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WILDFIRES AS A FACTOR OF LOSS OF BIODIVERSITY AND FOREST ECOSYSTEM FUNCTIONS

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Due to the ever-increasing anthropogenic impact and global climate change, wildfires are becoming more frequent and intense all over the world. The wildfire factor is turning into an acute problem for forested countries that requires prompt solutions as the areas of forest ecosystems are reducing catastrophically, which results in an irreparable loss of biodiversity that provides all ecosystem functions and services. Many biologists consider wildfires a factor destructive to biota that results in permanent loss of some species and groups of living organisms; even if it is possible for them to recover after a wildfire, they may need a lot of time to do so. However, some studies argue that wildfires do not reduce the biodiversity in forest ecosystems, but even increase it, thus contributing to species conservation and sustainable functioning of forests.

This article is aimed at analyzing the studies of how wildfires impact the main components, biodiversity, and functions of forest ecosystems. The authors answer the question of why wildfires while being a destructive factor, are sometimes considered a factor increasing biodiversity. The “positive” influence wildfires have on biodiversity mostly comes down to the formation of mosaic patterns, that is, forest canopy gaps that occur after a wildfire. However, analysis of references shows that the established opinion found in a number of studies that a certain frequency of wildfires is necessary to maintain forest communities may be associated with ignoring or misunderstanding the importance of biotic factors in the functioning of forests. In modern forest ecosystems, populations of keystone large mammal species have disappeared or greatly declined; therefore, there are no microsites they usually form, including large forest canopy gaps (glades) that provide opportunities for photophilous flora and pollinating insects to develop and generally maintain adequate conditions for multi-aged polydominant forest ecosystems with high biodiversity. In the forestry practice, there are measures to maintain mosaics. They include special types of felling, supporting populations of keystone animal species, etc., and are both significantly less catastrophic in comparison with the wildfire factor and substantiated biologically. The authors provide recommendations for the conservation and maintenance of biodiversity and ecosystem functions in modern forests.

Keywords: *forest, fires, vegetation, animals, keystone species, greenhouse gases, soil, climate, carbon, ecosystem services, emissions*

Wildfires are not only a modern global factor determining the state and functioning of forest ecosystems, exerting a powerful influence on the biogeochemical carbon cycle, hydrological regime and climate change, but also a historical factor in forest formation. The interaction of man and nature has been closely connected with fire since the middle of the Pleistocene (500 thousand years ago): drive hunting, slash-and-burn agriculture, fire clearing for meadows and pastures (Gowlett, 2006; Bowman et al., 2009; Bobrovskij, 2010; Tang, Yap, 2020; MacDonald et al., 2021). Therefore, when assessing the biodiversity of modern forests and the effectiveness of their ecosystem functions, it is necessary to take into account the anthropogenic history, in which fires in many territories were the most important factor of forest formation (Whitlock et al., 2010; Aleynikov et al., 2015). Currently, despite fundamentally different technologies in economic activity, wildfires remain an acute problem for forest countries, which requires solutions both in connection with global climate change and with a number of economic issues, such as loss of ecosystem services provided by forests, loss of forests as an important component amidst decarbonization of the economy. Many biologists consider wildfires as a destructive factor for biota, with slow recovery after exposure. If fragmentary "refugia" are preserved during a wildfire, in which individuals of different species survive, this does not necessarily mean that populations survive (Gongalsky, 2014). Therefore, the following consequences are seen:

(i) long-established coordinated functional relationships based on biodiversity are destroyed;

(ii) plant edificators are suppressed and populations of keystone animal species of above-ground and underground biota are reduced;

(iii) the ecosystem is thrown back to historically earlier stages of development and a round of fire-induced demutational succession is triggered; at a high frequency of wildfires, this leads to persistent digression and the formation of post-fire communities with limited species diversity.

At the same time, both in biology and forestry, there are ideas that wildfires are necessary, for example, for the germination of seeds of some plant species (Bell et al., 1993; Keeley, Fotheringham, 2000), the maintenance of pine and oak plantations (Cvetkov, 2013), etc. Currently, authors of some studies claim based on their findings that wildfires not only do not reduce, but also increase the biodiversity of forest ecosystems, and extinguishing large wildfires, in general, is economically impractical (Stephens et al., 2018; Kharuk et al., 2021). One of the arguments is that wildfires had also occurred prior to the beginning of global human influences on nature; therefore, they are necessary as a formation factor of forest ecosystems and even the evolution of biota (He et al., 2019). However, it should be kept in mind that, at present, the frequency, intensity and scale of wildfires (ninety percent of which, according to experts, occur due to human activity even in the most remote areas) have increased significantly, and this is exacerbated by the impact of climate change. The type of evolution of forest ecosystems under the influence of wildfires can be defined as "erasing evolution", according to the definition of L. G. Bogatyrev (2004), proposed for the development of forest litter.

The objective of this article is to analyze the results of studies of the impact of wildfires on the main components of forest ecosystems, their biodiversity and functions and to answer the question why wildfire as an obviously destructive factor is sometimes considered as a factor of increasing biodiversity.

THE SCALE OF WILDFIRES AND FIRE-INDUCED EMISSIONS OF CARBON COMPOUNDS IN THE FORESTS OF RUSSIA

The scale of wildfires

According to official statistics, 569.912 sites of wildfires were registered in the territory of the state forestry of the Russian Federation in 1992–2012, which averaged 26.805 foci per year (EMISS, 2021a). In 2009–2020, the area of state forestry lands covered by wildfires amounted to 43.945 million hectares (an average of 3.662 million ha per year) (EMISS, 2021b). Damage from wildfires in 2019, according to official statistics, amounted to 13.5 billion RUB (EMISS, 2021c). At the same time, according to various estimates, the proportion of major wildfires (with the area of more than 200 ha) in Russia is about 5% of the total, but their contribution by area is about 95%. In the forests of Russia, surface fires occur and spread most often, accounting for up to 98% of the total number of wildfires and more than 88% of the area covered by fire, whereas crown fires account for 1–2% and 12%, respectively (Isaev et al., 1995).

The data of satellite monitoring of wildfire areas, provided by various Russian and foreign experts, differ significantly from official statistics. Thus, A. Z. Shvidenko and D. G. Shchepashchenko, who have investigated the influence of climate on the wildfire situation in Russia in 1998–2010, cite data from various sources. On average, according to their estimates, the area of fires during this period was 8.5 million ha per year (Shvidenko, Shchepashchenko, 2013). From time to time, years with an abnormal frequency of fire occurrence with an area of up to 16–18 million ha are registered. Other authors (Lupyan et al., 2017) report that using satellite data, 5 to 20 thousand wildfires were registered annually in 2001–2016 in Russia, damaging forests with an area of 5–20 million ha. Similar estimates are given in the works of other Russian researchers (Ponomarev, Shvecov, 2015; Bondur et al., 2016).

Types of fire emissions and their assessment by surface methods

A significant contribution to the emissions of greenhouse gases (CO_2, CH_4, N_2O) and gases with an indirect greenhouse effect (CO, NO_x, non-methane volatile organic carbons) and other compounds are made by wildfires that occur annually in the forests of Russia over vast territories and often turn into natural disasters. The impact of wildfires on the carbon balance is determined by two main processes: the physicochemical process of “rapid” release of carbon compounds formed during incomplete combustion of organic matter (“fire” emissions) and the biological process of “slow” release of carbon compounds due to destruction and rotting of plants that died from wildfire, but had not been burnt (“post-fire” emissions). Fire emissions occur directly during the wildfires and can last from several hours to several days or weeks. Post-fire emissions begin with the death of woody plants and continue for several years or decades.

Surface studies of the intensity of combustion and the expenditure of various combustion conductors of forest fuels (FFs) show that the mass of above-ground FFs varies depending on the species and age of plantings, their productivity and degree of closure (completeness), the forest plant zone and the phenological state of vegetation. It usually ranges from 4.0 to 12.0 $t \times ha^{-1}$, which corresponds to the stock of needles, dry and small branches in the canopy (crowns) of coniferous stands most susceptible to wildfires (Molchanov, 1954; Kurbatskij, 1972; Grishin, 1981). Taking into account incomplete burning (not completely burnt, partially charred FFs), the mass of above-ground FFs burning during crown fires on average is about 7.0 $t \times ha^{-1}$.

The mass of above-ground FFs formed from living ground cover (mosses, lichens, shrubs) and litter (needles, leaves, small branches, etc.) varies widely depending on the species composition, age and closeness of stands, forest type, nutrient and water regime of soils. In most cases, FF stocks in this group range from 2.0 to 15.0 $t \times ha^{-1}$ (Vonskij, 1957; Konev, 1977). Taking into account incomplete burning, the mass of ground FFs burning during surface wildfires is 5 $t \times ha^{-1}$.

The mass of litter and organic soil horizons, consisting of dead parts of plants with varying degrees of decomposition and humus, in forest ecosystems usually varies in the range from 5.0 to 25.0 $t \times ha^{-1}$ (Molchanov, 1954; Vonskij, 1957). In most cases of crown and surface wildfires, the depth of burning does not exceed half the thickness of the forest litter layer, which corresponds to stocks of 3.0–12.0 t × ha^{-1}. In case of ground fires that occur in swamps and swampy forests with a developed peat horizon, the mass of organic materials involved in burning can be up to 150 t × ha^{-1} or more (Arcybashev, 1974; Sheshukov, 1979).

The stock of FFs from deadwood residues (deadwood, dead standing trees, stumps, dry branches) can reach several tens of tons per hectare. Most often, no more than half of the available stock of deadwood residues are burnt, which is commensurate in weight with the stock of living ground cover in forest areas.

Taking into account the above assumptions and stocks of the main FF groups, the mass of burning organic materials per ha of the area covered by wildfire is 30 t × ha^{-1}, 12 t × ha^{-1} and 120 t × ha^{-1}, respectively, for crown, surface, and ground wildfires.

Remote estimates of carbon emissions from wildfires

Quantitative estimates of direct fire emissions of carbon compounds and other greenhouse gases using satellite data differ by different researchers and are related to the methods of wildfire recognition and their consequences, models for measuring and estimating greenhouse gas emissions, as well as auxiliary data on Russian forests (maps of vegetation, woody fuels, etc.).

Direct measurements of fluxes and concentrations of gases (the "top-down" approach) in the Earth's troposphere are performed using satellite instruments (Amiro et al., 2001 a; Liu et al., 2005).

The conventional common "bottom-up" approach is also used, which is based on post-processing of satellite data on fires (area and degree of fire damage of vegetation) and data on stocks of plant combustion conductors of various types of wooody fuels (Isaev et al., 2002; Kasischke, Bruhwiler, 2003; Soja et al., 2004; Wiedinmyer et al., 2006; Sochilova, Ershov, 2007).

E. I. Ponomarev et al. use brightness temperature in the 3rd MODIS thermal channel (3.93–3.99 μm) to assess the intensity and type of wildfire, as well as its relationship with the FF consumption for various wood residues estimated according to literature (Ponomarev et al., 2017). The estimates of direct carbon emissions presented by the author for the time period 2002–2016 averaged 83 ± 21 Mt C per $year^{-1}$. The range of variation of direct carbon emissions in different years was 20–227 Mt C per $year^{-1}$. A. Z. Shvidenko and D. G. Shchepashchenko estimate the number of carbon emissions during 1998–2010 due to wildfires in Russia at 121 ± 28 Mt C per $year^{-1}$ with annual variability of 50 (2000) to 231 (2003) Mt C per $year^{-1}$ (Shvidenko, Shchepashchenko, 2013). Looking at some rough estimates of post-fire carbon emissions from wildfires of approximately 90–100 Mt C per year^{-1} (Shvidenko et al., 2010), the authors estimate total carbon emissions due to wildfires in recent decades at 180–200 Mt C per year^{-1}.

According to our estimates, direct fire carbon emissions in 2002–2018 amounted to 34 ± 19 Mt C per year^{-1}, ranging from 12 (2009) to 127 (2003) Mt C per year^{-1} (Ershov, Sochilova, 2020). At the same time, the areas of forest damage and the intensity of direct fire-induced carbon emissions increased 1.4 times after 2012. Until 2012, the average damage area and emissions were 3.95 million ha and 29.18 Mt C, whereas over the past 9 years those figures were 5.73 million ha and 41.07 Mt C, respectively. Differences in estimates as compared to other authors are due to the fact that only data from forest ecosystems (forested areas) are used, and there are no direct emissions data for large wood residues due to the lack of spatial data throughout Russia.

Thus, the extent of the forest area covered by wildfire and the amount of direct fire-induced emissions are evidences of a significant impact of wildfires on the state and biological diversity of forest ecosystems in Russia. Surface fires occur and spread most often in the forests of Russia, both in terms of the total number of wildfires and the area covered by fire, whereas major wildfires (with an area of more than 200 ha) make a significant contribution to the emissions of carbon compounds and other greenhouse gases. In addition to fire emissions corresponding to the duration of forest burning, post-fire emissions occur, which last for several years or decades.

PREREQUISITES OF IDEAS ABOUT WILDFIRES AS A FACTOR INCREASING BIOLOGICAL DIVERSITY

Modern forest ecosystems differ significantly from pre-anthropogenic forest-meadow systems that existed before the beginning of the Holocene when mass destruction of keystone animal species by humans occurred during the development of appropriating economy (Smirnova et al., 2021). In modern forests, biological diversity, including functional and structural, is reduced as compared to prehistoric forests (Vera, 2000; Orlova, 2013; Korotkov, 2017; Lukina et al., 2020). The mosaic of microsites of pre-anthropogenic forests was a result of treefalls or breaks due to either the natural death of trees or the activity of large vertebrates, which formed much larger gaps (breaks in the canopy of the forest) and clearings than the falls of single trees. Large phytophages had a great influence on the undergrowth of trees and shrubs through uneven grazing and trampling. As a result, a stand of different composition and different ages was formed (Vera, 2000). The renewal of light-demanding flora was not limited by the lack of light. Mammals and birds contributed to the spread of seeds, created additional micro-habitats for companion species, such as small mammals, insects and other invertebrates. Mosaic nanorelief was formed with different soil moisture and composition of soil fauna (Puchkov, 1992).

Currently, especially in boreal forests, the renewal of light-demanding flora is limited by a lack of light due to the continuous canopy of dark coniferous tree species, which is probably why a number of works claim that the preservation of modern pine, oak, and larch plantations is ensured by wildfires (Sannikov, 1997; Cvetkov, 2013; Robertson et al., 2019; Matveeva, 2020). However, there are studies showing that wildfires of any intensity also inhibit the renewal of pine trees (Allen et al., 2002; Makarov et al., 2016). According to available data, intra-forest clearings make a significant contribution to the floristic diversity of forest ecosystems (Smirnova et al., 1997; Evstigneev et al., 1999; Gornov et al., 2020). Succession changes of woody vegetation occur in the direction from light-demanding species to shade-tolerant, and a new demutation process is started after disturbances, such as blow-down, fire, logging, insect epidemics. However, after such large-scale disturbances, an even-aged stand with a small set of tree species that is vulnerable to external factors will be formed again.

Great importance in modern forests is assigned to deadwood as a common microsite of old-growth forests. Deadwood supports floral diversity (Evstigneev et al., 2012; Evstigneev, Gornova, 2017; Khanina, Bobrovsky, 2021), is a favorable habitat for dozens of species of vertebrates and hundreds of species of invertebrates, as well as fungi and bacteria (Goncharov, 2014; Geraskina, 2016; Ashwood et al., 2019; Evstigneev, Solonina, 2020; Jacobsen et al., 2020), which is especially relevant in the face of accelerating rates of loss of biological diversity (Lukina et al., 2021). Despite the fact that deadwood, especially in the late stages of decomposition, usually has higher humidity than the surrounding soil, it is also currently considered as a factor of increased fire danger (Paletto et al., 2012). This indicates a high degree of disturbance and vulnerability of modern forests since they practically lack such keystone species as moose, bison, beavers, etc., therefore, no natural barriers to the spread of wildfire are created due to the formation of gaps, trails, understocking, or intra-forest reservoirs. Felling of individual trees and creating gaps in order to prevent the spread of wildfire is recommended as one of ecological principles of wildfire protection (Allen et al., 2002).

Since fire is a historically long-standing factor, adaptations to wildfires have formed in a number of plants, i. e. significant thickening of external protective tissues of woody plants, activation of the seed bank of flowering plants under the influence of high temperatures (Keeley, Fotheringham, 2000; Lamont et al., 2018; Soos et al., 2019), opening of cones of gymnosperms (Sannikov, 1997; Agapov, 2019). For example, the giant sequoia (*Sequoiadendron giganteum*) is, in the big scheme of things, a fire-dependent plant, since it is generally believed that the cones of this species open only after exposure to wildfire (Harvey, Shellhammer, 1991). However, there are also natural biotic factors that ensure the spread and germination of seeds. Pine and cedar cones are eaten by birds (nutcrackers, jays), mouse-like rodents and squirrels, who release seeds from under the dense scales and make a stash in the litter and burrows, a large part of which most often is not found, so the seeds germinate (Rejmers, 2015). Giant sequoia cones serve as food for Douglas squirrel (*Tamiasciurus douglasi*), whose main food is the green scales of young sequoia cones, because the seeds are very small and have less nutritional value than large scales. The longhorn beetle (*Phymatodes nitidus*) is trophically very closely related to the cones of the giant sequoia: female beetles lay eggs on the surface of the cones, and hatching larvae eat the scales of the cones and release seeds (Weatherspoon, 1990). Besides, scales of cones dry and crack and the seeds fall down after exposure not only to wildfire, but also to direct sunlight, however, under the closed canopy of the stand due to the lack of open spaces as a result of extermination of large forest animals, this mechanism is often not implemented (Harvey et al., 1980).

The positive impact of wildfire on forest biodiversity is also believed to include:

- reduced root competition among different tree species (Matveeva, 2020),
- improved seed germination due to burning of the forest litter to the mineral layer (Karnel', Zabelin, 1978) and a decrease in number of small mammals that may damage seeds and plant sprouts (Farber, 2012);
- accelerated mineralization of organic matter (Wells et al., 1979);
- antiseptic effect of high temperatures on soils (Sokolov, 1973);
- reduced competition for light and precipitation on the burnt landscape (Agapov, 2019).

All these arguments are quite well supported by functional losses in the biodiversity of modern forests, since these effects implement biotic relationships between the components of forest ecosystems: the destruction of litter is provided by invertebrate saprophages and saprotrophic microorganisms, which also complete its mineralization and have a “sanitation” effect on soils, regulating the balance of different groups of bacteria (Byzov, 2005), the formation of structural diversity and reduction of competition between plants, including underground (root systems) provide zoogenic mechanisms in forest regulation (Puchkov, 1992; Vera, 2000; Smirnova et al., 2018).

Thus, in modern forests, where keystone species of large mammals have been lost together with the microsites formed by them and providing opportunities for the formation of multi-age polydominant forest ecosystems, wildfires are often considered as an important and necessary factor in maintaining biodiversity. Wildfires trigger positive feedback mechanisms; therefore, some forest communities (for example, pine forests) are now classified by researchers as fire-dependent. A number of plants have developed adaptation mechanisms to fire exposure. However, biotic factors play a high role in the functioning of forest ecosystems and the maintenance of biodiversity, and it must be taken into account when considering approaches to sustainable forest management and, if possible, lost ecosystem components should be restored.

THE IMPACT OF WILDFIRES ON PLANT COMMUNITIES

Wildfire affects plants directly by destroying them completely or partially, as well as indirectly through changes in living environment. Therefore, short-term and long-term effects of wildfires are distinguished. The short-term ones include the combustion of forest fuels, including phytomass, heating of the soil, burns (fire wounds) or death of plants, terrestrial vertebrates and soil animals, microorganisms (Melekhov, 1948; Wildland..., 2000; Il'ina, 2011; Suhomlinov, Suhomlinova, 2011, etc.). The long-term consequences of wildfires include fire-induced soil transformation, reduction of soil biota diversity, drying out and death of trees, accumulation of phytomass, postfire succession of vegetation (Kuleshova et al., 1996; Monitoring..., 2002; Tyler, Spoolman, 2011; Gorbunova et al., 2014; Ivanova et al., 2018, etc.).

Crown wildfires, when the fire spreads from the soil to the tops of trees, are the most destructive ones for forest vegetation. Crown fires can be running and independent (Zalesov, 2011; Il'ina, 2011). An independent wildfire is a disaster for the entire plant community, as it affects all its components. After the death of forest due to impact of a wildfire, there are sharp changes in the microclimate, hydrological and soil conditions, which, in turn, affect the formation of a new community depends, i. e. cause a change of phytocenoses. In some cases, the stand dies completely and falls out in a short time, forming blockages (Nesgovorova et al., 2015). Sometimes vegetation recovery is delayed due to severe burning of soils and lack of seed sources.

In case of surface wildfires, plants of the lower layers (moss-lichen and grass-shrub tiers, understory and undergrowth), as well as litter and humus horizon partially or completely burn out. Root systems are damaged, fire wounds form on tree trunks (Devyatova et al., 2014; Richter et al., 2019), deadwood, stumps and felling residues partially burn out. Surface wildfires, under some circumstances, can turn into crown wildfires. Fire-damaged and weakened trees are more severely damaged by insects and fungi (Melekhov, 1948; Popov, 1961; Parker et al., 2006). However, some studies argue that low-intensity wildfires can have a positive effect on the ability of some trees to protect themselves from insects, for example, the Eastern larch beetle (*Dendroctonus simplex*) (Hood et al., 2015). After surface fires, the understory mostly dies. The study by K. V. Levchenko (2017) emphasizes that the resistance of coniferous forests to surface wildfires is very low. In communities with understory and undergrowth, in the presence of slopes, a surface wildfire can turn into a crown one, and all components of the phytocenosis, including the ground cover, are completely destroyed.

Surface wildfires of different intensity affect vegetation differently (Pourreza et al., 2014; Ivanova et al., 2018). There are wildfires of low, medium and high intensity, which differ in the degree of burning out of litter and soil. After a weak impact, the stand is preserved, while the fire hazard of the territory is reduced for some time due to a decreased supply of fuels. After low-intensity wildfires, the abundance and diversity of grasses and mixed herbs may increase (Hutchinson et al., 2005). This is believed to be associated with the emergence of new ecological niches (Rosenzweig, 1995; Gorbunova et al., 2014). Medium-intensity wildfires, as well as low-intensity wildfires, weaken the stand and lead to the loss of trees (Ivanova et al., 2018). After high-intensity wildfires, the recovery time of the post-fire community is many times more (Ivanova et al., 2017). They significantly disrupt landscapes (Collins, Stephens, 2010) and lead to pronounced homogenization of the habitat, which significantly reduces biodiversity (Hessburg et al., 2016; Shive et al., 2018, Steel et al., 2018). Besides, after intense wildfires, the reserves of ground-based fuels increase and may exceed the pre-fire figures several times, providing conditions for the recurrence of a high-intensity wildfire (Ivanova et al., 2017). Sometimes, after such fires in high-light conditions, massive sprouting of woody plants is observed (Ivanova et al., 2018). However, due to increased soil temperature, insufficient moisture and infection with phytopathogens, these seedlings die. The understory is restored after 12–14 years.

Often after wildfires in forest communities, the proportion of light-loving plants increases, i.e. of pine forest and meadow species (Ivanova, Perevoznikova, 1996; Bizyukin, 1998), whereas, in some cases, the proportion of meadow-steppe species is increased (Shpilevskaya, Katkova, 2011). Moreover, the so-called pyrophytes often actively invade the burnt-out areas (Vostochnoevropejskie…, 2004; Afanas'eva, Berezina, 2011), the emerging "diversity" being qualified as pyrodiversity (He et al., 2019). It is believed that some plants have adapted to survive wildfires (Kelly, Brotons, 2017). These include, for example, the structure of seeds, which keeps the embryo alive after being exposed to wildfire, as well as the thick bark of trees that protects the cambium (Il'ina, 2011). Often, pyrophytes include fireweed (*Chamaenerion angustifolium*), which inhabits post-fire areas and forms closed plant aggregations (Bizyukin, 1998; Afanas'eva, Berezina, 2011; Shpilevskaya, Katkova, 2011). Pyrogenic communities may also be invaded by adventitious and ruderal species (Goryainova, Leonova, 2008; Shpilevskaya, Katkova, 2011).

Wildfire causes change in the vegetation composition of affected areas; that is, it leads to the formation of post-fire (pyrogenic) successions. They depend on the composition and condition of the initial community, fire intensity and duration (Kuleshova et al., 1996; Ivanova et al., 2017; Miller et al., 2019). At the first stages, the community is populated by pioneer (reactive) species, "pyrophytes" can often spread. Diasporas can stem from a soil seed bank and plants from undamaged sites. With no adult woody plants, the settlement of burnt areas will depend on seed transfer by animals (birds and small mammals) (Diaci, 1994). The importance of vegetative reproduction of plants increases as well (Ivanova, Perevoznikova, 1996; Kovaleva et al., 2012).

Although areas with higher illumination are invaded by pyrophyte species, wildfires always result in a decrease in plant species diversity (Chibilev, 1998; Il'ina, 2011; Richter et al., 2019). After wildfires, the stocks of seeds in the soil are significantly reduced (Il'ina, 2011; Miller et al., 2013). Rare flora may disappear entirely after wildfires (Kryukova, 2009; Makarov et al., 2019).

Post-fire recovery can take from several years to decades (Telicyn, Ostroshenko, 2008). Modern ecosystems are modified to varying degrees and are subject to anthropogenic impact (Richter et al., 2019). Therefore, the impact of wildfire on forests can manifest in different ways, depending on the composition of the original community and the history of wildfires in the specified area (Miller, Safford, 2020). In the review of D. A. Driscoll et al. (2021), wildfires and fragmentation of communities were shown to interinfluence depending on the conditions of interaction and its scale. For instance, after a wildfire, landscapes often become heterogeneous, while communities that have already survived such impact can restrain the spread of fire due to the areas covered by fire. Short-term increase in biodiversity that is observed in some cases is mainly due to the marginal effect.

Wildfires as a very powerful factor in development of forest ecosystems have had a huge impact on the modern appearance of boreal forests in both North America (Payette, 1992) and Eurasia (Gorshkov, 2001; Neshataev, 2017). Many researchers of boreal forests register the fact that in the modern vegetation cover of the taiga zone, most of the light and dark coniferous forests are not indigenous stands but various stages of forest recovery in the areas covered by fire (cited by Neshataev, 2017).

Modern dendrochronological studies show the influence of long-standing large wildfires (those that occurred more than a hundred years ago) on forest ecosystems. For example, the influence of a large wildfire in 1896 can still be seen in the growth pattern of trees and the depth of seasonal permafrost melting in Central Siberia. After the death of the stand and ground cover, there was a decrease in thickness of the organic soil horizon and an increase in thickness of permafrost, resulting in slow forest recovery after wildfires in most circumpolar boreal zones (Kirdyanov et al., 2020).

Amid climate change, the number of wildfires and their frequency will increase (Flannigan et al., 2000, 2006; Camia et al., 2017; Molina et al., 2019). Some post-fire systems may not restore the original composition of vegetation due to changes in soil conditions and the formation of deflation zones, despite reforestation already carried out (Gyninova et al., 2020).

Thus, wildfires of any intensity have a direct and indirect impact on the stand, understory and ground cover. Wildfires change the functioning conditions of all components of plant communities and make them more vulnerable to other environmental factors. The state of coenopopulations of plants that prevailed in pre-fire ecosystems deteriorates. The advent of light-demanding “pyrogenic” species does not make up for the overall level of decline in biodiversity after wildfires. Post-fire vegetation restoration requires considerable time, available diaspora sources and carriers.

THE EFFECT OF WILDFIRES ON VERTEBRATES

Despite high relevance, there are not so many studies of the impact wildfires have on vertebrates, which is stated in a number of works (Strategiya..., 2011; Pushkin, 2014; Barlow, Peres, 2006; Pastro et al., 2014; Gertini et al., 2021). Assessment of the impact of wildfires on animal populations is mainly based on change in their density over time: if population density increases in a certain area, a conclusion about the positive impact of wildfire is usually drawn, and if population density decreases, wildfire is believed to have a negative impact; alpha and beta diversity as well as spatial distribution of animals are analyzed as well (Revuckaya et al., 2018; Belyh et al., 2021; Cleary et al., 2004; Pastro et al., 2011; 2014).

Wildfires destroy habitat and food resources for vertebrates and increase the efficiency of predator hunting in post-fire landscapes (Letnic et al., 2005; Green, Sanecki, 2006; Kodandapani et al., 2008). Wildfires can be detrimental to the physiology of small mammals, for example, making it difficult for them to reproduce, as it has been shown in Australia regarding some quolls and antechinus species. In fact, major environmental changes destabilize animals at such stages of reproductive behavior as courtship, pregnancy, and offspring care (Banks et al., 2007). The impact of fire on individual animal species depends on the intensity and scale of wildfires (Cleary et al., 2004; Pastro et al., 2011).

In the oak forests of Pennsylvania, 4–12 months after the fire, the number of small mammals in the burned forests was significantly less than in the unburned forests, and two rodent species, i. e. *Microtus pennsylvanicus* and *Clethrionomys gapperi*, were not found at the fire sites (Kirkland et al., 1996). In a burned-out area of 15.000 ha in Arizona, the number of rodents of the Cricetidae family declined due to fire-induced disturbance of grass cover and returned to the pre-fire level only 6 years later (Bock et al., 2011). The abundance and diversity of small mammals in some parts of the eucalyptus forest in Australia recovered at least 9 years after a wildfire (Fox, McKay, 1981).

In some cases, the "benefits" of wildfires are listed for animals such as *Cervus elaphus* and *Alces alces*, which feed on herbaceous plants and understory of trees that appear on overgrowing fire sites (Kharuk et al., 2021). At first glance, this is corroborated by the established positive correlation between the increase in number of herbivores and the area covered by fire (Belyh, Sadovskaya, 2021). However, according to the authors of the study themselves, such a correlation may be due to forced migration of animals to the burnt-out areas from areas where the forest is still burning, in an attempt to escape the fire. The same explanation might be true for animals of the Canidae, Felidae, Ursidae, and Phasianidae families (Belyh, Sadovskaya, 2021). In the boreal forests of North America, foxes are more common at fire sites than wolves, which, however, reclaim the territories quite quickly. The dynamics of lynx population is largely determined by the population density of hares that are lynx's main prey (Fisher, Wilkinson, 2005).

In some studies, authors suggest that the effect of wildfires on animals is neutral (Pastro et al., 2014). For example, E. P. Lipatnikov, O. P. Vin'kovskaya (2012) did not find any dependence of the population of wild boar (*Sus scrofa sibiricus*) on the size of the areas covered by fire. At the same time, the very activity of wild boars affects wildfires: rooting damage caused by wild boar limits the spread of surface fires and protects woody understory (Lipatnikov, Vin'kovskaya, 2012), acting as a mineralized shelterbelt. At the same time, O. L. Revuckaya et al. (2018) found that the highest population density of wild boar, as well as Manchurian wapiti (*Cervus elaphus xanthopigus*), is recorded in areas with the least frequency of fire occurrence. Studies of the effect of controlled burning in *Pinus palustris* communities in the southeastern United States on small mammals and amphibians have not revealed significant differences in the number of animal species depending on the frequency of ignition: intervals of 1–3, 3–5 and more than 5 years (Darracq et al., 2016).

Wildfires have an extremely negative impact on Siberian musk deer (*Moschus moschiferus*) as their population on the burnt areas declines sharply, sometimes to the extent of disappearance, and does not recover for a long time (Domanov, 2017); sun bear *(Helarctos malayanus*) in South-East Asia (Fredriksson et al., 2007), tiger (Joshi et al., 2015), Indian elephant (Joshi et al., 2015), Amur leopard (Pikunov et al., 2009) and other rare mammals.

Most researchers are unanimous in their negative assessment of the impact of landscape wildfires on representatives of the Mustelidae family, in particular, sables (*Martes zibellina*) (Naumov, 2014; Pushkin, Mashkin, 2014; Revuckaya et al., 2018; Fedorova et al., 2020; Belyh, Sadovskaya, 2021). The work "Wildfires in the Siberian taiga" (Kharuk, 2021), on the contrary, argues that sables are attracted by overgrowing fire sites due to growing populations of hares and small mouse-like mammals they feed on. However, in the years of the maximum number of wildfires, there is a decrease in the number of sable populations (Fedorova et al., 2020; Belyh, Sadovskaya, 2021). Apparently, this is due to sable behavior in a wildfire. According to P. P. Naumov (2014), during a wildfire, sables do not try to escape from the impending fire, but hide. Therefore, they die from exposure to fire or smoke. During a crown wildfire, up to 100% of sables die (Naumov, 2014). Huge empty spaces remaining in the areas covered by crown fires cause damage to sable populations, hindering their reproduction and creating prerequisites for reduction of their range and population (Naumov, 2014). Damage caused by the destruction of the habitat of sables as a result of wildfires of 2019 in Krasnoyarsk Krai is estimated at more than 22 billion RUB (Krejndlin, 2019). These calculations show the lameness of conclusions about economic inexpediency of extinguishing wildfires. A negative effect of wildfires was also found for *Sciurus vulgaris* (Revuckaya et al., 2018) and *Lynx lynx* (Bekshaev, 2016).

Wildfires have a negative impact on populations of forest birds, especially highly specialized species (Bendel et al., 1974; Gil-Tena et al., 2009). Given the practice of burning felling residues, studies are being conducted on effects of such burning on birds nesting on clear cutting sites. Destruction of nests and death of broods are often noted, as well as forced abandonment of their nests by birds, including those that nested near the territory exposed to fire. However, despite the data obtained, some authors recommend the "method of controlled burning of felling residues on clear cutting sites in mountain forests as not causing significant change in animal communities" (Timoshkina, 2004). Considering that burning of felling residues during a fire season often leads to large wildfires (Yaroshenko, 2021), the negative effect of such burning can significantly increase.

Representatives of the herpetofauna (amphibians and reptiles) die from fire, smoke and oxygen starvation, despite the fact that these animals can potentially escape its influence. However, even fast-moving snakes and lizards get irreversible injuries, their shelters are destroyed and their food supply is depleted (Pausas, 2019).

Thus, open spaces with green food, including those that result from wildfires, can indeed attract large phytophagous animals and predators that feed on them. But in ecologically balanced ecosystems, such spaces arise and are maintained at the expense of keystone species (Vostochnoevropejskie lesa..., 2004). The heterogeneity of environmental conditions necessary to maintain biodiversity is created as a result of the population life of animals and plants, whose activities do not lead to catastrophic disturbances and losses that are inevitable after exposure to wildfire. In addition, often as a result of a large wildfire, huge homogeneous open spaces are formed, leading to the destruction of the natural heterogeneity of the living cover and, as a result, to a steady decline in biodiversity, including vertebrates.

THE EFFECT OF WILDFIRES ON SOIL PROPERTIES

Pyrogenesis is one of the leading processes in forests that affect soil properties. Wildfires cause changes in morphological and physicochemical properties, the composition of organic matter and mechanical composition of soils (Sapozhnikov, 1976; Trofimov, Bahareva, 2007; Kawahigashi et al., 2011; Dymov et al., 2014). Changes in morphological properties of soils are caused by burning out of organogenic horizons, loss of growing forest, deadwood and other plant residues and include formation of a pyrogenic horizon or appearance of signs of pyrogenesis in soil horizons. It has been found that morphological signs of fire influence can be found at a depth of up to 0.3 m (Dymov et al., 2018). Signs of pyrogenesis are manifested in the form of carbon-bearing inclusions in the lower part of the litter and mineral horizons, pyrogenic morphones. Signs of pyrogenesis include darkening of mineral horizons due to pyrogenic organic matter capable of active migration. The podzolic horizon becomes impregnated with mobile organic matter, hydrophobization is observed, and the upper mineral horizons are over-compacted.

Wildfires lead to decreased acidity of the litter and, on the contrary, increased acidity of the mineral horizons of soils, an increase in the content of exchangeable calcium in the mineral horizons of soils and their enrichment with carbon and nitrogen, a short-term increase in the availability of nutrients, a decrease in the biological activity of soils and the proportion of carbon of water-soluble compounds, a narrowing of the C : N ratio in the litter and other horizons that have experienced pyrogenic effects (Sapozhnikov, 1976; Sorokin et al., 2000; Certini, 2005; Bezkorovajnaya et al., 2007; Cibart, Gennadiev, 2009; Lukina et al., 2008; Dymov et al., 2014; Ludwig et al., 2018). The decrease in litter acidity on fire sites is associated with the influence of low-molecular organic compounds present in the soil solutions of the fire sites (Sapozhnikov et al., 2001). An increase in the carbon content is associated with its intake from burnt wood, an increase in the nitrogen content and exchangeable calcium is believed to be due to the massive intake of a large number of plant residues resulting from the impact of wildfires on woody and other plants.

Recent assessments of the effect of prolonged use of prescribed burning on the soils of south-western coastal plain pine forests in the United States demonstrate similar changes in their physicochemical properties. With an increase in the frequency of wildfires, the content of mobile calcium and manganese increases, the actual acidity, the content of potassium and sulfates in the ten-centimeter soil layer decreases (Coates et al., 2018). The authors believe these changes to be temporary. However, other authors demonstrate by the example of pyrogenic succession series lasting several hundred years that the effects of wildfires in the soils of forests in South Australia are observed after eighty years or more, and include depletion of soils with nutrients, in particular available phosphorus compounds and nitrates (Bowd et al., 2019).

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During wildfires in taiga biogeocenoses, there is a change and redistribution of organic matter pools between ecosystem components: a decrease in carbon and nitrogen reserves in the litter with their increase in the upper mineral horizons (Dymov et al., 2018). However, it should be emphasized that this increase in the carbon stock in the upper mineral horizons is accompanied by its huge fire-induced emissions into the atmosphere (section: The scale of wildfires and fire-induced carbon emissions in the forests of Russia).

Wildfires lead to change in the composition of soil organic matter. Due to fire, the content of hydrophilic organic compounds decreases and the content of hydrophobic compounds increases (Certini, 2005; Dymov et al., 2015 a). Increased soil hydrophobic properties lead to an increase in surface runoff and intensification of soil erosion processes. Wildfires contribute to an increase in the pyrogenic horizons of the content and proportion of polycyclic aromatic hydrocarbons (PAHs), which have carcinogenic and mutagenic properties. Naphthalene, whose content increased especially significantly, was also found in pyrogenic morphones at a depth of more than half a meter (Dymov et al., 2015 b).

The depth and scale of fire-induced changes in soil properties are, on the one hand, due to the nature of fire, its intensity, and on the other hand, due to the conditions (the level of soil moisture, precipitation, etc.) in which forests are formed, as well as types of forests.

In a changing climate, the frequency and intensity of wildfires are increasing. They lead to the release of carbon compounds from the buried organic matter of soils (legacy carbon) of boreal forests, which causes an increase in greenhouse gas concentrations and warming (Merzdorf, 2019). It has been shown that the restoration of litter in boreal forests after wildfires takes a lot of time (from 120 to 190 years) (Gorshkov et al., 2005).

Therefore, wildfires, the frequency and intensity of which are increasing in the modern circumstances of climate change, have a significant and negative impact on the properties of forest soils. As studies of long-term effects show, wildfires lead to reduced soil fertility, namely, to depletion of soils with available phosphorus and potassium compounds, to the release of carbon buried in the mineral horizons of soils, which causes a further increase in greenhouse gas concentrations. Wildfires contribute to an increase in soil hydrophobic properties and lead to an increase in surface runoff and intensification of soil erosion processes, as well as to an increase in the content of polycyclic aromatic hydrocarbons in soils, that have carcinogenic and mutagenic properties with inevitably detrimental effect on soil biota.

THE IMPACT OF WILDFIRES ON MICROBIOTA AND SOIL INVERTEBRATES

Wildfires have a destructive effect on the soil biota (Bowman, 1998; Doamba et al., 2014; Certini et al., 2021). Both crown and surface wildfires are dangerous, since both lead to the xerophytization of forest communities, which significantly changes the habitat conditions of both soil fauna and microorganisms. Charred wood (deadwood and tree trunks damaged by fire) is an unfavorable substrate for settlement of soil biota. Even among fungi, few species are known that can ensure the successful development of the pioneer stages of pyrogenic successions on wood (Safonov, 2006). In addition, direct burning of litter and deadwood leads to habitat loss for most species of soil biota. In general, wildfires reduce the biological activity of soils (Sorokin et al., 2000; Bezkorovajnaya et al., 2007; Sorokin, 2009; Sorokin, Afanas'eva, 2012).

Various studies focused on the effect of wildfires on microorganisms, most of which were short-term and conducted in the first years after the fires (Ahlgren, Ahlgren, 1965; Min, Haiqing, 2002; Mataix-Solera et al., 2009; Silva et al., 2020). Wildfire can affect the soil microbiome directly, through heating, and indirectly, changing the properties of the soil. The most important factors include the intensity and duration of wildfire, as well as soil properties. In the event of an intense, prolonged fire, the top layer of soil can undergo complete sterilization. The activity of soil microorganisms also decreases due to changes in the quality of organic matter. After depletion of easily mineralized organic compounds, the initial increase in microbial basal respiration quickly goes into a decrease, since the preserved forms of carbon and nitrogen are more resistant to the effects of microbiota. The increase in pH (due to deposition of ash) is the reason for the increased bacteria/fungi ratio (Mataix-Solera et al., 2009; Pressler et al., 2019). After medium- and high-intensity wildfires, rapid recolonization of the soil by photoautotrophic microorganisms (algae) can occur (Mataix-Solera et al., 2009).

In the middle taiga and southern taiga pine forests of Central Siberia, wildfires of medium and, especially, high intensity in the first year had a negative impact on the structure and functional activity of microbial complexes of sandy podzols. The number and biomass of nitrogen-carbon cycle microorganisms decreased, the qualitative composition became poorer, the enzymatic activity and intensity of microbial respiration decreased, the oligotrophicity of soils with respect to nitrogen increased (Bogorodskaya, 2006).

A surface wildfire of moderate intensity led to the decreased metabolic activity of the microbial community in the litter of the pine forest of the Novosibirsk region in the first two years after exposure (Naumova, 2008).

Analysis of the microbial community of Cambic Leptosols soils of Tolyatti pine forests after fires also showed that wildfires have a negative impact on the structure and metabolic activity of the microbial community of post-fire soil. It was found that the carbon content of microbial biomass and the rate of microbial respiration of the soil (in the upper organogenic horizons) of the sites after the wildfire significantly decreased as compared to the background figures (6.5 and 3.4 times, respectively). At the same time, at a depth of 10 cm in the soil, the effect of wildfire on these microbiological indicators has not yet been revealed (Maksimova et al., 2017).

Wildfires lead to a reduction in mycocenosis species diversity due to reduced quantity and quality of substrates (litter, wood residues) serving as a bank of spores and mycelium of fungi. The direct impact of wildfire on mycocenoses leads to a decrease in the species diversity of fungi. Burnt wood is slowly populated by xylotrophic fungi. As the deadwood accumulates after the fire, further development of mycocenosis occurs, but it goes in a direction different from the initial one (Safonov, 2006). Fungi are more sensitive to wildfires than bacteria (Pressler et al., 2019). Most studies of fungi forming arbuscular mycorrhiza have shown a negative effect (Mataix-Solera et al., 2009).

A meta-analysis of 1.634 field and 131 empirical studies of the impact of wildfires on microorganisms and mesofauna showed that wildfires have a strong negative impact on biomass, diversity, and distribution of soil biota. Wildfire reduces species richness and diversity of soil microorganisms and mesofauna by 88%–99%. The number of nematodes after wildfires is reduced by 88% (Pressler et al., 2019), Enchytraeidae — by 30–65% (Malmström et al., 2009), population and diversity of microarthropods are also reduced (Krasnoshchekova et al., 2008).

The monograph of K. B. Gongalsky (2014) focuses on the influence of wildfires on soil fauna and provides an overview of the world literature on the influence of wildfires of different scales on soil fauna. The results of field experiments on artificial burning of forest areas are presented, which showed 100% death of invertebrates of the litter and upper mineral soil horizons (Wikars, Schimmel, 2001); laboratory experiments with direct fire exposure to soil samples for 1 minute without subsequent extinguishing showed a 46% decrease in the total number of macrofauna; the survival rate of spiders was 49%, rove beetles — 27%, larvae of soldier beetles, click beetles and chironomids — 58–62%, whereas all cicadas, caterpillars (Noctuidae and Pyralidae) and molluscs were killed by wildfire (Gongalsky et al., 2012).

During surface fires, the inhabitants of the litter and mineral horizons of soils at a depth of 2–3 cm below the burning area are killed; death occurs both directly from high temperatures during a wildfire, and in the first few days after the fire due to intoxication by combustion products (Wikars, Schimmel, 2001). In the wildfire zone, mass mortality of ticks, collembolans, testate amoebas, insects and earthworms, i.e. groups closely related to the organogenic horizons of the soil, is recorded. “Mobile” insect groups are more resistant to wildfires, i.e. flying zoophages and phytophages (Moretti et al., 2006). At the same time, at the egg stage, almost 95% of insects die, at the larva and imago stages — 60% (Gongalsky, 2014).

Surface wildfires of any intensity have a negative impact on earthworms. During field studies in European forests after wildfires, it was expected that epigeic earthworms would suffer the most, since they are closely related to the litter, but it turned out that endogeic worm populations declined most and were extremely slow to recover due to the fact that cocoons and juvenile individuals of this group are located in the uppermost horizons of the soil. Wildfires also had a negative impact on the anecic earthworms group (Certini et al., 2021). At the same time, epigeic worms, as more mobile, probably found refuge in the trees and other fragments of woody remains in the forests. In the forests of the Russian Far East, significant differences in the population of earthworms in terms of decreased number, biomass, species diversity and composition of morpho-ecological groups have been revealed in forests often prone to wildfires, as compared to less disturbed forests (Geraskina, Kuprin, 2021).

Influence of wildfires on different taxonomic groups of meso- and macrofauna is a subject of numerous studies (Neumann, Tolhurst, 1991; Collett et al., 1993; Saint-Germain, 2005; Sackmann, Farji-Brener, 2006; Trucchi et al., 2009; Pressler et al., 2019; Gertini et al., 2021). Authors mostly report negative direct effects of wildfire on the density and species diversity of soil fauna, emphasizing their vulnerability and close relationship with the habitat. However, taking into account the indirect effects of wildfires, such as the emergence of open spaces, short-term development of microorganisms on mineralized due to fire organic residues, lack of competition in the first few years after a wildfire, etc., some authors report more favorable trophic and topic resources for individual taxonomic groups in the first years after a wildfire. For example, a number of Russian works show an increased diversity of ground beetles on fire sites in spruce forests: forest-meadow, meadow and field species appear, whereas the population of forest species of ground beetles decreases (Potapova, 1984; Uhova et al., 1999). At the same time, in the pine forests of Minnesota (Ahlgren, 1974) and the Spessart mountain range in Germany (Bauchhenss, 1980), a decrease in the diversity and population of ground beetles in the first two years after the fire was shown. A decrease in density and diversity of ground beetles in pine forests and an increase of these factors in spruce forests was found in Sweden, and the authors attribute this to better preservation of litter in spruce forests and its high humidity in comparison with pine forests. Insect larvae, earthworms, collembolans that ground beetles feed on have been preserved in the wetter litter. At the same time, the preservation of the diversity of ground beetles was directly correlated with the intensity of wildfire in both types of forest (Gongalsky, 2014).

In the first years after wildfires, irruptions of ants can be observed in the fire sites, which is believed to be due to the presence of a large amount of wood residues and high adaptation of ants to xerophilic conditions (Bess et al., 2002; Krugova, 2010). At the same time, it is known that even crown wildfires have a negative impact on some species of ants (Arnan et al., 2006).

The restoration of soil biota diversity after a wildfire is very slow, especially in groups of animals with low migration abilities, such as earthworms, millipedes, or molluscs (Gongalsky, 2014). Restoration of the soil population is possible due to the heterogeneity of the soil cover and the preservation of perfugiums — areas poorly affected by wildfire, where some invertebrates survive during a wildfire. Along with the inhabitants of the deep layers of soil, they are the first to populate the fire sites (Gongalsky, 2006; 2014). Mobility of invertebrates is of great importance for the subsequent recovery of population; for example, recovery of collembolan groups living in mineral horizons is much slower compared to the population of ground beetles living in the litter (Mordkovich, Berezina, 2009). It has been shown that spring burnings are more dangerous than autumn ones for collembolans, larvae of dipterans, butterflies, parasitic wasps and earthworms. After spring burnings, most of the taxa recover within one year, the earthworm population — within 3 years after the fire (Neumann, Tolhurst, 1991).

The long-term effects of wildfires on soil fauna have been studied in less detail than the short-term effects (Gongalsky, 2014). It takes at least 10 years to restore micro- and mesofauna (Pressler et al., 2019). It has been shown that, for example, in the fire sites in the Oka Nature Reserve (Ryazan region, Russia), no complete restoration of the soil fauna occurred 20 years after the wildfire due to the fact that the litter horizon did not return to its pre-fire state (Potapova, 2002).

Therefore, xerophytization of forest communities after a wildfire, loss of microhabitats, direct impact of fire and smoke on soil biota and indirect influence through changes in soil properties and destruction of trophic relationships has a negative impact on the biotically consistent structure of soil fauna. Irruptions of individual species or an increase in the diversity of individual groups (ground beetles, ants and other insects) are of a short-term nature, limited by trophic resources that are rapidly depleted on fire sites, and occur due to the formation of open spaces available for settlement by species with high migration abilities from neighboring biotopes.

THE IMPACT OF WILDFIRES ON ECOSYSTEM FUNCTIONS AND SERVICES OF FORESTS

Consideration of fire issues in the context of related socio-ecological systems that recognize the links between people and their natural environment is very relevant in the light of the increase in the world's population and, as a consequence, the increased demand for goods and services of forests. The terms "ecosystem functions" and "ecosystem services" are key in the concept of functional biodiversity. Ecosystem functions are a set of physical, biological, chemical and other ecosystem processes that support the integrity and conservation of ecosystems (Ansink et al., 2008). Ecosystem services are the benefits that people obtain from ecosystems, including provisioning services (fiber, wood, food, etc.), regulating services (erosion control, climate regulation, pollination, etc.), supporting services (soil formation, photosynthesis, etc.), cultural services (spiritual and religious, recreational, educational, etc.) (MEA, 2005). Forests simultaneously render forest ecosystem services (FESs) of all four categories, i.e. they are multifunctional (Byrnes et al., 2014; Manning et al., 2018; Van der Plas et al., 2018; Teben'kova et al., 2019). The transition to multifunctional forest management is considered as one of the key directions for achieving sustainable development of the forest-based sector (Bol'shakov et al., 2013). The multifunctional performance of forests can be considered at two levels: (1) the multifunctional performance of ecosystem functions, which are evaluated by fundamental studies of biological, geochemical and physical processes occurring in ecosystems; (2) the multifunctional performance of ecosystem services, which is defined as the joint provision of a number of ecosystem benefits in response to a request from society (Manning et al., 2018; Lukina et al., 2021). Taxonomic, functional, and structural biodiversity is the basis of multifunctional performance (Lukina et al., 2021). It has been shown that a greater number of species are needed to ensure multifunctionality than for single functions and services (Hector, Bagchi, 2007).

Later on, the impact of wildfires on each category of FESs is briefly reviewed.

1. Provisioning FESs

Provision with wood. Due to wildfires, there is a loss of wood biomass as a result of its complete or partial burning out, loss of value of wood resources due to trunk damage by fire and due to subsequent damage by wind, fungal diseases, and insects. In the case of a weak surface wildfire, when cambium is not damaged along the entire circumference of the trunk, its vital activity is partially preserved, and wood with a highly developed resin-forming apparatus begins to form, which is a response to fire damage. An increase in the number of annual rings was noted in the newly formed annual ring wood after damage. During a strong surface wildfire with a scorch height of 6–8 m, the tree loses its viability. Anatomical elements of the wood, most notably the resin canals, are completely or partially destroyed. The resin strongly impregnates the butt end of the trunk, which increases its density. Due to the destruction of anatomical elements, the sapwood of the upper part of the trunk shows a slight increase in the water absorption by wood and its decrease in the lower part due to resinosis. This affects the technology of storing lumber from fire-damaged forests (Isaenko et al., 2016). Moreover, favorable conditions are being created for the development of fungal diseases. After a severe wildfire, small and medium-sized roundwood has poor quality already in the first months after the wildfire and cannot be used as industrial wood (Kur'yanova et al., 2011). After wildfires, the growth of trees in the main canopy slows down, the understory and undergrowth are damaged (Gardiner et al., 2010). Moreover, this damage affects the economic aspects of the sale of biomass. For example, due to increased costs for timber harvesting and reforestation after a damage, the market is demoralized as a result of supply impulses (Prestemon, Holmes, 2004). After a wildfire, species composition of the forest changes, locations of raw-material bases are redistributed, which directly leads to changes in raw materials supplies to markets (Kogler, Rauch, 2019).

Provision of non-wood FESs. Since wildfire creates open spaces, despite its catastrophic effects on the ecosystem, fire is used to stimulate and increase the production of non-wood forest products, such as mushrooms, asparagus, medicinal and aromatic herbs, wild berries, nuts, etc. (Skulska et al., 2014). It is assumed that a low-intensity wildfire has a positive effect on regrowth of shoots of common hazel (*Corylus avellana*), raspberry

(*Rubus idaeus*), mountain ash (*Sorbus aucuparia*), prickly wild rose (*Rosa acicularis*), etc. (Johnston, Woodard, 1985; Panin, Zalesov, 2018). Under the influence of fire, the yield of the California hazelnut (*Corylus cornuta* var. *californica*) twigs increases, which are used for weaving (Marks-Block et al., 2019).

After low-intensity running and surface wildfires, the amount of lingonberries reaches the pre-fire level in 2–3 years and bog bilberries — in 3–5 years, after wildfires of average intensity — in 4–6 and 6–8 years, respectively, and after strong-intensity wildfires — in 10 and 15 years. The yield of berries increases in comparison with the pre-fire level by 30–60% due to improved lighting, temperature conditions and soil moisture. At the same time, subsurface and crown wildfires of high intensity lead to almost complete loss of berry plants from the ground cover of forest phytocenoses (Ostroshenko, 2012; Duchesne, Wetzel, 2004). In the areas covered by fire, European blueberry is actually eliminated from economic use for a long time (Panin, Zalesov, 2018; Duchesne, Wetzel, 2004).

The composition of fungal communities changes greatly under the influence of wildfire, which reflects changes in physical, chemical and biochemical properties of soils (Dahlberg et al., 2001). Wildfire intensity, stand age, soil pH, humidity, and C : N ratio are considered to be the main drivers of these changes (Waldrop, Harden, 2008; Reazin et al., 2016; Day et al., 2019). Moreover, the loss of vegetation cover and changes in plant composition are closely related to fungal communities that have symbiotic/saprophytic relationships with them (Cairney, Bastias, 2007). It is reported that in some cases, after wildfires, the number of carbotrophs increases, which is a special group of fungi using ash and charred wood as a substrate, as well as saprotrophs — fungi that feed on dead organic matter, and xylotrophs — fungi that feed on the wood of living and dead trees. Some morel species (saprotrophs) bear fruit abundantly in the first year after a fire (Larson et al., 2016). Most of the marketable yield in western North America consists of morels harvested in the first year after wildfires (Pilz et al., 2007). However, these effects are short-term and not always marked. Most often, after wildfires, there is a significant reduction in the number and biomass of edible and edible mycorrhizal fungal species (Gassibe et al., 2014). Fungal communities of boreal forests are the most vulnerable. One year after the wildfire, mycorrhizal fruit bodies were not found in these forests (Franco-Manchón et al., 2019). The number of species associated with mature trees is also decreasing. Restoration of symbiotic fungi is directly related to tree restoration. Boletus and saffron milk caps appear a few years after the wildfire at sites of self-sown pines (Smith et al., 2021). Fruit bodies of xylotrophic fungi, collected also in places covered by wildfires, are used in medicine. For example, a number of polypores are used in medicine, such as sulphur polypore, *Ganoderma applanatum*, *Ganoderma lucidum*, medicinal polypore, and chaga (Kochunova, 2014).

2. Influence on regulatory FESs

Regulation of carbon cycles. Wildfires lead to emissions into the atmosphere of large amounts of greenhouse gases and gases with an indirect greenhouse effect either directly as a result of burning out of living and dead wood, litter, as well as during the subsequent decomposition of dead wood, mineralization of litter and soil organic matter. Therefore, wildfires play an important role in the carbon cycle. It is wildfires, according to D. G. Zamolodchikov et al. (2013), that are the main cause of year-to-year variations in the carbon balance of forests in Russia. The negative impact of wildfires on carbon deposition is more often reported in the literature, mainly due to the reduction of aboveground biomass in the ecosystem (Bond-Lamberty et al., 2007; Bartalev et al., 2015; Zamolodchikov et al., 2017; Ershov, Sochilova, 2020), less often due to the burning of soil organic matter (Walker et al., 2018, 2019). It has been found that the time since the damage and wildfire intensity have an impact on the stocks of all carbon pools. So, on average, the differences in carbon stocks as compared to forests undisturbed by fire are –91.3 and +155.5% in the first year after the fire for live and dead wood, respectively, and increase by 0.6% for live and decrease by 1.4% for dead wood every year after the damage (Thom, Seidl, 2016). The study of the relationship between phytomass consumed by fire and mortality rate of trees in stands of mixed conifers and western yellow-pine (*Pinus ponderosa*) showed that burning of up to 13% of the available ground biomass led to mortality rate of 22%, while burning of 13%–35% was associated with mortality rate of 54% and of over 35% — with mortality rate of 98% (Meigs et al., 2009). Over time, forests restore biomass and, accordingly, the carbon stock that has been lost during the fire. This process depends on fire intensity and the resulting environmental conditions (soil-related, hydrological, light-loving vegetation overgrowth, etc.). For example, after a small surface wildfire, the Sierran mixed coniferous forest restores lost carbon in less than seven years, which is comparable to the historical interval between fires in such forests (Hurteau, North, 2009); Yellowstone National Park pine forests recovered about 90% of carbon within 100 years after the fire, with a historical average fire interval of 150–300 years (Kashian et al., 2013). This occurs not only due to active growth of woody plants, but also due to a decrease in soil respiration (Perez-

Quezada et al., 2021), due to changes in the structural and functional organization of soil microbiocenosis against the background of pyrogenesis (Medvedeva et al., 2020). Wildfires reduce the rate of carbon mobilization by soil biota. Shifts in soil trophic webs caused by wildfires have a significant short-term impact on the carbon cycle in forest soil; these effects vary depending on the type of forest and its geographical location (Gongalsky et al., 2021). Thus, if the frequency of fire occurrence will not increase significantly and become less than time needed for restoration of a ripe forest, wildfires should not cause net carbon emissions into the atmosphere (Campbell et al., 2012). But it also follows that if forests do not recover after a wildfire, the frequency of fire occurrence is high and there is not enough time to restore carbon stocks or there is a constant change in forest structure, leading to low carbon stocks, there will be a net loss of carbon over time. Therefore, it is so important to take measures to develop systems of forecasting, rapid fire detection and extinguishing.

However, it is believed that the protection of forests from wildfires increases the risk of fire. It has been shown that an effective fire detection and extinguishing system contributes to a significant accumulation of fuel in forests, which usually burns down during wildfires of low and moderate intensity. In combination with climate change, this can lead to a sharp increase in the frequency of fire occurrence. With such a system, in the case of large mega-fires, emission may exceed carbon deposition. Thus, in a number of countries, prescribed wildfires are used as a method of reducing the amount of fuels in such forests to reduce the risk of large catastrophic fires (Adams, 2013). At the same time, it is obvious that the trade-off with risks for environmental assets, such as biodiversity and ecosystem services, when using such a system is not entirely clear (Moritz et al., 2014; Harper et al., 2018). Prescribed burning leads to even greater frequency of fire occurrence (Yaroshenko, 2021).

Regulation of water regime. In many parts of the world, forests provide people with fresh water for domestic, agricultural, industrial and environmental needs. Forest stands affect the quantity and quality of water runoff by absorbing cations and anions from the solution, improving the bacteriological properties of water, purifying it from suspended solids and having an impact on the temperature regime of water bodies. Forest reduces peak loads of surface runoff, transforming it into underground one, and thereby reducing the risk of flooding (Rybalova, 2007). Wildfires can have devastating consequences for aquatic ecosystems and the potable water supply of the population. They can influence hydrological processes (interception, infiltration and evapotranspiration), which in turn affect the time and magnitude of river flow (base flow, peak flow and annual water production) (Shakesby, Doerr, 2006). The destruction of forest vegetation by wildfire reduces evaporation by intercepting precipitation and evapotranspiration, thereby increasing the amount of rain and snow reaching the ground and increasing soil moisture, runoff and volumes of water flowing into water bodies (Neary et al., 2003). Due to the greater amount of solar energy reaching the snow cover in the burned areas, there is a twofold increase in the rate of snow melting (Burles, Boon, 2011). Moreover, the thickness of snow cover in the areas covered by fire is less than in the undamaged areas (Maxwell et al., 2019). When the ground cover is damaged by wildfire, the natural water-repellent soil layer can be exposed (Doerr et al., 2009), which can reduce the infiltration of precipitation into the soil during heavy rains or snowmelt, contributing to an increase in surface runoff (Huffman et al., 2001). A two- to five-fold increase in peak runoff over 6–7 years is reported as a result of fire influence (Moody, Martin, 2001a). There is evidence that a combination of medium- and high-intensity wildfires in the context of intense short-term precipitation can increase peak runoff values up to 870 times (Neary et al., 2003; Moody, Martin, 2001b).

After wildfires, the role of forest canopy in the processes of precipitation interception decreases sharply, and the qualitative composition of the runoff changes. The consequence of this is an increase in the intensity of water, wind and soil erosion. As a result, the amount of dissolved substances, phosphorus, nitrogen, dissolved organic carbon, sulfates, chlorides, calcium, magnesium, sodium and potassium that are removed from the forest catchment increases sharply, which leads to an increase in their content in surface waters (Mikkelson et al., 2013, Smith et al., 2011; Emelko et al., 2011). As a result, the concentration of pollutants, including heavy metals and pathogenic microorganisms, may increase (Stone, Droppo, 1994), as well as the amount of sediment and debris in reservoirs, which leads to silting (Smith et al., 2011). For example, after the Hayman Fire in Colorado in 2002, twice as many nitrates were recorded in river water, and turbidity increased fourfold as compared to basins whose areas burned to a lesser extent; these indicators remained elevated for 5 years after the fire (Rhoades et al., 2011). This, in turn, affects the biological population of reservoirs, including valuable commercial fishery species. In Australia, populations of fish decreased by 95–100% due to an increase in bottom sediments after the fire and a subsequent decrease in dissolved oxygen levels in river water (Lyon, Connor, 2008).

From the perspective of water supply, wildfires increase the likelihood of impairment of water quality (taste, smell, color, chemical composition), deterioration of potable water purification processes and shortening of the working lifespan of the water intake and treatment system (Emelko et al., 2011). This is very important because, for example, it is known that almost two-thirds of municipalities in the United States and about one-third of the largest cities in the world, including Tokyo, Melbourne, Los Angeles and Rio de Janeiro, receive most of their potable water from forest catch basins (National Research Council, 2008). As a result of a heavy post-fire downpour in south-eastern Australia, for example, the concentration of arsenic, iron, lead and chromium in drinking water increased to levels exceeding the recommendations of the World Health Organization (Leak et al., 2003). Similarly, during the first two years after the Lost Creek Fire, total mercury concentrations in potable water during storms were many times higher than permissible sanitation standards (Emelko et al., 2011). Elevated concentrations of mercury were also found in fish (Garcia, Carignan, 2005).

Rapid reforestation can offset the negative effects of wildfires on aquatic ecosystems. In the first decade after large wildfires, as compared to mature intact forests, water consumption by forest stands more than doubles during their restoration, followed by a decrease for many decades (Lane, Feikema, 2010; Buckley et al., 2011; Benyon et al., 2007). This can be down not only to an increase in the area of foliage in total ("Kuczera effect", Kuczera, 1987), but also to the fact that, firstly, the stomatal conductance of newly developing and young leaves is much higher than that of the leaves of adult trees; secondly, both the sapwood area and the leaf area are significantly larger in young stands; and thirdly, night transpiration in young trees is also higher than in mature stands (Buckley et al., 2011).

Protection from avalanches, mudslides. An important regulatory function of forests, also related to water, is the protection of society and infrastructure from natural hazards, such as floods and avalanches. Disturbances weaken the buffer effect of forests on water runoff and increase the risk of avalanches and their collapse (Zurbriggen et al., 2014). Accelerated erosion combined with the emergence of hydrophobic soils, decreased rate of water infiltration, surface runoff or massive soil disturbance on hillsides can also sometimes lead to catastrophic mud streams (Doerr et al., 2009). It is estimated that the volume of sediments from mudslides after wildfires is 2–3 orders of magnitude higher than the annual rates of background erosion from areas of undisturbed forests. The volume of mudslides from slopes with a steepness of 18–62 percent varies from 539 to 33.040 cubic meters (Nyman et al., 2015). There are models for predicting mudslides that help make management decisions, such as RUSLE (Ying et al., 2021) or the US Geological Survey (USGS) Post-Fire Hazard Model (Ellett et al., 2019).

Air quality regulation. Since the late 1970s, wildfires have been recognized as an important source of air pollution (Crutzen et al., 1979; Rogers et al., 2020), and in the context of a changing climate, this contribution could soar due to increasing areas of wildfires (Amiro et al., 2001 b; Carvalho et al., 2011). It is known that when burning biomass, many different particles and gases are formed that affect atmospheric processes. These include carbon dioxide, carbon monoxide, methane, volatile and semi-volatile organic compounds (toluene, benzene, acetone, methanol, acetonitrile, isoprene, methyl vinyl ketone, etc.), nitrogen and sulfur compounds, halogenated hydrocarbon, solid volatile particles (soot, black carbon, etc.) (Yadav, Devi, 2018; Butt et al., 2020). The impact of these emissions can be seen at different levels: from temporary local atmospheric pollution (Miranda, 2004; Hodzic et al., 2007) to the global contribution to the greenhouse effect (Simmonds et al., 2005). Emissions of CO, CH_4 and volatile organic compounds into the air affect the oxidizing ability of the troposphere by reacting with OH· and NO· radicals, which leads to the formation of ozone and other photooxidants. CH_3Br emission causes ozone photodegradation in the stratosphere. Solid particles in the air can cause acidification of clouds, a change in the radiation balance of the Earth due to absorption and scattering of incoming solar radiation or formation of cloud condensation nuclei. This leads to a decrease in the size of cloud droplets, thereby increasing the albedo of clouds, which ultimately affects the nature of precipitation and the hydrological cycle (Yadav, Devi, 2018).

Smoke with dangerous fine solid particles and gaseous compounds resulting from biomass burning is one of the main atmospheric components affecting air quality in vast territories due to its massive plumes that can travel thousands of kilometers with the wind (Chen et al., 2017; Beig et al., 2020).

3. *Cultural services*

Recreation and meeting of spiritual needs. Recreational value of forest landscapes can be greatly reduced due to wildfires (Sheppard, Picard, 2006), because dead trees are often perceived as less picturesque than living stands and pose a danger to tourists. Therefore, recreational areas such as camping sites and trails are often closed after serious damage due to the risk of trees falling. On the other hand, wildfires provide researchers with opportunities to study a variety of issues, thereby contributing to the production of scientific knowledge. Moreover, many indigenous and traditional societies have a long experience of living with fire (i.e. cultural knowledge) and therefore can share it (Fowler, Welch, 2018).

The impact on people's health. The annual global mortality rate from the smoke of plant fires is estimated at about 339 thousand deaths per year (Cascio, 2018). Systematic reviews show that there is a positive association between exposure to wildfire smoke and mortality from respiratory diseases (Arriagada et al., 2019; Reid, Maestas, 2019; Xu et al., 2020). In a number of cases, an association has been recorded with the frequency of cardiovascular diseases, premature birth (Reid et al., 2016; Black et al., 2017), increased incidence of influenza (Landguth et al., 2020), the frequency of visits of patients with diabetes mellitus (Yao et al., 2020). In the areas surrounding a wildfire, cases of carbon monoxide poisoning are recorded very often (Tao et al., 2020; dos Santos et al., 2018). Heavy smoke can cause eye irritation and corneal damage (Finlay et al., 2012). Residents of affected areas are at greater risk of mental illness, including post-traumatic stress disorder, depression and insomnia (Belleville et al., 2019). The psychological effects of wildfires can persist for years (Bryant et al., 2018), and children and adolescents are particularly vulnerable (Brown et al., 2019). Experienced wildfires in childhood are associated with an increased likelihood of mental illness in adulthood (McFarlane, Van Hooff, 2009). Moreover, wildfires are associated with a subsequent decrease in the academic performance of children (Gibbs et al., 2019).

It is estimated that in the United States in 2008–2012, health care costs resulting from short-term exposure to particulate smoke from wildfires ranged from 11 to 20 billion US dollars per year, while the costs associated with long-term exposure to this factor range from 76 to 130 billion US dollars per year (US dollars in 2010) (Fann et al., 2017). In Tanzania, in 2010–2019, the total cost of health care related to the effects of wildfires amounted to 76 Australian dollars per day, which corresponds to 5.2% of annual health costs associated with smoking (Borchers-Arriagada et al., 2020).

4. Supporting services

Net primary production (*NPP*). After disturbances, NPP remains low for several years, partly due to the low leaf area index and their number; it reaches a maximum when the canopy closes and decreases slightly as the stand matures (Odum, 2014; Gower et al., 1996; Ryan et al., 1997; Howard et al., 2004; Goulden et al., 2011). In addition, repeated disturbances associated with stand replacement can prevent forests from reaching maximum NPP values (Gough et al., 2007), causing nitrogen losses due to leaching or a decrease in the amount of organic matter and soil fertility in general (Latty et al., 2004). The impact of fire frequency on NPP is particularly pronounced for coniferous forests which have a longer leaf lifespan and a longer recovery period (Peters et al., 2013).

Soil formation (See also the section “Influence of fires on the morphological and physico-chemical properties of soils"). During wildfires, there is a change in soil-forming processes (pyrogenesis of soils). Short-term and long-term post-fire changes are identified. During a wildfire, under the influence of high temperatures, the surface layers of soils lose organic matter, and roots, invertebrates, microorganisms, etc. die. Soil fertility depletion is observed. The contribution of organnic horizons to the total stock of soil carbon is reduced. In the soils of wildfire sites, aeration improves and oxidative processes, ammonification and nitrification are intensified, the degree of decomposition of litter fall within the soil and loss of total carbon increases. In the surface mineral horizons, the pH and base saturation increases as well as the content of mobile organic and mineral compounds increases. Wildfire changes the composition of carbon forms, increasing the proportion of hydrophobic compounds, which affects the structure of the soil system, and the biochemical composition and population of microorganisms in particular (Nadporozhskaya et al., 2020). The strongest impact on the soil has not the fire itself, but post-fire secondary changes in the biogeocenosis associated with the post-fire transformation of vegetation cover (Sapozhnikov et al., 2001). However, it is difficult to make prognoses of composition of vegetation after a fire, because it is influenced by many factors, such as the degree and area of the fire, the distribution of surviving trees, the volume of the seed bank, landscape fragmentation, climate change, invasion of species, the number of herbivores, changing accessibility of the territory, subsequent disturbances (McLauchlan et al., 2020).

Pollination. Since wildfires form open spaces, where populations of flowering plants are usually more represented than under the forest canopy, the density of pollinating insects is higher (Campbell et al., 2007; Hanula et al., 2015). Therefore, it has become more and more accepted that landscape mosaic with a variety of fire regimes and stand ages after wildfires contributes to the diversity of flowering plants and pollinators (Ponisio et al., 2016; Brown et al., 2017; Lazarina et al., 2019), which can also increase crop yields (Winfree et al., 2018; Mola, Williams, 2018). However, open spaces can be created by humans in ways that are less destructive to the ecosystem, for example, by logging, which also contributes to improving pollination efficiency (Goulson et al., 2015).

Economic damage from loss of ecosystem services as a result of wildfires

Despite the great economic importance of forest ecosystem services, there are few quantitative estimates in monetary terms of the impact of wildfires on forest ecosystem services (Lee et al., 2015). According to San Diego State University, the total economic impact of the 2003 wildfires in San Diego County is estimated at

$2.45 billion, of which the cost of extinguishing is less than two percent of the total losses. This does not take into account the long-term impacts of wildfires on the affected catch basins (Rahn, 2009). The Western Forestry Leadership Coalition estimates the true cost of wildfires in the western United States from two to thirty times higher than the cost of extinguishing (The true..., 2014). In our country, using the example of territories of two protected areas in the Irkutsk oblast, quantitative calculations of losses of ecosystem services of forests as a result of wildfires are given (Volchatova, 2019): for the Baikal National Park, annual total damage averages 136.26 million RUB, while for the Baikal-Lena Reserve — 1081.71 million RUB. It is emphasized that the territory of Siberia is extreme in terms of fire. For example, in Irkutsk Oblast, 77% of the forest fund is classified as the first three classes of natural fire danger. The situation is aggravated by the climatic and light conditions of the region — a sharply continental climate with a hot and arid summer period, sunshine over 2 thousand hours per year. An additional factor contributing to vulnerability of the forests of these protected areas is the predominance of pine forests in dry habitats with easily ignitable ground cover and high frequency of fire occurrence in pine stands. Damage caused by wildfire includes not only loss of standing wood, but also decreased ecological functions of the forest, pollution by combustion products, death of biota, which increases the amount of regulatory and support services of forests that were not received.

Thus, at present, wildfires are one of the leading factors regulating the functioning of forest ecosystems. Wildfires of any intensity have an impact on forest ecosystem functions and services of all categories. The short-term increase observed in some cases in the provision of non-wood products (berries, mushrooms, medicinal herbs) and such a supporting function as pollination resulting from the mosaic pattern of forest cover created by wildfires does not make up for the loss of other provisioning (wood, fibers), supporting (net primary production, soil formation, habitat maintenance), regulatory and cultural services. The extent of economic damage caused by wildfires, especially those of high intensity, is difficult to assess, since there is no clear understanding of the long-term effects of wildfires on biodiversity and ecosystem functions and services of forests as of yet. However, it is extremely important to take into account the impact of fire consequences on the functioning of ecosystems and economic development in the context of climate change when making management decisions.

CONCLUSION

The results of the studies regarding the fire impact on forest ecosystems show devastatingly powerful and long-term destructive impact of wildfires on the biodiversity and functions of forests. According to official statistics, in the last decade, hundreds of thousands of wildfires have been detected in Russia alone, with the total area covered by fire estimated at millions of hectares. Currently, the proportion of large wildfires (those with an area of more than 200 hectares) has increased. Due to global climate change, an increase in the frequency and intensity of wildfires is expected. The most common fire type in the forests of Russia are surface wildfires that have a destructive impact on soil and soil inhabitants, which leads to impaired soil formation and, consequently, decreased efficiency of all ecosystem processes. The restoration of litter in boreal forests after fires may take more than 120 years. In the mineral horizons of soils, "traces of fires", in the form of a change in chemical composition and depletion of elements of mineral nutrition are found over 100 years after the fires. No complete recovery of all components of the soil biota has been revealed in the first few decades after the fires, whereas results of longer observations are lacking. Vegetation restoration requires considerable time (tens and hundreds of years), if there are not enough diaspora carriers, i. e. birds and mammals, whose populations are also disrupted by wildfires and other causes. Wildfires are a factor that results in loss of genetic, taxonomic, and functional biodiversity, damage and destruction of habitats for plants, animals and microorganisms, loss of functions of forest ecosystems. Wildfires are a factor in the dynamics of forest ecosystems directed at "erasing of evolution".

Analysis of literary sources shows that an established opinion expressed in a number of works, that wildfires are, at a certain frequency, essential for the maintenance of forest communities, ignores or misunderstands the role of biotic factors in the functioning of forests. Populations of keystone large mammal species have been lost or drastically reduced in the modern forest ecosystems; consequently, there are no microsites formed by them, including large gaps in the forest canopy (glades) that provide opportunities for maintaining light-demanding flora, insect pollinators and conditions for the development of all-aged polydominant forest ecosystems with high biological diversity in general. Moose, bison, beavers, and other animals create natural barriers to the spread of fire due to formation of gaps, trails, sparse stands, and reservoirs in the forests.

It should be emphasized that an increased number and diversity of individual groups of invertebrates and vertebrates on fire sites is short-term, limited by trophic resources rapidly petering out on fire sites and is due to new open spaces becoming available for settlement by species from neighboring biotopes with high migratory abilities. Often, as a result of large wildfires, huge homogeneous open spaces are formed, which are very far from the sources of diasporas of many plant species and are difficult to be populated by "low-mobility" groups of animals, which results in a steady decline in biodiversity. Wildfires as a powerful factor trigger positive feedback mechanisms leading to the elimination of species, which is why some forest communities have been identified by researchers as fire-dependent.

Wildfires of any intensity have an impact on forest ecosystem functions and services of all categories. The short-term increase observed in some cases when providing some non-wood products (berries, mushrooms, medicinal herbs, pollination) resulting from the mosaic pattern of the forest cover created by wildfires does not make up for the loss of other functions and services of forests. The extent of economic damage is difficult to assess, since the long-term effects of wildfires on the climate, soil formation, water regimen regulation, and human health are not taken into account.

It is essential to ensure continuous maintenance and restoration of populations of endangered animal species in modern forests, especially large mammals that create zoogenic clearings and gaps in the forest canopy, regulating the density of the stand and the mosaic pattern of the ground cover.

Based on the performed analysis of the impact of wildfires, we can give the following recommendations for the conservation and maintenance of biodiversity and ecosystem functions of forests in the modern forests:

- take action to prevent wildfires: educate people on how to prevent wildfires; completely ban burning of felling residues during the fire-hazardous season; ban agricultural and any prescribed burning of dry grass vegetation (Postanovlenie…, 2015; Sosnovchik, 2016; Volchatova, 2019; Vacchiano et al., 2018; Yaroshenko, 2021);
- take action for timely detection and rapid and prompt localizing of fires: abolition of "control zones" where it is allowed not to extinguish fires; increase the staff and funding of road and air forest protection several times; continuous road, air and space monitoring of fire danger in forests (Korovin, Isaev, 1997; Gomes et al., 2006); develop safety barriers that would prevent the spread of wildfires, including channels and water reservoirs to be used for fire extinguishing (Češljar, Stevović, 2015);
- harvest large wood residues in areas of massive blow-downs, provided that the deadfall of individual tree trunks is preserved to maintain the biological diversity of xylobionts (Lust et al., 2001);

• maintain and restore populations of endangered animal species in modern forests, especially large mammals that create zoogenic clearings and gaps in the forest canopy, regulating the density of the stand and mosaic pattern of the ground cover (Van Meerbeek et al., 2019; Van Klink et al., 2020), as well as beavers as the main representatives of “forest firefighters” regulating the groundwater level, creating intra-forest reservoirs that serve as natural barriers to the spread of fire (Evstigneev, Belyakov, 1997; Aleynikov, 2010; Zav’yalov et al., 2016). That is, it is necessary to restore the biotic factor that forms the structural diversity in forest ecosystems (Lukina et al., 2021);

• ensure haymaking and grazing of domestic animals near human settlements. These impacts would, on one hand, prevent the formation of communities with large reserves of dry grass and rags, which create a high fire hazard, and, on the other hand, support biological diversity and productivity of ecosystems (Smirnova et al., 2021; Evstigneev, Gornov, 2021).

• form mixed stands as more fire stable during forest restoration after wildfires and during plantation management (Korotkov, 2016, 2017; Gomes et al., 2006);

• if necessary, conduct gap felling with planting or sowing of light-loving tree species in the gaps (Metodicheskie..., 1989; Korotkov, 2016, 2017).

• fell individual trees and groups of trees to prevent the spread of fire (Allen et al., 2002).

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