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Wildfire as an ecological factor in the forests of Central Europe

Disertační práce

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Prohlášení:

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Podpis

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The Havraní skála rock in the Bohemian Switzerland National Park, burned in 2006. Nine years after the fire.

Contents

Abstract
On the Northern Hemisphere, wildfires are considered to be an integral part of natural dynamics mainly in boreal forests and Mediterranean ecosystems, and most recently also in temperate forests of Northern America. By contrast, in temperate forests of Central Europe, the importance of wildfire for forest ecosystems has been traditionally marginalised despite documented frequent wildfire occurrence and existence of fire-prone forests. Apparently, the reason of this rooted attitude does not lie in the specific environmental conditions of Central Europe, but more likely in the traditional forest ecology approach, which generally does not consider the effect of disturbances on the shape of vegetation communities and strictly excludes human activity from natural processes since its beginnings. This attitude resulted in the lack of knowledge about local vegetation-wildfire relationship and patterns of wildfire occurrence in the landscape. The general aim of this thesis was to clarify the ecological role of wildfires for Central European forest ecosystems with a focus on *Pinus sylvestris* forests and using the Czech Republic as a model area for a broader region.

Chapter 1 deals with the spatial analysis of the occurrence of forest fires in the Czech Republic. We found that the presence of wildfire in this cultural landscape is controlled mainly by the environmental factors, while the wildfire frequency is driven mainly by the human factors, the most common ignition trigger. However, wildfire frequency was driven also by the density of cloud-ground lightning strikes. We traced naturally fire-prone areas in the landscape, which are determined mainly by a high proportion of coniferous forests in lower altitudes, ruggedness of the relief and occurrence of drainable soils. Striking example of such areas are the sandstone “rock towns” of the North Western part of the Czech Republic.

Chapter 2 is focused on one of such “rock town” areas in the Bohemian Switzerland National Park. We used a combination of recent forestry data and soil charcoal concentration values to compare the factors influencing wildfire occurrence patterns on decadal and millennial scales. The results of both analyses corresponded with the main driving factors of the wildfire incidence being topographic features, namely the heat load index and presence of rocks. An additional important factor was especially the *Pinus sylvestris* abundance, while human factors were of marginal importance. Since the topographic factors were stable over the time, we concluded that wildfires, regardless whether of human or natural origin, have been occurring in similar fire-prone habitats at least since the Subatlantic period which could result on such sites in the development of fire-adapted vegetation. The results of the analyses were also used for the creation of the wildfire risk prediction for the National Park territory.

Chapter 3 deals with the study of 192 years lasting spontaneous post-fire vegetation development of semi-natural *Pinus sylvestris* forests of four sandstone regions. The survey was focused on the forest resistance and resilience to wildfire and the role of fire severity and environmental factors on the post-fire vegetation dynamics. We found that the resistance of the tree layer turned out to be dependent on species composition and fire severity, while even low-severity fires induced great changes in the understorey species composition. The forests displayed structural and compositional resilience, resulting in fast recovery of the vegetation cover and return to a similar species composition to pre-fire stands after about 140 years. We noticed a continuous shift from initial prevalence of the regeneration of *Pinus sylvestris* and broad-leaved pioneer species towards higher proportional abundance of shade-tolerant and fire-sensitive tree species. Thus, periodic wildfires occurring at least once in 200 years seem to be a factor maintaining *Pinus sylvestris* forests in temperate sandstone landscapes.

These results indicate the wildfire occurrence in Central European landscape is subjected to similar rules like in the other regions, where wildfire is considered an integral part of forest dynamics. Moreover, wildfire turned out to be an important factor shaping Central European forest vegetation in the long-term, at least within certain regions and forest types.

Abstrakt
V rámci lesů severní polokoule je požár považován za přirozenou součást dynamiky zejména v mediteránních ekosystémech a boreálních lesích a nově také v temperátních lesích Severní Ameriky. V případě temperátních oblastí střední Evropy byl však ekologický význam požárů pro lesní ekosystémy tradičně přehlížen i přes jejich relativně častý výskyt, zejména v některých oblastech a lesních typech. Příčinou tohoto přehlížení nejsou specifické přírodní podmínky střední Evropy, ale spíše tradiční přístup lesnické ekologie, který v úvahách o fungování lesních společenstev nebere v potaz vliv disturbancí a striktně vyčleňuje vliv člověka z přírodních procesů již od jeho prvopočátků. Tento přístup vedl k současnému nedostatku studií o vlivu požáru na vegetaci a zákonitostech výskytu požárů v krajině. Hlavním cílem této práce bylo objasnit ekologickou roli požárů pro středoevropské lesní ekosystémy se zaměřením na borové lesy, přičemž území České republiky bylo využito jako modelová oblast pro širší geografický region.

Kapitola 1 se zabývá prostorovou analýzou výskytu lesních požárů v České republice. Zjistili jsme, že výskyt požárů v této kulturní krajině je řízen především faktory prostředí, zatímco frekvenci požárů ovlivňují zejména lidské faktory, které jsou nejčastějším zdrojem zážehu. Frekvence požárů však závisela také na hustotě výskytu blesků, přirozené příčině požárů. Identifikovali jsme tak v krajině oblastizvláště náchylné k požárům, které se vyznačují především vysokým podílem jehličnatých lesů v nižších nadmořských výškách, členitostí terénu a výskytem propustných půd. Typickým příkladem takovýchto oblastí jsou pískovcová skalní města severozápadní části České republiky.

Kapitola 2 je zaměřena na konkrétní pískovcovou oblast, NP České Švýcarsko. Použili jsme kombinaci současných lesnických dat a hodnot koncentrace uhlíků v půdě k porovnání faktorů, které ovlivňují výskyt požárů na desetileté a tisícileté škále. Výsledky obou analýz si odpovídaly. Výskyt požárů nejvíce ovlivňovaly topografické faktory, konkrétně index tepelného požitku a větší zastoupení skal. Dalším důležitým faktorem bylo zejména zastoupení borovice, zatímco lidské faktory měly pouze okrajový vliv. Vzhledem k tomu, že topografické faktory jsou v čase neměnné, dospěli jsme k závěru, že požáry se vyskytovaly na podobných k požárům náchylných stanovištích přinejmenším od Subatlantiku. Na těchto lokalitách se tak mohla během tohoto období vyvinout vegetace podmíněná pravidelným výskytem požárů. Výsledky těchto analýz byly také použity pro vytvoření predikce požárového rizika pro území NP České Švýcarsko.

Kapitola 3 se zabývá výzkumem spontánní, 192 let trvající sukcese vegetace polopřirozených borů čtyř pískovcových oblastí po požáru. Cílem výzkumu bylo zjistit, jak jsou tyto lesy rezistentní a resilientní k požáru a jak intenzita požáru a další faktory prostředí ovlivňují dynamiku vegetace po požáru. Zjistili jsme, že rezistence stromového patra závisí na intenzitě požáru a jeho druhovém složení, zatímco i požáry nízké intenzity způsobily výrazné změny druhového složení podrostu. Bory projevily značnou resilienci k požárům, což vedlo k rychlé obnově pokryvnosti všech vegetačních pater a podobného druhového složení jako před požárem po přibližně 140 letech. Zaznamenali jsme kontinuální posun od počátečního hojného výskytu semenáčků borovice a pionýrských druhů listnáčů směrem k vyššímu poměrnému zastoupení zmlazení stínumilných a požáru citlivých druhů dřevin. Proto se požáry vyskytující se s frekvencí nejméně jednou za 200 let zdají být faktorem udržujícím borové lesy v pískovcových oblastech temperátní střední Evropy.

Tyto výsledky naznačují, že výskyt požárů ve středoevropské krajině podléhá podobným zákonitostem jako v jiných oblastech světa, kde je požár považován za nedílnou součást dynamiky lesních ekosystémů. Požár se navíc zdá být důležitým faktorem, který ovlivňoval podobu středoevropských lesů v dlouhodobém horizontu, což se týká alespoň některých lesních typů a oblastí.

Introduction

Wildfire represents a disturbance factor that has shaped forest ecosystems worldwide (Engelmark, 1987; Skre et al., 1998; Pausas and Vallejo, 1999; Podur et al., 2003) and throughout the whole history of terrestrial life with an important evolutionary effects on the biota (Pausas and Keeley, 2009). The main natural cause of wildfire is the lightning strike (Pyne et al., 1996), while the other possible sources of ignition might be, for example, volcanic eruptions, meteoritic impacts, sparks from falling rocks or spontaneous combustion (Kozlowski and Ahlgren, 1974). Since the humanity mastered the fire, the most important source of ignition in many parts of the world is man. However, spatio-temporal fire occurrence patterns with important consequences for the development of ecosystems are controlled by a complex interplay of climatic, biotic, and abiotic conditions, combined with human activity (Marlon et al., 2013). Thus, in considerations on the importance and effects of fire on ecosystems, it is necessary to take into account all these variables.

Such close connection of humans with fire, in contrast to other natural disturbance factors, has probably led in its long-term negligence in scientific considerations on the functioning of natural ecosystems. The importance of fire for forest ecosystems started to be evident at first to the ecologists during the second half of the 20th century due to the striking changes that followed after the period of intensive fire suppression related to the development of industrial forestry (Zackrisson, 1977). A new branch of ecology, fire ecology, emerged with a focus on studying species fire-adaptive strategies and fire-dependent ecosystems (Arno and Allison-Bunnell, 2002). In the context of the Northern Hemisphere, as fire-dependent ecosystems have been recognized mainly Mediterranean ecosystems, boreo-continental coniferous forests, temperate pine forests and most recently also mixed and deciduous forests of Northern America (Kozlowski and Ahlgrlen, 1974; Abrams, 1992; Goldammer and Furyaev, 1996; Pausas and Vallejo, 1999). Although some of these forest ecosystems have comparable species composition and physiognomy to Central European temperate forests, the common attitude of modern Central European forest science is that fire is not considered to be a factor that plays an important role in local forest ecosystems and thus this scientific topic is traditionally neglected (Clark and Merkt, 1989; Ellenberg, 1996; Tinner et al., 2005; Stähli et al., 2006; Niklasson et al., 2010). The emerging question is whether the reason for such striking negation of fire, in contrast with recent ecological knowledge from other regions, lies in natural conditions of Central Europe or whether this is just a scientific relic. The clarification of the ecological role of fire for the forests of Central European region is the general topic of this thesis. More detailed information on the above mentioned topics is provided in the following text.

Fire ecology

Fire ecology is the study of the interaction between wildfire and biotic and abiotic environment, where wildfire is recognized as a natural process and often an integral part of the ecosystem in which it occurs (nature.com). It represents a relatively new branch of modern ecology that developed in the second half of the 20th century as a scientific reaction to commonly deep-rooted attitude on wildland fire being an alien and destructive factor for ecosystems (Boerner, 1981). Such attitude was typically demonstrated by the forestry practice which was focused on strict wildfire suppression in forests. However, the U.S. ecologists became aware that alteration of natural pre-settlement fire regimes of coniferous fire-prone forests resulted in the degradation of ecosystems and simultaneously in the occurrence of catastrophic wildfires of high intensity due to fuel accumulation. Thus, fire ecology was closely associated with the search for the suitable forest management practice of the purpose of wildfire prevention and nature conservation (Arno and Allison-Bunnell, 2002).

The basis of fire ecology is formed by the following concepts:

1) **Fire dependence and adaptation**: This concept assumes that certain natural communities are fire-dependent. They are composed of fire-dependent species, requiring fire to persist and thrive and the fire-adapted species, which are capable of living in a recurrently burned ecosystem. This provides them an advantage in competition with other species in such conditions (fws.gov; Keeley et al., 2011).

2) **Fire History**: This concept describes how often fires have occurred in a given geographical area. Recent past period can be studied using the historical records, more distant periods by dendrochronological analysis of fire-scarred trees or by various palaeoeological methods (interwork.sdsu.edu).

3) **Fire Regime**: A natural fire regime is the total pattern of fires over time that is typical for a natural region or ecosystem. It describes the patterns of fire seasonality, frequency, size, spatial continuity, intensity, type (crown fire, surface fire, or ground fire), and severity. A fire regime is a generalization based on the characteristics of fires that occurred over a long period. Fire regimes are often described as “cycles” or “rotations” with the estimation of the fire return interval because natural wildfires usually occur in forest ecosystems periodically (fs.fed.us; Sannikov and Goldammer, 1996).

The specifics of fire disturbance

The most important natural disturbance factors influencing forest dynamics are, apart from fire, wind, snow, flooding and insect outbreaks (Angelstam, 1998). Similarly to other types of disturbance, the activity of fire temporarily reduces vegetation biomass and changes local biotic and abiotic conditions (Agee, 1998; Lloret et al., 2005). However, the effects of fire on forest ecosystem differ in some features from other disturbances types. Fire eliminates low and sensitive species in favour of species that are able to survive or easily regenerate in burned places. Apart of the change of light and thermal regime caused by vegetation cover removal, it also directly affects chemical, physical and biological qualities of the soil (Agee, 1998; Lloret et al., 2005).

Generally, fire consumes organic soil layers that is accompanied by rapid release of available nutrients in inorganic form (mainly N and P) and by the increase of pH due to the denaturation of organic acids and the release of the alkaline cations (Ca, Mg, K, Na) bound to organic matter. The marked changes in soil properties are usually of short nature, lasting from several months to several years (Certini, 2005). However, these changes depend strongly on fire temperature and duration where high intensity fires can decrease the amount of nutrients due to its volatilization, which concerns mainly N and S (Hernández et al., 1997). Other important product of combustion is the charcoal. It acts in the soil similarly to the active carbon by adsorbing inhibitive allelopathic phytotoxins and humic acids, supporting thus the germination of seeds and the seedling recruitment (Hille and den Ouden, 2005; Zackrisson et al., 2010).

In contrast to wind disturbances, fire reduces forest necromass that is followed by rapid nutrients release (Uotila et al., 2005) and baring of mineral soil in larger extent than after windthrow. Wind blows down mainly large mature trees while shade-tolerant understory trees are released. By contrast, fire preferentially destroys understory which is usually replaced by the regeneration of light-demanding tree species (Sinton et al., 2000). However, the immediate effect of a disturbance depends on its severity. Thus, the impact of fire varies from totally stand-replacing crown fires to low-severity surface fires which do not almost disrupt the tree canopy with consequences for further stand development (Baird et al., 1999; Weisberg, 2004). Periodic fires can shift the ecosystems from the equilibrium with local environmental conditions towards "fire climax" dominated by fire-adapted species (Meeker and Merkel, 1984).

Plant adaptations to fire

There are many traits which provide a fitness advantage for plant species in ecosystems facing recurrent fires and these markedly vary with given fire regime. That happens because species are not simply "fire-adapted" but are rather adapted to a particular fire regime, which mainly includes fire frequency, fire type, fire intensity and the patterns of fuel consumption (Keeley et al., 2011). The main division in the function of adaptive plant traits to fire is between the adaptations to the fire regimes characterized by less frequent but high-intensity stand-replacement (crown) fires and by more frequent low-intensity surface fires.

Tree species adapted to surface fire regimes tend to resist the fires. These occur typically in Western USA forests and in Savanna ecosystems. Their adaptations can be demonstrated on the example of a thick bark protecting the cambium from the heat, height and self-pruning of dead lower branches which ensures a gap in fuels between the dead surface litter and live canopy (Pausas et al., 2004). Such adaptations occur with many coniferous species like North American *Pinus ponderosa*, *P. rigida*, *P. resinosa*, *Pseudotsuga menziesii*, *Larix occidentalis* (Starker, 1934), *Sequoiadendron giganteum* (Chang, 1996), European species like *Pinus canariensis*, *P. pinea*, *P. sylvestris*, *P. nigra* (Fernandes et al., 2008) and *Quercus* spp. (Starker, 1934; Graves et al., 2014). The resistance to fire usually rises with the increasing age of a tree individual (Fernandes et al., 2008).

The adaptations on high-intensity crown fire regimes are characterized by different traits mostly affecting species resilience. One example is serotinous cones of coniferous species that require the heat from a fire to open and release seeds. Species with serotinous cones typically have thin bark and retain lower dead branches allowing the fire to reach tree crown so they are mostly killed by the fire. These traits are claimed to be simultaneously an adaption for nutrient-poor conditions where the lack of nutrients does not allow sufficient growth to keep the canopy away from surface fuels. Nutrient-rich seeds stored in tough cones are thus protected against herbivores better than in the soil bank (Keeley et al., 2011).

Examples of such species are North American *Pinus contorta*, *P. banksiana*, *P. attenuata*, European *P. halepensis* and *P. brutia* (de las Heras et al., 2012). However, also many other species have serotinous cones or fruits, including e.g. *Sequoiadendron giganteum* and Australian taxa *Eucalyptus* spp. and *Banksia* spp. (Crawford et al., 2011).

Many species can survive and quickly recover after high-intensity fires by resprouting from underground or aboveground organs even if 100% of aboveground part was scorched by fire. However, resprouting ability after a disturbance is a widespread trait among the plants and it is assumed it also evolved under different evolutionary pressures other than fire (Lloret et al., 2005). An example of a clear adaptation to fire is the lignotuber, a woody swelling located at the root-stem transition containing storage nutrients and morphologically protected dormant buds enabling the plant to resprout after a fire event. Plants possessing lignotubers include *Eucalyptus* spp., *Banksia* spp., *Arbutus* spp. and some species of oaks, e.g. Mediterranean *Quercus suber*, where lignotuber occurs only in seedlings stage (Molinas and Verdauguer, 1993; Paula et al., 2015). Another type of resprouting associated with fire disturbance is epicormic sprouting which enables resprouting from scorched aboveground stems from dormant buds set beneath the bark. Species capable of epicormic sprouting include *Eucalyptus* spp., *Banksia* spp., *Quercus suber*, *Pinus canariensis* or *P. rigida* (Govindaraju and Cullis, 1992; Pausas, 1997; Climent et al., 2004).

Some species survive and regenerate after fire from propagules (seeds, fruits) stored in a canopy seed bank (serotinous species) or in a persistent soil seed bank. The germination of the seeds is often triggered by heat shock or combustion chemicals (Pausas et al., 2004). The majority of these species occur in Mediterranean fire-prone ecosystems including European Mediterranean basin. Heat-stimulated germination is linked to the rupture of the seed coat in species with water-impermeable seeds, e.g. in *Cistaceae* and *Fabaceae*. Smoke-stimulated germination independent on the heat-shock was proved e.g. in *Ericaceae* (*Erica umbellata, E. terminalis, E. multiflora*), *Lamiaceae* (*Lavandula latifolia, L. stoechas, Thymus vulgaris, Rosmarinus officinalis*) and *Primulaceae* (*Coris monspeliensis*) (Moreira et al., 2010).

Some plants in fire-prone environments have no persistent seed bank when fire occurs. These species rely on post-fire (pyrogenic) flowering and the production of non-dormant seeds to exploit favorable post-fire establishment and growth conditions. Typically, it concerns Australian flora, e.g. *Doryanthes* spp. and *Telopea* spp. (Denham and Auld, 2002).

Plant flammability that increases the frequency and intensity of fire can be seen as another type of fire adaptation. The traits increasing flammability include e.g. small leaves, volatile organic compounds or retention of dead leaves and branches. This strategy could be selected to gain a competitive advantage over more fire-sensitive neighbors or due to enhanced seedbank survival by limiting deposition of dead fuels on the soil surface (Keeley et al., 2011). However, the adaptive value of such strategy, referred also as “Mutch hypothesis” (Mutch, 1970) or “Kill thy neigbour” strategy (Bond and Midgley, 1995), was not sufficiently proved, thus it still remains highly disputable (Bowman et al., 2014).

Fire-dependent forests ecosystems of the Northern Hemisphere

This section focuses on forest ecosystems of the temperate and continental/boreal climatic zone of the Northern Hemisphere, in accordance with the Köppen–Geiger climate classification system (Peel et al., 2007), where fire has been recognized an important driver of natural dynamics.

<u>Northern America</u>

Ponderosa pine forests

Ponderosa pine (*Pinus ponderosa*) ecosystems occur as a transition between grasslands and deserts at lower elevations and higher level Alpine communities up to about 3200 m a.s.l., thus occurring in both dry and moist conditions. These ecosystems are found in the Western part of the USA, sometimes as nearly pure stands of *P. ponderosa*, and sometimes mixed with other species, such as *Pseudotsuga menziesii*, *Populus tremuloides, Larix occidentalis, Pinus contorta, Abies grandis*, *A. concolor* or *Thuja plicata.* The characteristic surface cover in a ponderosa pine forest is a mix of grass, forbs, and shrubs. The natural fire regime has a cycle of approximately 20 years in dry sites up to approximately 60 years in mesic sites. These fires tend to be low-intensity ground fires that remove woody shrubs and favor grasses, creating open, park-like ponderosa stands.

P. ponderosa is well adapted species to high-frequency, low-intensity fires. These fires burn litter and release soil nutrients, thus providing a good seedbed for ponderosa pine seeds. For the first five years of their life cycle, ponderosa pines are vulnerable to fire. Eventually, at about five or six years of age, the tree begins to develop thick bark, deep roots and shed lower branches. These factors increase its ability to withstand fire and decrease the possibility of crown fire, which can kill ponderosa pines. Ponderosa needles on the ground facilitate the spread of low intensity ground fires and reduce grasses that can intensify ground fires. *P. menziesii* is commonly found in association with ponderosa pine, but is able to survive without fire. However, also *P. menziesii* is resistant to fire, even more than most other conifers. Additionally, *P. menziesii* regenerates readily on sites that are prepared by fire. In fact, nearly all the natural stands of *P. menziesii* in the USA originated following the fire. Fire exclusion in ponderosa forests caused the shift of species composition towards higher proportion of *P. menziesii* and *Abies* spp., in changes in stand structure and accumulation of fuel, which resulted in destructive high-intensity crown fires (nifc.gov; Graham and Jain, 2005).

Lodgepole pine forests of the Rocky Mountains

Lodgepole pine (*Pinus contorta*) forests occur mostly in upper montane to subalpine elevations of the Rocky Mountains and adjacent regions, including the Yellowstone National Park. These forests can both be maintained by recurrent fires as various post-fire seral stages or can be edaphically dependent, occurring on well-drained, shallow and nutrient-poor acidic soils on pumice deposits, volcanic ash, glacial till or fractured quartzite bedrock. In this ecosystem, a mean fire interval is 100-200 years, and about 80% of these fire events are high-intensity stand-replacement crown fires. *P. contorta* produces nonserotinous (open) cones for

20-30 years and afterwards serotinous cones that release seeds after fire, resulting in fast post-fire regeneration. The most fire-prone developmental stages are dense regeneration and over-mature stage with accumulated fuel. Fire-free intervals less than the life span of *P. contorta* favor its dominance while greater intervals and the loss of standing dead trees with closed cones, favor dominance by other trees. Since *P. contorta* is light-demanding species, old unburned forests are replaced by shade-tolerant coniferous species like *Abies grandis, A. lasiocarpa, Pseudotsuga menziesii or Picea engelmannii* (Crawford, 2011).

Jack pine forests of the Great Lakes region

These forest communities typical for the boreal region of the Great Lakes are also known as Jack pine barrens. They occur on flat glacial lake plains with nutrient-poor, acidic, drained sandy soils, sandy riverine terraces and glacier moraines. The ecosystem is formed by a shifting mosaic of pine stands and dry sand prairie, with species composition and community structure varying with fire frequency and fire intensity. The dominant tree is Jack pine (*Pinus banksiana*) which is mixed with other tree species like *Pinus resinosa, P. strobus, Quercus ellipsoidalis, Prunus serotina, Populus* spp. (aspens) or *Betula papyrifera*. The understory is composed of dwarf shrubs (e.g. *Vaccinium angustifolium*), *Salix humulis, Pteridium aquilinum* and graminoids like *Carex* spp., *Avenella flexuosa, Koeleria macrantha* or *Stipa spartea.* Severe crown fires occur in this ecosystem with a return interval of about 100-200 years (Whitney, 1986). *Pinus banksiana* is a fire-adapted tree species requiring mineral soil for germination, with serotinous cones that release seed after crown fires. When fire is withheld from *P. banksiana* stands, they are replaced by other boreal tree species and the hardwoods that occur in this ecosystem. Fire also limits the dominance of mat-forming *Carex pensylvanica*, maintaining a higher diversity of grasses and forbs. Fire suppression also causes changes to the ecosystem structure, shifting opened vegetation mosaic into closed canopy forests. Fire management is an important tool to restoration and continued existence of this ecosystem, since these forests were strongly affected by human activity after European settlement (mnfi.anr.msu.edu; nifc.gov).

Atlantic coastal pine barrens

The Atlantic Coastal Pine Barrens is a disjunctive ecoregion of the coastal plain of New Jersey and adjacent regions. It differs from neighboring ecoregions by the combination of hydrologic, soil and vegetation conditions and related fire regimes. The region has a wide variety of ecosystems, including swamps, meadows, stunted pine and oak forests, peat bogs, heathlands and coastal salt ponds, dune systems. The region has humid continental climate but it lies on nutrient-poor, acidic and excessively drained soils. The upland forests are commonly dominated by *Pinus rigida* (Pitch pine) and in lesser extent by several species of oak, with understorey formed of *Ericaceae* heaths (*Gaylussacia* spp. and *Vaccinium* spp.) with other fire-adapted species such as *Pteridium aquilinum*. Fires are frequent in such forests due to drained soils and thick litter layer (Boerner, 1981). *Pinus rigida* has various adaptations to frequent fire, including thick bark, the ability to resprout from basal or epicormal buds, early initiation of reproduction and variable levels of serotiny. Its seedlings are shade intolerant and require bare mineral soil establish, suggesting that its dominance is disturbance-dependent (Landis et al., 2005). The post-fire recovery of the ecosystem is quick since most of its biomass survives after the fire. Also, the co-occurring oak species such as *Quercus velutina, Q. marilandica and Q. ilicifolia Q. prinus, Q. stellata, Q. falcata, Q. coccinea, Q. alba* and *Q. prinoides* exhibit basal sprouting, high early growth rate of sprouts, prolific early seed production and development of large root crowns under a regime of frequent fires (Boerner, 1981). Thus, frequent wildfires with fire return interval of 5-30 years have historically maintained this highly fire-adapted ecosystem (nifc.gov).

Northern American boreal forests

The Northern American boreal forest is a mosaic of pure deciduous and mixed deciduous-coniferous to pure coniferous stands. The prevailing tree species are *Pinus banksiana* (Jack pine), *P. contorta* (Lodgepole pine), *Picea mariana* (Black spruce), *P. glauca* (White spruce), *Abies balsamea* (Balsam fir), *Betula papyrifera* (White birch), *Populus tremuliodes* (Quaking aspen) and *Thuja occidentalis* (White cedar). Wildfires that are caused by lightning-strike or human activities are the main disturbance factor shaping boreal forest, which is actually a mosaic of stands of different ages since they last burned (Fauria and Johnson, 2008). The most fire-dependent species are *Pinus banksiana* and *P. contorta* with serotinous cones, which would have probably disappeared as a natural component of the boreal forest landscape in the absence of fire. They colonize the early post-fire successional phases together with *Populus tremuloides* and *Betula papyrifera*, which are able to recolonize disturbed areas also vegetatively by stem sprouts and root suckers (Weber, Michael G. and Stocks, 1998). Typical plant species to be found in burnt areas is the fireweed (*Epilobium angustifolium*). *Picea mariana* is another species adapted to crown fires. It possesses semi-serotinous cones enabling the tree regeneration immediately after a fire. However, this species grows slower on open sites than the pioneer species. Without a fire in more than 100 years, it can replace the post-fire cohort of pioneer species, being more shade-tolerant and capable of establishing under canopy layer (Johnstone et al., 2009). In contrast, species as *Abies balsamea*, *Picea glauca* and *Thuja occidentalis* have no special adaptations to fire and are, in fact, late-successional species. Thus, these species are rare in areas that are repeatedly severely burned (nrcan.gc.ca).

<u>Eurasia</u>

Eurasian boreal forest

Eurasian boreal forest (Taiga) is less rich in tree species than boreal forest of North America. Although Eurasian boreal tree species lack pronounced fire adaptations like serotiny or epicormics sprouting, past and recent fire frequencies seem to be rather comparable between both continents (Zackrisson, 1977; Rogers et al., 2015). Equally, throughout the 20th century, fire has been recognized as an important driver of natural dynamics and a pre-requisite for long-term stability of boreal forest also in Eurasia (Zackrisson, 1977), which can be identically to North American boreal forest regarded as a mosaic of various post-fire developmental stages (Gromtsev, 2002). However, there are differences in typical fire regimes, due to the fact that, in contrast to North America, crown fires occur seldom in Eurasia while the surface fires prevail (Gromtsev, 2002; Granström, 1996; Rogers et al., 2015).

Taiga's classification is split into "dark taiga", consisting of shade-tolerant tree species (e.g. *Picea abies*, *P. obovata*, *Abies sibirica*, *Pinus sibirica*), and "light taiga", consisting of light-demanding species (e.g. *Pinus sylvestris*, *Larix sibirica*, *Larix* spp.). Light taiga occurs only where shade-tolerant species fail to grow either due to climatic or edaphic reasons (Mühlenberg et al., 2012; Schulze et al., 2005). Dark taiga species are fire-sensitive species and fires occur there less frequently than in light taiga, which is composed of more fire-tolerant species (Sannikov and Goldammer, 1996). *Pinus sylvestris* is considered to be the most fire-adapted species of boreal Eurasia. It is adapted on prevailing frequent surface fires of low to moderate fire intensity, to which mature trees are resistant due to thick bark, deep root system and self-pruning of lower dead branches, keeping the canopy away from surface fires (Agee, 1998; Fernandes et al., 2008). Fire also stimulates the release of the seeds from cones on the mineral substrate prepared by fire, even though this fire trait is less pronounced than in serotinous pine species (Sannikov and Goldammer, 1996). Recurring fires favour *Pinus sylvestris* against shade-tolerant species *(e.g. Picea abies)* and can therefore maintain pine stands in places where shade-tolerant (climax) species would otherwise prevail due to site conditions (Engelmark, 1987; Angelstam, 1998; Gromtsev, 2002).

Within the Eurasian taiga biome, the frequency of natural (lightning-ignited) fires increases with raising continentality from the West (Fenno-Scandinavia) towards East with the maximum in Western Siberia, and towards South. Farther to the East, the lightning fire frequency rapidly decreases again, probably due to the lower inflammability of the litter of *Larix* spp. which dominates in Eastern Siberia. However, apart from this general pattern, fire regimes are considerably shaped by edaphic and microclimatic conditions driven by topography *(*Sannikov and Goldammer, 1996). Generally, fires occur more frequently in dry and nutrient-poor conditions. Taiga is thus further classified into several types with distinct natural fire regimes, according to site-specific conditions.

1) Permanently wet sites located near the source of water (e.g. water courses), typically dominated by *Picea abies* or deciduous species (*Alnus glutinosa*, *A. incana*, *Salix* spp.). Fire is almost absent there and forest disturbance regime is driven by internal gap-phase dynamics (Angelstam, 1998). These sites represent "no-fire refugia" from where the fire-sensitive species can colonize surrounding burnt areas (Gromtsev, 2002).

2) Moist sites dominated by *Picea abies*. Fire occurs seldom there with frequency < once per 100 years, happening only during extreme droughts. Such fires are usually stand-replacing, followed by succession of deciduous species (*Populus tremula, Betula pendula, B. pubescens*) and later coniferous trees (Angelstam, 1998). The time period between the fire events there is usually long enough for the climax vegetation to be established again (Gromtsev, 2002).

3) The vegetation of the most common mesic sites consists usually of the mixture of *Picea abies* and *Pinus sylvestris* with understory formed by *Vaccinium* spp. and *Empetrum hermaphroditum* dwarf shrubs and plerocarpous mosses such as *Pleurosium schreberii* and

Hylocomium splendens, which provide good fuels during dry seasons. Mean fire-return interval in these sites is below 100 years, where fire probability raises from about 50 years after previous fire due to fuel accumulation and successional development of plerocarpous mosses. After long periods of drought, peat bogs with *Sphagnum* spp. have similar fuel characteristics. Burned coniferous forest is replaced by deciduous phase (*Populus tremula, Betula* spp.), which can be sometimes kept almost permanent by intermittent fires (Angelstam, 1998).

4) Dry sites, dominated mostly by *Pinus sylvestris* with understory of *Calluna vulgaris* and ground lichens (*Cladonia* spp.) burn rather often, with mean fire-return interval of 40-60 years. The tree mortality after the fire is low due to low fuel accumulation and the resistance of pine. Burned gaps are colonized by pine seedlings without deciduous post-fire phase. This process creates typical multi-cohort structure of the natural pine stands (Angelstam, 1998).

The boreal forest vegetation is highly resilient and adapted to recurrent natural disturbances including fires (Zackrisson, 1977; Rydgren et al., 2004). Moreover, wildfire in boreal forests is important in rejuvenating soil properties and encouraging tree regeneration and growth (Zackrisson et al., 1996). Thus prolonged absence of fire may affect the whole forest ecosystem and its functioning by changing the stand structure, species composition and richness. For example, the occurrence of *Populus tremula* in Fenno-Scandinavian boreal forest is fire-dependent (Lankia et al., 2012). This tree species is claimed to be the keystone species for preserving the local ecosystem biodiversity, as many organisms from other trophic levels are dependent on it (Latva-Karjanmaa et al., 2006). The exclusion of fire in Fennoscandia possibly caused a continuous decline in the cover of dominant ericaceous dwarf shrubs *Vaccinium myrtillus*, *V. vitis-idaea* and *Calluna vulgaris* accompanied by the increase of thickness and cover of moss layer. Other ericaceous dwarf shrubs, such as *Empetrum nigrum*, may become dominant without fire (Nilsson and Wardle, 2005). As a species with allelopathic effects, it alters ecosystem function by, for example, reducing tree seedling establishment, microbial activity, and decomposition rates (Hekkala et al., 2014).

Post-fire succession in European boreal forests

The effect of fire on forest vegetation depends on many factors as fire type, intensity and duration, stand composition, age and structure and on local abiotic conditions. These factors influence fire severity, the rate of disruption of vegetation cover and soil organic horizons (Keeley, 2009), that impacts further post-fire vegetation development. Successional pathways also differ geographically depending on local species pool (Engelmark et al., 1998), thus this part is focused mainly on European boreal region.

The post-fire changes in soil chemical and physical properties together with almost complete destruction of ground vegetation (tree regeneration, lichens, mosses, dominant dwarf shrubs) induce changes in understory species composition in the early post-fire stages (Sannikov and Goldammer, 1996). The initial change in species composition and overall species turnover during the stand development is markedly more pronounced after fire than after non-fire forest disturbances (Rees and Juday, 2002; Hekkala et al., 2014). Striking changes occur in moss layer where formerly predominant forest mosses like *Pleurosium* *schreberii*, *Hylocomium splendens* and *Dicranum* spp. are replaced by the constant mixture of fire-related species such as *Ceratodon purpureus, Funaria hygrometrica, Marchandsia polymorpha, Polytrichum juniperinum* and *P. piliferum.* Ericaceous dwarf shrubs are typically replaced by meadow-forest forbs and grasses such as *Epilobium angustifolium, Conyza canadensis*, *Pteridium aquilinum, Avenella flexuosa, Agrostis capillaris, Calamagrostis epigejos* or *Luzula pilosa.* Fire is also followed by intensive regeneration of pioneer tree species such as *Pinus sylvestris, Betula spp*., *Populus tremula* and *Salix capraea* (Rees and Juday, 2002; Marozas et al., 2007; Hekkala et al., 2014). Even though the regeneration of these tree species is markedly stimulated by fire, they can also regenerate in lesser extent in unburned sites or in late successional stages. The only exception is *Populus tremula* whose regeneration in the Taiga was observed only in burned sites (Lankia et al., 2012; Hekkala et al., 2014). Dwarf shrubs such as *Vaccinium spp*. and *Calluna vulgaris* are able to survive even the fire of high intensity in underground rhizomes and to resprout after the fire. During the succession, their abundance increases and it recoveries into the pre-fire values in 5-15 years depending on initial fire severity (Gorshkov and Bakkal, 1996; Marozas et al., 2007, Hekkala et al., 2014). The complete recovery of species composition and characteristics of moss-lichen layer was observed 60-140 years after the fire, depending on vegetation type (Gorshkov and Bakkal, 1996, Gromtsev, 2002).

On the mesic sites, prevailing in European Taiga, the post-fire succession of tree layer begins with deciduous phase dominated by *Betula* spp. and *Populus tremula* with understory of more slowly growing coniferous species (Angelstam, 1998). During this phase which lasts for about 40 years, the probability of the next fire is low due to wet and hardly inflammable litter of deciduous species. After that, the proportion of coniferous species increases due to the self-thinning of deciduous canopy. Without fire, the species composition of the tree layer recoveries after about 120-140 years with only few persisting *Betula* spp. individuals of the post-fire cohort. Than in mature Taiga stands, *Betula* spp. occurs only sparsely in lower canopy. In contrast, *Populus tremula* can regenerate even in later developmental stages by vegetative root suckers. It also has greater competition ability than *Betula* spp. being higher in mature age and due its interconnected root system. Thus, it can retard the succession towards coniferous stage (Gorshkov and Bakkal, 1996, Schulze et al., 2005).

Global history of wildfire

Three essentials are needed to burn a fire: oxygen, fuel, and the source of ignition. Since the source of heat has probably been available throughout the whole history of Earth in the form of lightning, volcanoes or meteorite impacts, the main precondition for fire occurrence was the development of photosynthetic organisms producing oxygen and of terrestrial plants serving as a fuel (Pausas and Keeley, 2009). Thus, the first evidence of wildfire comes from Silur (440 million years ago [mya]) in the form of charred remains of ancient *Rhyniophyta* plants (Glasspool et al., 2004). The global wildfire activity in Paleozoic reflected fluctuating atmospheric oxygen concentration, where combustion was possible from the oxygen concentration above 13%. Although there is the evidence of wildfires from Devon, extensive charcoal deposits did not appear until late Paleozoic when atmospheric oxygen concentration reached 31% in Carboniferous (Pausas and Keeley, 2009). Permic coal contains large proportion of charcoal produced by combustion where high oxygen concentration made even moist vegetation flammable (Bowman et al., 2009). The major fall in oxygen concentration during Triassic can explain relatively sparse fire evidence from that period. However, during the rest of Mesozoic, fires were increasingly important. There is also an evidence of distinct fire regimes comparable with recent fire-dependent vegetation, where Devonian and Carboniferous (395-345 mya) protogymnosperms underwent high-frequency and low-intensity surface fires. In contrast, the wetland lepidodendron forests of the Carboniferous underwent low-frequency crown fires (Pausas and Keeley, 2009). These facts indicate that fire must have had evolutionary effects on terrestrial biota throughout the Earth history (Bowman et al., 2009). However, a substantial peak in charcoal deposits in marine sediments bearing an evidence of increased global fire activity occurs in the late Tertiary, characterized by more seasonal climate (7-8 Mya). It is related with spread of C_4 grasses in open-canopy landscape and forming of the savanna biome which due to its high flammability produced a climatic, self-perpetuating feedback (Bowman et al., 2009; Pausas and Keeley, 2009).

The expansion of the open landscape of African savanna probably markedly influenced the evolution of fauna and promoted the development of bipedal hominids. It has been suggested that the origin of *Homo* spp. about 2.5 Mya in such highly flammable environment probably contributed to the implementation of fire into the evolution of mankind (Ségalen et al., 2007). The earliest evidence of the use of fire by humans comes from about 1.9 Mya and the routine domestic use of fire began around 100 - 50 kya (Bowman et al., 2009). During the Paleolithic and Mezolithic, fire was extensively used also for the non-agrarian land management for various purposes like clearing the ground for human habitats, hunting or maintaining plant resources. Since the Neolithic, fire has been widely used to open forests for agriculture and for managing pastures (Pausas and Keeley, 2009, Vannière et al., 2015).

The global fire activity generally increased since the last Glacial Maximum (ca. 21 kya) which can be attributed to both global warming and increasing human population (Vannière et al., 2015). According to many studies, human activity has positive effect on fire frequency but on the other hand, it reduces the total amount of burned biomass by land-use practice leading to the reduction of fuel load and continuity, and since the modern industrial era, also by the active fire suppression (Marlon et al., 2012; Vannière et al., 2015). However, the human-driven increase in fire frequency in populated areas probably markedly influenced the vegetation composition and development during the Holocene period (Tinner et al., 1999). In summary, one can state that since the onset of human presence in the landscape, climatic- and human-driven fire patterns became interconnected and hardly distinguishable. Thus, observed fire regimes should be regarded as the result of the complex combination of climate, local environmental factors including vegetation and human activities (Pausas and Keeley, 2009; Marlon et al., 2013).

Global wildfire occurrence and the Central European perspective

Wildfires occur most frequently in warm climatic regions with long-lasting dry seasons following after moister periods of vegetation growth, e.g. in Australia, Africa, Mediterranean and South Western USA. In the context of forests of Northern Hemisphere, wildfires are considered to be an integral part of natural dynamics mainly in Mediterranean ecosystems and boreal forests of North America and Eurasia (Agee, 1998; Engelmark, 1993; Skre et al., 1998; Pausas and Vallejo, 1999). The majority of ecological studies concerning wildfire thus come from these regions. The role of wildfire in temperate zone is less clear, however, it is increasingly viewed as an important process for Northern American temperate coniferous, mixed and even for the oak-dominated forests (Abrams, 1992; Odion et al., 2004; Sturtevant et al., 2004; Hoss et al., 2008; Flatley et al., 2011; Brose et al., 2013). Specific forest formations dependent on frequent wildfire occurrence are the pine barrens, a temperate pine-oak forests on sandy soils of North Eastern USA (Boerner, 1981; Scheller et al., 2011). By contrast, the general perception of wildfire in temperate Central Europe is quite different. In this region, ecological role of the fire for functioning of local forest ecosystems has been traditionally neglected (Clark and Merkt, 1989; Ellenberg, 1996; Tinner et al., 2005; Stähli et al., 2006; Niklasson et al., 2010) and wildfire has been perceived just as an adverse product of human activity without any relevance to natural processes. Therefore, this topic has been almost left out from ecological studies of the Central European region.

However, the reasons for this attitude towards wildfire seem to be a complex matter. Part of the temperate Northern American region of numerous fire ecology studies, including New Jersey pine barrens, has the climate that is similar to those of the Central Europe in accordance to the Köppen–Geiger climate classification system (Peel et al., 2006). Thus, the climate of the Central Europe does not seem to be an important reason. The Central European wildfire perspective can more likely be related to the local tradition in forest ecology, namely to the traditionally accepted concept of the potential natural vegetation (Tüxen, 1956) or similar forestry typology (Randuška, 1982) which generally does not consider the effect of disturbances on the shape of vegetation communities (Falinski and Falinska, 1986; Korpel, 1995; Splechtna et al., 2005). When the impact of disturbance on forest dynamics is taken into consideration, it is usually the wind storms and insect outbreak that are mentioned most often (Kulakowski and Bebi, 2004; Svoboda et al., 2010). The other reasons for traditional negation of ecological role of wildfire in Central European forests can be relatively dense human population and long-lasting land-use associated with strong influence of natural vegetation and processes, compared to e.g. Northern America or boreal Eurasia. It appears that the lack of large intact forest areas in Central Europe has hampered the understanding of the natural disturbance regimes (Angelstam and Kuuluvainen, 2004). Broadleaved deciduous forests are hypothetically the most widespread climax vegetation in Central Europe (Chytrý et al 2012) and they are generally perceived as a vegetation type that is not prone to fires, or at least less so than coniferous forests (Clark et al. 1996; Moreira et al. 2001; Sturtevant et al. 2004, Parisien et al. 2011). However, wildfires can occur even in broadleaved forests (Corona et al. 2014; Ascoli et al. 2015). Thus, the relatively frequent occurrence of wildfires in recent man-made coniferous forests has usually been interpreted as a mere adverse consequence of human activity (e.g. Šomšák et al. 2009) and has received little attention of ecologists due to the unnaturalness of such forests. However, contemporary paleoecological studies indicate that coniferous species (especially *Picea abies* and *Pinus sylvestris*) had been much more abundant in lowland forests of the Czech Republic in the Middle and Late Holocene than used to be assumed (Novák et al. 2012; Bobek 2013; Abraham 2014), also because of the consideration of the role of disturbances on the shape of vegetation communities. The other possible reason of traditional overlooking of wildfires in Central Europe in comparison with e.g. Northern America could be the pattern of typical wildfire behavior. Although recent fire frequencies in boreal forests of Northern America and Eurasia almost do not differ, forest fires in Northern America exhibit more likely as spectacular high-intensity crown fires, whereas in Eurasia prevail low-intensity surface fires that rarely reach tree crowns. It has not been explained by different climate but more likely by different fire-adaptive strategies of the tree species. Coniferous forests of Northern America are composed mainly of fire "embracers", whose life strategy is to be killed by the crown fire and subsequently to regenerate from (semi-)serotinous cones that release seeds when burned. The morphological adaptation of such species, which allows fire to reach tree crowns, is the retention of lower branches until the tree maturity. In contrast, Eurasian fire-adapted tree species, like e.g. *Pinus sylvestris*, are more likely fire "resisters", which suppress crown fires by self-pruning of lower branches and resist surface fires owing the protective, thick bark (Rogers et al., 2015).

Either way, wildfire has been recently recognized as an important process also in Central Europe, namely in Alpine regions (Delarze et al., 1992; Tinner et al., 1999; Stähli et al., 2006; Müller et al., 2013; Valese et al., 2014) and in hemiboreal *Pinus sylvestris* forests of Southern Lithuania and Eastern Poland (Marozas et al., 2007; Niklasson et al., 2010; Zin et al., 2015).

The statistics on forest fires in Europe for whole countries indicate that wildfires recently occur in Central Europe (e.g. in the Czech Republic) relatively frequently, markedly more than e.g. in Northern countries. The fires are usually small-scaled, mainly in comparison with Mediterranean countries (Fig. 1). However, wildfire incidence differs among regions within the countries. Thus the southern regions of Fenno-Scandinavian countries seem to be similarly fire-prone to the Czech Republic (www.eea.europa.eu/publications/european-forest-ecosystems, page 43).

If one asks about "naturalness" of the wildfire occurrence which is independent on human activity, some estimation can be provided by the comparison of the spatial density of lightning-ignited forest fires, which reaches in some parts of the USA and in European Alpine regions up to 0.9 fires/(year 100km^2). In the Mediterranean Europe, the average density was estimated on 0.12 fires/(year 100 km^2). In the Czech Republic, which constitute a main study area of this thesis, the average density (0.065) is slightly lower than in Western Siberia (0.075) but higher than in Northern European boreal countries (0.039) (Granström, 1993; Larjavaara et al., 2005; Kula and Jankovská, 2013; Müller et al., 2013). However, this value is regionally specific and such comparison can be distorted also by the quality of the input data, where the numbers of lightning-ignited fires are often underestimated (Larjaavara et al., 2005).

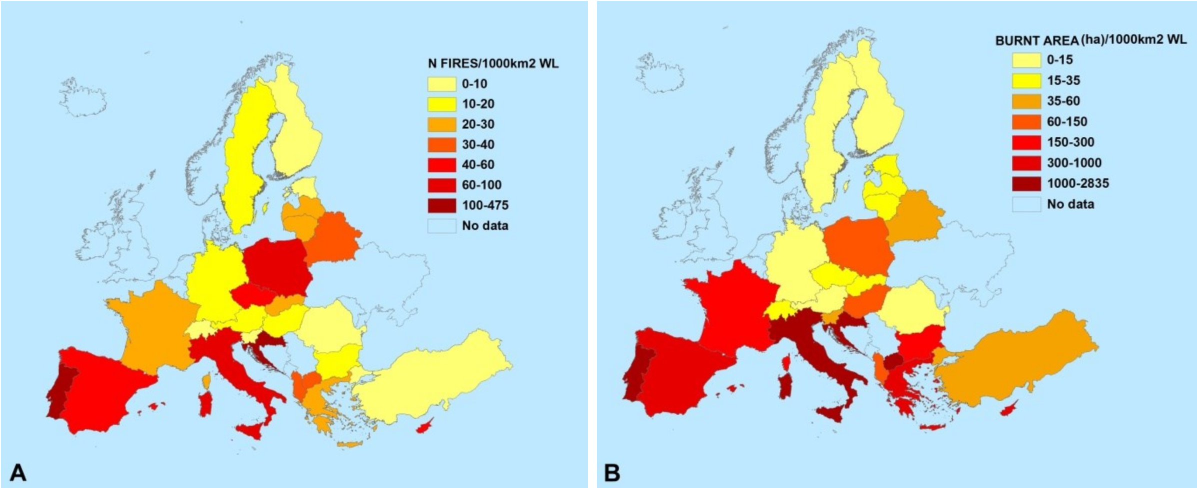

Fig. 1. Mean number of wildfires (**A**) and average burnt area [ha] (**B**) per year per 1000 km^2 of wooded land (WL) in the period of 1980-2010.

Data source:
Forest fires statistics: European Forest Fire Information system (EFFIS); http://effis.jrc.ec.europa.eu
Forest coverage in Europe: State of Europe´s forests 2007: The MCPFE report on sustainable forest management in Europe; http://www.foresteurope.org

Although the forest fire is a natural phenomenon, the main cause of ignition in populated landscapes is the human activity. In Europe, 97% of forest fires of known cause within the period of 2006-2010 were directly or indirectly caused by human agents (Ganteaume et al., 2013). Also, many palaeoecological and fire-history studies suggest that during the Holocene period, fire incidence was markedly positively influenced by human presence in the landscape (Niklasson and Granström, 2000; Vannière et al., 2008; Molinari et al., 2013). Equally, overwhelming majority of recent forest fires in the Czech Republic is caused by humans. From annual average of about 1200 forest fires, 69% are human-caused (fire raising, smoking, and forestry management), 30% are of unexplained causes and 1.4 % are ignited by the lightning strike (Kula and Jankovská, 2013). Since human influence has been long-lasting and integral component of Central European landscape, it is necessary to consider even human-caused fires as a factor shaping Central European forest vegetation through the Holocene period, similarly like in other regions (Tinner et al., 1999; Abrams and Nowacki, 2008).

Considering these facts, the reason of the traditional negation of the ecological role of wildfire in Central European landscape seems to be mostly a matter of socio-cultural memory (Le Goff, 1992) rather than an objective result of specific Central European natural conditions. Thus, overlooking of the role of wildfire resulted in the lack of studies on the fire-vegetation relationship and on environmental factors influencing the wildfire incidence in Central European landscape that can be also applied for the production of predictive models.

Patterns of the wildfire occurrence in the landscape

The spatial distribution of wildfire occurrence in the landscape depends on many factors which determine either the availability of ignition triggers or fire-proneness of a site. Such factors can be anthropogenic, biotic or abiotic and the wildfire occurrence patterns depend mostly on their specific combination, which varies geographically and depends on the spatial and temporal scale (Cardille and Ventura, 2001; Yang et al., 2007; Avila-Flores et al., 2010). Biotic factors, like the vegetation cover, structure and composition, influence the fuel type, load and flammability; abiotic factors, like climate, topography or the soil type, influence the fuel moisture and the spread of the fire (Engelmark, 1987; Cardille and Ventura, 2001; Díaz-Delgado et al., 2004). The frequency of wildfires is generally higher in dry conditions, on convex terrain sites and south-facing slopes and it decreases with increasing humidity, e.g. towards poles, with raising altitude and oceanity of the climate (Angelstam, 1998; Skre et al., 1998; Pew and Larsen, 2001; Futao et al., 2016). Human activity acts mainly as the ignition trigger but it can also indirectly influence the wildfire occurrence by changing the landscape fire-proneness according to the land-use practice (Moreira et al., 2001, Ganteaume et al., 2013). It has been suggested that the human factors can more or less obscure the effects of environmental factors as the climate or topography (Flatley et al., 2011; Zumbrunnen et al., 2012). On the other hand, spatial distribution even of human-caused wildfires can be strongly dependent on environmental factors, where the occurrence of a fire ignition is more dependent on the ability of the fuel to be ignited than on the presence of an ignition agent (Pew and Larsen, 2001).

Forest vegetation characteristics is one of the most important drivers of the fire ignition occurrence, as it directly influences the quality and load of the fuel. It comprises especially the species composition and to a lesser degree the stand age and structure (Bessie and Johnson, 1995; Krawchuk et al., 2006; Fang et al., 2015). Wildfires occur more likely in coniferous forests than in deciduous, correspondingly in Mediterranean, temperate and boreal regions (Díaz-Delgado et al., 2004, Sturtevant et al., 2004, Parisien et al., 2011). However, fire proneness varies also among particular coniferous species. In the Eurasian boreal zone, wildfires are associated mainly with *Pinus sylvestris* forests (Engelmark, 1987; Tanskanen, 2007) whereas the other dominant boreal coniferous species, *Picea abies*, is claimed to be less fire-prone but more fire-sensitive (Wallenius, 2002; Tryterud, 2003). *Pinus sylvestris* grows usually under drier conditions, produces resiny and easily flammable litter and its mature stands form a relatively sparse canopy allowing the ground layer to dry out (Lecomte et al., 2005). At the same time, *Pinus sylvestris* possesses fire-adaptation traits allowing to resist surface fires and to regenerate afterwards (Agee, 1998; Rogers et al., 2015). Other species occurring in pine forests, such as *Vaccinium spp.*, *Calluna vulgaris* or *Pteridium aquilinum* are also fire-adapted (Boerner, 1982; Keatinge, 1975; Tinner et al., 2000). Regular fires can thus 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).

In temperate Central Europe, the conifer-dominated forests occur as well (e.g. Bendel et al., 2006). In the Czech Republic, except of man-made conifer plantations of the production purpose (mainly *Picea abies* and *Pinus sylvestris*), there naturally occur montane spruce forests and pine or pine-oak forests in lower altitudes (Chytrý, 2012). Occurrence of natural pine(-oak) forests is there, according to traditional perspective, restricted on sites with edaphically unfavorable conditions for other tree species, like dry rock tops with shallow soils or on extremely nutrient poor and drainable sandy and gravel soils. Apart from dry sites, *Pinus sylvestris* also naturally occurs on the opposite side of the wetness gradient, in permanently moist peat bogs (Chytrý, 2012). However, during the prolonged periods of drought, peat bogs can burn as well (Angelstam, 1998).

Natural pine formations are known also as "relic pinewoods" because they are claimed to represent a remnants of the vegetation of early postglacial period (Mikeska, 2008). Larger areas of semi-natural pine-dominated forests on nutrient poor substrates are nowadays considered to be a geographically disjunct analogy of boreo-continental pinewoods or a lowland taiga due to their similar physiognomy and species composition to boreal pinewoods (Chytrý, 2012; Novák et al., 2012). The largest region of such pine forests is situated in North Western part of the Czech Republic and is characterized by sandstone bedrock with occasional occurrence of areas of specific sandstone rocky landscapes, so-called "rock towns" (e.g. Elbe Sandstones). Present-day wildfire occurrence in this region is markedly more frequent than in the rest of the country (Kula and Jankovská, 2013) and references about local forest fires are found also in archival historical records (Belisová, 2006). The evidence of pre-historic wildfire occurrence in this region was lately found in the form of charred plant material in the peat and sandy sediments (Pokorný and Kuneš, 2005; Abraham, 2006; Sádlo and Herben, 2007) and pedoanthracological surveys newly confirmed continuous occurrence of *Pinus sylvestris* charcoals through whole Holocene period (Novák et al., 2012; Bobek, 2013). These facts indicate that such ecosystems have been influenced by recurrent wildfires in the long-term. However, the question whether the fire disturbance could play an important role in the dynamics and long-term development of these pine forests, similarly to e.g. American pine barrens or analogous Eurasian boreal forests, and contribute thus to preserve „relict pinewoods“ until recent, still remains unresolved. Such findings would change the traditional perspective on the occurrence of naturally pine-dominated forests of Central Europe to be delimited only by edaphic conditions.

Taking into account the lack of the studies on ecological role of wildfire for Central European forests, it appears useful to study the wildfire occurrence patterns in recent and distant past landscape and to observe the long-term forest vegetation response on the wildfire events to resolve this problem.

Aims of the thesis

The aim of this dissertation thesis is to clarify the ecological role of wildfire in forests of Central Europe with the focus on the Czech Republic as a model area for a broader region. With regard to consistency of the results and availability of suitable study plots, the main focus of the thesis was pointed towards just one conspicuously fire-prone forest type, namely the *Pinus sylvestris*-dominated forests of Czech and German sandstone region. The great advantage of this region, except enough of burnt plots, was also the concentration of protected natural areas, what enabled me to observe the effect of wildfire on relatively preserved forest ecosystems and without post-fire forestry intervention.

Specifically, I asked:

1) Which factors influence the wildfire occurrence in the Central European landscape on various geographical scales?

2) Is the spatial pattern of wildfire occurrence in the cultural landscape driven more by anthropogenic or natural environmental factors?

3) Which environmental factors define the naturally fire-prone areas in Central European landscape?

4) How does wildfire influence the development and species composition of the vegetation of *Pinus sylvestris*-dominated forests of sandstone regions?

5) How resilient and resistant are these forest to wildfires?

6) Is wildfire an important factor conditioning the persistence of “relict pinewoods” in Central European landscape?

Main results

In **Chapter 1**, we aimed to reveal the factors influencing the spatial distribution of forest fires in the landscape of the Czech Republic. We compared the role of environmental and human factors for wildfire occurrence (presence / absence) and frequency (counts) and between two geographical scales: whole country and selected fire-prone region situated in the North Western part of the Czech Republic. Thereafter, we aimed to trace the areas with specific naturally driven fire-prone conditions. As the input data, we used a database of in total 15985 forest fires of the period 1992-2004, localized and digitalized into municipality cadasters. The database was kindly provided by Zuzana Jankovská (Jankovská, 2006; Kula and Jankovská, 2013) and it is a manually verified and further processed forest fire evidence, provided originally by the General Directorate of Fire Rescue Service of the Czech Republic (GR HSZ CR). The predictors of wildfire occurrence were processed as GIS layers of human, topographic, climatic, geological, pedological and forest composition factors. We identified the most important drivers of wildfire occurrence and frequency using GLM and compared their relative importance by the hierarchical partitioning method. We found that the spatial distribution of wildfires in densely populated landscape of the Czech Republic is driven by combination of human, biotic and abiotic environmental factors. Wildfire presence was controlled more by environmental factors, while human factors like the population density strongly influenced the frequency of wildfires, being the most common ignition trigger. However, wildfire frequency on the country scale was positively affected also by the density of cloud-ground lightning strikes, a potential natural source of ignition. We identified the naturally driven fire-prone conditions in the landscape, which consisted mainly of higher abundance of *Pinus sylvestris*, *Picea abies* and *Betula spp.* in lower altitudes, ruggedness of the relief and occurrence of drainable soils. An example of the landscape type, where all these factors interact, are the sandstone "rock towns". In the selected region, where such conditions are prevalent, the effect of environmental factors on wildfire incidence was even more pronounced than on the country scale. The wildfire frequency in local fire-prone *Pinus sylvestris* forests was driven also by the density of lightning strikes of positive polarity. The combination of the fire-prone conditions with the availability of ignition triggers has probably led to the development of local fire-dependent ecosystems.

In **Chapter 2,** we asked whether there is the continuous long-term fire history in the sandstone rocky landscape, the Bohemian Switzerland National Park and whether spatial distribution of recent and ancient wildfires is driven by the same environmental factors. In this interdisciplinary study, we used a combination of contemporary forestry data from the period of 1974-2008 and of pedoanthracological approach to reveal wildfire events in the present-day landscape and in the distant past. As the input data, we used digitalized locations of recent wildfire occurrences and soil probes with measured soil charcoal concentration and GIS layers of topographic factors, derived from LiDAR digital elevation model of resolution 5m, forest age and composition and anthropogenic factors. The time span of analysed ancient wildfires was estimated as ca. 0-3500 years BP by ^{14}C dating of 14 charcoal particles. The recent wildfire distribution was analysed in relation with all available factors using the ENFA method, the soil charcoal concentration was analysed in relation to temporally stable topographic factors only, using linear regression. We identified the factors influencing fire occurrences in the landscape on two temporal scales, decadal and millennial. The results of the analyses of soil charcoal concentrations corresponded with those of contemporary forestry data. The main driving factors affecting the wildfire incidence in such rugged landscape were topographic features, namely the heat load index and the presence of rocks. Additional important factors were forest composition features, especially the abundance of *Pinus sylvestris*. Quite surprisingly, even though the landscape is populated and attractive to tourists, present-day anthropogenic factors like the proximity of villages, tourist paths and roads had only marginal effects on wildfire occurrence. The results indicate that fires have been occurring in similar fire-prone habitats, namely the elevated rock plateaus and south western slopes, at least since the Subatlantic period. The vegetation of such sites, which is recently represented mostly by semi-natural *Pinus sylvestris*-dominated stands, thus has to be influenced by recurrent wildfires for millennia. Considering how well *P. sylvestris* and its understorey species are adapted to fire, we assumed that the natural occurrence of Scots pine forests in the landscape of the Bohemian Switzerland National Park partly depends on wildfire activity. This especially concerns *P. sylvestris* stands on deeper soils, where other tree species like beech or oak are presumed to form climax forests.

Additionally, we created the map of the wildfire risk for the Bohemian Switzerland National Park territory based on the recent wildfire spatial distribution, using the ENFA method (Fig. 2). This practical output was conducted for the purposes of the national park authority and was published in the study of Adámek et al. (2013), which is not included into this thesis.

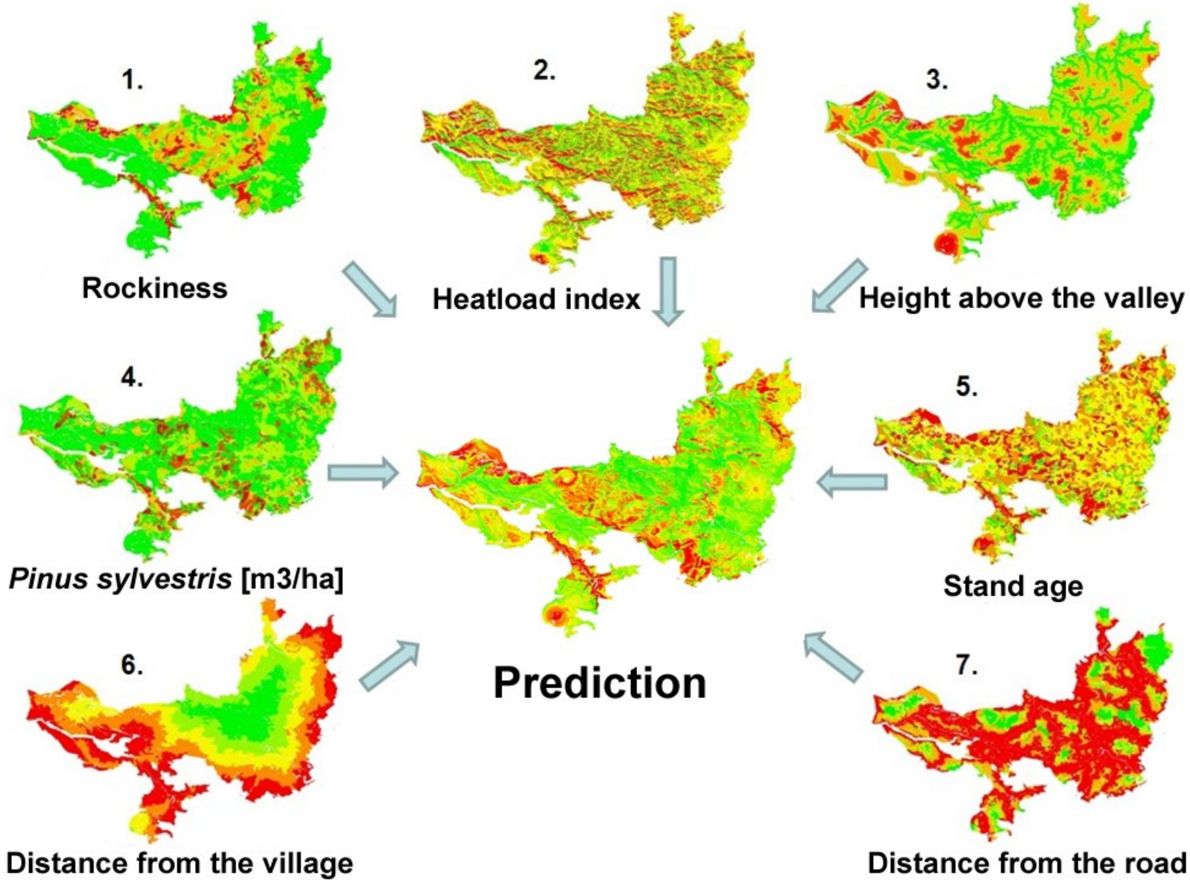

Fig. 2. Wildfire risk prediction for the Bohemian Switzerland National Park territory, based on the raster layers 1-7 and processed using the ENFA method (Hirzel et al., 2002a) in the Biomapper software (Hirzel et al., 2002b).

In **Chapter 3**, we studied post-fire vegetation development and environmental factors explaining changes in species composition of burnt forests. We focused on semi-natural forests dominated by *Pinus sylvestris* of four sandstone regions within the Czech Republic and adjacent part of Germany. Due their physiognomy and species composition such pinewoods resemble boreo-continental pine forests, which are claimed to be fire-adapted. Since forest fires are in Czech sandstone areas markedly frequent even though commonly perceived as adverse for local forests, we examined the wildfire importance for them. 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. Some of these forests occur even on sites with deeper soils, where not pinewoods but more likely beech-fir stands are considered natural vegetation. We thus asked whether wildfires can be the factor supporting the preservation of pine-dominated forests in such sites.

Our study took 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 and resilient the forests are to fire in terms 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, while even low-severity fires induced great changes in the understorey species composition. 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. Thus, periodic wildfires occurring at least once in 200 years, regardless whether human- or lightning-caused seem to be a factor maintaining forests dominated by *Pinus sylvestris* in temperate sandstone landscapes.

Conclusions

<u>Drivers of forest fire occurrence in the Central European landscape</u>

The wildfire occurrence in the cultural landscape of the Czech Republic is driven by both human and natural environmental factors. Environmental factors like vegetation composition, topography, soil type and climatic conditions determine the fire-proneness of a site while human presence and activity, as the main sources of ignition, have stronger impact on wildfire frequency. Even in such a densely populated country as the Czech Republic, the effect of the environment including the lightning density as a potential driver of natural ignitions was not totally overridden by human factors. Local fire regimes are thus a complex result of biotic, abiotic and human factors. This result indicates that wildfire occurrence in Central European landscape is subjected to similar rules like in other parts of the world, where fire ecology is a well-established scientific line.

<u>Naturally fire-prone areas of Central Europe</u>

Although forest fires are there relatively frequent, naturally-driven fire-prone conditions are not omnipresent in the Central European landscape. They are more likely restricted to specific regions. Such conditions encompass namely the prevalence of coniferous, especially pine forests in lower altitudes and rugged relief forms with drainable soils. When we focus, from an ecologist's point of view, on places where such vegetation occurs more or less naturally (in the long run), the sandstone landscapes with high proportion of pine forests emerge as a striking example of such fire-prone area. Our study that focused in detail on one of the sandstone regions largely confirmed the results from the country scale and even more emphasized the driving effect of environmental factors on wildfire occurrence in this rugged landscape, which was consistent also across temporal scales.

Fire-dependent forests of Central Europe

The vegetation field study conducted in pine forests of sandstone regions provided an insight into the mechanism how wildfire can preserve local pine-dominated forests in the long run. The results indicate that the natural pine forests of Central Europe are not only edaphically-dependent but can also be preserved in the long run by recurrent fires on sites where other species would potentially form climax vegetation. These results are comparable with the well-known fire-driven dynamics of Eurasian boreal forests or Northern American pine forests despite different species that interact in these ecosystems.

These results indicate that even in temperate Central Europe wildfire can be the important factor shaping forest vegetation in the long-term perspective, at least within certain regions and forest types. When one accepts the human presence, a major source of wildfire ignitions, as a long-term and integral part of Central European landscape, then there is no reason for further marginalization of the wildfire importance for naturally fire-prone ecosystems.

Additional contribution to the knowledge of the wildfire-vegetation relationship in Central Europe can be provided by a detailed study of post-fire regeneration of key tree species of the region (Fig. 3); by the comparison of the post-fire forest successional trajectory with those of different disturbance types, together with a study of wildfire effect on the soil nutrient content. These data are currently in process of being analyzed.

Fig. 3. Experimental plots for the study of post-fire tree regeneration.

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Chapter 1

Drivers of Forest Fire Occurrence in the Cultural Landscape of Central Europe

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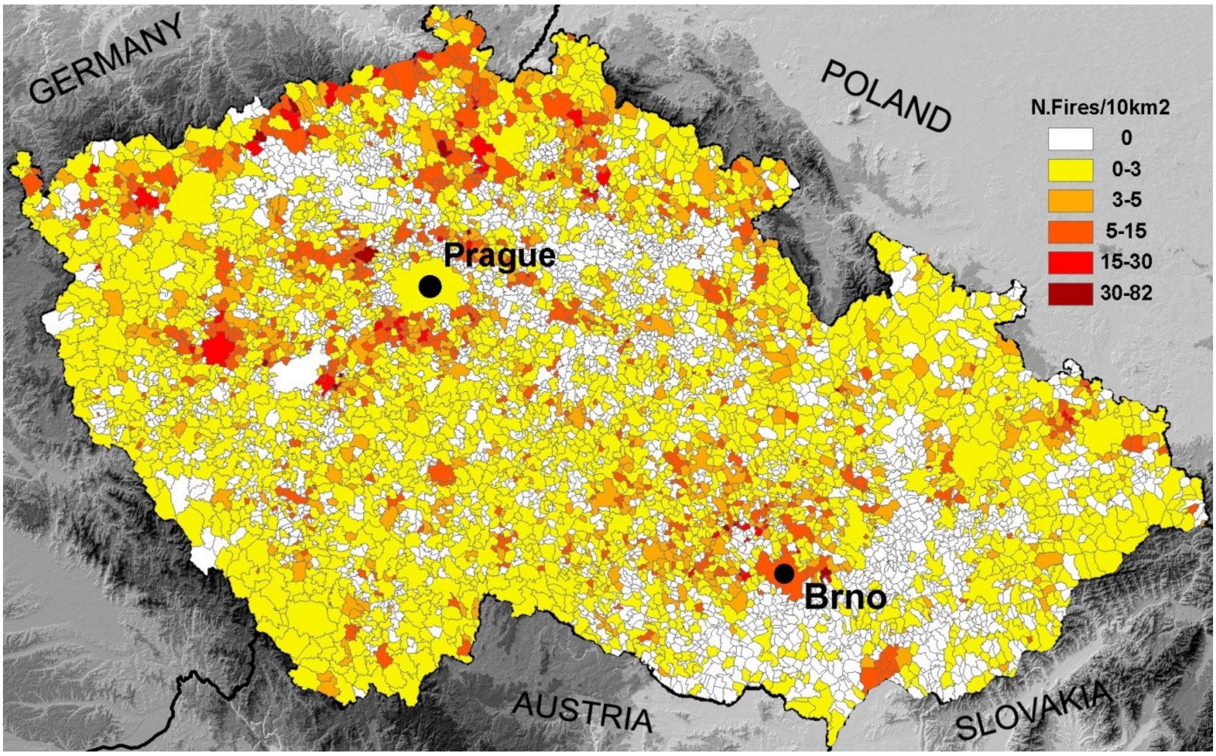

The frequency of forest fires in the Czech Republic in the period of 1992-2004.

Abstract

Wildfires in Central European temperate forests have traditionally been perceived as a mere consequence of human activity without any relevance to natural forest development, despite their documented frequent occurrence. As a result, our knowledge about local fire ecology and patterns of wildfire occurrence in the landscape is lacking. In this study, we aimed to reveal the factors influencing the spatial distribution of forest fires in the Czech Republic as a model area for the broader Central European region. Specifically, we aimed (1) to compare the importance of environmental and human factors for wildfire incidence across the country and within a selected fire-prone region; (2) to examine the relationship between lightning strikes and wildfire incidence; (3) and to identify specific areas with naturally driven fire-prone conditions. We took data on 15,985 forest fire records covering a period of 12 years and explored their distribution using GIS layers of human, topographic, climatic and vegetation composition factors. Using GLM and hierarchical partitioning, we singled out important factors that determine the distribution of wildfires in the landscape. We found wildfire occurrence to be controlled mostly by environmental factors whereas wildfire frequency was strongly driven by human factors. In the selected region, where fire-prone conditions are prevalent, the effect of environmental factors was more pronounced. Wildfire frequency in local fire-prone *Pinus sylvestris* forests is also driven by CG+ lightning strikes. The combination of the fire-prone conditions with the presence of ignition triggers has probably led to the development of local fire-dependent ecosystems.

Key words: Wildfire; Spatial pattern; Temperate; *Pinus sylvestris*; *Picea abies*; *Betula*; Ruggedness; Population density; Lightning strikes; Polarity

1. Introduction

Fire is an important disturbance factor shaping forest vegetation worldwide (Engelmark 1993; Skre et al. 1998; Pausas and Vallejo 1999; Podur et al. 2003). On the Northern Hemisphere, fire is generally supposed to be an integral part of natural dynamics of boreal forests and Mediterranean ecosystems. In temperate regions of Central Europe, by contrast, the role of fire in the functioning of local forest ecosystems has been traditionally neglected, and wildfires have been perceived as a mere adverse consequence of human activity without any relevance to natural processes (Clark and Merkt 1989; Ellenberg 1996; Tinner et al. 2005; Niklasson et al. 2010). That is why this topic had long been neglected by ecological studies from this region, including the analysis of factors influencing the wildfire incidence in the landscape. However, wildfires have recently been recognized as an important factor also in Central Europe, namely in Alpine regions (Delarze et al. 1992; Tinner et al. 1999; Stähli et al. 2006; Müller et al. 2013; Valese et al. 2014) and in *Pinus sylvestris* forests of Lithuania, Poland and the Czech Republic (Marozas et al. 2007; Niklasson et al. 2010; Adámek et al. 2015; Zin et al. 2015).

A major natural cause of wildfires are lightning strikes (Pyne et al. 1996). The proportion of lighting-ignited fires varies substantially worldwide. In the period of 2006-2010, lightning strikes ignited 7.3% of forest fires in Northern Europe, 0.5% in Central Europe and 4.7% in Southern Europe, whereas in Canada and the USA, the proportion of naturally caused fires is about 48% (Cardille and Ventura 2001; Ganteaume et al. 2013). This proportion, however, depends on the local population density, as lightning-caused fires prevail in remote areas with low populations (e.g. Flannigan et al. 2000). Different perspective can be provided by comparing the spatial density of lightning-ignited forest fires, which in some parts of the USA and in European Alpine regions reaches up to 0.9 fires/(year 100km^2). In Mediterranean Europe, the average density has been estimated to be 0.12 fires/(year 100 km^2). In the Czech Republic, the area of our study, the average wildfire density (0.065 fires/(year 100 km^2), is slightly lower than in W Siberia (0.075) but slightly higher than in Northern European boreal countries (0.039) (Granström 1993; Larjavaara et al. 2005; Kula and Jankovská 2013; Müller et al. 2013), even though in the Czech Republic, there is a higher proportion of mixed and broadleaved forests, which are considered less fire-prone than coniferous forests (Clark and Royall 1996; Moreira et al. 2001).

Although forest fires are a natural phenomenon, their main cause in populated landscapes is human activity. In Europe, 97% of forest fires of known cause within the period of 2006-2010 were directly or indirectly caused by humans (Ganteaume et al. 2013). Moreover, palaeoecological and fire-history studies suggest that during the Holocene period, the frequency of fire events was markedly positively influenced by human presence in the landscape (Niklasson and Granström 2000; Vannière et al. 2008; Molinari et al. 2013). Equally, the overwhelming majority of recent forest fires in the Czech Republic is caused by humans.

Besides ignition triggers, the distribution of wildfires in the landscape is also influenced by environmental factors of both anthropogenic and natural origin (Cardille and Ventura 2001; Yang et al. 2007; Avila-Flores et al. 2010). Thus, human presence in the landscape usually acts as an ignition trigger, while environmental factors influence wildfire probability. Such factors can be biotic, such as the vegetation cover influencing the fuel type, load and inflammability, or abiotic, such as the climate, topography or soil type influencing fuel moisture and spreading of the fire (Engelmark 1987, Cardille et al. 2001, Díaz-Delgado et al. 2004). Anthropogenic factors influencing fire occurrence can be socio-economic, such as population density, the rate of unemployment, etc., as well as socio-environmental, such as land use (Moreira et al. 2001, Ganteaume et al. 2013). However, the effect of all these factors on fire incidence varies among habitat types and depends on the temporal and spatial scale, as, for example, climatic variables usually operate on a broader than regional scale (Yang et al. 2007; Avila-Flores et al. 2010; Miranda et al. 2012).

Since the Central European landscape is influenced by long-term human presence, human-ignited fires could be an important factor shaping forest vegetation throughout the Holocene period (Tinner et al. 2005). Stable natural conditions increasing the fire-proneness of a locality can promote the development of specific fire-adapted vegetation even in cultural temperate landscapes (Adámek et al. 2015). Knowledge of how the environment affects patterns of wildfire occurrence is therefore important for understanding the processes influencing the development of the Central European landscape. Moreover, this knowledge can be useful for fire prevention planning, especially at present, when the fire risk in Europe is rising due to the climate change (Lindner et al. 2010).

This study presents the results of the first quantitative investigation of the influence of human, biotic and abiotic factors on the spatial distribution of recent forest wildfires in the temperate Central European region, characterized by a long-term and relatively dense human presence. Specifically, we aimed to find out: a) which factors influence the occurrence and frequency of the forest fires on the country scale and in a selected fire-prone region; c) what is the role of lightning strikes in wildfire occurrence in the cultural temperate landscape; and d) which factors determine naturally fire-prone areas in the landscape, where wildfires might influence ecosystems in the long-term.

2. Methods

2.1. Study area

We aimed to reveal the drivers of the occurrence of forest fires operating at different geographical scales. We therefore selected two model areas. The large (country) scale is represented by the Czech Republic, which has an area of 78,866 km^2 (**Fig. 1**). The country is situated in in Central Europe, in the middle of the temperate zone of the Northern Hemisphere. Its climate is mild with four seasons, transitional between oceanic and continental, and characterized by prevailing western winds, intensive cyclonal activity and relative high precipitation. The average temperature varies between ca. -3°C (January) and 17°C (July), and average annual precipitation across more than 60% of the country's area is 600-800 mm (Tolasz 2007). The climate is, however, considerably influenced by the relatively rapidly changing elevation and relief. The elevation varies ranges from 115 to 1,603 m a.s.l. with a median of 430 m a.s.l.. The prevailing relief type are hills and highlands. The naturally dominant vegetation formation in the Czech Republic are mixed beech-fir forests transitioning towards broadleaved oak-dominated forest in the lowlands and towards coniferous spruce-dominated forests inat higher altitudes (Chytrý 2012). However, as a result of intensive forestry management, practised since the 19th century, the present forest composition differs markedly from the natural state. Forests at present cover 33.9% of the country and are mainly composed of *Picea abies* (52%), *Pinus sylvestris* (17%), *Fagus sylvatica* (7%), *Quercus spp*. (7%), *Larix decidua* (4%), *Betula pendula* (3%), *Abies alba* (1%). Other broad-leaved species (e.g. *Carpinus betulus*, *Acer spp*., *Fraxinus spp*,. *Populus spp*., *Salix spp*., *Tilia spp*.) occupy ca. 8% of the forested area (www.uhul.cz). The average population density of the Czech Republic is 133 persons/km^2. In the period of 1992-2004, the average number of forest fires in the country per year was 1,230, with a mean burned area of 0.49 ha/fire. The causes of fire were: unexplained (29.9%), human-caused – mostly fire raising, smoking and forestry management (68.7%), and lightning strike (1.39%) (Kula and Jankovská 2013).

The regional scale was represented by an area of 4,925 km^2, located in the NW part of the Czech Republic. It was chosen due to its characteristic natural conditions and markedly frequent occurrence of wildfires (Kula and Jankovská 2013). The region is characterized by a relatively low population, high forest cover with preserved semi-natural forests and a related aggregation of natural protected areas, including, for example, Bohemian Switzerland National Park. The topography and geology of the region is very diverse, encompassing tertiary volcanic hills, quartzite mountain ranges, sandstone rocky areas, river valleys and tablelands. The elevation ranges between 115 m a.s.l. (Elbe river valley) and 1,012 m a.s.l. (Ještěd mountain). A large part of the region is characterized by sandstone bedrock with a typical rugged relief ("rock towns") with *Pinus sylvestris* as the dominant tree species. Forests on volcanic bedrock are mainly composed of broadleaved tree species such as *Fagus sylvatica* and *Quercus* spp. Other parts of the regions are covered mainly by forests dominated by *Picea abies*. The semi-natural coniferous forests of this region have recently been recognized as an extrazonal lowland taiga that has probably been shaped by recurrent wildfires over millennia (Novak et al. 2012; Chytrý 2012; Adámek et al. 2015). We therefore focused on this specific region to test the drivers of wildfire occurrence on a narrower geographical scale, where the effect of climatic factors is suppressed and where precise data on the density of cloud-ground lightning strikes can be used to test their role as a potential natural ignition trigger.

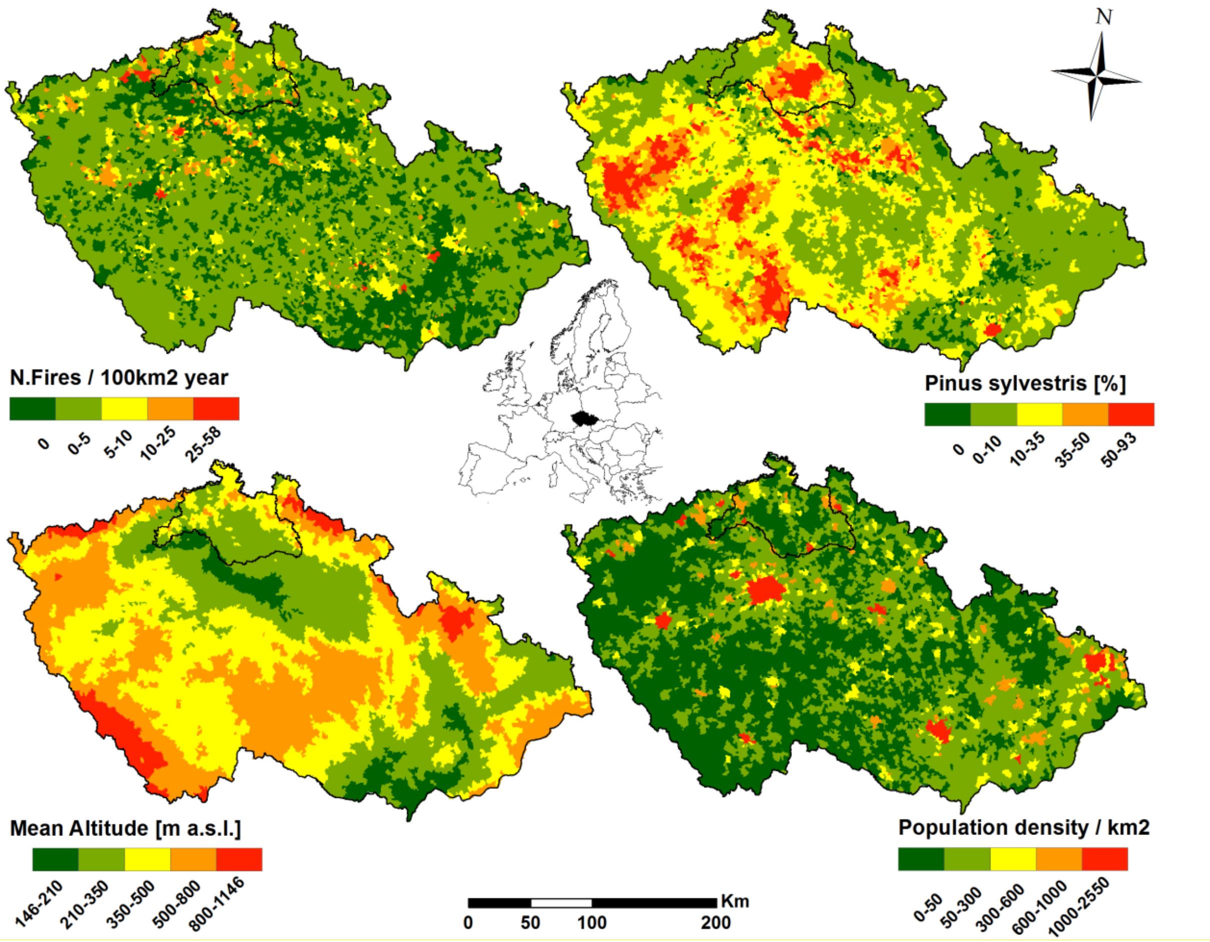

Fig. 1. Localization of the study area in the European context (country scale) and within the Czech Republic (selected region). Maps show the number of wildfires / 100 km^2 of forested area per year and values of important drivers of wildfire occurrence in municipality cadastres: *Pinus sylvestris* abundance, Mean altitude; Population density.

2.2. Data on forest fire occurrence

In our analyses, we used a database of 15,985 forest fires that occurred in the Czech Republic in the period of 1992-2004. The dataset originated from the General Directorate of Fire Rescue Service of the Czech Republic (GR HSZ CR) and was manually verified to exclude non-forest fires (Kula and Jankovská 2013). All fire records were localized into 3,474 cadastres (corresponding to LAU2 units of the Nomenclature of Territorial Units for Statistics of European Union) from the total of 6,251 existing in the Czech Republic. Prior to our analyses, we excluded cadastres without forest cover, military areas due to missing or inaccurate data and the two largest cities, Prague and Brno. The final dataset thus included 6,170 cadastres on the country scale and their subset of 343 on the regional scale. The area of the cadastres analysed ranged from 0.25 to 214.9 km^2 (mean 12.4 km^2, median 8.1 km^2, SD 13.6). Fire counts per cadastre ranged from 0 to 191 (2.5, median 1, SD 7).

2.3. Fire occurrence predictors

We computed the values of particular factors used to explain the occurrence of wildfires in each cadastre polygon using ArcGIS 10.1. software (www.esri.com). For a complete list of factors used in our analyses, see **Tab. 1**. The data source for human factors such as the population density and the number of accommodation facilities (a proxy for the rate of tourism) in cadastres was the Czech Statistical Office (www.csu.cz). Distance from the nearest city was computed as the distance from the nearest settlement with more than 50,000 inhabitants. The mean precipitation and temperature figures for each municipality for the period 1992-2004 were computed from grid data (cell size 500 m) on mean annual temperature and sum of annual precipitation provided by the Czech Hydrometeorological Office (CHMI; www.chmi.cz). The data on lightning strikes density came from of the Central European Lightning Detection Network (CELDN) provided by the CHMI. The number of cloud-ground (CG) lightning strikes, a potential ignition trigger, was calculated from annual sums for the period of 2002-2009. The only available data for the whole country were the sums of all CG flashes in 77 districts of the Czech Republic. For the region of the NW Czech Republic, we used sums of flashes in cadastres from the same period computed from gridded data (1x1 km), where flashes were divided according to their polarity into negative (CG-) and positive (CG+) flashes. We used these categories as separated factors because CG+ flashes are claimed to be a stronger source of the wildfire ignition than the more frequent CG- flashes (Latham and Williams 2001), although this is still disputed (e.g. Flannigan and Wotton 1991; Nauslar 2013). Topographic factors such as mean altitude and the ruggedness index (Riley et al. 1999) of each cadastre were computed from the LiDAR Digital Elevation Model (DEM) of the Czech Republic provided by the Czech Office for Surveying, Mapping and Cadaster in the form of the DMR 4G service, resampled to a grid cell size of 20 m. The area proportion of particular soil types was computed from the digitized pedological map of the Czech Republic (Tomášek 1995). The percentage abundance of particular tree species in the forested area of each cadastre was computed from grid data of 500 m cell size, provided by the Czech Forest Management Office (www.uhul.cz).

Tab. 1 (next page). Factors used as fire predictors and their descriptive statistics.
† Factors excluded from GLM analyses due to collinearity
* *Betula pendula, B. pubescens*
**Populus nigra, P. alba, P. x canadensis*
* *Tilia cordata, T. platyphyllos, T. x vulgaris*

Factors	Country scale Min.	Max.	Mean	SD	Regional scale Min.	Max.	Mean	SD
Anthropic								
Population/km2	0.9	2362	91.4	138	5.2	1486	94.6	153.8
N. of accomodation/km2	0	28.1	0.08	0.4	0	2.3	0.1	0.2
Distance from city [km]	0	75	22.2	13.6	0	49.7	15.1	11.2
Climatic								
Precipitation [mm]	434.8	1355	660.7	125	434.8	1090	718	125.3
Temperature [°C]†	4.1	10	8.3	0.9	6.5	9.6	8.2	0.6
N. of all flashes / km2	17.2	51.2	27.6	5.3	NA	NA	NA	NA
N. of CG- flashes / km2	NA	NA	NA	NA	0	32.9	15.6	4.3
N. of CG+ flashes / km2	NA	NA	NA	NA	0	13.1	4.8	1.9
Topographic								
Altitude [m a.s.l.] †	146.2	1145	412.4	144	146.2	606.7	348.1	84.1
Ruggednes index	0.3	22.4	4.7	2.9	1.1	22.4	6.9	3.3
Soil type [%]								
Alpine soil	0	30	0	0.7	NA	NA	NA	NA
Anthrosol	0	100	0.2	3.1	0	8.9	0	0.5
Arenosol	0	100	0.8	6.8	NA	NA	NA	NA
Cambisol acidic	0	100	40	42.7	0	100	11.2	24.1
Cambisol eutrofic	0	100	1	7.7	0	100	9.6	22.1
Cambisol lithic	0	100	17.7	30	0	100	21.3	25.4
Cambisol terrace	0	100	3.2	12.7	0	76.8	3.2	11.8
Fluvisol	0	100	3.6	13.7	0	86.2	0.8	7.3
Chernozem	0	100	8.3	23.4	0	100	6.1	21.5
Leptosol	0	100	2	10.8	0	98.6	1.5	9.7
Luvisol	0	100	11.4	24.6	0	100	22.4	30.4
Peaty soil	0	73.3	0.2	2.5	0	37.2	0.5	3.1
Pelosol	0	100	3	13.8	0	99.6	3.4	13.3
Podzosol	0	100	3	12.8	0	97.9	15.3	23.2
Pseudogley	0	100	8.7	22.5	0	100	6.7	18.8
Vertisol	0	100	0.3	4.3	0	37	0.3	2.3
Forest composition [%]								
Abies alba	0	33.1	0.5	1.2	0	0.8	0.1	0.1
Betula pendula	0	85	3.4	4.5	0	36.7	6	4.2
Carpinus betulus	0	47.2	1.9	3.8	0	22.8	2.2	3.3
Fagus sylvatica	0	65.4	3.5	6	0	57.5	5	6.1
Larix decidua	0	40	3.6	3.8	0	15.1	3.1	2.5
Picea abies	0	100	32.4	25.6	0	70.4	23.9	17.8
Pinus sylvestris	0	92.1	18	18.3	0	76	19.6	19.1
Populus spp.	0	87	2.2	7.1	0	80	1	4.9
Populus tremula	0	26	0.5	1.2	0	5.7	0.6	0.7
Quercus petraea	0	74.8	2.7	7.2	0	54.9	3.5	8.1
Quercus robur	0	100	9	12.1	0	76	12.6	12
Robinia pseudacacia	0	100	3.4	10.6	0	42.3	2.7	6.8
Tilia spp.	0	83.3	2.1	4.2	0	20	1.8	2.9
Forested area [km^2]	0.25	167	9.1	11.4	0.25	167	10.9	14.5

2.4. Data analyses

We performed our analyses on two geographical scales to compare the drivers of fire occurrence for the whole country and for a region selected for its specific natural conditions. For the regional scale, we used more precise flash data divided into two factors (CG- and CG+), summed for each cadastre. For both spatial scales, we performed analyses with two dataset types: a) fire presence/absence data to reveal the general pattern of fire occurrence and b) fire counts > 0 data to reveal factors influencing the fire frequency. On the country scale, we finally included 6,170 cadastres using presence/absence data and 3,467 cadastres using the fire counts data. In the regional-scale analyses, we included 343 and 226 cadastres for presence/absence and frequency data, respectively. When the correlation of two factors exceeded the arbitrary threshold of Spearman's $r_S = 0.7$, we only retained the better interpretable factor for further analyses. We thus excluded altitude, which was critically correlated with temperature, *Picea abies* abundance and prevalence of Cambisol acidic soils. We also excluded temperature, which was critically correlated with precipitation. The presence/absence data were analysed using generalized linear models (GLM) with binomial distribution of errors; for counts data, we used GLM with a quasi-Poisson distribution to account for overdispersion. In the analyses, we incorporated all available factors, including the Forested area [ha] as a covariable to be filtered out, and selected clearly interpretable interactions of tree species abundance with other factors (climatic, topographic and anthropic). For all four analyses, we subsequently produced a minimal adequate model (MAM) containing all significant factors. To compare the relative importance of significant factors (percentage of explained variance), we used the hierarchical partitioning method using the R package hier.part (Mac Nally and Walsh 2004). For this comparison, we used a maximum of nine significant factors with the highest z/t values from each analysis due to the inaccuracy of the hier.part method with > 9 factors included (Olea et al. 2010). The significance of these factors was tested using the randomization test method (rand.test) of the hier.part package. Within the selected NW region, we examined the relationship of the density of CG- and CG+ flashes with altitude and precipitation, using linear regression. We additionally visualized the total number of fires in cadastres classified by the dominant tree species, related to the area of forest dominated by the given tree species (number of fires / 100 km^2 of forest). Similarly, we visualized the frequency of fires across altitudinal zones using average altitude values for each cadastre: planar (146-210 m a.s.l.), colline (210-500 m a.s.l.), submontane (500-800 m a.s.l.), montane (800-1145 m a.s.l.). On the regional scale, we similarly visualized the effect of geology and geomorphology on fire frequency. We distinguished four landscape categories: areas with prevailing granodiorite bedrock (Granite); landscapes with volcanic basalt hills (Basalt); sandstone "rock towns" with a characteristic rugged relief formed by cliffs, rock walls, pillars, canyons and narrow gorges (Rock towns); relatively flat areas with sandstone bedrock (Sandstone); and areas with prevailing loess or loess-like loam sediments (Loess). Geological areas were distinguished according to the geological map of the Czech Republic 1:50000 (www.geology.cz), and sandstone "rock towns" identified using the digital map of landscape typology of the Czech Republic (Löw and Novák 2008).

3. Results

3.1. Country scale

The occurrence of forest fires in the Czech Republic in the period of 1992-2004 in the sense of the presence or absence of fire events depended more on environmental than on human factors. The incidence of wildfires increased with increasing abundance of *Picea abies* (explained variance 19.9%), *Pinus sylvestris* (13.1%) and *Betula spp.* (0.5%), and with increasing ruggedness index (7.9%). Conversely, the incidence of wildfires decreased with increasing precipitation (4.2%), which was strongly correlated with altitude and temperature (r_S = 0.63 and r_S = - 0.74, respectively); the latter factors were excluded from the analysis (see Data analyses). The abundance of *Betula spp.* and *Ouercus robur* in interaction with the ruggedness index also had a positive effect. Moreover, fire occurrence was influenced also by the soil type, the strongest predictor being the proportion of cambisol soils on the river terraces (0.7%). Somewhat weaker predictors of fire occurrence were human factors. Fire occurrence increased with population density (4%) and the density of accommodation facilities (2.7%). Conversely, it decreased the distance from the nearest large city (> 50.000 inhabitants). There was also a significant positive effect of the interaction of *P. abies* abundance with population density.

The frequency of fires in cadastres, by contrast, was driven mostly by population density (37.2%), and the other human factors were significant as well. Fire frequency was significantly influenced also by environmental factors. It was positively influenced by the abundance of *Betula spp.* (4.8%) and *P. sylvestris* (2.5%), which were significant also in interaction with human factors, by the density of cloud-ground strikes (4.3%), the ruggedness index (3.3%) and the proportion of anthrosols (1.1%), and negatively by precipitation (1.3%). Significant positive effects were found for the interaction of *P. sylvestris* and *Betula spp.* with the ruggedness index and of *Fagus sylvatica* with the frequency of CG flashes (**Tab. 2**).

The most fire-prone were forests dominated by *Betula* spp. (64 fires / 100 km^2 of forest of such composition), *Pinus sylvestris* (39 fires / 100 km^2) and *Fagus sylvatica* (34 fires / 100 km^2), and the least fire-prone were forests dominated by *Larix decidua* (4 fires / 100 km^2), *Tilia spp*. (6 fires / 100 km^2) and *Populus spp*. (12 fires / 100 km^2). In the most widespread forest type, dominated by *Picea abies,* fires occurred with a similar frequency as in *Quercus robur*-dominated forests – 25 fires / 100 km^2 (**Fig. 2A**). As for the different altitudinal zones, the highest fire frequency was in forests of the colline and planar zones and decreased markedly towards higher altitudes (**Fig. 2C**).

Tab. 2. Factors significantly influencing spatial distribution of wildfires. Given are z/t values from GLM analyses of presence/absence and fire frequency data, and the proportion of explained variance of max. 9 selected factors from hierarchical partitioning (I column). Plus/minus signs indicate a positive or negative effect. *Factors significant in the randomization test of the hier.part package. [int]Factors significant only in interactions.

	Country scale				Regional scale			
	Pres/Abs		Counts		Pres/Abs		Counts	
Factors	**z - val.**	**I [%]**	**t -val.**	**I [%]**	**z - val.**	**I [%]**	**t -val.**	**I [%]**
Human								
Population/km2	+9.1	4.03*	+30.7	37.17*	NS		+7.1	10.74*
Accomodation/km2	+3.8	2.73*	+4.2		+2	4.48*	+5.1	9.64*
Distance from city	-3.7		-3.5		NS		NS	
Climatic								
Precipitation	-7.6	4.17*	-4.5	1.3*	NS		NS	
Flashes / km2	NS		+5.3	4.27*	NA		NA	
CG+ flashes / km2	NA		NA		NS		int	
Topographic								
Ruggednes index	+3.9	7.98*	+7.8	3.27*	int		+3.4	2.82
Soil type [%]								
Alpine soil	-3.2		NS		NS		NS	
Anthrosol	+2.8		+5.9	1.13*	NS		NS	
Arenosol	NS		+3.4		NS		NS	
Chernozem	-3.2		NS		NS		NS	
Cambisol lithic	+2.4		+2		NS		NS	
Cambisol terrace	+4.4	0.68*	+2.6		+2.6	2.03*	NS	
Leptosol	+3.2		NS		NS		NS	
Peaty soil	NS		+2.5		NS		NS	
Forest composition [%]								
Abies alba	NS		-2.6		NS		+2.1	2.5
Betula spp.	+5.4	0.45*	+4.7	4.84*	NS		NS	
Carpinus betulus	+2.2		-2.8		NS		NS	
Fagus sylvatica	+3.5		+2.7		NS		NS	
Larix decidua	NS		+2.9		NS		NS	
Picea abies	+16.1	16.88*	+3.5		+3.8	12.97*	int	1.2
Pinus sylvestris	+15.1	13.1*	+8.9	2.46*	+5.6	25.19*	+2.9	10.01*
Populus tremula	-2		-4.7		NS		NS	
Quercus robur	+3.2		NS		int		NS	
Forested area [ha]	+21.6	49.99*	+41.5	44.81*	+6	55.33*	+12.2	62.22*
Interactions								
Betula : Population/km2	NS		+4.5		NS		NS	
Pic.abi : Population/km2	+5.1		+10.3		NS		+3.2	
Pin.syl : Population/km2	NS		+10		NS		+4	
Pin.syl : Accomodation/km2	NS		+4.5		NS		NS	
Betula : Ruggedness i.	+3.9		+3.2		NS		NS	
Pin.syl : Ruggedness i.	NS		+3.7		NS		NS	
Que.rob : Ruggedness i.	+3.5		NS		+2.5		NS	
Fag.syl : Flashes/km2	NS		+4.3		NA		NA	
Pin.syl : CG+ Flashes	NA		NA		NS		+3.6	

3.2. *Selected NW region of the Czech Republic*

In the selected NW region, the location of the "lowland taiga", we found that pattern of wildfire occurrence partly depends on the density of lightning strikes. The frequency of wildfires was significantly driven by the interaction of positive (CG+) flashes with the abundance of *Pinus sylvestris.* Negative (CG-) flashes did not exhibit any significant effect, and, similarly to the country scale, the density of lightning strikes regardless of polarity did not affect wildfire incidence. CG+ flashes, which are about three times less frequent than CG- (**Tab. 1**), occurred in the region more frequently at lower altitudes (p-value = < 0.001, R^2 = 0.113) and in places with low precipitation (p-value = < 0.001, R^2 = 0.33). CG- flashes, by contrast, were slightly more frequent at higher altitudes (p-value = 0.013, R^2 = 0.014), but without a significant relationship with precipitation (**Fig. 3**).

Overall, the results of the analyses showed a similar pattern to the broader country scale, but the effect of environmental factors on the incidence of wildfires in the selected region was more pronounced. Fire occurrence was driven mainly by environmental factors, especially by the abundance of *Pinus sylvestris* (25.2%) and *Picea abies* (13%). A significant positive effect was also found for the proportion of Cambisol soils on river terraces (2%) and the interaction of *Quercus robur* with the ruggedness index. The only significant human factor was the density of accommodation facilities (4.5%). Similarly to the country scale, the frequency of wildfires was driven more by human factors like population density (10.7%) and the density of accommodation facilities (9.6%), than by environmental factors. The interactions of *Pinus sylvestris* and *Picea abies* with population density also had a significant positive influence. The strongest environmental factor increasing wildfire frequency was *P. sylvestris* abundance (10%). According to the results of our GLM analyses, but without support of the randomization test of the hier.part package, the other significant factor was the ruggedness index (**Tab. 2**).

The limited environmental conditions of the selected region harboured a lower diversity of forest types. The most fire-prone forests were those dominated by *Betula spp.* (238 fires/ 100 km^2) followed by *Pinus sylvestris* (63 fires / 100 km^2) and *Picea abies* (55 fires / 100 km^2). The least fire-prone were forests dominated by *Quercus petraea* (no fires), *Fagus sylvatica* (8 fires / 100 km^2) and *Robinia pseudacacia* (11 fires / 100 km^2). *Q. robur* forests exhibited intermediate proneness to fires (28 fires / 100 km^2) (**Fig. 2B**). The highest fire density occurred in areas with sandstone bedrock, especially in sandstone "rock towns", where the density of wildfires was almost double that of less rugged sandstone areas. Less fire-prone were forests in areas with granodiorite bedrock, in landscapes with volcanic basalt hills and on loess sediments (**Fig. 2D**).

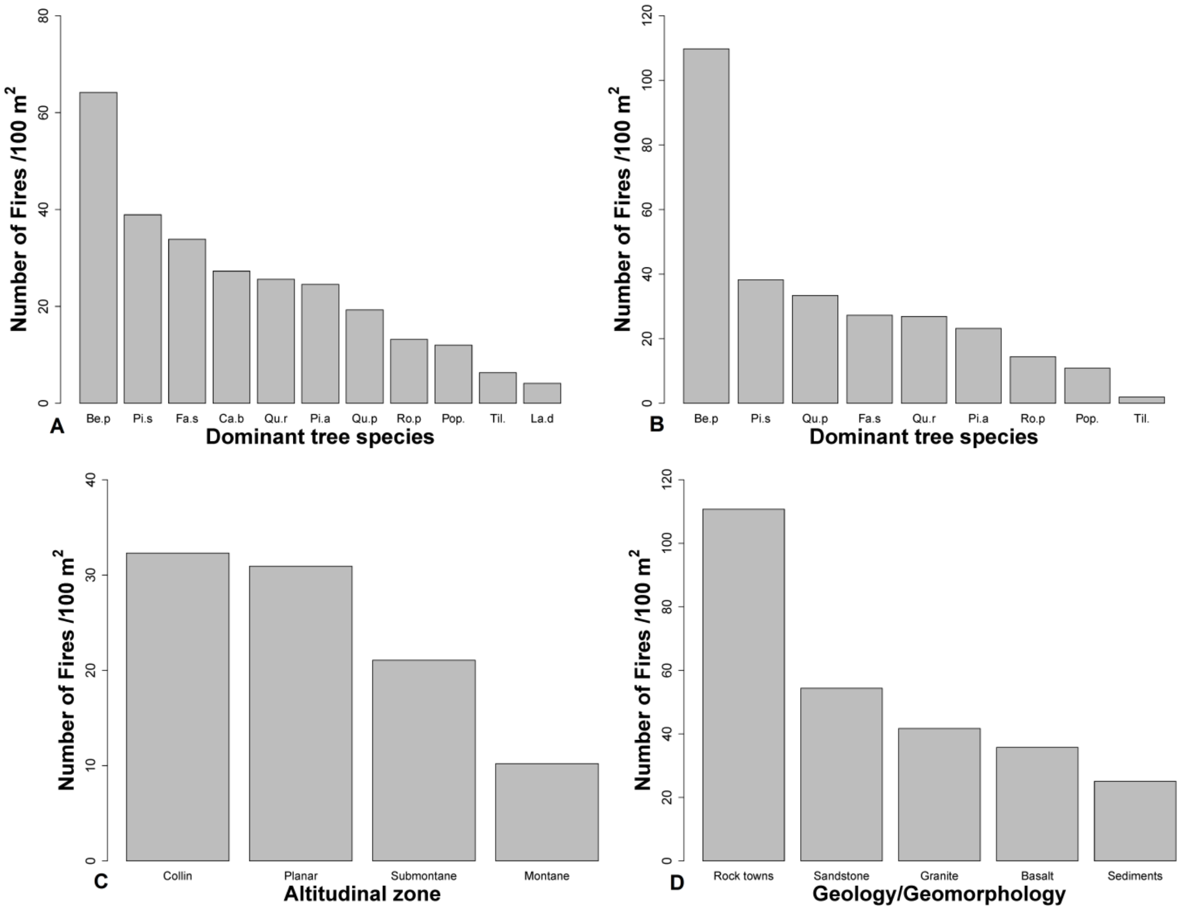

Fig. 2. Wildfire counts per 100 km^2 of forested area of given characteristics. Fire densities by tree dominant on the country scale (A) and the regional scale (B); Wildfire densities on the country scale by altitudinal zone (C) and according to geology/geomorphology on the regional scale (D). The prevalent sandstone bedrock is divided into two categories: sandstone "rock towns" and other sandstone areas.

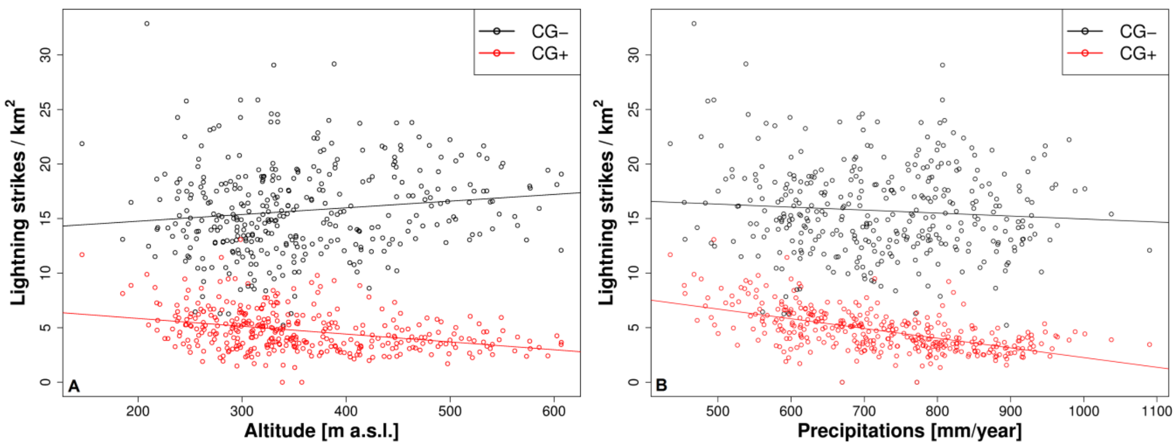

Fig. 3. Density of cloud-ground lightning strikes of negative (CG-) and positive (CG+) polarity in the NW region, related to altitude (**A**) and precipitation (**B**). **A.** CG-: p-value = 0.013, R^2 = 0.014; CG+: p-value = < 0.001, R^2 = 0.113. **B.** CG-: p-value = 0.131; CG+: p-value = < 0.001, R^2 = 0.33.

4. Discussion

Our results show that the spatial pattern of wildfire occurrence in the temperate Central European landscape (represented by our model country, the Czech Republic) is driven by a combination of human and environmental biotic and abiotic factors. We found that environmental factors mainly influence the location of wildfires whereas human factors mostly determine their frequency. Similar results concerning the occurrence and frequency of forest fires have been reported by Martínez-Fernández et al. (2013). This suggests that the frequency of wildfires in environmentally conditioned fire-prone areas depends mainly on the availability of ignition triggers, which in the conditions of Central Europe are mostly of human origin (Kula et Jankovská 2013, Ganteaume et al. 2013). However, wildfire frequency is also driven, even though to a lesser extent, by the density of cloud-ground (CG) lightning strikes.

Biotic drivers of wildfire incidence

Our findings regarding the susceptibility of coniferous forests to fire, especially those dominated by *Pinus sylvestris*, is in agreement with ecological studies where *P. sylvestris* is claimed to be a fire-adapted and simultaneously fire-attracting species due its easily flammable, resiny litter and sparse canopy that enables the ground layer to dry out (e.g. Agee 1998; Angelstam 1998; Gromtsev 2002; Lecomte et al. 2005). *Betula spp*. also markedly enhanced the probability of forest fires. This broadleaved species often accompanies *Pinus sylvestris* in nutrient-poor conditions, which might be one explanation of the effect of birch. It also dominates on anthrosols, where wildfires were markedly frequent as well. Simultaneously, it is a pioneer tree species that typically colonizes burnt areas (Huotari et al. 2008; Reyes and Casal 2012), so an alternative explanation might be the abundance of birch is actually a consequence of previous fire occurrence. However, wildfires are usually not as extensive to explain the prevalence of birch in the region, and, moreover, almost all burnt areas have been reforested by tree species that are economically more valuable. Furthermore, birch possesses a specific characteristic that might be linked to wildfires. It has highly flammable bark that remains on the forest ground after decaying of old trunks and branches. In the case of a fire, this could increase the likelihood of its spreading. Indeed, the abundance of *Betula* spp. did influence fire frequency. Wildfires, to some extent, nevertheless also occurred in forests dominated by *Fagus sylvatica* or *Quercus* spp. Especially *Quercus robur* forests in rugged landscapes seem to be a fire-prone biotope. This result supports the theory that temperate oak forests are associated with the occurrence of wildfires (Abrams 1992; Brose et al. 2013). The least fire-prone were forests dominated by *Populus* spp. and *Tilia* spp. (**Fig. 2 A, B**), which grow in relatively moist conditions of flood plains and shady scree slopes, respectively (Chytrý 2012).

Abiotic drivers of wildfire incidence

The occurrence of wildfires depended on abiotic environmental factors such as the relief, climate and altitude. Although we did not use altitude as a predictor, since it highly correlated with precipitation and temperature, its effect was clearly evident in our comparison of fire density, which was markedly lower at higher altitudes (**Fig. 2C**). Numerous other studies have found a negative effect of altitude and precipitation on wildfire incidence (e.g. Engelmark 1987; Pew and Larsen 2001; Futao et al. 2016). However, in drier climatic conditions, the effect of these factors can be the opposite, as fuel availability increases with increasing precipitation values (Martínez-Fernándes et al. 2013).

In our study, the occurrence and frequency of wildfires increased with increasing ruggedness of the relief, which is consistent with the results of similar studies (Kalabokidis and Vasilakos 2002; Ganteaume et al. 2013). In rugged landscapes there are more fire-prone sites than on flat land, such as south-oriented slopes and convex rock tops with shallow soils dry out more easily (Angelstam 1998; Mouillot et al. 2003). A previous study by Adámek et al. 2015 has found that the most fire-prone sites in sandstone "rock town" areas of the NW Czech Republic region are steep SW-facing slopes and elevated rock plateaus. Additionally, such protruding, convex sites attract CG lightning strikes, the main natural ignition trigger (Engelmark 1987; Vogt 2011).

The density of CG flashes turned out to have a significant positive effect on wildfire frequency also in more populated landscapes, although they provably cause only about 1.4% of forest fires in the Czech Republic (Kula and Jankovská 2013). Using more precise data on the density of lightning strikes, we found wildfire frequency to be driven by positive (CG+) flashes in interaction with *Pinus sylvestris* abundance. CG+ flashes, in contrast to negative (CG-) flashes, occurred more frequently in the areas with lower altitudes and precipitation (**Fig. 3**), which vary strongly in forest composition, from thermophilous broadleaved forests on volcanic basalt to *Pinus sylvestris* forests on sandstone. The effect of CG+ flashes thus interacts with the fire-prone conditions of pine forests, which can be more likely to get ignited by lightning. CG+ flashes are claimed to be a stronger ignition trigger than CG- flashes, even though they are less frequent. This has been explained by their larger magnitude or temperature (Latham and Williams 2001) and by the fact that they more often accompany convective or so-called "good weather" thunderstorms, which last a short time and bring little rainfall, which is in accordance with our results. CG- flashes, by contrast, occur more frequently with frontal thunderstorms accompanied by higher rainfall (Larjavaara et al. 2005). This result indicates a possible interconnection between the occurrence of a fire-adapted lowland pine taiga in the region and the frequency of CG+ lightning strikes as a natural ignition trigger.

Wildfire incidence also depended on the soil type, which, however, more likely indicates certain specific site conditions. The negative effect of alpine soils and chernozems thus points to the non-fire-prone conditions of montane spruce forests of highest altitudes and lowlands vegetation in the largest river flood plains, respectively. The significant effect of cambisol lithic soils probably indicates more frequent fire events on sites with shallow, drainable soils. The proportion of cambisol soils on river terraces, which only showed a significant positive effect on wildfire occurrence, probably reflects the fire-prone conditions of drainable soils on sand and gravel river sediments. A positive effect of coarse soils on the incidence of wildfires was also found by Cardille et al. (2001). The only soil type that had a significant effect on fire frequency were anthrosols, which occur in coal mining regions at the NW boarder of the Czech Republic.

The frequency of wildfires in the NW region strikingly differed depending on geological conditions. It was higher on sandstone bedrock, where the pine-dominated lowland taiga occurs (Novák et al. 2012; Chytrý 2012), and lower on more fertile basalt and loess bedrock with a higher cover of broadleaved forests. However, the most fire-prone areas of the region were sandstone “rock towns” (**Fig. 2D**), which is probably related with the high abundance of *Pinus sylvestris* touristic attractiveness and ruggedness of the landscape.

Human drivers of wildfire incidence

According to numerous studies, human factors, especially population density and distance from human settlements and infrastructures, explain a large proportion of wildfire ignitions (e.g. Pew and Larsen 1999; Cardille et al. 2001; Zumbrunnen et al. 2012; Ganteaume et al. 2013; Martínez et al. 2013; Futao et al. 2015). It has also been suggested that human factors can more or less obscure the effects of environmental factors such as the climate or topography (Flatley et al. 2011; Zumbrunnen et al. 2012). In our study, however, environmental factors did have an apparent effect despite the high population density whereas human factors mostly influenced fire frequency. The strongest factor was population density, followed, to a lesser extent, by the density of accommodation facilities as a proxy for tourism intensity and distance from the nearest large city. In the NW region, the effect of tourism was more important than on the country scale, probably due to the intensity of tourism and relatively sparse population in the region. Further strong predictors were the interactions of human factors with abundance of fire-prone coniferous species. The significant interactions between vegetation composition and human factors on wildfire incidence suggest that human activity and the vegetation are connected.

Conclusions

The pattern of wildfire distribution in the Czech Republic follows similar rules as in other regions of the world, even those where wildfire is considered part of the natural dynamics of local ecosystems. In the densely populated cultural landscape of Central Europe, the distribution of wildfires, not surprisingly, depends strongly on human factors. However, people act mainly as a ubiquitous ignition trigger whereas natural environmental factors determine the susceptibility of habitats to being ignited. The main natural conditions that increase the likelihood of wildfires are: a rugged relief at lower altitudes, drainable soils with a prevalence of coniferous forests, especially of *Pinus sylvestris*, sometimes mixed with *Betula spp*. If sufficient ignition triggers are available, be it of human or natural origin, such conditions can in the long term lead to the development of fire-adapted ecosystems. Natural conditions, including CG+ lightning strikes as a potential natural ignition trigger determine the susceptibility of habitats in the sandstone landscapes of NW Bohemia. This region is a good example of a naturally conditioned fire-prone area within temperate Central Europe where fire-dependent vegetation is shaped also by lightning-ignited wildfires.

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Chapter 2

Forest fires within a temperate landscape: a decadal and millennial perspective from a sandstone region in Central Europe

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Traces of an old wildfire in the Bohemian Switzerland NP.

Abstract

In Europe, fire is considered an integral part of forest dynamics only in the Mediterranean and in Fenno-Scandinavia. In Central Europe, the ecological role of fire is largely neglected and deemed unimportant. To fill this knowledge gap, we studied ancient and recent fires in temperate coniferous forests of a sandstone landscape. We used palaeoecological and contemporary forestry data to reveal wildfire events in the present-day landscape and in the distant past. Using linear regression and the ENFA method, we identified the factors influencing fire occurrences in the landscape on two time scales. Analyses of soil charcoal concentrations correspond with contemporary forestry data. The main driving factors affecting the incidence of fires were topographic features, namely the heat load index and presence of rocks. Additional important factors were forest composition features, especially the abundance of *Pinus sylvestris*. Even though the landscape is populated and attractive to tourists, present-day anthropogenic factors, surprisingly, have only marginal effects. Fires have been occurring in similar fire-prone habitats at least since the Subatlantic period, regardless of whether they were caused by humans or lightning. Our results therefore show that fire affects long-term forest vegetation development also in temperate forests of Central Europe. This has far reaching consequences for forest management because, contrary to prevailing beliefs, fire must be considered a natural driver of forest vegetation patterns even in this temperate region.

Keywords: Wildfire; Fire-regime; Charcoal records; Sandstone landscape; Temperate forests; *Pinus sylvestris*

1. Introduction

Wildfires are an important disturbance factor influencing forest ecosystems. They have a strong impact on both biotic and abiotic conditions. Fire eliminates sensitive species in favour of species that are able to survive or easily regenerate in burned places (Agee, 1998; Lloret et al., 2005). They alter the local light and thermal regime as well as physical, chemical and biological qualities of the soil (Certini, 2005). The occurrence of wildfires depends on complex interactions among the climate, topographic characteristics, vegetation structure and composition and the presence of natural or anthropogenic ignition triggers. Forest fires are more frequent during dry climatic periods, on convex relief forms and on south facing slopes (Angelstam, 1998). The frequency of wildfires decreases with increasing humidity, for example, towards the poles, higher elevations and a regions with a more oceanic climate (Angelstam 1998; Skre et al., 1998). The most common natural cause of wildfires is lightning (Tinner et al., 1999; Goldammer and Page, 2000; Niklasson and Granström, 2000). Generally, a gradual increase in biomass burning during the Holocene has been detected on the continental scale in Europe (Carcaillet et al., 2002; Power et al., 2007). It has been proposed that climate warming following deglaciation is responsible for this trend (Marlon et al., 2012). However, recent studies from the Alps (Stahli et al., 2006), Pyrenees (Rius et al., 2011) and the Pannonian Basin (Feurdean et al., 2013) have shown substantial regional variation indicating a predominant role of anthropogenic drivers acting during the mid- and late Holocene (Molinari et al., 2013).

Wildfires in Europe are associated mainly with the Mediterranean region and the Boreal forest zone. In these areas, fire is considered to be the main forest vegetation disturbance factor (Engelmark, 1993; Skre et al., 1998; Pausas and Vallejo, 1999), and its ecological role and history are well studied there (Niklasson et al., 2010). In northern Eurasia, fires are often associated with forests of Scots pine (*Pinus sylvestris*). This coniferous tree species often occurs in drier conditions and produces resiny, easily inflammable litter. At the same time, Scots pine possesses several physiological and morphological adaptations to fire, for example, thick bark, a deep root system and an ability to quickly regenerate after fire in places with mineral soil (Agee, 1998). Regular fires can maintain pine stands also in places where other tree species would otherwise prevail due to site conditions (Engelmark, 1987; Angelstam, 1998; Gromtsev, 2002). Natural fire disturbances are thought to be of such importance that emulating them has been considered a legitimate forest management practice (Bergeron et al., 2002, Kuuluvainen, 2002).

The situation in Central Europe, where the most prevalent natural forests are composed of temperate broadleaf species, is entirely different. The ecological role of fire has traditionally been neglected (Clark and Merkt, 1989; Ellenberg, 1996), and forest fires are regarded as purely adverse results of human activity. But even in temperate Central Europe, fire can play an important ecological role, at least in some forest types, where it shapes their stand structure, dynamics and species composition (Tinner et al., 2005; Niklasson et al., 2010). A comparable situation exists in North America where the perception of the importance of fire in temperate deciduous forests is increasing, but still remains to be disputable. On the other hand, no one doubts, for example, the fire-driven dynamics of the

Pine Barrens, a temperate pine forests on sandy soils in north eastern USA (Abrams, 1992; Hoss et al., 2008). In Central Europe, there is evidence that wildfires normally occur in natural Scots pine-dominated forests in sandstone areas, which are considered a geographically disjunct analogy to boreal coniferous forests of northern Europe (Novak et al., 2012). There is also evidence that wildfires occurred throughout the Holocene period (i.e. the last 10000 years). Charred plant material has been found in sedimentary peat bog records (Pokorný and Kuneš, 2005; Abraham, 2006) and in sand sediments under rocks (Sádlo and Herben, 2007). However, the spatial and temporal dynamics of forest fires, and the environmental factors responsible for their occurrence over millennia had so far not been studied in the area.

Changes in the temporal distribution of fire events on the millennial scale are usually inferred from the sedimentary charcoal record in lakes or peat-bogs (Rius et al., 2011). This approach can reveal the frequency of fires in ancient times; however, the spatial distribution of ancient fires remains uncertain. On the contrary, spatially explicit fire histories can be derived from fire scar chronologies, which usually span only the last several centuries, however (Niklasson et al., 2010). In any case, well preserved traces of fire in the tree-ring record are rather infrequent and fragmentary in Central Europe due to the rarity of old scared trees caused by intensive forestry. Another possible reason is the prevalence of low-severity fires, which usually do not leave scars on mature pine trees (Piha et al., 2013).

The goal of this study was to determine the role of environmental factors affecting the frequency and distribution of forest fires on two temporal scales. We traced the occurrence of wildfires over the last three decades and in the last millennium combining two complementary approaches – the study of historical forest management records and assessment of charcoal content in the topmost layer of forest soil. Comparing fire patterns on two different time scales, but using similar environmental correlates, strengthens the inferences about processes controlling the distribution of forest fires in the landscape. Specifically, we aimed to reveal:

1/ Whether the region under study has a continuous long-term fire history;

2/ Whether the spatial distribution of wildfires is driven by the same environmental factors over decades as over millennia; and

3/ Whether the spatial distribution of wildfires in the landscape is driven more by anthropogenic or natural factors.

We also discuss the implications of our findings for forest management practice in protected natural areas of Central Europe.

2. Materials and methods

2.1. Study area

We worked in the Bohemian Switzerland National Park (BSNP), situated in the NW region of the Czech Republic (Fig. 1). It is part of a larger landscape territory – the Elbe Sandstones, which also include the Saxon Switzerland National Park in Germany. The BSNP was established in 2000 and covers an area of 79 km^2. Elevations vary from 116 to 619 m a.s.l.. The bedrock is composed of quartzose sandstone rocks of Cretaceous origin with occasional outcrops of Tertiary volcanic bodies. The terrain is very rugged, with cliffs, pillars, rock walls, arches, gorges, canyons and several conic volcanic hills. The depth of some gorges exceeds 200 m. Such landscape heterogeneity results in great variation in habitat conditions within a relatively small area, for example, frequent alternation of moist shady gorges with steep slopes and dry insolated rock tops (Fig 1).

Fig. 1. Common topography of the BSNP landscape (Pravčický důl valley).

The main part of the BSNP is covered by forest. The natural vegetation is an acidophilous beech and mixed spruce-fir-beech forest (*Luzulo-Fagetum*). Other forest communities occur in special habitats – Norway spruce (*Picea abies*) stands in narrow gorges with climatic inversion, acidic Scots pine and oak-pine forests (*Dicrano-Pinetum*; *Vaccinio vitis-idaeae-Quercetum*) on sandstone rock tops, and herb-rich beech forest (*Melico-Fagetum*) on several volcanic hills (Mikuláš et al., 2007).

The contemporary forest is dominated mainly by spruce and pine plantations; natural vegetation remains mainly in inaccessible terrain (rock tops, gorges, hill slopes, etc.). The approximate present BSNP forest composition is: 71% Norway spruce *(Picea abies);* 16% Scots pine *(Pinus sylvestris);* 6% European beech *(Fagus sylvatica);* 3% European larch *(Larix decidua),* which is not native in this region; 2% invasive White pine *(Pinus strobus)* and 1% silver birch *(Betula pendula).* The abundance of other occurring species, for example, sessile oak *(Quercus petraea),* European ash *(Fraxinus excelsior)* and black alder *(Alnus glutinosa)*, etc., is less than 1%.

The earliest traces of human presence in the region date to the Mesolithic age (9500–5500 BC), when hunters and gatherers settled rock shelters (Svoboda, 2003). There is weak evidence that humans occupied the area during the Neolith and Bronze Age. Since that time, there is no evidence of any important human presence up until the early Middle Ages (Jenč and Peša, 2003).

Compared to the rest of the Czech Republic, forest fires are markedly more frequent in this area (Jankovská, 2006). References about local forest fires are found in historical records (Belisová, 2006) and also in present mass media. Nowadays, all fires are suppressed by the fire brigade, although the very jagged terrain hinders early detection of fires and makes them difficult to extinguish.

Actual forest management in the BSNP is focused on active transformation of even-aged spruce plantations into a forest with natural tree species composition. Forest typology maps (Randuška, 1982) based on a concept similar to that of potential natural vegetation (Tüxen, 1956) are used as a benchmark for natural forest composition. Non-native species are removed, *Picea abies*, which is nowadays very abundant, is suppressed, and *Fagus sylvatica* and *Abies alba*, currently rare, are supported and planted. Natural *Pinus sylvestris* stands are proposed to occur only on dry rock cliffs with shallow soils.

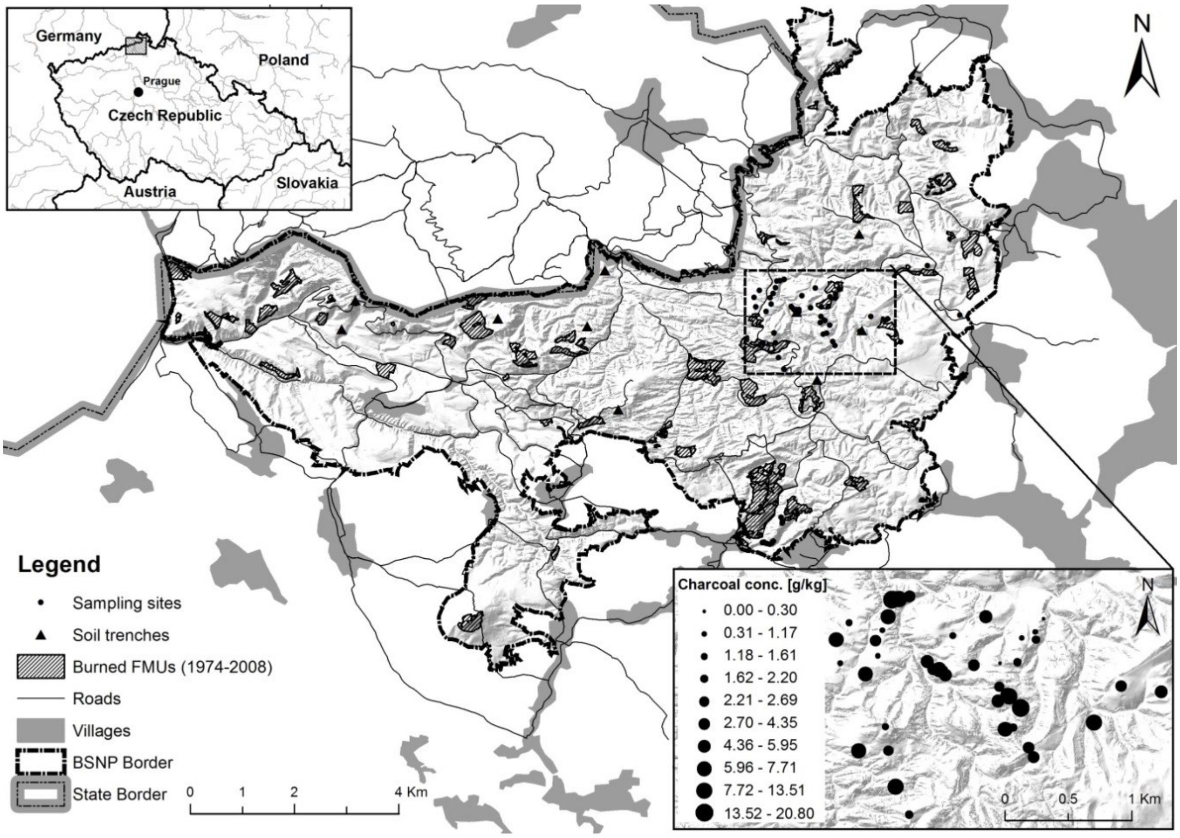

Fig. 2. Map of the study area with soil charcoal sampling sites and fire-affected Forestry Management Units (FMUs). The map section shows the distribution of soil charcoal sampling sites within the pilot area. Dots size corresponds to charcoal concentrations in the upper 20 cm of soil. Triangles represent soil trenches from which samples for radiocarbon dating were taken.

2.2. Ancient forest fires

2.2.1. Charcoal spatial pattern

To detect the spatial distribution of ancient fires, we selected a pilot area of 4 × 2 km situated within the core zone of the BSNP (Fig. 2, inset graph), where we assessed the spatial pattern of charcoal concentration in the topmost soil layer (0–20 cm). We consider this area to be representative of the rest of the protected sandstone landscape because it covers the common altitudinal gradient and has a typical relief configuration.

Charcoal can be retransported by various processes, including water erosion or wind dispersion, resulting in homogenization of spatial signal. The selection of proper sampling sites and charcoal size fraction can minimize the effect of post-depositional processes (Clark, 1995). We therefore selected sampling sites only in flat areas and on gentle slopes. Based on the digital elevation model, we identified places with an inclination not exceeding the arbitrarily chosen angle of 6° and occurring outside the accumulation area at the bottoms of valleys. Finally, we randomly selected 61 sampling sites within the pilot area where soil trenches were dug down to the topmost part of the mineral B-horizon (average depth 6.5 cm, SD=5.6), where the highest charcoal content could be expected. To eliminate intra-site heterogeneity in soil charcoal concentration (Touflan and Talon, 2009), we collected 100 cm^{-3} soil samples from four subsamples taken in the corners of the trench (approx. 1 m^2 plot). The final spatial distribution of sampling sites mainly covered flat ridges and larger plateaus at various heights above the valleys. The minimum distance between two nearest sites was 4 m, the maximum distance was 1136 m, and the mean distance was 165 m.

We determined the charcoal content of the soil samples by a modified method proposed by Winkler (1985) based on chemical quantification of carbonized residues of organic matter in the upper soil layer. Dried soil samples (12 hrs at 60°C) were weighed, and organic matter mixed with charcoal was separated from the mineral part by flotation. The floating fraction was captured on a 125 μm sieve. This dried sample was homogenized in a grinding mortar, and decomposable organic matter was subsequently removed by digestion with concentrated hot nitric acid (68% HNO_3, 30 min, 90°C). Sample residue captured on ashless filter paper was dried and weighed. To completely oxidize pyrogenic carbon, each sample was placed in a furnace at 550°C for the 2 hour. The final inorganic residue was weighed again, and the difference represented charcoal mass. The resulting concentration of charcoal was expressed as the proportion of charcoal pieces greater than 125 μm to the dried weight of the soil sample.

2.2.2. Radiocarbon dating

We had 14 samples radiocarbon dated to build a time frame of charcoal formation. The samples for radiocarbon dating were taken from ten trenches within a larger area inside the BSNP (app. 10 × 5 km) to minimize the risk of multiple dating of single fire events and to capture the landscape scale variability in fire occurrence. The raw time scale of charcoal assemblage age within the sampled soil layer (down to 20 cm depth) was based on absolute radiocarbon dating. However, the age-depth relationship in the soil profile could have been distorted due to bioturbation or tree uprooting (Carcaillet, 2001). We therefore only take into account the most frequent age range. The exact probe location was chosen on the flat surface without any trace of former tree uprooting.

Samples (10–15 l each) were taken from the uppermost part of the mineral B-horizon (down to 20 cm) in each trench. Four trenches were sampled at two depth levels to obtain a more detailed insight into the fine soil stratigraphy. The dried soil samples were processed by flotation and wet sieving. Charcoals larger than 5 mm were hand-picked under a stereomicroscope to extract fragments suitable for radiocarbon dating carried out at the University of Salento. The calibrated age of 13 charcoals (one sample of modern age was excluded) were calculated using OxCal 4.1 (Ramsey, 2009) and IntCal09 (Reimer et al., 2009). To establish a "minimal insight" (Robin et al., 2013) into the frequency of fires in the study area, we attempted to distinguish single fire episodes. We thus plotted cumulative probability curves of calibrated radiocarbon dates (Fig. 3) to explore the possible temporal overlaps of fire events.

2.3. Recent forest fires

We used archival forest fire records for the period 1974–2008 provided by the administration of the national park (2000–2008) and by two local forestry administrations – in Děčín (1992–2000, 1/3 of the current NP area) and in Rumburk (1974–2000, 2/3 of the current NP area). From these records, we extracted the date of the fire, the code of the affected forestry management unit (FMU), the size of the burned area and the cause of fire. The FMU code (stated in 96% of records) enabled us to localize most fire events in the map using archival and current forestry maps with the accuracy of FMUs. The FMU area varied from 0.015 to 25.7 ha, with the mean value of 1.7 ha and the median value of 0.75 ha, which provides relatively rough fire localization. The other possibility was to precisely localize sites of fires by surveying the field, but we were unable to detect all recorded fires, probably because of their small areas, low fire intensity that left no visible traces after several decades, former forestry management, etc. We therefore preferred to analyse a less precise but larger dataset of fires localized with the precision of the FMU area (Fig. 2).

Digitized FMUs were classified into two categories: A) Burned FMUs and B) Other FMUs. Burned units were FMUs affected by fire between 1974 and 2008 (96 FMUs in total). Other units were all FMUs with no fire detection within the given time period with the exception of FMUs intersecting the 50 m buffer zone around burned units (3277 FMUs in total). Burned FMUs were digitized from scanned forestry maps of ages relevant to the wildfire dates. Other FMU polygons came from the vector FMU map of 2001.

2.4. Fire incidence correlates

To identify the agents of fire incidence, we tested three groups of factors (Tab. 1) chosen according to the current knowledge of wildfire occurrence: A) Topographic factors, B) Forest canopy composition, and C) Anthropogenic factors. For each factor, a continuous layer covering the entire study area was created using GIS software.

A) Topographic factors were calculated using SAGA GIS (SAGA Development Team 2007) from a detailed digital elevation model (DEM) generated by the LiDAR technology

(TU Dresden, IPF, 2005). To reduce local variation, we resampled the original 1 m LiDAR DEM to a 5 m DEM through multilevel B-spline interpolation (Lee et al., 1997). We then calculated the following topographic factors from the resampled DEM: 1) Height above the valley that corresponds to the elevation of the site above the neighbouring valley bottom; 2) Heat load index (Boehner and Antonic 2009) indicating the thermal influx computed from slope and aspect with a maximum on SW and a minimum on NE slopes; 3) Rock height; and 4) Rockiness, a measure of rock abundance in the FMU. The vector layer of rocks used to compute factors 3–4 was created from a raster layer of slopes by arbitrarily considering slopes steeper than 55° as rocks. Rock height was computed as the difference between the minimum and the maximum elevation of each particular rock polygon. The Rockiness factor was computed as the sum of the areas of all rock polygons in the FMUs divided by the total FMU area. Factors 1–3 were used as the maximum value for each FMU polygon. Particular FMU shapes broadly reflect the relief, but in many FMU polygons, abiotic conditions vary immensely (e.g. FMUs along the slope profile from the valley bottom to rock tops). As the highest factor values are supposed to indicate the most favourable conditions for fire ignition, we operated with the maximum values of environmental factors (relief and distances).

B) The forest canopy composition factors were inferred from current and archival forestry management plans (FMP). The factors were abundances of particular tree species in FMUs measured in wood supply units (m^3/ha) and stand age in decades. We included abundances of tree species occurring in more than 5% of FMUs: *Picea abies, Fagus sylvatica, Pinus sylvestris, Pinus strobus, Betula pendula* and *Larix decidua.* The archival FMP was used to find out the tree species composition of Burned FMUs in the time immediately before fire events. The FMP from the 2001 was used for the Other FMUs.

C) Anthropogenic factors were represented by each FMU’s distance from the nearest village and the nearest road (in the sense of all asphalt roads inside and outside the BSNP area and marked tourist paths). The distance was measured from the nearest edge of the FMU polygon. GIS layers representing the road network and villages were vectorized from raster maps (1:10000). The current FMP was provided by the BSNP administration.

Table 1. List of environmental variables used in analyses.

Variable code	Analysis	Variable description	Min	Max	SD
Heat load	ancient	Max. heat load value within 30 m radius around sampling site [unitless]	−0.1	0.7	0.2
Heat load	recent	Max. heat load value within the FMU* [unitless]	−0.5	0.9	0.2
Height_valley	ancient	Height above the valley bottom at the sampling site [m]	0.5	19.1	4.1
Height_valley	recent	Max. height above the valley bottom within the FMU [m]	2.1	327.9	35.5
Rockiness	ancient	Total area of the rocks surface within 30 m radius around sampling site [m^2]	0	722.3	166.9
Rockiness	recent	Total area of the rock surface within the FMU related to its area [m^2/100 m^2]	0	41.2	5.5
Rock height	ancient	Max. height of the rock wall within a 30 m radius around the sampling site [m]	0	56	14.6
Rock height	recent	Max. height of the rock wall within the FMU [m]	0	126.1	22.1
Age	recent	Stand age of the FMU [decades]	0	17	4.3
Bet_pen	recent	Abundance (wood stock) of *Betula pendula* within the FMU related to its area [m^3/ha]	0	97	8.5
Fag_syl	recent	Abundance (wood stock) of *Fagus sylvatica* within the FMU related to its area [m^3/ha]	0	626	47.2
Lar_dec	recent	Abundance (wood stock) of *Larix decidua* within the FMU related to its area [m^3/ha]	0	290	20.7
Pic_abi	recent	Abundance (wood stock) of *Picea abies* within the FMU related to its area [m^3/ha]	0	564	139.8
Pin_str	recent	Abundance (wood stock) of *Pinus strobus* within the FMU related to its area [m^3/ha]	0	272	19.0
Pin_syl	recent	Abundance (wood stock) of *Pinus sylvestris* within the FMU related to its area [m^3/ha]	0	357	59.0
Roads	recent	Distance from the edge of the FMU to the nearest road or tourist path [m]	0	1060	179.3
Villages	recent	Distance from the edge of the FMU to the nearest village [m]	0	3517	846.4

* FMU = Forestry Management Unit

2.5. Data analysis of ancient fires

To analyse the relationship between charcoal concentrations and fire-driving factors, we used linear models with Pearson's correlation coefficient as a measure of the strength of linear relationships among variables. The following topographic predictor variables were used in the model: Rock height, Height above the valley, Rockiness and Heat load index. These predictor variables are the same as in the analyses of recent fires and were selected because they are stable over time. It was thus possible to draw a comparison between drivers of ancient and recent fires. Taking into account the possibility of restricted charcoal dispersion during fire events (Ohlson and Tryterud, 2009) and subsequent post-fire downfall of charred stumps, we used maximum values for derived topographic factors and the sum of all rocks for Rockiness within the radius of 30 m around each sampling site to approximate the spatial scale on which wildfires operate. Charcoal concentrations (n=61) were transformed prior to the regression analysis using a common logarithm. To investigate which factors significantly explain charcoal concentration, we used multiple linear regression and forward selection of variables as implemented in STATISTICA 8.0 (Hill and Lewicki, 2007).

2.6. Data analysis of recent fires

Relationships between the environment and presence-absence data on the occurrence of an observed phenomenon are traditionally computed by regression models or their generalized forms (GLM, GAM) that define the probability of the phenomenon's occurrence along a gradient of an environmental factor (Guisan and Zimmerman, 2000; Guisan et al., 2002). An essential condition for successful model calibration is a high-quality presence and absence dataset. The occurrence of wildfires is well documented by presence data, but to prove that a concrete locality was not affected by fire in the studied period is impossible without a detailed field survey. Moreover, the dataset available to us is limited by a relative short time period covered by the archival forestry record. We therefore cannot exclude the possibility that wildfires occurred in any of the FMUs before this period.

Special techniques for assessing relationships between the environment and the occurrence of phenomena that consider only presence data have been developed to deal with such cases (Elith et al., 2006; Phillips et al., 2006; Tsoar et al., 2007). For our purpose, we used the ENFA (Ecological Niche Factor Analysis) method developed by Hirzel et al. (2002), which is more focused on probable causal relationships between particular factors and a certain phenomenon than merely on predicting its occurrence. The ENFA is based on an ecological niche of a species (wildfires in our analyses) defined as an n-dimensional space composed of particular environmental factors. The niche position in the space is described using two measures: *marginality* and *specialization*. *Marginality* is in our case the difference between the mean of whole area factor values (all FMUs) and the mean of wildfire presence factor values (Burned FMUs). Higher absolute values of *marginality* imply higher differences between factor values of localities with fire occurrence and those for the whole study area. Factors with higher absolute *marginality* values have stronger effects on the incidence of wildfires. A positive number shows a shift towards higher mean factor values in the plots with a localized fire; the negative sign indicates an indirect proportional effect. *Specialization* is computed as the ratio of the standard deviation of factor values for the whole area to those in places with wildfire presence. Higher *specialization* values indicate narrower species niches, i.e. more restricted distribution of the habitat within the available environment. The analysis resembles principal component analysis (PCA). The *marginality* axis is extracted as the first axis, followed by several uncorrelated *specialization* axes until the number of initial variables is exhausted (Hirzel et al., 2002; Basille et al., 2008).

To cope with the different areas of FMUs, which could account for the observed fire incidence, but was beyond our interest, we subsampled the total number of 3277 Other FMUs according to their area, resulting in a subsample of 1000 units which have the same probability distribution function of FMU area as a set of 96 Burned FMUs. This sample set constitutes the landscape matrix used in the ENFA. This analysis was performed using the Adehabitat package (Calenge, 2006) for R (R Core Team, 2012). We tested the significance of the *marginality* values of particular factors by a randomization test of 1000 repetitions to distinguish the factors whose *marginality* values cannot be exceeded by a random distribution of presences (to be significant at least in 95% cases). Spatially defined information was processed using ArcGIS software, version 9.2 (ESRI, 2007).

3. Results

3.1. Ancient fire events

Charred material larger than 125 μm was present in all 61 soil samples analysed within the pilot area. However, the abundance of charcoal in the topmost 20 cm of the soil profile varied considerably from 0.0006 $g.kg^{-1}$ to 20.7964 $g.kg^{-1}$ (mean 4.68, SD=4.37). Low charcoal concentrations under 1 $g.kg^{-1}$ made up only 13% of the whole dataset, suggesting ubiquitous occurrence of charcoals in forest soils of the sandstone area. We also found substantial variation of charcoal concentration between proximate sites, indicating a non-uniform distribution of charcoals following fire events. Since we performed homogenization of sub-samples within 1 m^2, we were unable to assess small-scale variability. However, the maximum difference between the nearest sampling sites was 3.1 $g.kg^{-1}$.

The regression Model 1 including all proposed topographic predictors was statistically significant; however, only because the Heat load index factor had a significant effect (Tab 2). In the stepwise forward selection procedure, only the Heat load index contributed significantly to the model's explanatory power, and thus remained in the minimal adequate regression model (Model 2). Other environmental factors included in the analysis did not improve the model fit significantly. The positive estimated slope for the Heat load index indicates that charcoal concentrations in soil increase with increasing Heat load index, i.e. with high exposition to solar radiation (southwest-facing slope orientation).

The radiocarbon dating of 14 charcoal samples performed to assemble a time frame of charred matter formation revealed that 70% of forest fires occurred during the last millennium. We also obtained much older (3399 cal. yrs BP) and recent (276 cal. yrs BP) dates within the investigated topmost soil layer (Tab. 3). Thus, the measurements of charcoal concentration within this soil layer represent an outcome of fire activity at a given site throughout the Subatlantic period (2500 cal. yrs BP - present). The spatial distribution of dates shows no apparent pattern with respect to the environmental gradients. The ranges of calibration intervals (2 σ) formed three major clusters during the Middle Ages and Early Modern Period and two non-overlapping fire events in the Bronze Age (Fig 3).

Table 2. Multiple regression results. Model 1: Linear regression of charcoal concentration in the topmost soil layer as a dependent variable and topographic parameters as independent variables, R= 0.41; R^2= 0.167; F(4.56)=2.8047; p<0.03415 ; Model 2: Stepwise linear regression with forward selection of variables, R= 0.40; R^2= 0.164; F(2.58)=5.6724; p<0.00562

	Model 1				Model 2				
Variables	*β*	SE *β*	*t*	*p*-value	Step	*β*	SE *β*	*t*	*p*-value
Intercept			5.894	0.000				6.762	0.000
Heat load	0.561	0.205	2.737	0.008	1	0.503	0.160	3.136	0.003
Rockiness	-0.018	0.256	-0.070	0.945					
Rock height	-0.078	0.273	-0.284	0.777					
Height_valley	-0.164	0.169	-0.970	0.336					

Table 3. ^{14}C ages of charcoal fragments extracted from the topmost 20 cm of soil profiles distributed across the whole BSNP area. Calibrated ages include the median probability of the calibration probability distribution and 2 σ range.

Site	Lab code	Depth (cm)	^{14}C age (BP)	Calibrated age (cal yrs BP ± 2 σ)
Ponova louka	LTL8214A	0–6	Modern	
Pravčický důl-hrana	LTL8206A	3–10	236 ± 45	276 (1–452)
Jedlina	LTL8211A	9–12	340 ± 45	396 (307–493)
Zadní Jetřichovice	LTL12356A	8–10	370 ± 35	431 (316–503)
Pryskyřičný důl	LTL8208A	4–8	368 ± 30	434 (316–502)
Piket	LTL12353A	10–15	818 ± 35	728 (680–788)
Pravčický důl-ústí	LTL12357A	7–13	938 ± 45	851 (746–931)
Jedlina	LTL8212A	15–20	1074 ± 40	984 (927–1060)
Česká silnice	LTL12347A	11–15	1351 ± 45	1281 (1182–1341)
Mlýny	LTL12358A	2–10	1399 ± 40	1313 (1271–1376)
Mlýny	LTL8202A	15–20	1449 ± 45	1345 (1285–1472)
Ponova louka	LTL8215A	6–20	1650 ± 45	1552 (1413–1692)
Pryskyřičný důl	LTL8209A	10–16	2626 ± 40	2755 (2716–2844)
Eustach	LTL8203A	12–16	3174 ± 50	3399 (3249–3553)

3.2. Recent fire events

In the period of 1974–2008, 71 fire events affected 96 FMUs within the territory of the BSNP (Fig. 2). Some of the FMUs were affected by fire repeatedly over the course of the study. The real number of fires was probably higher because some of the fire records were impossible to localize (the FMU code was not stated) and due to a hiatus in the archival data from the W part of the BSNP in the period of 1974–1992.

The average fire frequency in the BSNP was two fires per year. The mean, median and mode size of the burned area was 0.75 ha, 0.08 ha and 0.01 ha, respectively. The largest fire was 17.92 ha. The causes of most fires were unknown or unstated (83%), 10% were caused by open fires (foresters, tourists) and 4% by cigarettes and 3% by lightning.

Using ENFA, we indicated the factors responsible for the wildfire distribution in the BSNP. These factors have a significant *marginality* value in the randomization test (Tab. 4). Fire incidence was primarily influenced by the factors Rockiness and Heat load index, followed by Height over the valley and Rock height. The factors with the least but still significant effects were Scots pine abundance and Stand age (Tab. 4 and Fig. 4). Factors representing the abundance of other tree species were deemed insignificant by the randomization test of *marginality*. The influence of anthropogenic factors is of marginal significance. The ENFA did not show any noticeable trends in *specialization* (Fig. 5). The highest values of *specialization* are related to Rockiness and Rock height. This can be interpreted as a partial limitation of wildfire occurrence on FMUs with rocks.

In summary, the results indicate that wildfires are more frequent at the following sites (in descending order of importance): 1) rocky and elevated places (typically rock tops); 2) more insolated places (S, SW slopes); 3) stands with higher Scots pine abundance; 4) older forest stands; and 5) areas close to villages, roads, tourist paths and other places of human activity (with marginal effect).

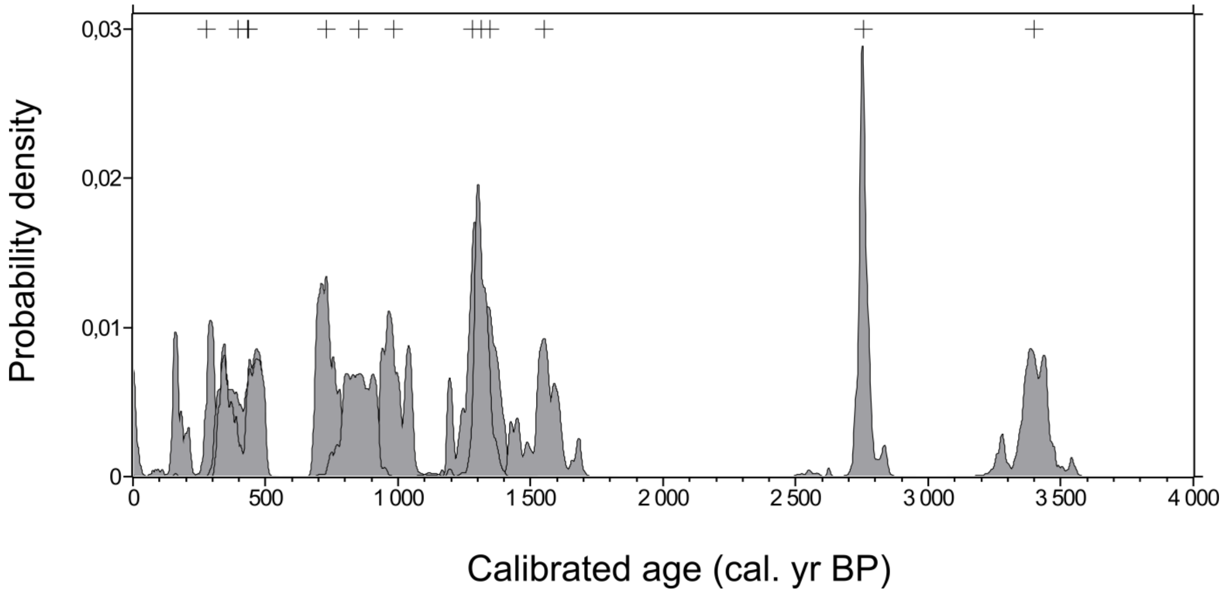

Fig. 3. Distribution of the cumulated probability of calibrated ^{14}C dates (n=13, one modern sample excluded) of charcoal fragments extracted from soil profiles located across the whole BSNP area. The crosses denote the median probability of the 2 σ calibration interval.

Table 4. *Marginality* values of environmental variables and their correlations with the *specialization* axes of the ENFA (Spe1, Spe2). The factors are sorted in descending order of *marginality* values and tested for *marginality* significance by a randomization test (p-value). Factors with significant *marginality* ($p < 0.05$) are highlighted in **bold.**

Variables	*Marginality*	p-value	Spe1	Spe2
Rockiness	0.563	**0.001**	0.557	0.121
Heat load	0.531	**0.001**	−0.159	0.552
Height_valley	0.435	**0.001**	0.203	−0.198
Rock height	0.431	**0.001**	−0.770	−0.494
Pin_syl	0.347	**0.001**	−0.024	−0.168
Age	0.272	**0.006**	0.063	0.279
Villages	−0.192	0.058	−0.061	0.076
Roads	−0.192	0.052	−0.076	−0.053
Pin_str	0.146	0.150	−0.049	0.023
Lar_dec	−0.145	0.124	0.036	0.471
Bet_pen	−0.105	0.246	0.066	−0.025
Fag_syl	0.096	0.324	0.041	0.015
Pic_abi	−0.059	0.550	0.079	0.243

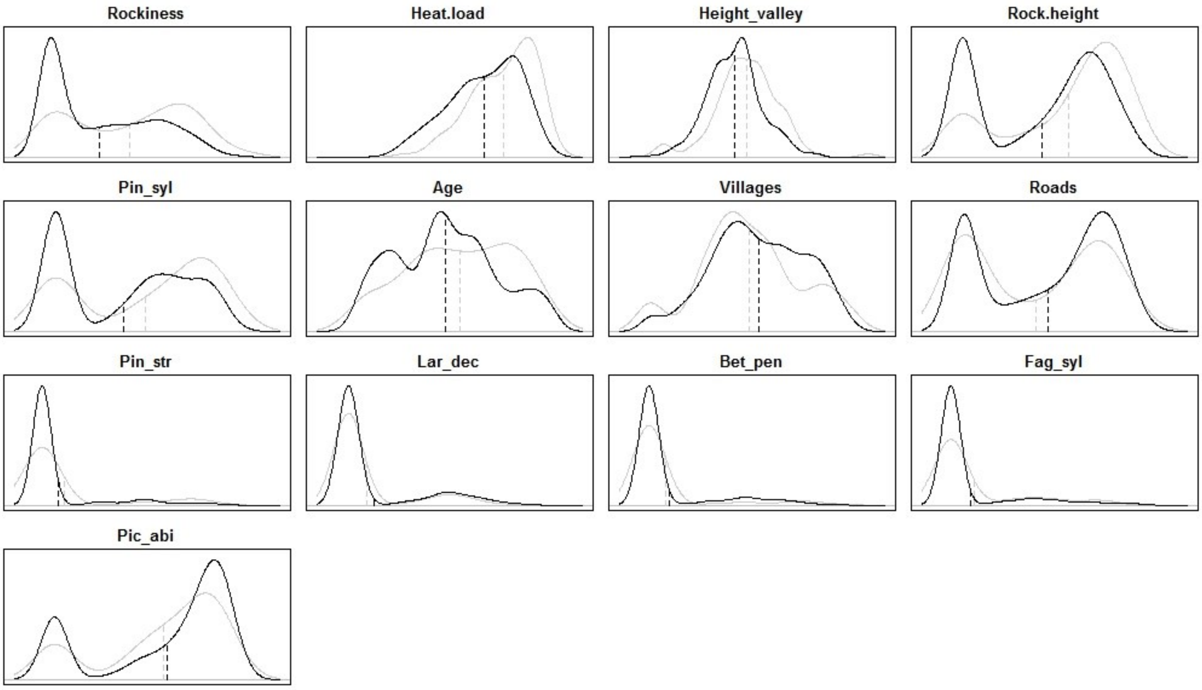

Fig. 4. Graphic output of ENFA. Kernel density estimates (smoothed histograms) of values of particular environmental variables. The grey line represents factor values of FMUs affected by wildfires; the black line represents values of all FMUs.

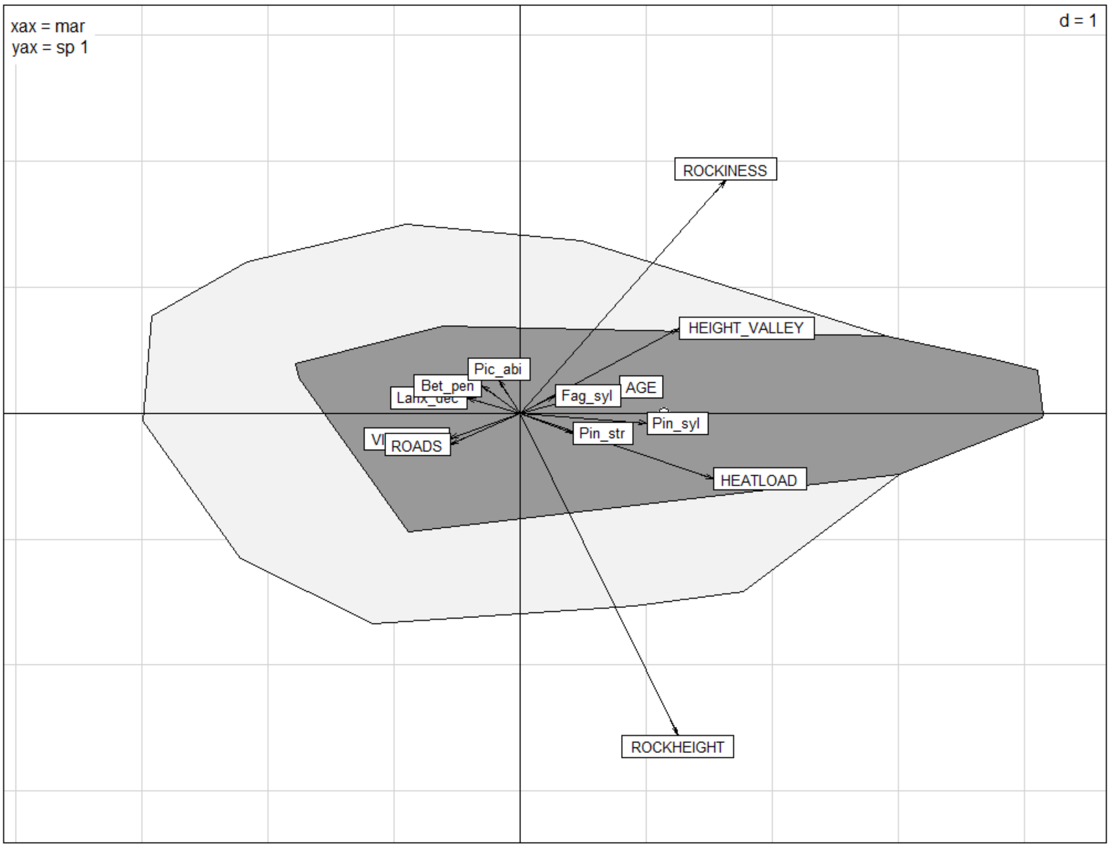

Fig. 5. Graphic output of ENFA. Biplot of the ENFA formed by the *marginality* axis (X axis) and the first *specialization* axis (Y axis). The light and dark areas correspond to the minimal convex polygon enclosing the projections of all and burned FMUs, respectively. The white dot G corresponds to the centroid of burned FMUs. The arrows are projections of environmental variables.

4. Discussion

4.1. Topographic determinants of fire distribution

The results of our two approaches describing the spatial pattern of forest fires on the time scale of the last 34 years and the scale of the last two millennia are comparable. The distribution of wildfires in the present-day BSNP landscape is largely explained by topographic factors. Biotic variables including vegetation composition and stand age have weaker control over the occurrence of wildfires. Long-term fire occurrence inferred from charcoal content in mineral soil varies with the Heat load index. Sandstone landscape landforms thus determine a mosaic of fire-prone sites with higher fire occurrence probability. The overriding effect of Rockiness is probably connected with convex relief forms, shallow sandy soils and reduced canopy density, which increases the irradiation of the soil surface. A higher rate of evaporation at such sites results in a local decrease of humidity and the formation of fire-prone conditions. The significant effect of the Heat load index (i.e. site-specific thermal regime), thus also explains part of the variability connected with moisture distribution at the landscape level. Other parameters with marginal albeit significant effects could also be related to the thermal regime, for example, position along the valley slope profile or height of rocks. However, their positive effect also determines the elevated position of fire-prone areas above the surrounding landscape, thus increasing the probability of lighting strike, which is the most common natural trigger of wildfires (Gromtsev, 2002).

Since we consider topographic characteristics to be constant over the given time period, we also used them as explanatory variables of ancient wildfire distribution. We assume a simple process driven by gravity during which charcoal mass left on the surface by a forest fire is gradually incorporated into mineral soil and moves downwards through the profile (Preston 2006). Subsequent fire events can partly consume charcoal in organic soil layers but simultaneously adds charcoal material, thus increasing its concentration. The total amount of charcoal in mineral soil therefore corresponds to the number of fires which had occurred at a given place. We found that soil charcoal content as a proxy for former fire incidence significantly increases with the increasing Heat load index within a 30 m radius around the sampling site. Our model, however, explained only part of the observed variability (16%), thus implying the role of other factors not included in the model. These missing parameters are related to former vegetation cover and past anthropogenic activity – data on which it is impossible to obtain at stand-scale resolution. It is, however, more probable that the low proportion of observed variation comes down to the chosen methodological approach, which focused on *a priori* selected sites with a minimal risk of redeposition of charcoal (i.e. less than 6° slopes and places outside bottoms of valleys) due to fluvial transport. This selection reduced the total variability of topography-based factors pertaining to steeper slopes and relative vertical elevation (i.e. Heat load and Height above the valley) in the charcoal analyses. Within the context of our sandstone landscape, we suppose that fire spreads from optimal conditions until it reaches a barrier such as an edge of a plateau. We therefore searched for maximum values of the Heat load index inside the 30 m radius around our sampled plots, which represents the minimum distance of charcoal dispersion due to falling burned trees. The relationship could moreover be affected by post-depositional processes generated during the fire event such as small-scale (<1m^2) heterogeneous charcoal distribution. This variability has also been reported by other authors (Touflan and Talon 2009), who related it to the distribution of coarse woody debris on the surface prior to fire events. We partly eliminated this problem by using a sub-sampling strategy from several pits to get an average value of charcoal concentration.

4.2. Biotic determinants of fire distribution

Forest canopy composition and anthropogenic factors were tested in relation to present-day fire occurrence only. According to the ENFA results, the vegetation factors influencing the incidence of fires are only the abundance of Scots pine (*Pinus sylvestris*) and stand age, both with a positive effect. These results correspond to findings from northern Eurasia, where fires are often associated with Scots pine forests. Scots pine occurs often in dryer habitats, and its abundant resiny litter accumulated in developed older forests is easily inflammable (Ellenberg, 2009). At the same time, it is supposed to be one of the most fire-adapted tree species of the region, and the existence of certain Scots pine formations can be conditioned in the region by regular fires (see Engelmark, 1987; Agee, 1998; Angelstam, 1998; Gromtsev, 2002). Higher stand age may increase the probability of fire due to accumulation of organic litter and reduced canopy density (Angelstam and Kuuluvainen, 2004). Based on an interpretation of pollen analyses (Pokorný and Kuneš, 2005; Abraham, 2006), the natural occurrence of Scots pine in the BSNP landscape was always restricted to sandstone rock tops with shallow soil. However, its present-day distribution is much broader and includes slopes and larger plateaus with deeper soil. We thus suppose that the occurrence of Scots pine influences the incidence of fires also in other relief types apart from rock tops.

The anthropogenic influence was approximated as the distance from the nearest road and village. These factors have a marginal effect on fire occurrence compared to the relief and vegetation. This indicates the dominance of natural factors over factors associated with human presence in the landscape as a trigger of fire incidence. Although forest management statistics provide strong evidence for the prevalence of human-lit forest fires in the BSNP area, it is obvious that this ignition trigger is only one presumption from a complex group of preconditions necessary for a fire to break out.

4.3. Local versus landscape drivers

As summarized above, our results indicate a positive effect of the variable landscape surface on fire occurrence. This does not correspond with the situation in regions with frequent fires (MFI < 39 yrs), where the variability of the landscape surface is negatively correlated with fire frequency (Stambaugh and Guyette, 2008). If a landscape is predominantly flat, barriers limiting the spread of fire are infrequent, and the distribution of fuel is continuous. Fires should be more frequent under these conditions than in a variable landscape (Stambaugh and Guyette, 2008). However, in regions climatically less favourable for the occurrence of wildfires, fire-prone conditions occur more frequently on convex landforms than in the flat surrounding landscape (Angelstam, 1998).

This also means that factors operating at the stand scale are more responsible for variation in forest fire incidence than landscape-scale drivers (i.e. the climate) (Iniguez et al., 2008). We suggest that in climatic regions without pronounced drought periods, bottom-up processes are responsible for wildfire occurrence. The specific environmental features of the BSNP sandstone landscape, such as sharp gradients in soil moisture content and numerous fire spread barriers, result in a small-scale pattern of plots affected by fire. The size of most present-day fires does not exceed 0.1 ha, although they are difficult to locate and put out in the rugged landscape. Moreover, our results from radiocarbon dating of soil charcoal do not provide any evidence of large-scale (>100 ha) fire events. The calibration ranges of all fourteen ^{14}C dates collected within the whole BSNP area are clustered in several groups, which could indicate a possibility of synchronous fire events during certain time intervals (Fig. 3). However, the sampling sites are separated by long distances (max distance between soil trenches ~10 km) and numerous barriers to the spread of fire. Based on the available evidence, we find the concept of a larger number of singular events to be more likely.

4.4. Fire frequency

Because our radiocarbon dates are distributed over an extensive area and the number of analyses is low, we were unable to calculate any parameter describing fire frequency. On the other hand, the dates indicate a marked increase in fire occurrence after the beginning of the Early Middle Ages (approx. 500 AD). This could constitute evidence for logging or pastoral activity within areas not permanently settled based on available archaeological and historical data (Jenč and Peša, 2003). During the subsequent High Medieval colonization, human pressure, including establishing of settlements, was concentrated in the surrounding regions. We can reasonably expect an interaction between human activity and other factors influencing the fire regime, resulting in a change of fire frequency. Such a positive effect on wildfire occurrence as a consequence of human activity has been detected in the palaeoecological record all across Europe (Rius et al., 2011). However, the spatial pattern of the most fire-prone areas is driven mainly by non-anthropogenic factors such as relief characteristics, fuel distribution and vegetation type. Moreover, fire disturbances also occurred during the Middle and Early Holocene, as we know from ^{14}C dating of charcoal extracted from deeper soil layers and microcharcoal (>125 um) deposited in peat-bogs (Bobek, 2013). We therefore hypothesize that the topography-driven distribution of fires has a long-term influence on the sandstone landscape.

4.5. Fire as a natural driver in the temperate zone

Our results could significantly alter the current attitudes towards wildfires in Central Europe. Our findings concerning the incidence of wildfires in the BSNP landscape are in accordance with information from regions where wildfires are considered a natural part of forest dynamics. The correspondence between the results of two different methodical approaches and the weak effect of anthropogenic factors indicate that wildfires occurred in similar places at least during the Subatlantic period (from about 2500 years ago to the present day), although fires had probably been less frequent in periods without noticeable human activity. Vegetation occurring on rock tops and plateaus (typically *Pinus sylvestris* stands) has been influenced by human- or lightning-lit fires for centuries. Considering how well *P. sylvestris* and its understorey species are adapted to fire, we assume that the natural occurrence of Scots pine forests in the BSNP landscape partly depends on wildfire activity. This especially concerns Scots pine stands on deeper soils, where other tree species like beech or oak are presumed to form climax forests.

4.6. Implications for forest management

For a long time, wildfires have not been considered to be an important natural disturbance factor in Central Europe. Forest managers and conservationists therefore have not taken them into account. The present management practice in the area under study and similar protected areas is mostly driven by the concept of potential natural vegetation (Tüxen, 1956) or similar forestry typology (Randuška, 1982). This concept, which is based solely on remnants of what is thought to be natural vegetation in equilibrium with the recent climate and soil, does not take into account any disturbance event because it is, by definition, static (see Carrión & Fernández, 2009 and the follow-up discussion). This has an impact, for example, on *Pinus sylvestris* stands in elevated positions characterized by more favourable soil conditions, where pine prevails thanks to the influence of wildfires. Current management policies consider these pine stands as being far from the natural state. They are thus supposed to be replaced by stands with presumed natural tree composition. Our study, however, strongly supports the idea that contemporary Central European forest restoration should accept non-equilibrium states as regular aims of natural conservation. Fire is a natural and important agent forming such states in at least part of this region.

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Chapter 3

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

Martin Adámek, Věroslava Hadincová, Jan Wild

Natural regeneration of *Pinus sylvestris* four years after the wildfire in the protected area Kokořínsko.

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.

Keywords

Scots pine; succession; sandstone; Central Europe; fire severity; tree regeneration

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 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 Fenno-Scandinavian 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 resiny 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 B.C.). 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 km^2 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 suppressed by the fire brigade, although the very rugged terrain of rocky areas hinders their early detection and extinguishment, and also makes reforestation more difficult, so burnt plots are often left to develop spontaneously.

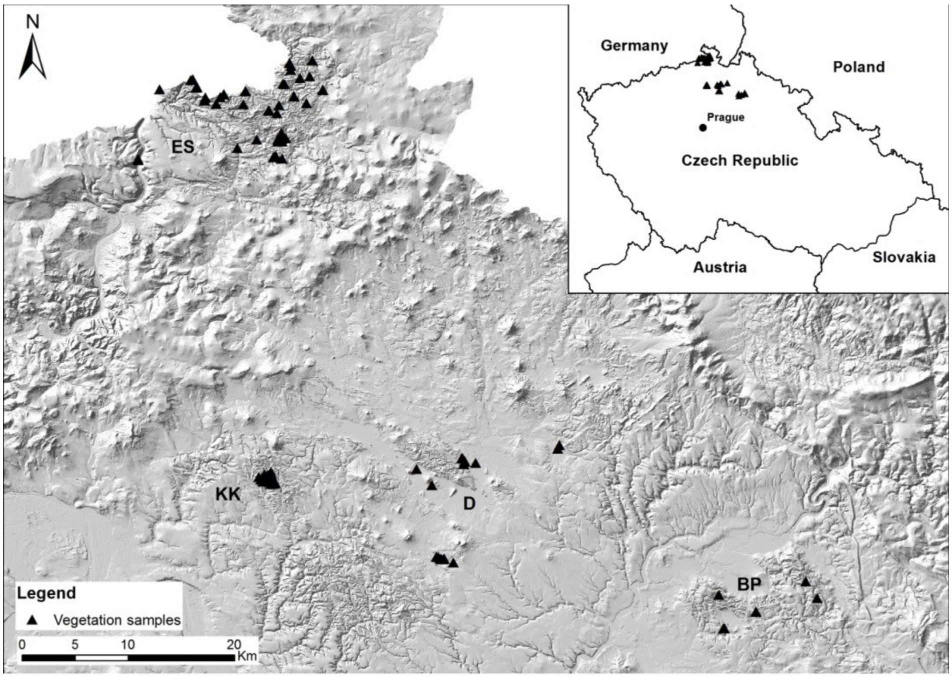

Fig. 1. Localization of the study regions and vegetation plots. ES – Elbe Sandstones; KK – Kokořínsko; D – Doksy region; BP – Bohemian Paradise

2.2. Forest fires occurrences

Information about the approximate place and date of each wildfire was obtained from local nature protection and forestry authorities. Information about wildfires that occurred more than 100 years ago was found in archival forestry maps and records. Individual burnt places were identified based on observable traces of fire such as scorched tree trunks, charred wood on the ground, remnants of charred bark on living trees and the presence of larger charcoal particles in upper soil horizons. We focused on burnt areas that had not been artificially reforested to observe spontaneous post-fire succession. Although the local forest legislation mandates that clearings or naturally disturbed areas have to be reforested within two years, it allows for certain exceptions. Thus, burnt areas of National parks, management-free zones in protected areas, inaccessible localities and small burnt areas are usually left to spontaneous succession. Moreover, some low-severity fires did not critically disrupt the tree canopy, so no forestry interventions were applied.

We found 70 burnt areas 0.01-18 ha large that had developed naturally for 1–192 years. In each homogeneous area, we selected one plot, in which we recorded the composition of vegetation and characteristics of the environment. In larger burnt areas with different angles of slope, aspect or relief type, we sampled more plots to encompass the whole variation in environmental conditions (up to 3 plots per burnt area) and considered these records independent. The final dataset thus included 102 vegetation plots.

2.3. Vegetation and environmental data

We recorded the vegetation composition in 102 post-fire plots 100 m^2 large in burnt areas of known age that had not undergone artificial reforestation. Alongside the vegetation of each burnt area, we recorded vegetation plots with similar environmental conditions and pre-fire tree canopy composition in nearby unburnt stands, representing the mature stage of forest development, further referred to as unburnt plots (55 plots). The unburnt plots were mostly in stands planted after clear-cut logging. To assure that the unburnt plots were not influenced by fire in the past, we checked them for the presence of larger charcoal particles in upper soil horizons and traces of fire on the bark of trees. Percentage cover of the tree layer (woody species > 5 m), the shrub layer (woody species 1–5 m), of juveniles (woody species < 1 m), the herb layer, the moss layer (bryophytes) and the ground lichen layer was recorded in each vegetation plot. All vascular plant and bryophyte species and their abundances were recorded within each of the vegetation layers using the Braun-Blanquet nine degree semi-quantitative scale (Westhoff and van der Maarel, 1973). The species of ground lichens were not determined.

For each vegetation plot, the following data were recorded: region (categories ES, KK, BP, D), post-fire age (i.e. time since the last fire), GPS coordinates, slope, aspect and horizon angle in eight directions to calculate potential direct solar irradiation (Gutzerová and Herben, 2001), fire type (burnt or preserved organic soil layer) and flame height (height of scorching on tree trunks < 2m or > 2m) , thickness of the organic layer (O, measured without the top fresh litter), and thickness of the soil humus horizon (A_h), slope, cover of rocks and of dead wood (%). Stand age of the unburnt plots (time since the last reforestation) was determined from forestry management plans.

We arbitrarily divided the plots into five post-fire age categories comprising a comparable number of plots, utilizing missing values in the dataset as breaking points of the continuous variable: initiation stage (1-6 years old, n = 34), early succession (8-13 yrs, n = 21), shrub stage (15-22 years, n = 17), young forest (25-50 years, n = 19) and mature forest (93-192 years, n = 11). The age category of 51-92 years is missing because of lacking forestry and archival evidence.

To analyse the fire-surviving ability of tree species, we counted the numbers of living and dead mature individuals of each tree species. As mature, we regarded individuals with trunk DBH ≥ 20 cm (age ≥ ca 50 years), which corresponds to the mature forest category (high forest stemwood) according to the local forestry classification. To ascertain the intensity of fire that the species under study are able to withstand, we classified the plots into three levels of fire severity (see below). It was possible to clearly identify the effect of fire on tree survival only in younger plots where fire-damaged trees were not felled, which was sometimes done for safety reasons. To secure a sufficient amount of data on tree survival, we added plots from other areas of pinewoods within the Czech Republic, lying outside the sandstone regions under study but having a similar vegetation composition. Altogether, we thus counted trees in 95 plots aged 1-35 years.

To explore how forests respond to fire disturbances, it is necessary to estimate the extent of their effect. Because we worked with historical fire records, we had to estimate their effect retrospectively based on field proxy data only, namely the extent of charring of the organic and humus horizons (completely burnt or preserved) and the height to which tree trunks were charred. The effect of fire on organic soil horizons was clearly visible in the form of a compact black burnt layer containing charred twigs and needles or (partly) preserved brown organic horizons with its typical structure. This was assessed using three soil probes per plot, all reaching the B-horizon. Traces of flames on tree trunks served as an indication of flame height. Although we did not directly measure the loss of organic matter, we are convinced that both these parameters well describe the impact of fire and can therefore be used as proxies of fire severity in terms of recent terminology in fire ecology (Keeley 2009; Vega et al., 2013).

We assigned three levels of fire severity to all plots with post-fire age under 35 years. Up to this age, traces of fire on tree trunks and in the soil profile were still clearly recognizable, even under newly deposited litter. First, we distinguished plots with at least partly unburnt (Low severity) or completely burnt organic and humus horizons. Plots with burnt horizons were divided into the following two categories according to the height of flames: flames reaching up to the height of 2 m (Medium severity) and flames reaching above the height of 2 m (High severity).

2.4. Data analyses

2.4.1. Forest structure and species composition development

To evaluate differences in vegetation characteristics between post-fire plots of various age and unburnt plots, we used percentage cover of vegetation layers (tree, shrub, herb, moss, lichen, juvenile trees), the number of species and humus thickness, and tested for differences between the groups using the non-parametric Wilcoxon rank-sum test with the Benjamini-Hochberg correction (Benjamini and Hochberg, 1995) in R (R Core Team, 2012).

2.4.2. Dynamics of ecological species groups

To observe changes in the cover of plant species depending on their ecology, we defined ten groups of species. Four groups were distinguished within the herb layer: dwarf shrubs, forbs, graminoids and ferns. The species within the moss layer were divided into three groups following Watson (1955) and Kremer and Muhle (1991): pioneer, forest and indifferent bryophytes. Regenerating trees were sorted into climax and pioneer species, and the most abundant and fire-adapted tree species *Pinus sylvestris* was placed into a separate category. The cover of each tree species resulted from the sum of covers of juveniles and individuals in the shrub layer. We plotted the covers of individual ecological groups against post-fire age of the plots (time since fire) and visualized the trend of this relationship using the loess function in R (R Core Team, 2012).

2.4.3. Effect of fire strength and tree survival

To determine the role of fire severity on forest resistance and post-fire vegetation resilience under the three fire severity levels, we measured Bray-Curtis dissimilarity (Bray and Curtis, 1957) for each pair of burnt and unburnt plots based on species abundance data. Only burnt plots up to 35 years after the fire and their corresponding unburnt plots were used in the analyses comparing responses under the three levels of fire severity, as we did not have data on fire severity for older plots. Bray-Curtis dissimilarity among the plots was computed using the R package vegan (Oksanen et al., 2013). Differences between the three levels of fire severities were visualized using polynomial regression fitting (loess function) within the groups, with the degree of smoothing set to 0.8 (Cleveland et al., 1992).

The post-fire survival ability of different tree species under the three levels of fire severity was counted as the percentage of surviving individuals of particular species summed over all observed plots.

2.4.4. Environmental effects on species composition

To detect the environmental factors influencing species composition in post-fire plots, we performed multiple Redundancy analyses (RDA) with implemented Monte Carlo permutation test using Canoco 5 software (Ter Braak and Šmilauer, 2012) with species abundances expressed on an ordinal scale from 1 to 9. Species with only one occurrence in the dataset were excluded from the analysis. We analysed the importance of each environmental factor on the vegetation as a whole and on the individual vegetation layers separately. The analyses of the effects of the fire severity took into consideration the effect of flame height and burning of the organic layer separately. Since vegetation records were available for fire severity analyses only up to the post-fire age of 35 years, we used the same time interval also for the other analyses (n = 85) to obtain a consistent dataset containing all levels of ecological factors. We tested the effects of particular factors on vegetation separately. The tested factors were: age of the burnt area (coded as age categories), region, organic O layer thickness, humus A_h horizon thickness, fire type, flame height, potential direct solar irradiation, slope, cover of rocks and cover of dead wood. To reveal the pure effect of age and region, we used all other factors as covariables. In analyses of effects of environmental factors, by contrast, only 'age' and 'region' were used as covariables to prevent distortion of the results by possible collinearity of factors.

2.4.5. Species composition development

To reveal and visualize the changes in species composition during the post-fire succession and differences from the unburnt plots, we performed RDA analysis in the same way as described above, but with all vegetation plots included (102 post-fire plots and 55 unburnt plots). The categories representing different time intervals of post-fire succession and unburnt plots were used as an explanatory variable, and the region code was used as a covariable. We then performed two additional RDA analyses to test whether the two oldest categories of post fire succession still differed from the unburnt plots. The type of treatment (Fire vs Unburnt) was used as a categorical variable and the plot code (plots paired with unburnt plots) as a covariable. In the first analysis, we used 19 plots of 25-50 years old post-fire vegetation together with 13 unburnt plots aged 61-170 years. The second RDA analysis was performed in the same way with 11 post-fire plots aged 93-192 years and 8 unburnt plots aged 120-170 years.

To illustrate changes in species' nutrient demands during post-fire succession, we used Ellenberg's species indicator value (EIV) for nutrients (Ellenberg et al., 1992). EIVs of herbaceous species were averaged for each vegetation plot using Juice 7 software (Tichý, 2002). Differences between post-fire age categories were tested by the Wilcoxon rank-sum test.

A detailed list of species included in the analyses with their percentage frequencies based on presence/absence data and average non-zero species covers in the age categories is given in Appendix 1. The list was generated using Juice 7 software (Tichý, 2002).

3. Results

3.1. Forest structure development

We found significant changes in the cover of different vegetation layers among the post-fire age categories (Fig. 2 A-D). The tree layer developed within two decades, but its cover was significantly lower than in the unburnt plots until 25-50 years after fire (Fig. 2A). The great variability in the early phases corresponds to variation in fire severity. Low-severity fires did not disrupt the tree layer almost at all whereas high-severity fires could burn it completely, resulting in different vegetation development under different levels of fire severity (Tab. 1). The main part of the shrub layer was destroyed even by low-severity fires (Fig. 2B). During the first six years, shrubs and young trees (high 1-5 m) were almost absent, as were lichens.

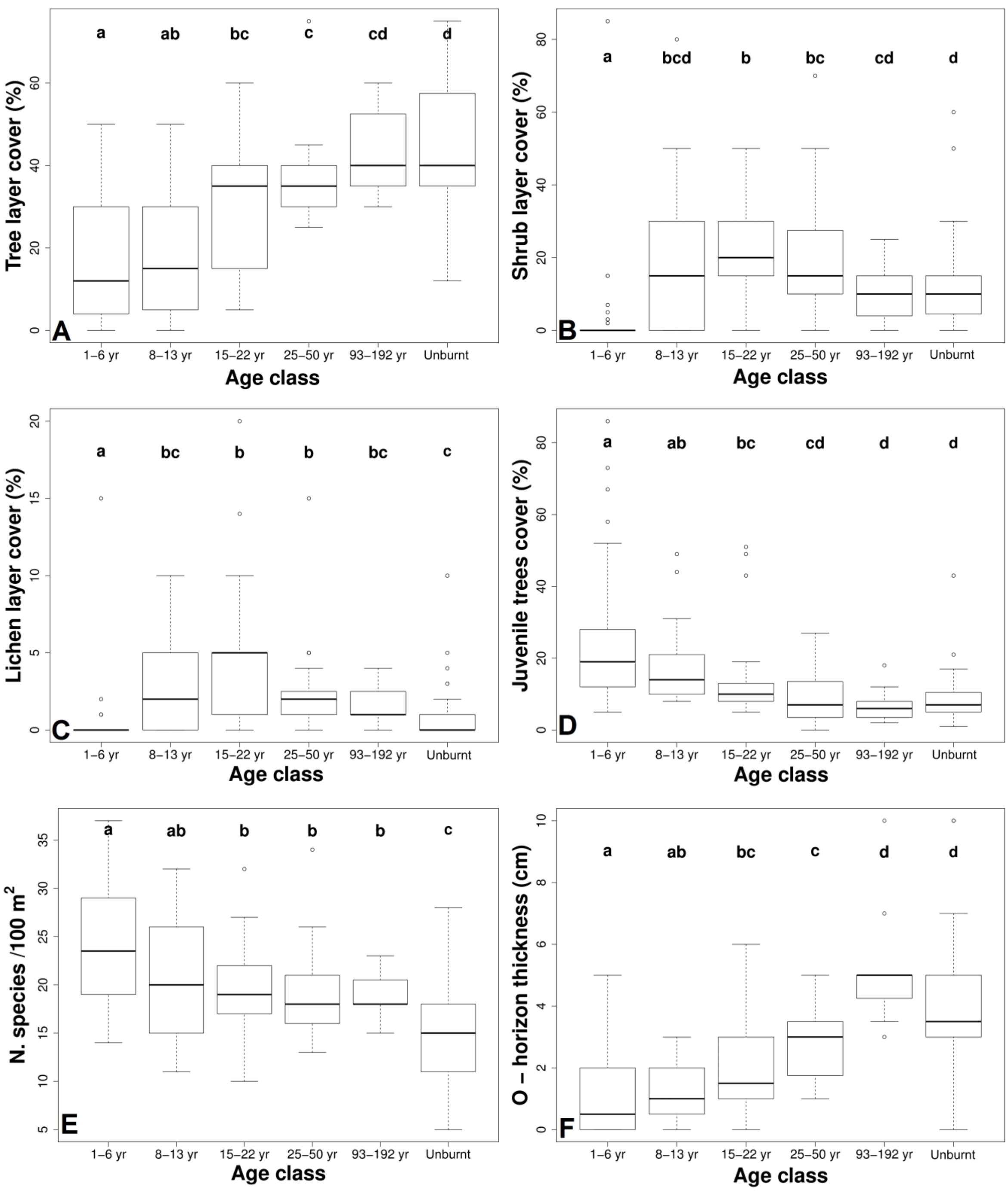

Fig 2. Differences in the cover of vegetation layers (A-D), number of species (E) and thickness of the organic horizon (F) among post-fire age categories and unburnt plots. The different letters indicate significant differences among the age classes and control plots resulting from multiple comparisons using the Wilcoxon's rank-sum test.

Later on, lichens increased and remained significantly more abundant in comparison with the unburnt plots (Fig. 2C). The cover of tree juveniles (high < 1m) was markedly high in early post-fire stages (up until 15-22 years old phase), but then it continuously decreased towards later successional phases, in which it was as low as in the unburnt plots (Fig. 2D). The cover of the herb and bryophyte layers did not significantly differ among age categories and unburnt plots. What did differ, however, was species composition. The total number of species per plot was significantly higher in stands of all post-fire ages compared to the unburnt plots (Fig. 2E). The organic layer (O), if it got burnt, was not restored until the last stage of vegetation development (Fig. 2F).

3.2. Dynamics of ecological species groups

To get an insight into the general trends of vegetation development, we observed changes in the abundance of species grouped together according to their ecology. In the herb layer (Fig. 3A), the main trend was an initial increase in the cover of forbs followed by a sharp decrease, while quite the opposite trend was observed in dwarf shrubs. Tree regeneration was characterized by the usual interaction between pioneer and climax species. Initially, the high cover of regenerating pioneer trees species started to decrease after approximately 15 years and got replaced by climax species. The cover of regenerating *Pinus sylvestris* developed similarly to that of pioneer species, but its initial growth was not so quick. After ca 100 years, the cover of regenerating *Pinus sylvestris* again tended to rise slightly whereas pioneer species continued to fade away (Fig. 3B). A similar shift from pioneer to forest (climax) species occurred in the bryophyte layer (Fig. 3C).

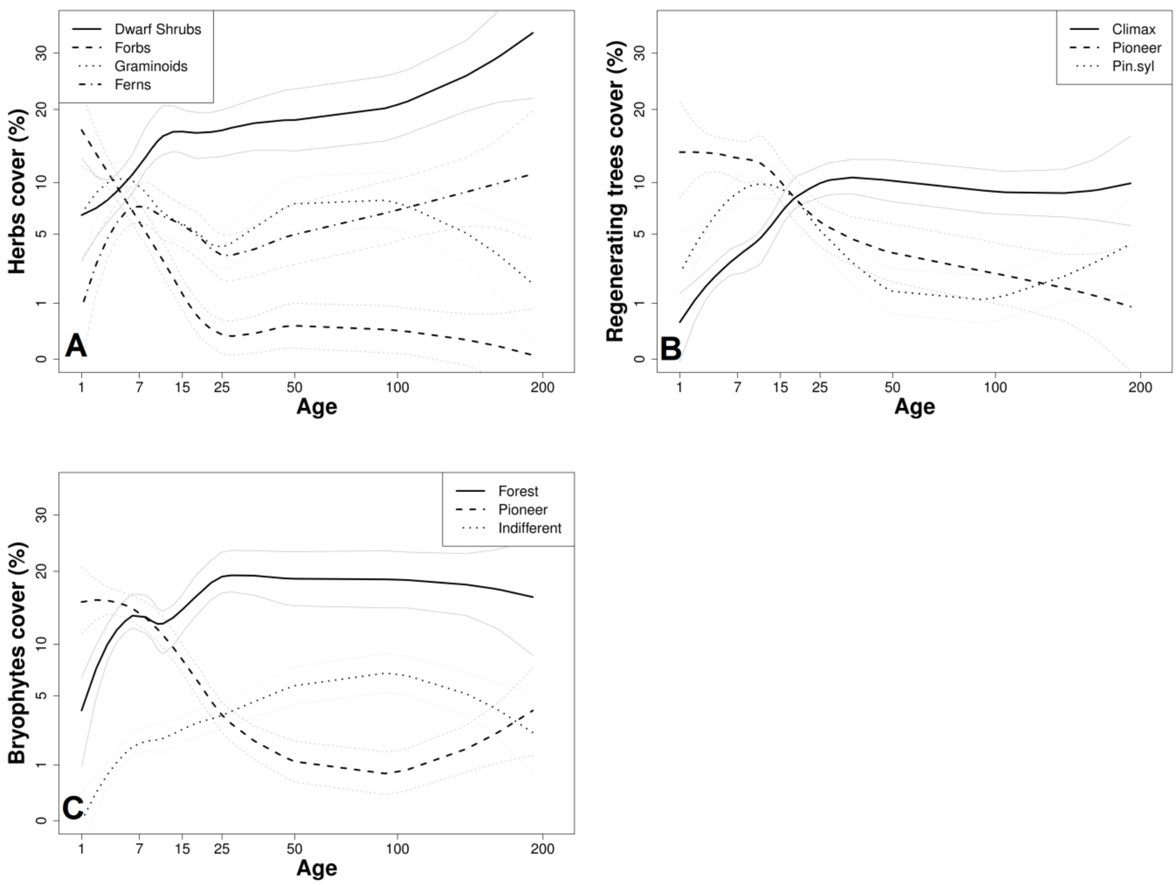

Fig. 3. Post-fire vegetation cover development. Species were merged into groups by their ecology: **A)** Herbs: Dwarf shrubs (*Ericaceae*), Forbs, Grasses, Ferns; **B)** Tree regeneration: Climax, Pioneer, *Pinus sylvestris;* **C)** Bryophytes: Forest, Pioneer, Indifferent. Local regression (loess) visualization with grey lines indicating ± 1 SEM; both axes were square-root transformed.

3.3. Effect of fire severity on forest recovery

Fire severity significantly influenced post-fire vegetation changes measured as Bray-Curtis dissimilarity between post-fire and unburnt plots. Plots affected by high- and medium-severity fires (plots with burnt organic and humus horizons) showed a stronger initial deviation in vegetation composition from unburnt plots than plots with low fire severity (plots with unburnt organic horizons). Plots of high and medium fire severity (classified based on flame height) differed markedly only in the first seven years after fire. Unexpectedly, plots with low fire severity also considerably differed from the unburnt plots. The standard error of the mean (SEM) of Bray-Curtis dissimilarity curves for plots affected by fires of all three severities started to overlap after the 17th year (Fig. 4).

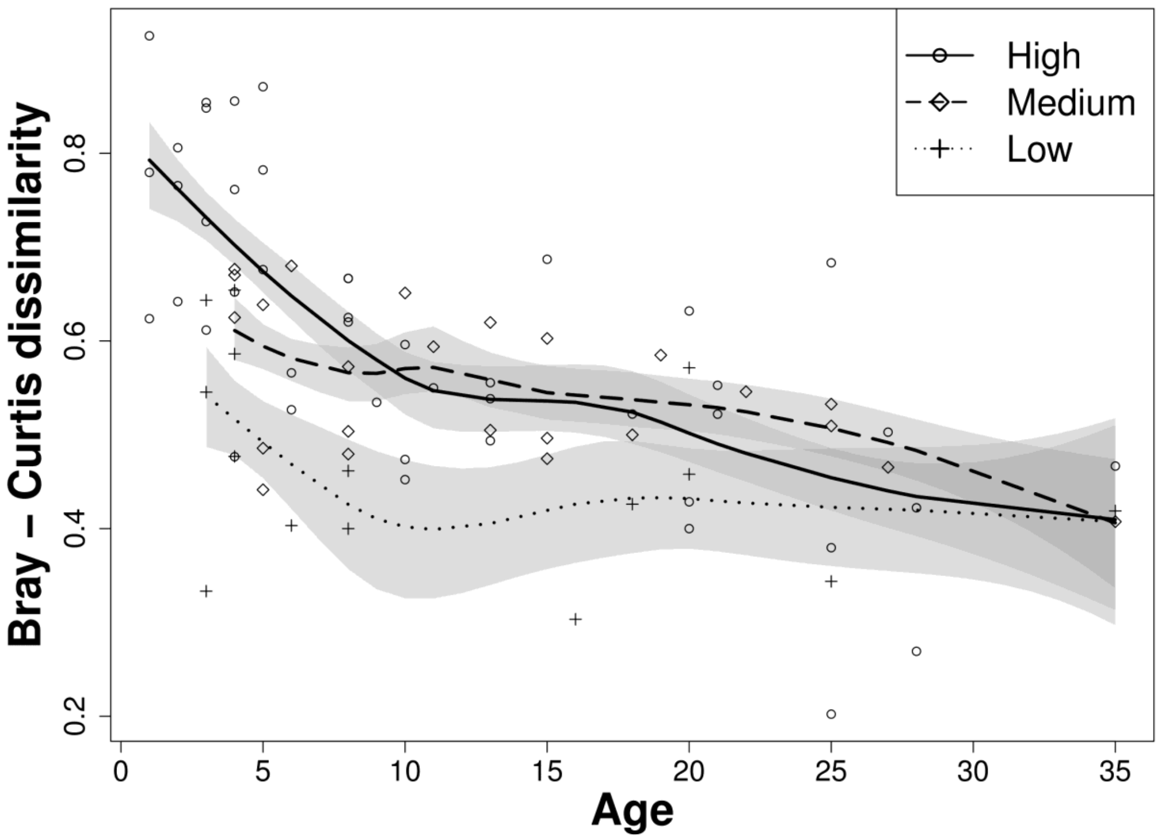

Fig. 4. Post-fire development of Bray-Curtis dissimilarity between burnt and unburnt (control) plots. Local regression (loess) visualization with grey lines indicating ± 1 SEM. Burnt plots up to 35 years after fire were categorized into three groups by fire severity (High, Medium, Low).

3.4. Tree survival

Our analysis of the ability to survive fires of three severity levels revealed differences among the observed tree species. Under low fire severity, all the tree species except *Picea abies* and *Sorbus aucuparia* exhibited a notably high survival rate (more than 60 % of trees survived). With increasing fire severity, species tended to differ in their sensitivity. The most resistant were *Quercus petraea* and *Larix decidua,* whose survival rate was practically uninfluenced by increasing fire severity. More sensitive was *Pinus sylvestris* followed by *Betula pendula,* whose survival rates decreased continuously with rising severity to 39 % and 25 %, respectively. Even more sensitive was the invasive species *Pinus strobus*, which could withstand fires of medium severity (37%) but almost never survived high-severity fires, like the most fire-sensitive species *Picea abies* and *Sorbus aucuparia*. The survival ability of *Fagus sylvatica* was unclear due to the low number of observations. However, it seems to be resistant to fires of low and medium severity, similarly to *Betula pendula,* but more sensitive to high fire severity (Tab. 1).

Tab. 1. Post-fire survival ability of tree individuals (trunk diameter > 20 cm) by fire severity (High, Medium and Low) expressed as the number (N) and percentage of surviving individuals.

Fire severity	**Low**		**Medium**		**High**	
Tree species	**N**	**Surviving [%]**	**N**	**Surviving [%]**	**N**	**Surviving [%]**
Quercus petraea	11	90.9	1	100	8	87.5
Larix decidua	28	71.4	30	66.7	14	85.7
Pinus sylvestris	287	81.5	231	57.6	122	39.3
Fagus sylvatica	8	62.5	6	83.3	4	0
Pinus strobus	5	100	19	36.8	60	5
Betula pendula	42	61.9	43	41.9	12	25
Picea abies	44	31.8	42	11.9	25	0
Sorbus aucuparia	11	18.2	0	-	1	0

3.5. Environmental effects on post-fire vegetation composition

Species composition was significantly influenced by the environment, and the effects differed depending on the vegetation layer. The factors with the strongest effect on species composition were post-fire age (coded as a categorical variable), with the strongest explaining power for bryophytes, and the region, which explained the composition of the shrub layer the most. The overall vegetation and the composition of tree species in all vegetation layers responded significantly to potential direct solar irradiation. The type of wildfire was significantly important for the overall vegetation and for the herb, tree and juvenile layers. Flame height was significantly important only for juveniles. The next important factors were thickness of the soil humus horizon (A_h), explaining the composition of all vegetation layers except the bryophyte layer, and thickness of the organic layer (O), which significantly explained the overall vegetation and species composition of juveniles. Other environmental factors did not affect the vegetation and are not presented in Tab. 2.

3.6. Species composition development

RDA analysis of 157 vegetation plots from all four study regions revealed significant differences in species composition between individual post-fire successional phases and unburnt plots (pseudo-F = 6.0, p-value = 0.002, explained variance = 16.8%; Fig. 5). Early successional phases (1-13 years) differed most from the unburnt plots. In later phases, the species composition of post-fire plots became progressively more similar to that of the unburnt plots. In the last phase, the differences ceased to be significant. Early successional phases (1-13 years) were colonized by more nutrient-demanding species than later phases and unburnt plots (Fig. 6). Significant differences between post-fire and unburnt plots remained up to the 25-50 years old phase (pseudo-F = 2.1, p-value = 0.01, expl. var. = 9.5%). Forests 93–192 years after fire did not differ significantly from the unburnt plots (pseudo-F=1.0, P-value = 0.436. expl. var. = 7.2%). The graphical output of the RDA comparing the unburnt plots and the 25-50 years old phase is presented in Appendix A.

Tab. 2. Environmental factors significantly influencing the overall species composition and composition of vegetation layers in post-fire plots: Age (1-6, 8-13, 15-22, 25-35 years), Region (ES, KK, BP, D), Potential direct solar irradiation (PDSI), Fire type ($O+A_h$ burnt/unburnt), Flame height (<2, >2 m). Results of multiple RDA (explained variance in %, p-value) are presented separately for each vegetation layer. NS = not significant.

factor / layer	**All**	**Tree**	**Shrub**	**Herb**	**Juvenile**	**Moss**
Age	10.5% p = 0.002	8.2% p = 0.002	9.9% p = 0.004	9.5% p = 0.002	10.8% p = 0.002	12.1% p = 0.002
Region	7.6% p = 0.002	7.4% p = 0.01	15.4% p = 0.002	8.1% p = 0.002	7.7% p = 0.002	7.4% p = 0.002
PDSI	4.1% p = 0.004	7.6% p = 0.002	8.7% p = 0.028	- NS	2.8% p = 0.048	- NS
Fire type	2.4% p = 0.002	4.9% p = 0.002	- NS	2.0% p = 0.022	2.8% p = 0.006	- NS
Flame height	- NS	- NS	- NS	- NS	2.90% p = 0.004	- NS
A_h thickness	1.7% p = 0.01	2.6% p = 0.046	3.7% p = 0.028	2.2% p = 0.01	1.7% p = 0.054	- NS
O thickness	1.5% p = 0.024	- NS	- NS	- NS	2.1% p = 0.018	- NS

The first post-fire phase (**1-6 years** old plots in our dataset) was characterized by massive regeneration of the pioneer tree species *Populus tremula*, *Salix capraea*, *Betula pendula* and *Pinus sylvestris*, and less often *Larix decidua.* Seedlings of *P. tremula* and *S. capraea* usually did not survive until later phases, probably due to unfavourable habitat conditions. In this stage, many herb and bryophyte species appeared that were never found in later phases or in the unburnt plots. Typical were species of the *Asteraceae* family (*Taraxacum sect. Ruderalia, Hypochaeris radicata* and *Mycelis muralis*) and the bryophytes

Marchantia polymorpha and *Funaria hygrometrica*. Several alien species were also recorded in this phase (*Conyza canadensis*, *Digitalis purpurea*).

The second phase (**8-13 years old**) was characterized by an expansion of *Calluna vulgaris* and *Polytrichum juniperinum* that continued at a lower rate into the next two phases and by a high frequency of *Rubus fruticossus agg.* and *Pohlia nutans*, both of which occurred more frequently in all post-fire plots than in the unburnt plots. A similar trend was observed for the invasive moss species *Campylopus introflexus*.

In the third phase (**15–22 years old**), surviving juveniles of *Pinus sylvestris*, *Betula pendula*, *Picea abies*, *Larix decidua* grew to form the shrub layer whereas *Picea abies* and the alien *Pseudotsuga menziensii* still remained in the juvenile stage. Ground lichens (such as *Cladonia* sp., *Cetraria* sp.) strongly increased in abundance and frequency, and remained, to a certain degree, in the plots until the next phases of post-fire development.

The fourth phase (**25-50 years old**) was the last phase that significantly differed from the unburnt plots. *Betula pendula* and *Populus tremula* grew to form the tree layer, and their abundance in the shrub layer reached its maximum frequency. Mature *P. tremula* individuals were found neither in any of the other phases nor in the unburnt plots. They, however, occurred very rarely throughout our dataset. This post-fire stage differed from the vegetation in the unburnt plots of the same age most markedly in the higher frequency and abundance of the fern *Pteridium aquilinum*, moss species *Dicranella heteromala*, *Polytrichum formosum* and abundant ground lichens. In the unburnt plots, *Fagus sylvatica* and typical spruce forest species (*Picea abies, Trientalis europea*, *Calamagrostis villosa, Pleurosium schreberi*, *Bazzania trilobata*) were more abundant than in the post-fire plots.

In the fifth, latest phase (**93-192 years old**), *Pinus sylvestris* and *Picea abies* reached the tree layer, but *P. abies* remained mostly in the lower canopy. *Betula pendula* trees became senescent. The herb layer was composed mainly of dwarf shrubs, namely *Vaccinium myrtillus* and *V. vitis-idaea*. This phase was characterized by the presence of *Molinia* sp., *Calamagrostis villosa* and *Pteridium aquilinum* in the herb layer and typical forest bryophytes *Leucobryum glaucum*, *Dicranum scoparium*, *Hypnum cupressiforme*, *Campylopus flexuosus* or *Bazzania trilobata* in the moss assemblage.

Unburnt plots were characterized by the presence of a tree layer composed mostly of *Pinus sylvestris* and *Picea abies,* which was the most abundant in these plots. Full-grown *Betula pendula* was present only in 35% of the plots, unlike the last two post-fire phases, in which its frequency exceeded 80%. The ground layer was composed mainly of dwarf shrubs and forest bryophytes, similarly as in the last post-fire phase.

For a detailed species list with percentage frequencies and average abundance in age categories and species shortcuts used in figures, see Appendix B.

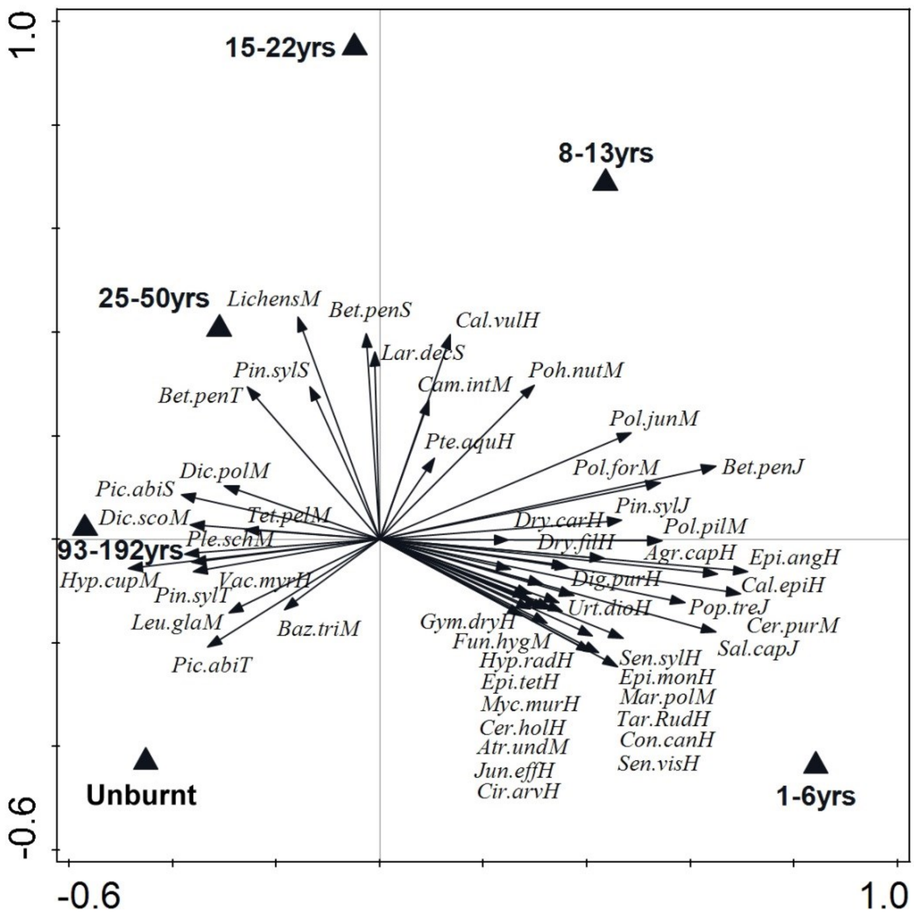

Fig. 5. RDA. Post-fire changes in species composition. Graphic output of RDA of 157 vegetation plots. Categorized post-fire age of burnt plots and a category comprising unburnt plots were used as an explanatory variable, the region code being used as a covariable. The capital letter at the end of each species code marks the vegetation layer: T = tree, S = shrub, H = herb, J = juvenile, M = moss. Pseudo-F = 6.0, P-value = 0.002, explained variance = 16.8%.

Fig. 6. Differences in Ellenberg's species indicator value (EIV) for nutrients among post-fire age categories and unburnt plots. The different letters indicate significant differences among the age classes and unburnt plots resulting from multiple comparisons using Wilcoxon's rank-sum test.

4. Discussion

4.1. Forest recovery

Wildfires have considerably influenced the vegetation structure and composition of temperate pine-dominated forests of Central European sandstone areas. Our results suggest that post-fire stands differed from the unburnt plots at least for 25-50 years. After about 140 years (median age of the last stage), however, the differences were almost undetectable. Our unburnt plots, chosen to represent the pre-disturbance stage of each burnt area, were mainly in mature forests developed from plantations of mostly *Pinus sylvestris*. It is believed that, without subsequent forestry intervention, they develop into semi-natural forests, as other plant species enter the stands (Winter et al., 2010). Vegetation in our post-fire plots can thus be expected to be undergoing succession towards the same type of forests, which represent the semi-natural vegetation of the study regions. This assumption was justified in the case of stand structure and species composition. As for vertical vegetation structure, succession produced the usual stand layers with the same cover as in the unburnt plots (see Fig. 2). The species composition of the last post-fire stage did not significantly differ from unburnt plots either. We thus infer that pine forests in our study areas possess structural and compositional resilience to fire disturbances, as it developed after ca 140 years into a pre-disturbance-like state representing semi-natural vegetation of the study regions. This is in accordance with the findings for boreal forests, whose biodiversity is completely restored after about 120–140 years following a fire (Gorshkov and Bakkal, 1996).

4.2. Effect of fire severity

The most important factor influencing the character of post-fire plots and vegetation development in early succession phases was fire severity. More important than flame height, which was significant only in the case of juvenile trees, was the extent to which the organic and humus horizons were burnt. Surprisingly, the forest understorey possessed only low compositional fire resistance even to fires of low severity that did not completely burn the organic layers and were mostly survived by mature pine trees. However, Bray-Curtis dissimilarity analyses demonstrated that low-severity fires changed the species composition markedly less than those of medium and high severity. After about 17 years, forest stands that underwent fires of all three levels of severity differed in species composition from the unburnt plots to a similar extent. The initial differences can be explained by stronger changes in site conditions, caused by more intense fires, and physical, chemical and biological properties of the soil (Certini, 2005). High-severity fires often caused total destruction of the tree and shrub layer and burnt the organic and humus soil layers. Low-severity fires often did not harm mature trees and did not burn the humus layer, thus preserving the dominant *Ericaceae* dwarf shrubs in the herb layer, which can quickly re-sprout from unharmed underground organs (Parro et al., 2009).

4.3. Vegetation dynamics

In early post-fire phases of succession, previously dominant *Ericaceae* dwarf shrubs and forest bryophytes vanished in favour of herbaceous species and pioneer bryophytes. The cover of dwarf shrubs and forest mosses reverted to the original state after 15-25 years. Burnt areas in the earliest phase hosted a specific flora that almost did not occur in later successional stages or in unburnt forests. The occurrence of these generally more nutrient-demanding species was probably related to a temporarily increased availability of nutrients that were released by fire from organic layers, where they were bound in an inaccessible form in organic layers (Certini, 2005). Other species benefited from fire for longer and often persisted until the oldest post-fire phases. Even 25-50 years following a fire, we found 18 species of vascular plants, bryophytes and juvenile trees never encountered in the unburnt plots. That many of the species recorded in our study plots respond positively to wildfires has been reported from boreal and hemiboreal pine-dominated forests (Marozas et al., 2007; Kwiatkowska-Falinska, 2008; Hekkala et al., 2014a). Fire also significantly benefited ground lichens (*Cladonia* spp*., Cetraria* spp.), which spread the most in later post-fire phases (15-50 years). A positive effect of fire on the abundance of ground lichens has also been observed in Scandinavian and Canadian boreal forests (Engelmark, 1987; Goward, 1999).

4.4. Tree regeneration

Post-fire changes in site conditions also induced massive tree regeneration that remained increased, compared to unburnt vegetation, until the 15-22 years post-fire phase. Fire markedly enhanced the regeneration of *Betula pendula* and *Pinus sylvestris*. Several previous studies also document a positive effect of fire on the germination and early establishment of these species (Hille and Ouden, 2004; Marozas et al., 2007; Huotari et al., 2008). Burnt sites were colonized also by tree species that normally do not regenerate in such forests, such as *Populus tremula* and *Salix capraea*. These findings correspond with the situation in Fenno-Scandinavian boreal forests, where the occurrence of *P. tremula* and partly of *S. capraea* is fire-dependent. These species are claimed there to be the keystone species for preserving the biodiversity of this ecosystem, as many organisms from other trophic levels are dependent on them (Lankia et al., 2012; Latva-Karjanmaa et al., 2006). Although the survival of *P. tremula* and *S. capraea* seedlings until later phases was very low in our study regions, several *P. tremula* individuals that reached the shrub or tree layer were recorded even in plots 25-50 years post-fire. Not one mature individual or a single seedling of any of these species was found in non-post-fire forests (aged between 30 and 170 years).

The enhanced post-fire tree regeneration was probably enabled mainly by changes in light conditions, reduced cover of dwarf shrubs and burning of the organic layer. Humus of the mor type and litter produced by conifers and ericaceous dwarf shrubs, prevailing in the forest type under study, hamper the germination and regeneration of many tree species, including *Pinus sylvestris* (Lecomte et al. 2005). The presence of charcoal probably also significantly enhanced seed germination by adsorbing inhibitive allelopathic phytotoxins and humic acids (Hille and den Ouden, 2005; Zackrisson et al., 2010).

4.5. Long-term effects of wildfires on pine forests

According to numerous studies of boreal forests in Northern Europe, a certain frequency and severity of fires can maintain *Pinus sylvestris* stands also in places where other tree species would otherwise prevail due to site conditions (Engelmark, 1987; Angelstam, 1998; Gromtsev, 2002). Most of the pine forests in our study plots are in sites with deeper soils, where oak-pine or beech stands are the supposed natural vegetation. We observed increased pine regeneration in early post-fire phases that decreased rapidly after about 30 years. From then on, regeneration of *Fagus sylvatica* and *Picea abies*-dominated under the tree canopy of mainly pine and birch. Although the results indicate a slight rise of pine regeneration after approximately 100 years, possibly connected with lightening of the canopy in mature stands, a continuous shift towards stands with higher proportional abundance of temperate climax or shade-tolerant species was found in the oldest stage of succession, and a further increase can be expected during subsequent forest development without wildfires. The next wildfire event would remove especially spruce, and probably also beech and the invasive white pine from the stand whereas full-grown pines, oaks and non-native larches would survive and regenerate. Considering this mechanism, we assume that long-term persistence of stands dominated by *Pinus sylvestris* at sites with deeper soils in our study area is probably dependent on occasional wildfires occurring once in approximately ca 200 years. Based on Bray-Curtis analyses and tree survival, it seems that even low-intensity fire is sufficient to induce typical post-fire changes in species composition and to suppress more shade-tolerant tree species. This idea is supported by recent results of a pedoanthracological analysis from the Elbe Sandstones region, which proves the continuous presence of pine and wildfires throughout the Holocene period (Bobek, 2013).

4.6. Implications for forest management

Post-fire vegetation development resulted in significantly increased species diversity in all successional stages in comparison with unburnt plots. The higher species richness might be evidence of a positive effect of spontaneous development on stand heterogeneity enhancing species richness, for example, by increasing the variation in light availability (Standovár et al., 2007). Early post-fire phases also provide suitable habitats for rare pyrophilous and saproxylic species of fungi and invertebrates dependent on dead wood accumulated after a wildfire, as has been reported from Scandinavian boreal forests (Hekkala et al., 2014b) and newly also from our study area (Marková et al., 2011; Bogusch et al., 2014). Considering also the positive effect of wildfires on tree regeneration, fire should be accepted by local nature conservation authorities as a natural process to which Central European pine forests are well adapted and from which they are able to quickly recover spontaneously.

5. Conclusions

Post-fire succession in temperate Scots pine-dominated forests of Central European sandstone landscapes shows a markedly similar course as in forests of the European boreal zone, where wildfires are considered an integral part of ecosystem dynamics. Stands surveyed in this study exhibited structural and compositional resilience, resulting in recovery of the plant cover in all vegetation layers and a species composition undistinguishable from that of surrounding unburnt forests. However, plant species richness remained enhanced, compared with the unburnt plots, even after ca 140 years of post-fire succession. Fire favorably affected the regeneration of *Pinus sylvestris* in early phases of succession as well as its ability to compete with climax species (*Fagus sylvatica*, *Picea abies*), which have a tendency to dominate the undergrowth in late phases. Periodic fires occurring once in about 200 years thus seem to be a factor maintaining forests dominated by Scots pine in temperate sandstone landscapes. Fire also showed an enhancing effect on overall biodiversity and tree regeneration, pointing to possible beneficial effects of wildfires, from which pine forests are able to recover easily and without any forestry intervention.

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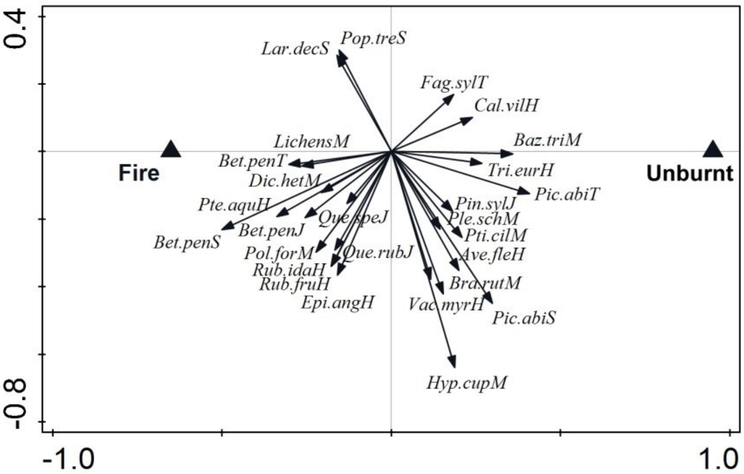

Appendix A. Differences in species composition between the 25-50 years old post-fire stage and unburnt control plots. Graphical output of RDA. The capital letter at the end of each species code marks the vegetation layer: T = tree, S = shrub, H = herb, J = juvenile, M = moss. Pseudo-F = 2.1, P-value = 0.01, explained variance = 9.5%.

Appendix B. Synoptic table of all plant species present in the study plots with their percentage frequency and average non-zero cover within particular post-fire age categories and unburnt plots. The capital letter behind each species name marks the vegetation layer code: T = tree, S = shrub, H = herb, J = juvenile, M = moss.

		1-6 yrs		**8 -13 yrs**		**15-22 yrs**		**25-50 yrs**		**93-192 yrs**		**Control**	
Species	**Shorcut**	**fq**	**cover**	**fq**	**cover**	**fq**	**cover**	**fq**	**cover**	**fq**	**cover**	**fq**	**cover**
Abies alba T	*Abi.albT*	0	0	0	0	0	0	0	0	0	0	2	4
Betula pendula T	*Bet.penT*	17	4.2	43	6.2	68	14.2	86	11.6	82	13.2	35	8.4
Carpinus betulus T	*Car.betT*	0	0	0	0	0	0	0	0	9	4	0	0
Fagus sylvatica T	*Fag.sylT*	11	6.5	10	8	21	11.3	5	18	36	14.3	23	20.8
Larix decidua T	*Lar.decT*	9	8	5	3	16	7.7	10	18	18	10.5	9	9.2
Picea abies T	*Pic.abiT*	11	4.3	19	4	21	3.8	19	4.8	73	8	51	20.5
Pinus strobus T	*Pin.strT*	6	6	5	8	11	3.5	5	4	0	0	12	17.1
Pinus sylvestris T	*Pin.sylT*	77	15.3	76	19	89	21.1	81	29.8	91	27	93	28.7
Populus tremula T	*Pop.treT*	0	0	0	0	0	0	10	3	0	0	0	0
Quercus petraea T	*Que.petT*	14	5.6	0	0	5	3	0	0	9	8	5	16
Quercus rubra T	*Que.rubT*	0	0	0	0	0	0	0	0	9	4	4	3
Sorbus aucuparia T	*Sor.aucT*	0	0	0	0	0	0	5	2	0	0	0	0
Betula pendula S	*Bet.penS*	14	17	48	16.8	58	9.5	62	5.1	27	9.3	21	4.1
Fagus sylvatica S	*Fag.sylS*	3	2	5	3	21	3.5	14	8.3	18	10.5	14	4.9
Frangula alnus S	*Fra.alnS*	3	3	0	0	0	0	5	2	0	0	4	2
Larix decidua S	*Lar.decS*	0	0	14	4.7	32	12.5	14	9.7	9	2	4	2.5
Picea abies S	*Pic.abiS*	0	0	24	7	68	6.5	38	13	64	5.3	60	7
Pinus strobus S	*Pin.strS*	3	3	5	4	26	3.2	19	10.5	9	2	14	9.9
Pinus sylvestris S	*Pin.sylS*	6	10.5	52	17.7	58	9.3	43	5.6	27	9.7	28	11.1
Populus tremula S	*Pop.treS*	9	14.7	5	38	0	0	10	3	0	0	0	0
Pseudotsuga menziesii S	*Pse.menS*	0	0	0	0	5	3	0	0	0	0	0	0
Quercus petraea S	*Que.petS*	0	0	0	0	0	0	0	0	0	0	5	8
Quercus rubra S	*Que.rubS*	0	0	0	0	0	0	0	0	0	0	2	2
Salix caprea S	*Sal.capS*	3	3	0	0	0	0	0	0	0	0	0	0
Sorbus aucuparia S	*Sor.aucS*	0	0	5	2	0	0	5	3	9	3	2	3
Abies alba J	*Abi.albJ*	0	0	0	0	5	1	0	0	0	0	2	1
Acer platanoides J	*Ace.plaJ*	0	0	0	0	0	0	5	3	0	0	0	0
Acer pseudoplatanus J	*Ace.pseJ*	0	0	0	0	0	0	10	2.5	0	0	0	0
Betula pendula J	*Bet.penJ*	100	6.9	95	4.3	84	2.3	29	2.7	9	2	37	1.8
Carpinus betulus J	*Car.betJ*	3	1	0	0	0	0	5	3	9	1	2	2
Crataegus species J	*Cra.speJ*	0	0	0	0	5	1	0	0	0	0	0	0
Fagus sylvatica J	*Fag.sylJ*	37	2.2	29	1.8	32	1.8	38	2.4	36	2.8	35	2.1
Frangula alnus J	*Fra.alnJ*	14	1.4	10	2	16	1.3	14	2	9	2	18	1.7
Fraxinus excelsior J	*Fra.excJ*	0	0	0	0	0	0	5	1	0	0	0	0
Larix decidua J	*Lar.decJ*	43	1.7	14	2	42	2.8	24	2.8	0	0	19	2
Picea abies J	*Pic.abiJ*	69	2.3	62	2.3	89	7.6	67	2.3	64	3.3	67	3.4
Pinus species J	*Pin.speJ*	0	0	0	0	0	0	0	0	0	0	7	2.3
Pinus strobus J	*Pin.strJ*	31	2	24	3	32	2	24	3.8	18	2	32	2.4
Pinus sylvestris J	*Pin.sylJ*	97	6.3	100	4.7	79	2.6	57	2.2	82	1.8	74	2.3
Populus tremula J	*Pop.treJ*	83	5.2	29	7.3	16	1.7	0	0	0	0	0	0
Prunus avium J	*Pru.aviJ*	0	0	10	1.5	0	0	0	0	0	0	0	0

Prunus spinosa J	*Pru.spiJ*	0	0	0	0	0	0	10	1	0	0	0	0
Pseudotsuga menziesii J	*Pse.menJ*	0	0	0	0	11	1	0	0	0	0	2	2
Pyrus species J	*Pyr.speJ*	0	0	0	0	0	0	5	1	0	0	0	0
Quercus species J	*Que.speJ*	40	1.6	38	1.4	42	1.8	62	2.1	9	1	49	1.7
Quercus rubra J	*Que.rubJ*	6	1	0	0	5	1	14	2	9	1	5	1.3
Salix caprea J	*Sal.capJ*	71	2.5	33	1.9	16	1.7	0	0	0	0	0	0
Sorbus aucuparia J	*Sor.aucJ*	37	1.3	48	1.7	47	1.9	24	1.6	55	1.8	32	1.6
Ulmus glabra J	*Ulm.glaJ*	0	0	5	1	0	0	0	0	0	0	0	0
Agrostis capillaris H	*Agr.capH*	46	2.1	10	3.5	26	2.6	10	10.5	0	0	0	0
Agrostis stolonifera H	*Agr.stoH*	0	0	5	2	0	0	0	0	0	0	0	0
Alopecurus pratensis H	*Alo.praH*	3	1	0	0	0	0	0	0	0	0	0	0
Anemone nemorosa H	*Ane.nemH*	0	0	0	0	11	1.5	0	0	0	0	0	0
Athyrium filix-femina H	*Ath.filH*	6	2.5	0	0	0	0	0	0	0	0	0	0
Avenella flexuosa H	*Ave.fleH*	60	9.1	67	4.9	79	6.1	86	14.9	91	3.4	67	7.3
Blechnum spicant H	*Ble.spiH*	3	2	0	0	0	0	0	0	0	0	0	0
Calamagrostis arundinacea H	*Cal.aruH*	0	0	5	2	11	2.5	0	0	9	2	0	0
Calamagrostis epigejos H	*Cal.epiH*	80	5.4	62	4.8	21	2.5	10	13	0	0	2	1
Calamagrostis villosa H	*Cal.vilH*	9	3	19	3.5	21	2	14	2	36	2.5	12	3.3
Calluna vulgaris H	*Cal.vulH*	60	2.2	86	9.1	74	3.9	57	2.3	27	4.7	40	3
Carduus nutans H	*Car.nutH*	9	1.3	0	0	0	0	0	0	0	0	0	0
Carex canescens H	*Car.canH*	0	0	5	1	0	0	0	0	0	0	0	0
Carex leporina H	*Car.lepH*	3	3	5	2	0	0	0	0	0	0	0	0
Carex nigra H	*Car.nigH*	3	2	0	0	0	0	0	0	0	0	2	3
Carex pilulifera H	*Car.pilH*	9	2.3	10	2	16	3.7	19	2.5	0	0	5	2.3
Carex species H	*Car.speH*	3	2	0	0	0	0	0	0	0	0	2	1
Carum carvi H	*Car.carH*	3	1	0	0	0	0	0	0	0	0	0	0
Cerastium holosteoides H	*Cer.holH*	14	1.6	5	1	0	0	0	0	0	0	0	0
Chenopodium album H	*Che.albH*	0	0	5	1	0	0	5	1	0	0	0	0
Cirsium arvense H	*Cir.arvH*	26	2	5	2	0	0	0	0	0	0	0	0
Cirsium vulgare H	*Cir.vulH*	3	2	5	1	0	0	0	0	0	0	0	0
Conyza canadensis H	*Con.canH*	37	1.9	0	0	0	0	0	0	0	0	0	0
Crepis biennis H	*Cre.bieH*	3	1	0	0	0	0	0	0	0	0	0	0
Crepis capillaris H	*Cre.capH*	3	1	0	0	0	0	0	0	0	0	0	0
Dactylis glomerata H	*Dac.gloH*	3	1	0	0	0	0	0	0	0	0	0	0
Digitalis grandiflora H	*Dig.graH*	0	0	5	8	0	0	0	0	0	0	0	0
Digitalis purpurea H	*Dig.purH*	20	12.9	10	2	11	2	14	4.7	0	0	0	0
Dryopteris carthusiana H	*Dry.carH*	54	1.9	24	2.4	32	1.8	29	2.5	9	1	19	2.2
Dryopteris dilatata H	*Dry.dilH*	0	0	10	2.5	0	0	0	0	0	0	0	0
Dryopteris filix-mas H	*Dry.filH*	23	2	10	2	5	2	0	0	0	0	0	0
Epilobium angustifolium H	*Epi.angH*	83	2.2	57	2.3	11	1	10	2	0	0	0	0
Epilobium montanum H	*Epi.monH*	26	2	5	1	0	0	0	0	0	0	0	0
Epilobium parviflorum H	*Epi.parH*	3	1	0	0	0	0	0	0	0	0	0	0
Epilobium tetragonum H	*Epi.tetH*	23	2.1	5	2	0	0	0	0	0	0	0	0
Eupatorium cannabinum H	*Eup.canH*	3	2	5	1	0	0	0	0	0	0	0	0
Festuca ovina H	*Fes.oviH*	0	0	5	2	0	0	0	0	0	0	0	0
Filago arvensis H	*Fil.arvH*	6	2	5	2	0	0	0	0	0	0	0	0

Fragaria moschata H	*Fra.mosH*	3	2	0	0	0	0	0	0	0	0	0	0
Galeopsis species H	*Gal.speH*	3	1	5	2	5	1	5	3	0	0	0	0
Galium saxatile H	*Gal.saxH*	6	2	5	2	11	2	14	4.3	0	0	2	2
Genista germanica H	*Gen.gerH*	3	2	0	0	0	0	0	0	0	0	0	0
Geranium pusillum H	*Ger.pusH*	3	1	0	0	0	0	0	0	0	0	0	0
Gnaphalium sylvaticum H	*Gna.sylH*	9	1.3	5	1	0	0	0	0	0	0	0	0
Gymnocarpium dryopteris H	*Gym.dryH*	9	2	5	2	0	0	0	0	0	0	0	0
Hieracium lachenalii H	*Hie.lacH*	3	2	0	0	0	0	0	0	0	0	0	0
Hieracium pilosella H	*Hie.pilH*	6	2	0	0	0	0	0	0	0	0	0	0
Hieracium sabaudum H	*Hie.sabH*	3	1	0	0	0	0	0	0	0	0	0	0
Holcus lanatus H	*Hol.lanH*	3	2	0	0	0	0	0	0	0	0	0	0
Hypericum maculatum H	*Hyp.macH*	0	0	0	0	5	1	0	0	0	0	0	0
Hypericum perforatum H	*Hyp.perH*	0	0	5	2	0	0	0	0	0	0	0	0
Hypochaeris radicata H	*Hyp.radH*	20	1.3	0	0	0	0	0	0	0	0	0	0
Juncus bufonius H	*Jun.bufH*	3	2	0	0	0	0	0	0	0	0	0	0
Juncus effusus H	*Jun.effH*	20	2.7	5	1	11	2	0	0	0	0	0	0
Juncus tenuis H	*Jun.tenH*	0	0	5	2	0	0	0	0	0	0	0	0
Lactuca serriola H	*Lac.serH*	3	1	0	0	0	0	0	0	0	0	0	0
Ledum palustre H	*Led.palH*	0	0	0	0	0	0	0	0	0	0	2	2
Leontodon hispidus H	*Leo.hisH*	6	1	0	0	0	0	0	0	0	0	0	0
Lotus corniculatus H	*Lot.corH*	3	2	0	0	0	0	0	0	0	0	0	0
Luzula campestris agg. H	*Luz.camH*	0	0	5	2	0	0	0	0	0	0	0	0
Luzula luzuloides H	*Luz.luzH*	0	0	0	0	16	3	0	0	0	0	0	0
Luzula pilosa H	*Luz.pilH*	0	0	0	0	5	3	0	0	0	0	0	0
Lysimachia vulgaris H	*Lys.vulH*	0	0	0	0	0	0	0	0	0	0	2	2
Maianthemum bifolium H	*Mai.bifH*	0	0	0	0	11	2	0	0	0	0	4	2.5
Melampyrum pratense H	*Mel.praH*	0	0	19	2	16	2.3	10	2.5	0	0	9	2.2
Milium effusum H	*Mil.effH*	0	0	0	0	5	2	0	0	0	0	0	0
Moehringia trinervia H	*Moe.triH*	0	0	5	63	11	2	10	2	0	0	0	0
Molinia species H	*Mol.speH*	11	11.5	10	6	21	2	29	7.2	55	2.2	11	22.3
Mycelis muralis H	*Myc.murH*	17	1.8	0	0	0	0	0	0	0	0	0	0
Myosoton aquaticum H	*Myo.aquH*	3	2	0	0	0	0	0	0	0	0	0	0
Orthilia secunda H	*Ort.secH*	0	0	0	0	0	0	0	0	0	0	2	2
Oxalis acetosella H	*Oxa.aceH*	0	0	0	0	11	2.5	0	0	0	0	2	2
Persicaria lapathifolia H	*Per.lapH*	0	0	5	1	0	0	0	0	0	0	0	0
Phragmites australis H	*Phr.ausH*	3	4	0	0	0	0	0	0	0	0	2	3
Plantago major H	*Pla.majH*	3	1	0	0	0	0	0	0	0	0	0	0
Poa annua H	*Poa.annH*	0	0	5	2	0	0	5	1	0	0	2	1
Poa nemoralis H	*Poa.nemH*	0	0	0	0	5	2	0	0	0	0	0	0
Poa pratensis H	*Poa.praH*	3	1	0	0	0	0	0	0	0	0	0	0
Poa trivialis H	*Poa.triH*	3	2	0	0	0	0	0	0	0	0	0	0
Polygonum aviculare H	*Pol.aviH*	0	0	0	0	5	1	0	0	0	0	0	0
Polytrichum formosum H	*Pol.forH*	0	0	0	0	0	0	5	3	0	0	0	0
Potentilla anglica H	*Pot.angH*	0	0	0	0	5	1	0	0	0	0	0	0
Prenanthes purpurea H	*Pre.purH*	0	0	0	0	0	0	5	3	9	2	0	0
Pteridium aquilinum H	*Pte.aquH*	49	13.8	57	24.6	63	7.7	62	9.8	91	10.5	49	4.4

Ranunculus repens H	*Ran.repH*	3	1	0	0	0	0	0	0	0	0	0	0
Rubus fruticosus agg. H	*Rub.fruH*	11	2.3	24	2.4	11	1.5	19	3	9	2	0	0
Rubus idaeus H	*Rub.idaH*	17	2.8	10	2	0	0	10	3.5	0	0	2	1
Rumex acetosa H	*Rum.aceH*	3	1	5	1	0	0	0	0	0	0	0	0
Rumex acetosella H	*Rum.aceH*	3	2	10	2.5	5	2	0	0	0	0	0	0
Rumex obtusifolius H	*Rum.obtH*	0	0	5	1	0	0	0	0	0	0	0	0
Senecio ovatus H	*Sen.ovaH*	3	1	0	0	0	0	0	0	0	0	0	0
Senecio sylvaticus H	*Sen.sylH*	46	2.9	10	2	0	0	0	0	0	0	2	1
Senecio viscosus H	*Sen.visH*	29	2.3	5	2	0	0	0	0	0	0	0	0
Senecio vulgaris H	*Sen.vulH*	6	2	0	0	0	0	0	0	0	0	0	0
Solidago canadensis H	*Sol.canH*	6	1	0	0	0	0	0	0	0	0	0	0
Sonchus asper H	*Son.aspH*	6	1.5	0	0	0	0	0	0	0	0	0	0
Sonchus oleraceus H	*Son.oleH*	3	1	0	0	0	0	0	0	0	0	0	0
Spergula morisonii H	*Spe.morH*	6	3	0	0	0	0	0	0	0	0	0	0
Stellaria graminea H	*Ste.graH*	3	1	0	0	0	0	0	0	0	0	0	0
Stellaria media H	*Ste.medH*	0	0	0	0	0	0	0	0	0	0	2	2
Taraxacum sect. Ruderalia H	*Tar.RudH*	43	1.9	0	0	0	0	0	0	0	0	0	0
Trientalis europaea H	*Tri.eurH*	0	0	5	2	0	0	5	1	9	2	7	1.8
Trifolium dubium H	*Tri.dubH*	3	2	0	0	0	0	0	0	0	0	0	0
Tussilago farfara H	*Tus.farH*	3	2	0	0	0	0	0	0	0	0	0	0
Urtica dioica H	*Urt.dioH*	17	1.8	10	1.5	5	2	0	0	0	0	0	0
Vaccinium myrtillus H	*Vac.myrH*	80	9.2	90	10.4	89	13.6	90	17.2	100	22.5	91	26.5
Vaccinium uliginosum H	*Vac.uliH*	0	0	5	18	0	0	0	0	0	0	2	4
Vaccinium vitis-idaea H	*Vac.vitH*	43	3.4	52	4.1	42	5.3	52	6	73	3.1	60	5.3
Veronica chamaedrys H	*Ver.chaH*	6	2	0	0	0	0	0	0	0	0	0	0
Veronica officinalis H	*Ver.offH*	0	0	0	0	5	3	0	0	0	0	0	0
Viola palustris H	*Vio.palH*	0	0	0	0	0	0	0	0	0	0	2	3
Viola riviniana H	*Vio.rivH*	0	0	0	0	5	3	0	0	0	0	0	0
Atrichum undulatum M	*Atr.undM*	29	5	5	2	11	2.5	5	2	0	0	2	1
Aulacomnium androgynum M	*Aul.andM*	3	2	0	0	11	3.5	0	0	0	0	0	0
Aulacomnium palustre M	*Aul.palM*	0	0	0	0	0	0	0	0	0	0	2	3
Bazzania trilobata M	*Baz.triM*	0	0	0	0	0	0	0	0	18	3	11	2.7
Brachythecium rutabulum M	*Bra.rutM*	40	4.7	38	4	47	6.7	43	3.7	55	2.5	32	5.6
Brachythecium velutinum M	*Bra.velM*	0	0	0	0	5	1	10	3	9	2	2	1
Bryum species M	*Bry.speM*	14	1.8	5	1	0	0	0	0	0	0	0	0
Calypogeia integristipula M	*Cal.intM*	0	0	0	0	5	2	0	0	0	0	2	2
Campylopus flexuosus M	*Cam.fleM*	3	4	10	2.5	21	4.5	43	3.2	45	4	18	3
Campylopus introflexus M	*Cam.intM*	17	2.5	33	3	21	8.5	19	3.5	36	2.8	5	2.3
Cephalozia bicuspidata M	*Cep.bicM*	0	0	0	0	0	0	0	0	9	2	2	2
Ceratodon purpureus M	*Cer.purM*	89	3.9	57	2.8	21	2.5	5	2	9	2	7	1.5
Lichens M	*LichensM*	6	10.5	57	4.5	84	4.8	76	3.3	82	2.4	40	2.7
Dicranella heteromalla M	*Dic.hetM*	69	3.4	62	3.6	84	3.6	90	2.5	91	3.3	72	3.4
Dicranodontium denudatum M	*Dic.denM*	0	0	5	3	0	0	5	3	0	0	0	0
Dicranum polysetum M	*Dic.polM*	14	2.6	43	2.4	58	3.2	67	4.4	36	2.8	44	6.1
Dicranum scoparium M	*Dic.scoM*	23	4.1	62	3.4	53	3.3	71	2.9	100	4.4	60	5.8
Funaria hygrometrica M	*Fun.hygM*	17	2.2	0	0	0	0	0	0	0	0	0	0

Hylocomium splendens M	*Hyl.splM*	0	0	0	0	0	0	0	0	0	0	2	18
Hypnum cupressiforme M	*Hyp.cupM*	20	3	52	3.8	47	2.8	90	4.1	91	5	75	6.6
Lepidozia reptans M	*Lep.repM*	0	0	0	0	0	0	0	0	9	2	2	2
Leucobryum glaucum M	*Leu.glaM*	11	1.8	5	2	16	1.7	24	2.2	64	2.6	37	3.8
Lophocolea bidentata M	*Lop.bidM*	9	1.3	14	2.3	21	1.8	5	2	9	2	7	2.3
Marchantia polymorpha M	*Mar.polM*	43	4.4	0	0	0	0	0	0	0	0	0	0
Mylia taylorii M	*Myl.tayM*	0	0	0	0	0	0	0	0	0	0	2	3
Plagiomnium affine M	*Pla.affM*	0	0	0	0	11	2	0	0	0	0	2	3
Plagiomnium cuspidatum M	*Pla.cusM*	3	1	0	0	0	0	0	0	0	0	0	0
Plagiothecium species M	*Pla.speM*	0	0	10	2	16	7.3	14	2	9	2	11	2.2
Plagiothecium undulatum M	*Pla.undM*	0	0	0	0	0	0	0	0	0	0	2	2
Pleurozium schreberi M	*Ple.schM*	3	8	19	2.3	47	17.4	52	12.8	55	7	46	25.1
Pogonatum urnigerum M	*Pog.urnM*	0	0	0	0	5	2	0	0	0	0	0	0
Pohlia nutans M	*Poh.nutM*	77	2.8	86	3.4	79	3.1	76	2.5	55	3.3	40	2.3
Polytrichum commune M	*Pol.comM*	26	16.3	14	2.7	11	2	5	3	0	0	2	3
Polytrichum formosum M	*Pol.forM*	94	10.3	81	12.5	79	3.8	62	2.7	64	3	39	2.7
Polytrichum juniperinum M	*Pol.junM*	51	6.5	62	6.9	37	5	5	1	0	0	0	0
Polytrichum piliferum M	*Pol.pilM*	46	6.1	43	6.6	11	2.5	0	0	0	0	0	0
Ptilidium ciliare M	*Pti.cilM*	0	0	5	3	11	2.5	14	1.7	9	2	12	2.1
Scleropodium purum M	*Scl.purM*	0	0	0	0	11	2.5	0	0	0	0	4	3
Sphagnum species M	*Sph.speM*	6	1.5	5	4	11	2.5	5	8	9	2	7	3
Tetraphis pellucida M	*Tet.pelM*	6	2	10	2	32	2	48	2.3	45	2.4	32	2.3
Thuidium tamariscinum M	*Thu.tamM*	0	0	0	0	5	2	0	0	0	0	5	3

Contribution of Martin Adámek to the papers included in the thesis:

Adámek, M., Jankovská, Z., Hadincová, V., Kula, E., Wild, J.: **Drivers of Forest Fire Occurrence in the Cultural Landscape of Central Europe.** *Manuscript*

Idea: 100%
Data collection: 10% (+ZJ, EK)
GIS layers processing: 100%
Data analyses: 80% (+JW)
Writing: 80% (+JW, VH)

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

Idea: 50% (+PB, VH)
Data collection: 50% (+PB)
GIS layers processing: 33% (+PB, MK)
Data analyses: 40% (+PB, JW)
Writing: 50% (+PB, JW, VH, MK)

Adámek, M., Hadincová, V., Wild, J.: **Long-term effect of wildfires on temperate *Pinus sylvestris* forests: vegetation dynamics and ecosystem resilience.** *Under review in Forest Ecology and Management*

Idea: 30% (+VH)
Data collection: 100%
Data analyses: 100%
Writing: 80% (+VH, JW)