



Long-term effect of wildfires on temperate *Pinus sylvestris* forests: Vegetation dynamics and ecosystem resilience



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ABSTRACT

In Europe, wildfires are considered an integral part of forest dynamics mainly in the Mediterranean region and Fenno-Scandinavia. In temperate forests of Central Europe, by contrast, the ecological role of fire has largely been neglected even though the high frequency of wildfires in naturally fire-prone forests is well documented. In this study, we focused on semi-natural forests dominated by *Pinus sylvestris* in Central European sandstone regions that resemble boreo-continental pine forests, which are claimed to be fire-adapted. We studied the ability of these forests to recover spontaneously after a fire event. Specifically, we observed the development of vegetation composition and diversity, the role of fire severity and the ability of tree species to resist fire, and asked whether wildfires can contribute to the preservation of pine-dominated forests in the region.

Our study takes a space-for-time substitution approach based on a quantitative analysis of vegetation data collected in spontaneously regenerating burnt forest plots of post-fire age ranging from 1 to 192 years. This time span allowed us to reveal the complete successional trajectory and to assess how resistant or resilient the forests are to fire in respect of severity of damage and time needed to return to the pre-fire state.

The resistance of the tree layer turned out to be dependent on species composition and fire severity. The forest understorey, by contrast, could not resist fires even of low-severity. All study stands displayed structural and compositional resilience, resulting in fast recovery of the vegetation cover in all stand layers and return to a similar species composition as in pre-fire stands after about 140 years. However, the species richness remained increased up to the latest successional stage in comparison with mature non-post-fire forest stands. In early post-fire phases, broad-leaved pioneer species and *Pinus sylvestris* regeneration prevailed, but during stand development, there was a continuous shift towards stands with higher proportional abundance of more shade-tolerant and fire-sensitive tree species. Periodic wildfires occurring at least once in 200 years thus seem to be a factor maintaining forests dominated by *Pinus sylvestris* in temperate sandstone landscapes.

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1. Introduction

Fire is an important disturbance factor influencing forest ecosystems worldwide. In the context of the Northern Hemisphere, wildfires are associated mostly with the boreal forest zone or regions with a Mediterranean climate, where it is regarded as an integral part of forest dynamics (Engelmark, 1993; Skre et al.,

1998; Pausas and Vallejo, 1999). The situation in the temperate zone is different. Fire-driven vegetation dynamics has been well documented in temperate pine forests on sandy soils in the NE USA (Hoss et al., 2008); however, the ecological role of fire in temperate Central Europe has traditionally been neglected (Clark and Merkt, 1989; Ellenberg, 1996; Tinner et al., 2005; Niklasson et al., 2010) and wildfires have been regarded only as an adverse consequence of human activity.

However, several recent studies propose that fire plays an important role in the dynamics, stand structure and species composition of specific forest types also in Central Europe (Niklasson et al., 2010; Tinner et al., 2005; Zin et al., 2015). The Holocene

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history of fires and the drivers of fire incidence have newly been documented in temperate *Pinus sylvestris* forests of a Central European sandstone region (Adámek et al., 2015). Such pine forests have a similar species composition and physiognomy as Fennoscandinavian boreal forests (Novák et al., 2012), but in contrast to forests in the boreal region, very little is known about their post-fire vegetation dynamics and succession trajectory.

In the Eurasian boreal zone, wildfires occur mainly in forests of *Pinus sylvestris* growing under drier conditions, where *P. sylvestris* produces resinous and easily flammable litter and forms a relatively sparse canopy allowing the ground layer to dry out (Lecomte et al., 2005). At the same time, *Pinus sylvestris* possesses several fire-adaptation traits: for example, a thick bark, a deep root system and quick regeneration in barren places with mineral soil. Other species occurring in pine forests, such as the dwarf shrubs *Vaccinium* spp. and *Calluna vulgaris*, are also fire-tolerant (Agee, 1998). Regular fires can maintain pine stands also in places where other tree species (e.g. *Picea abies*) would otherwise prevail due to site conditions (Engelmark, 1987; Angelstam, 1998; Gromtsev, 2002). However, this process depends on the frequency and intensity of wildfires. If they are too frequent, young pine trees do not have the time to create a hardy, thick bark, leaving them vulnerable to the next high-intensity fire (Hille and Ouden, 2004). When fires are infrequent or of low intensity, fire-sensitive species are able to survive and outcompete pine species (Niklasson and Drakenberg, 2001; Boucher et al., 2014). Pine-dominated boreal forests are claimed to be resistant or at least resilient to fire, depending on its severity; they stay untouched by wildfires of low severity and recover fast from highly severe fires (Thompson et al., 2009).

Whether fire is an important disturbance factor shaping coniferous and mixed forests of the European temperate zone remains unresolved. So far, no Central European study has dealt with post-fire vegetation development in detail at more than one locality over a period of more than 10 years. Another shortcoming of post-fire vegetation recovery studies is that ecologists have paid little attention to understorey components of the forest. However, understanding understorey vegetation ecology is important for forest conservation and management, since the species composition of the understorey strongly affects tree regeneration (Nilsson and Wardle, 2005).

Detailed knowledge of long-term post-fire forest dynamics of all components of vegetation is essential for understanding the role of wildland fires in Central Europe and is important also for nature conservation and forestry management, as many of such forests are located in natural protected areas. It is probably impossible to apply all the principles being used in northern boreal forests in Central Europe, if only because certain tree species not occurring in the north are some of the principal components of Central European forest communities (e.g. *Abies alba*, *Acer pseudoplatanus*, *Fagus sylvatica*, *Quercus petraea*, *Q. robur*).

To describe post-fire vegetation dynamics, we performed a quantitative analysis of vegetation data collected in spontaneously regenerating forest plots burnt 1–192 years ago. This time span enabled us to reveal the complete successional trajectory and to assess whether fire disturbances can contribute to the preservation of pine-dominated forests even in Central Europe. Specifically, we aimed to answer the following questions:

- (1) What is the rate and dynamics of forest recovery after a fire event?
- (2) How does fire severity influence tree species survival and post-fire vegetation development?
- (3) Which environmental factors explain changes in species composition of burnt forests?

2. Material and methods

2.1. Study regions

The field investigations were undertaken in four protected natural areas in the NW part of the Czech Republic (Fig. 1). Three of the selected regions are sandstone rocky areas characterized by a rugged relief: the Elbe Sandstones (ES) (including the National Park Bohemian-Saxon Switzerland), Kokořínsko (KK) and the Bohemian Paradise (BP). Fourth is the Doksy region (D), a relatively flat sandstone tableland with occasional rocks, characterized as a sandstone pseudokarst in its last stage of development (Novák et al., 2012).

All the study regions are highly forested and situated within the altitudinal range of ca 200–500 m a.s.l. Precipitation and temperature means vary among the regions between 500 and 850 mm and 7 and 8.5 °C, respectively. The prevailing well-drained, nutrient-poor and acidic sandy soils determine a relatively unproductive sites with species-poor acidophilous vegetation, naturally composed of pine and oak-pine forests (*Pinus sylvestris*, *Quercus petraea*) in dryer conditions (typically on sandstone rock tops and upper slopes), beech forests (*Fagus sylvatica*) in moister conditions (middle slopes) and spruce stands (*Picea abies*) in deep and narrow gorges. These communities belong to the vegetation units *Dicrano-Pinetum*, *Vaccinio vitis-idaeae-Quercetum*, *Luzulo-Fagetum* and *Bazzanio-Picetum* (Mikuláš et al., 2007) of the traditional phytosociological system (Braun-Blanquet, 1964).

The first notable traces of human settlement in regions under study come from the Mesolithic (9500–5500 BCE). However, due to unfavourable natural conditions outside fertile lowland areas, the human population there was sparse and restricted to smaller communities of hunters, gatherers, prospectors or outcasts inhabiting rock shelters and having relatively little impact on the ecosystem (Jenč and Peša, 2007). Human impact increased during the Medieval colonization in the 13th century in the form of selective forest harvesting without organized reforestation, wood pasture and the production of tar and charcoal. This took place mainly in easily accessible sites whereas remote areas of rugged terrain remained almost intact. From the beginning of 19th century, the forests started to be managed in an industrial way involving clearcutting and reforestation by target tree species, accompanied by strict fire exclusion. The intensity of management, however, was always more or less influenced by terrain accessibility. This practice ceased during the last decades due to regulations imposed by nature conservancy (Kačmar, 2013). Because of the past intensive forestry management, the regions are mainly covered with stands dominated by planted *Pinus sylvestris* and *Picea abies*. However, during the natural succession since the last harvest (up to the approximate age of 170 years), other species enter the plantations, and thus forests stands can be considered as semi-natural (Winter et al., 2010).

Compared to the rest of the Czech Republic, forest fires occur markedly more frequently in these regions (Kula and Jankovská, 2013), probably because of the prevalence of easily flammable *Pinus sylvestris* forests on sandy substrates (e.g. Engelmark, 1987; Agee, 1998; Angelstam, 1998; Gromtsev, 2002; Wallenius, 2002). The frequency of fires is on average three per year per 100 km² of forested land. The extent of burnt areas varies among the regions. The average and median size of burnt areas ranges from 0.75 ha and 0.08 ha on rugged rocky terrain (ES) to 2.47 ha and 0.57 ha on relatively flat terrain (D). The majority of fires are caused by people (e.g. tourists or forestry workers), but lightning-ignited fires occur regularly as well (Adámek et al., 2015). Mentions of local forest fires are found also in historical records (Belisová, 2006) and were detected in a recent palaeoecological survey (Bobek, 2013). Nowadays, all fires are being

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