra* forest, eastern Spain. *Forest Ecology and Management* 255: 1234–1242.
Genko, N. 1902-1903. Kharakteristika Belovezhskoi pushchi i istoricheskiya o nei dannyya. *Lesnoi Zhurnal* 32; 33: 1012–1056, 1269–1302; 1022–1056.
Gill, A.M. 1995. Stems and fires. In: Gartner, B. (ed.) *Plant Stems: Physiology and Functional Morphology*, pp. 323–342. Academic Press, San Diego.
Granström, A. 2001. Fire management for biodiversity in the European boreal forest. *Scandinavian Journal of Forest Research*: 62–69.
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 B-Biological Sciences* 363: 2353–2358.
Grissino-Mayer, H.D. 2016. Fire as a Once-Dominant Disturbance Process in the Yellow Pine and Mixed Pine-Hardwood Forests of the Appalachian Mountains. In: Greenberg, C.H. & Collins, B.S. (eds.) *Natural Disturbances and Historic Range of Variation. Type, Frequency, Severity, and Post-disturbance Structure in Central Hardwood Forests USA*, pp. 123–146. Springer International Publishing, Switzerland.
Gutowski, J.M. & Jaroszewicz, B. 2004. Białowieża Primeval Forest as a refuge of the European entomofauna. *Wiadomości Entomologiczne* 23 Supl. 2: 67–87.
Gutowski, J.M. & Jaroszewicz, B. 2001. *Catalogue of the fauna of Białowieża Primeval Forest*. Instytut Badawczy Leśnictwa, Warszawa.
Gutsell, S.L. & Johnson, E.A. 1996. How fire scars are formed: Coupling a disturbance process to its ecological effect. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 26: 166–174.
Halme, P., Allen, K.A., Aunins, A., Bradshaw, R.H.W., Brumelis, G., Cada, V., Clear, J.L., Eriksson, A.-M., Hannon, G., Hyvärinen, E., Ikauniece, S., Iršėnaitė, R., Jonsson, B.G., Junninen, K., Kareksela, S., Komonen, A., Kotiaho, J.S., Kouki, J., Kuuluvainen, T., Mazziotta, A., Mönkkönen, M., Nyholm, K., Olden, A., Shorohova, E., Strange, N., Toivanen, T., Vanha-Majamaa, I., Wallenius, T., Ylisirniö, A.-L. & Zin, E. 2013. Challenges of ecological restoration : Lessons from forests in northern Europe. *Biological Conservation* 167: 248–256.

Hannah, L., Carr, J.L. & Landerani, A. 1995. Human disturbance and natural habitat – a biome level analysis of a global data set. *Biodiversity and Conservation* 4: 128–155.
Hare, R.C. 1965. Contribution of Bark to Fire Resistance of Southern Trees. *Journal of Forestry* 63: 248–251.
Harley, G.L., Grissino-Mayer, H.D. & Horn, S.P. 2013. Fire history and forest structure of an endangered subtropical ecosystem in the Florida Keys, USA. *International Journal of Wildland Fire* 22: 394–404.
Hedemann, O. 1939. *L'histoire de la forêt de Białowieża (jusqu'a 1798)*. Institut de Recherches des Forêts Domaniales, Warszawa.
Heyerdahl, E.K. & Card, V. 2000. Implications of paleorecords for ecosystem management. *Trends in Ecology & Evolution* 15: 49–50.
Higuera, P.E., Sprugel, D.G. & Brubaker, L.B. 2005. Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. *Holocene* 15: 238–251.
Hille, M. & den Ouden, J. 2004. Improved recruitment and early growth of Scots pine (*Pinus sylvestris* L.) seedlings after fire and soil scarification. *European Journal of Forest Research* 123: 213–218.
Huntley, B. & Birks, H.J.B. 1983. *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 years ago*. Cambridge University Press, Cambridge.
Jaroszewicz, B. 2004. Białowieża Primeval Forest – a treasure and a challenge. In: Jędrzejewska, B. & Wójcik, J.M. (eds.) *Essays on mammals of Białowieża Forest*, pp. 3–12. Mammal Research Instiute, Polish Academy of Sciences, Białowieża.
Jaroszewicz, B. 1993. Stopień podobieństwa krzywych dendrochronologicznych (telekoneksja) między świerkami z Puszczy Białowieskiej i z Babiej Góry. *Parki Narodowe i Rezerwaty Przyrody* 12: 13–19.
Jaroszewicz, B., Bobiec, A. & Eycott, A.E. 2016. Lack of demographic equilibrium indicates natural, large-scale forest dynamics, not a problematic forest conservation policy – a reply to Brzeziecki et al. *Journal of Vegetation Science*. DOI: 10.1111/jvs.12458.
Jedrzejewska, B., Jedrzejewski, W., Bunevich, A.N., Miłkowski, L. & Krasiński, Z.A. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriologica* 42: 399–451.
Jędrzejewska, B. & Jędrzejewski, W. 1998. *Predation in Vertebrate Communities. The Białowieża Primeval Forest as a Case Study*. Springer, Berlin – Heidelberg – New York.
Karcov, G. 1903. *Belovezhskaya Pushcha. Eya istoricheskii ocherk, sovremennoe okhotnich'e khozyaistvo i Vysochaishiya okhoty v Pushche*. A. F. Marks, St. Petersburg.
Karpiński, J.J. 1948. *Les Traces de L'ancienne Apiculture sur le Terrain du Park National de Białowieża*. Institut de Recherches des Forêts Domaniales, Kraków.
Keeley, J.E. 2012. Ecology and evolution of pine life histories. *Annals of Forest Science* 69: 445–453.
Keeley, J.E. & Zedler, P.H. 1998. Evolution of life histories in *Pinus*. In: Richardson, D.M. (ed.) *Ecology and biogeography of Pinus*, pp. 219–250. Cambridge University Press, Cambridge.
Kirby, K.J. & Watkins, C. 2015. *Europe's Changing Woods and Forests: from Wildwood to Cultural Landscapes.* CABI, Wallingford.
Kolström, T. & Kellomäki, S. 1993. Tree survival in wildfires. *Silva Fennica* 27: 277–281.
Koop, H. 1989. *Forest Dynamics. SILVI-STAR: A Comprehensive Monitoring System*. Springer-Verlag, Berlin – Heidelberg – New York – Tokyo.
Koprowski, M. & Zielski, A. 2008. Extremely narrow and wide tree rings in the Norway spruce (*Picea abies* (L.) Karst.) of the Białowieża National Park. *Ecological questions* 9: 73–78.
Kozulko, G.A. 2003. Państwowy Park Narodowy "Biełowieżskaja Puszcza" jako białoruski obszar szczególnie chroniony. In: de Bruijn, O., Kozulko, G. & Okołów, C. (eds.) *Puszcza Białowieska w trzecim tysiącleciu. Wyzwania stojące przed ochroną przyrody i zrównoważonym rozwojem*, pp. 57–64. Północnopodlaskie Towarzystwo Ochrony Ptaków, Białystok.
Krasińska, M. & Krasiński, Z.A. 2007. *European bison: the nature monograph*. Mammal Research Institute, Polish Academy of Sciences, Białowieża.
Krüdener, A.A. 1909. Iz vpechatlenii o tipakh nasazhdenii Belovezhskoi Pushchi i ob opustosheniyakh, proizvedennykh v nei monashenkoi. *Lesnoi Zhurnal* 39: 1–26.
Krzyściak-Kosińska, R., Arnolbik, V. & A., A. 2012. Nomination Dossier to the UNESCO for the Inscription on the World Heritage List. *(manuscript)* Białowieski Park Narodowy, Białowieża.

Kuijper, D.P.J., Cromsigt, J.P.G.M., Jędrzejewska, B., Miścicki, S., Churski, M., Jędrzejewski, W. & Kweczlich, I. 2010. Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *Journal of Ecology* 98: 888–899.
Kuuluvainen, T. 2016. Conceptual models of forest dynamics in environmental education and management: keep it as simple as possible, but no simpler. *Forest Ecosystems* 3: 1–9.
Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: The complexity challenge. *Ambio* 38: 309–315.
Kuuluvainen, T. & Aakala, T. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica* 45(5): 823–841.
Kwiatkowski, W. 1994. Vegetation landscapes of Białowieża Forest. *Phytocoenosis* 6: 35–87.
Latałowa, M., Tobolski, K. & Nalepka, D. 2004. *Pinus* L. subgenus *Pinus* (subgen. *Diploxylon* (Koehne) Pilger) – Pine. In: Ralska-Jasiewiczowa, M., Latałowa, M., Wasylikowa, K., Tobolski, K., Madeyska, E., Wright Jr., H.E. & Turner, C. (eds.) *Late Glacial and Holocene history of vegetation in Poland based on isopollen maps*, pp. 165–177. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
Latałowa, M., Zimny, M., Jędrzejewska, B. & Samojlik, T. 2015. Białowieża Primeval Forest: a 2000-year interplay of environmental and cultural forces in Europe's best preserved temperate woodland. In: Kirby, K.J. & Watkins, C. (eds.) *Europe's Changing Woods and Forests: From Wildwood to Managed Landscapes*, pp. 243–264. CAB International, Oxfordshire - Boston.
Lentile, L.B., Smith, F.W. & Shepperd, W.D. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 35: 2875–2885.
Linder, P., Jonsson, P. & Niklasson, M. 1998. Tree mortality after prescribed burning in an old-growth Scots pine forest in northern Sweden. *Silva Fennica* 32: 339–349.
Marozas, V., Racinskas, J. & Bartkevicius, E. 2007. Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. *Forest Ecology and Management* 250: 47–55.
Maruszczak, H. 1999. Wpływ rolniczego użytkowania ziemi na środowisko przyrodnicze w czasach historycznych. In: Starkel, L. (ed.) *Geografia Polski. Środowisko przyrodnicze*, pp. 189–202. Wydawnictwo Naukowe PWN, Warszawa.
Matuszkiewicz, J.M. 2007. Ogólne kierunki zmian w zbiorowiskach leśnych Polski, ich przyczyny oraz prognoza przyszłych kierunków rozwojowych. In: Matuszkiewicz, J.M. (ed.) *Geobotaniczne rozpoznanie tendencji rozwojowych zbiorowisk leśnych w wybranych regionach Polski*, pp. 555–816. Instytut Geografii i Przestrzennego Zagospodarowania im. Stanisława Leszczyckiego PAN, Warszawa.
Matuszkiewicz, W. 1984. *Die Karte der potentiellen natürlichen Vegetation von Polen*. Istituto di Botanica dell' Università di Camerino, Camerino.
Maycock, P.F. 1967. Paczoski, J. – founder of science of phytosociology. *Ecology* 48: 1031–1034.
McBride, J.R. 1983. Analysis of tree rings and fire scars to establish fire history. *Tree-Ring Bulletin* 43: 51–67.
McRae, D.J., Conard, S.G., Ivanova, G.A., Sukhinin, A.I., Baker, S.P., Samsonov, Y.N., Blake, T.W., Ivanov, V.A., Ivanov, A.V., Churkina, T.V., Hao, W.M., Koutzenogij, K.P. & Kovaleva, N. 2006. Variability of fire behavior, fire effects, and emissions in Scotch pine forests of Central Siberia. *Mitigation and Adaptation Strategies for Global Change* 11: 45–74.
Mirek, Z., Piękoś-Mirkowa, H., Zając, A. & Zając, M. 2002. *Flowering plants and pteridophytes of Poland. A checklist*. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
Mitchell, F.J.G. & Cole, E. 1998. Reconstruction of long-term successional dynamics of temperate woodland in Białowieża Forest, Poland. *Journal of Ecology* 86: 1042–1059.
Niklasson, M. 1998. *Dendroecological Studies in Forest and Fire history. Silvestria 52.* PhD Doctoral thesis, Swedish University of Agricultural Sciences, Umeå.
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.
Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T., Jędrzejewska, B., Gutowski, J.M. & Brzeziecki, B. 2010. A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology* 98: 1319–1329.
Novák, J., Sádlo, J. & Svobodová-Svitavská, H. 2012. Unusual vegetation stability in a lowland pine forest area (Doksy region, Czech Republic). *Holocene* 22: 947–955.

Ochyra, R., Żarnowiec, J. & Bednarek-Ochyra, H. 2003. *Census Catalogue of Polish Mosses*. Institute of Botany, Polish Academy of Sciences, Kraków.
Okołów, C., Karaś, M. & Bołbot, A. 2009. *Białowieża National Park. Know it – understand it – protect it*. Białowieski Park Narodowy, Białowieża.
Paczoski, J. 1930. *Die Waldtypen von Białowieża*. Państwowa Rada Ochrony Przyrody, Poznań.
Pausas, J.G., Blade, C., Valdecantos, A., Seva, J.P., Fuentes, D., Alloza, J.A., Vilagrosa, A., Bautista, S., Cortina, J. & Vallejo, R. 2004. Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice – a review. *Plant Ecology* 171: 209–220.
Pausas, J.G. & Keeley, J.E. 2009. A Burning Story: The Role of Fire in the History of Life. *Bioscience* 59: 593–601.
Peterken, G.F. 1996. *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge.
Pierzgalski, E., Boczoń, A. & Tyszka, J. 2002. Variability of precipitation and ground water level in the Białowieża National Park. *Kosmos* 51: 415–425.
Pilcher, J.R. 1990. Sample preparation, cross-dating, and measurement. In: Cook, E.R. & Kairiukstis, L.A. (eds.) *Methods of Dendrochronology*, pp. 40–51. Kluwer Academic Publishers, Dordrecht, Boston, London.
Przybylski, W. 1863. Notatki z wycieczek po kraju. Puszcza Białowieska i żubry. *Tygodnik Ilustrowany* 200; 201; 202; 203: 287–290; 296–299; 310–311; 319–320.
Pucek, Z. 2004. European bison – history of a flagship species. In: Jędrzejewska, B. & Wójcik, J.M. (eds.) *Essays on mammals of Białowieża Forest*, pp. 25–34. Mammal Research Institute, Polish Academy of Sciences, Białowieża.
Pyne, S.J. 1997. *Vestal Fire. An Environmental History, Told through Fire, of Europe and Europe's Encounter with the World*. University of Washington Press, Seattle and London.
Ralska-Jasiewiczowa, M. & van Geel, M.B. 1992. Early human disturbance of the natural environment recorded in annually laminated sediments of Lake Gościąż, Central Poland. *Vegetation History and Archaeobotany* 1: 33–42.
Recke, G.v.d. 1928. Naturverjüngung der Kiefer durch Brandkultur. *Der Deutsche Forstwirt* 10: 652–653.
Ronke, E. 1830. Do W. Jarockiego professora Kr. War. Uniwer. Niektóre uwagi względem Puszczy Białowieżskiey. *Powszechny Dziennik Krajowy* 84; 85: 418; 423–424.
Rösch, M. 2000. Long-term human impact as registered in an upland pollen profile from the southern Black Forest, south-western Germany. *Vegetation History and Archaeobotany* 9: 205–218.
Rotherham, I.D. 2013. *Cultural Severance and the Environment: the Ending of Traditional and Customary Practice on Commons and Landscapes Managed in Common*. Springer, Dordrecht.
Samojlik, T. 2007. *Antropogenne przemiany środowiska Puszczy Białowieskiej do końca XVIII wieku.* PhD Doctoral thesis, Mammal Research Institute, Polish Academy of Sciences, Białowieża – Jagiellonian University, Kraków.
Samojlik, T. 2005. *Conservation and hunting. Białowieża Forest in the time of kings*. Mammal Research Institute, Polish Academy of Sciences, Białowieża.
Samojlik, T. 2006. The grandest tree – a history of Scots pine (*Pinus sylvestris* L.) in Białowieża Primeval Forest until the end of the 18th century. *Rocznik Dendrologiczny* 54: 7–27.
Samojlik, T. & Jędrzejewska, B. 2004. Utilization of Białowieża Forest in the times of Jagiellonian dynasty and its traces in the contemporary forest environment. *Sylwan* 148: 37–50.
Samojlik, T. & Kuijper, D.P.J. 2013. Grazed wood pasture versus browsed high forests – impact of ungulates on forest landscapes from the perspective of the Białowieża Primeval Forest. In: Rotherham, I.D. (ed.) *Trees, Forested Landscapes and Grazing Animals – a European Perspective on Woodlands and Grazed Treescapes*, pp. 143–162. Routledge, London and New York.
San-Miguel-Ayanz, J., Ståhl, G., Vidal, C., Bonhomme, C., Cienciala, E., Korhonen, K., Lanz, A. & Schadauer, K. 2011. Criterion 1: Maintenance and Appropriate Enhancement of Forest Resources and their Contribution to Global Carbon Cycles. In: *FOREST EUROPE, UNECE and FAO 2011: State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe*, pp. 17–27. Ministerial Conference on the Protection of Forests in Europe, Oslo.

Sannikov, S.N. & Goldammer, J.G. 1996. Fire ecology of pine forests of Northern Eurasia. In: Furyaev, V.V. & Goldammer, J.G. (eds.) *Fire in Ecosystems of Boreal Eurasia*, pp. 151–167. Kluwer Academic Publishers, Dordrecht – Boston – London.
Schama, S. 1996. *Landscape and Memory*. Vintage Books, New York.
Schelhaas, M.J., Hengeveld, G., Moriondo, M., Reinds, G.J., Kundzewicz, Z.W., ter Maat, H. & Bindi, M. 2010. Assessing risk and adaptation options to fires and windstorms in European forestry. *Mitigation and Adaptation Strategies for Global Change* 15: 681–701.
Schelhaas, M.J., Nabuurs, G.J., Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology* 9: 1620–1633.
Schimmel, J. & Granström, A. 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77: 1436–1450.
Schimmel, J. & Granström, A. 1997. Fuel succession and fire behavior in the Swedish boreal forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 27: 1207–1216.
Schmuck, G., San-Miguel-Ayanz, J., Camia, A., Durrant, T., Santos de Oliveira, S., Boca, R., Whitmore, C., Giovando, C., Libertá, G., Corti, P. & Schulte, E. 2011. *Forest Fires in Europe 2010. European Commission, Joint Research Centre – Institute for Environment and Sustainability, JRC Scientific and Technical Reports, Report No 11*. Publications Office of the European Union, Luxembourg.
Schweingruber, F.H., Eckstein, D., F., S.-B. & U., B.O. 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia* 8: 9–39.
Selva, N. 2016. Defining Forest, Habitat, and Wilderness in a Changing World. *Conservation Biology* 30: 1140–1142.
Sokołowski, A.W. 2004. *Lasy Puszczy Białowieskiej*. Centrum Informacyjne Lasów Państwowych, Warszawa.
Sokołowski, A.W. 1999. Succession of forest communities in the Starzyna reserve in the Białowieża Forest. *Parki Narodowe i Rezerwaty Przyrody* 18: 31–59.
Speer, J.H. 2010. *Fundamentals of tree-ring research*. The University of Arizona Press, Tucson.
Stephens, S.L., Fry, D.L., Collins, B.M., Skinner, C.N., Franco-Vizcaino, E. & Freed, T.J. 2010. Fire-scar formation in Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 40: 1497–1505.
Stephens, S.L., Skinner, C.N. & Gill, S.J. 2003. A dendrochronology-based fire history of Jeffrey pine - mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 33: 1090–1101.
Stokes, M.A. & Smiley, T.L. 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago.
Stokland, J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecological Bulletins* 49: 71–83.
Storaunet, K.O., Rolstad, J., Toeneiet, M. & Blanck, Y.L. 2013. Strong anthropogenic signals in historic forest fire regime: a detailed spatiotemporal case study from south-central Norway. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 43: 836–845.
Svenning, J.C. 2002. A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104: 133–148.
Swetnam, T.W. & Baisan, C.H. 1996. *Fire effects in southwestern forests*. Proceedings of the Second La Mesa Fire Symposium, March 29–31, 1994, Los Alamos, USDA Forest Service Gen. Tech. Rep. RM-GTR-286.
Swetnam, T.W., Baisan, C.H., Caprio, A.C., Brown, P.M., Touchan, R., Anderson, R.S. & Hallett, D.J. 2009. Multi-millennial fire history of the Giant Forest, Sequoia National Park, California, USA. *Fire Ecology* 5: 120–150.
Szczygieł, R., Ubysz, B. & Zawiła-Niedźwiecki, T. 2009. Spatial and temporal trends in distribution of forest fires in Central and Eastern Europe. In: Bytnerowicz, A., Arbaugh, M., Riebau, A. & Andersen, C. (eds.) *Wildland Fires and Air Pollution* pp. 233–245. Elsevier, Amsterdam – Oxford.
Timbal, J., Bonneau, M., Landmann, G., Trouvilliez, J. & Bouhot-Delduc, L. 2005. European non-boreal conifer forests. In: Andersson, F. (ed.) *Ecosystems of the World. Coniferous Forests*, pp. 131–162. Elsevier, Amsterdam – San Diego – Oxford – London.

Touchan, R., Baisan, C., Mitsopoulos, I.D. & Dimitrakopoulos, A.P. 2012. Fire History in European Black Pine (*Pinus nigra* Arn.) Forests of the Valia Kalda, Pindus Mountains, Greece. *Tree-Ring Research* 68: 45–50.
Tüxen, R. 1956. Die heutige potentielle natürliche Vegetation als Gegenstand der Vegetationskartierung. *Angewandte Pflanzensoziologie (Stolzenau/Weser)* 13: 4–52.
Van Horne, M.L. & Fulé, P.Z. 2006. Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 36: 855–867.
Vera, F. 2000. *Grazing Ecology and Forest History*. CABI Publishing, Wallingford.
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.H., Pennanen, J. & Burton, P.J. 2011. Long-term decreasing trend in forest fires in northwestern Canada. *Ecosphere* 2: 1–16.
Walter, H. 1968. *Die Vegetation der Erde in öko-physiologischer Betrachtung. Band II: Die gemäßigten und arktischen Zonen*. VEB Gustav Fischer Verlag, Jena.
Wardle, D.A., Walker, L.R. & Bardgett, R.D. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305: 509–513.
Więcko, E. 1984. *Puszcza Białowieska*. Państwowe Wydawnictwo Naukowe, Warszawa.
Wirth, C., Schulze, E.D., Schulze, W., von Stunzner-Karbe, D., Ziegler, W., Miljukova, I.M., Sogatchev, A., Varlagin, A.B., Panvyorov, M., Grigoriev, S., Kusnetzova, W., Siry, M., Hardes, G., Zimmermann, R. & Vygodskaya, N.N. 1999. Above-ground biomass and structure of pristine Siberian Scots pine forests as controlled by competition and fire. *Oecologia* 121: 66–80.
Wodzicki, T.J. & Zajączkowski, S. 1983. Variation of seasonal cambial activity and xylem differentiation in a selected population of *Pinus silvestris* L. *Folia Forestalia Polonica. Seria A* 25: 5–23.
Yamaguchi, D.K. 1991. A Simple Method for Cross-Dating Increment Cores from Living Trees. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 21: 414–416.
Zackrisson, O. 1977. Influence of forest fires on North Swedish boreal forest. *Oikos* 29: 22–32.
Zajączkowski, G., Jabłoński, M., Jabłoński, T., Małecka, M., Kowalska, A., Małachowska, J. & Piwnicki, J. 2014. *Raport o stanie lasów w Polsce 2013*. Państwowe Gospodarstwo Leśne Lasy Państwowe, Dyrekcja Generalna Lasów Państwowych, Centrum Informacyjne Lasów Państwowych, Warszawa.
Zimny, M. 2014. *Późnoholoceńska historia roślinności Puszczy Białowieskiej.* PhD Doctoral thesis, Uniwersytet Gdański, Gdańsk.
Zin, E., Drobyshev, I., Bernacki, D. & Niklasson, M. 2015. Dendrochronological reconstruction reveals a mixed-intensity fire regime in *Pinus sylvestris*-dominated stands of Białowieża Forest, Belarus and Poland. *Journal of Vegetation Science* 26: 934–945.
Zin, E., Niklasson, M. & Szczygieł, R. 2014. Past and present fire regimes in temperate forest zone of lowland Central Europe. In: Viegas, D.X. (ed.) *Advances in Forest Fire Research*, pp. 575–582. Imprensa da Universidade de Coimbra, Coimbra, Portugal.

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