

Natural Disturbance Dynamics in the Boreal Forests of European Russia: a Review

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In the European part of the Russian boreal zone the dynamics of pristine forests (taiga) has been studied by several generations of researchers. Many studies have examined the patterns and role of fire, windthrow, insect outbreaks and other natural disturbances. An attempt is made to provide a brief review of these studies. The reviewed studies show that lightning strikes were the only natural source of fires in taiga. The frequency of fires varied in various types of pristine landscape from 1–2 per century to 1–2 per millennium. Fires maintained a dynamic equilibrium between compositionally different forest communities or their certain ratio and areal occurrence. Fires favored the regeneration and recovery of pine forests and prevented the replacement of shade-intolerant species (e.g. pine) by shade-tolerant ones (e.g. spruce). Taiga forests generally displayed a mosaic pattern that varied from pioneer plant communities, growing in open burns, to climax communities that were extremely seldom affected by fire. The reviewed studies suggest that fires were a powerful ecological factor in pristine taiga, being largely responsible for the structure and spontaneous dynamics of forest communities. Windfalls were also common in pristine taiga landscapes and they regulated spontaneous dynamics in a gap-mosaic regime, which is most characteristic of spruce forests.

Key words European Russia, boreal forests, disturbance dynamics, fires, windthrow

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1 Introduction

Pristine forests are continuously changing, even under relatively stable climate conditions. The successional stage of forest communities range widely, from a relatively stable dynamic balance (climax) to catastrophic dieback induced by cata-

strophic natural disturbances (fires, windthrow, massive insect outbreaks, etc.) followed by the establishment of pioneer plant communities. In the European part of the Russian boreal zone the dynamics of pristine forests has, for a long time, been one of the central subjects of research. In many of the papers forest dynamics is considered

in connection with various natural disturbances.

The taiga zone of European Russia covers an area of ca. 170 million hectares. It extends from the Gulf of Finland and the Russian-Finnish state border in the west to the Urals in the east (Fig. 1).

The taiga zone changes to forest tundra northwards and to mixed (coniferous-deciduous) forest zone (so-called "subtaiga") southwards. This territory is part of Europe's two largest physico-geographic regions (natural countries) that differ considerably in forest cover pattern:

a) Fennoscandia in the Baltic crystalline shield, which is dominated by a denudation-tectonic hilly-ridge relief, including low-mountain areas, and is clearly dominated by pine stands. b) The Russian (East European) Plain with chiefly flat interfluves and a morainic-hilly relief clearly dominated by spruce stands. The boundary between these two contrasting geographic areas extends approximately along the administrative border between the Republic of Karelia and the Arkhangelsk province. The taiga zone is subdivided into north-, middle- and south-taiga subzones, depending on the structural characteristics of stands, such as density, productivity and the live ground cover, affected by north-south climatic variations.

In the Fennoscandian part of the region the forest cover is formed by conifers such as (scientific names are according to Russian nomenclature) *Pinus sylvestris* L., *Picea abies* (L.) Karst. and *P. obovata* Ledeb. It should be noted that a cycle of hybridogenic forms, intermediate between *Picea* species and collectively known as *Picea × fennica* (Regel) Kom), prevails. *Betula pendula* Roth (*B. verrucosa* Ehrh.), *B. pubescens* Ehrh. and *Populus tremula* L. usually occur as admixture. *Alnus incana* (L.) Moench, *A. glutinosa* (L.) Gaertn. and *Salix caprea* L. are also encountered in pristine forests, whereas *Tilia cordata* Mill., *Acer platanoides* L. and other broad-leaved species grow in southernmost areas.

On the Russian Plain, another forest-forming species (i.e. species that form forest cover) is *Larix sibirica* Ledeb. The European part of its area is often regarded as the independent species *L. sukaczewii* Djil. spec. nov. Larch forests cover about 1/3 mln. ha. Other forest-forming species that occur in the easternmost part of European

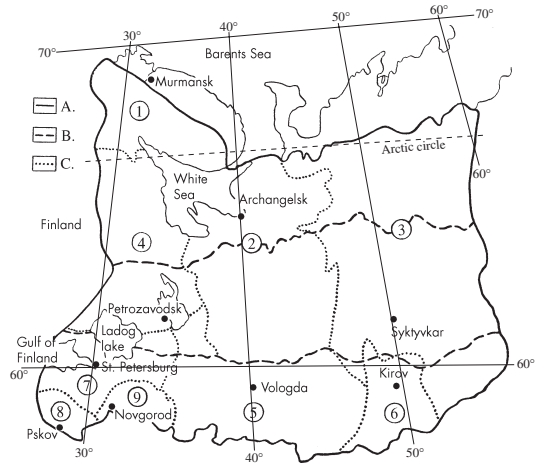


Fig. 1. Taiga zone of the European Russia and administrative regions. Administrative regions – Murmansk (1), Arkhangelsk (2), Komi Republic (3), Karelia Republic (4), Vologda (5), Kirov (6), Leningrad (7) and Novgorod (8). A. border of taiga zone. B. border between northern, middle and southern taiga subzones. C. border of the administrative regions.

Russia's taiga zone are *Abies sibirica* Ledeb. and *Pinus sibirica* Du Tour. Fir stands are scarce (in the Ural foothills) and Siberian cedar stands are extremely rare.

One of Russia's largest forest regions covers the Murmansk, Leningrad and Arkhangels provinces, the Republic of Karelia, the Komi Republic and the northern parts of the Vologda, Novgorod, Pskov and Kirov provinces. By the early twenty-first century, pristine forests will have survived as fragments only in the north-taiga subzone along the Russian-Finnish border and along the White Sea coast. The largest pristine forests are in the areas adjoining the forest-tundra zone of the Arkhangels province and in the foothills of Urals.

Mainly in the second half of the twentieth century a number of monographs, describing the structure, productivity and spontaneous dynamics of the forest cover, were published in Russia (Tkachenko 1911, Voropanov 1950, Levin 1959, Kazimirov 1973, Zybchenko 1984, Dyrenkov 1984 and others). Part of them also discussed the problems of anthropogenic forest dynamics and forestry. The monographs mention or discuss

various aspects of pristine forest dynamics in connection with different kinds of natural disturbances. Most of the information on this theme is. However, found in a large number of more specific research papers (the references only list the key publications). The review is an attempt to make a brief overview of these studies. In order to give a structured account of the topic, the analyzed publications are grouped according to disturbance factor.

2 Forest Fires

About 90% of all analyzed publications are devoted to the role of forest fires in the natural dynamics of the forest. The reason for such great interest of researchers on this topic is obvious. Fires have been the most powerful ecological factor shaping the structure and dynamics of pristine forests. Some of the central publications in these respects are the monographs by Melekhov (1947, 1948), Korchagin (1954), Vakurov (1975).

There also exist some methodological papers. For example, Savchenko (1987) proposes a whole system of principles by which research about the effect of fires on forests can be organized. He suggests the fires to be considered "... not only as a reason for pyrogenic forest dynamics, but also as a source of potential pyrogenic stability of certain forest biogeocenosis [term of Sukatchev 1964] types" (Savchenko 1987, p. 31). He also stresses that conclusions based on the study of pyrogenic dynamics of forest communities in small burnt areas cannot be extrapolated for large burnt areas, and vice versa.

2.1 Ignition Sources

Ignition sources are central for identifying the ecological role of forest fires, while ever since human activities started in boreal areas they have become the main reason for fire ignitions. This is true especially in connection with the spread of slash-and-burn agriculture. While the only source in European pristine boreal forests is lightning strikes. It can be estimated that 3 to 70% of

fires in the European part of the Russian boreal zone are initiated by lightning (Listov and Borodin 1964, Fjodorchyuk and Ovchinnikov 1965, Listov 1967, Vakurov 1975, Kurbatsky 1976, Noga and Tikhonov 1979, Stolyarchyuk and Belaya 1982). Kurbatsky (1976) analyzed the mechanisms of lightning-induced fires and claims that a forked lightning can hit a group of trees simultaneously.

2.2 Conditions of Fire Emergence.

A number of papers deal with the climatic and weather conditions under which fires start. The boreal zone of European Russia, lying mostly north of the 59th parallel, is part of the so-called May-June forest fire belt typical of the northern and middle taiga subzones (Melekhov 1946). The duration of the fire danger period is 90–100 days in the northern, and 125–135 days in the southern part of the belt. The maximum number of fires is usually recorded in July. Fires are most numerous in the driest years. The main parameter used for determining the probability of fires is air humidity, which determines the "pyrogenic ripening of fuels" (Kurbatsky 1970). Calculations and forecasts of the fire danger also take into account the air temperature, moisture deficit and other weather variables (Melekhov 1939, Nesterov 1940).

2.3 Frequency and Extent of Fires

The frequency of fires ranges widely, due to the great diversity of landscape conditions in the European north of Russia. In general fires can be divided into local fires (occurring within individual habitats, e.g. lichen and cowberry pine stands) and regional fires (covering vast areas).

In the Archangels region fires repeated, on average, once in 40–44 years in dry forest types, 64–68 years in moister forest types and 130–200 years in spruce forests (Melekhov 1971). In the central part of northern Karelia rapid ground fires occurred once in 20–40 years, and more stable fires recorded throughout the research area 1–2 times in a century (Zyabchenko 1984, p. 65). According to the data from the literature, the

years noted for heavy droughts and fires were 1363–1372, 1518–1534, 1630–1646, 1717–1743 and 1826–1840 (Voropanov 1950).

Some researchers report that some fires in boreal forests have embraced areas up to 30000 ha (Tkachenko 1911). Voropanov (1950) deems that “deforested areas were created by forest fires that in some historical epochs covered enormous territories” (Voropanov 1950, p. 110). These open, burned areas became covered with new natural tree regeneration gradually (within 10–15 years).

2.4 Types of Fires

Melekhov (1947) developed a classification of forest fires that is widely used in Russia. Fires are grouped into surface fires (the main fuel is ground, litter-humus, understory-shrubs and tree-fall-stumps), crown fires (main fuel is tree crowns and stems) and underground (peat) fires. According to statistics, surface fires account for 76–86%, crown fires for 16–24% and underground fires less than 0.1% of the total number of fires (Melekhov 1947).

In terms of flammability (the risk of fire emergence) Melekhov (1947) grouped all forest sites into 5 categories (in the descending order of flammability risk) from dead standing forests and windbreak to deciduous forests. In Russia this simple classification is commonly used in evaluating fire risk. Melekhov (1947) also suggested a similar classification for burnt areas where the following groups were defined and described: 1) stands totally destroyed, 2) stands with dead standing and fallen trees, 3) stands with living trees: a) a minor proportion (less than 10%) of living trees in the first layer and completely dead understory, b) a greater proportion (more than 10%) of living trees and completely dead understory, c) with partial die-back only in the subordinate layers or even their complete survival.

2.5 Landscape Specificity of Natural Fire Regimes

Some researchers point out the need to analyze the landscape-specific characteristics of the con-

ditions of fire ignition and spread. They stress the importance of analyzing the spatial arrangement of forest communities which pre-determine potential flammability within a landscape (Kolesnikov 1985). Kuleshova (1981, p. 1542) notes that “the spread and cycle of fires depend on the plant cover characteristics and the site moistening pattern ... these parameters being different ... in the neighboring structural units of the same landscape”.

According to Dyrenkov (1968, 1984) the ratio of forests of different “burnability” (pine and spruce) depends on the “fire cycle” (or period between fires). This means that in landscapes where fires are rare spruce has time to substitute pine stands, and spruce stands reach the climax (absolutely uneven-aged structure). In landscapes where the fire disturbance is more frequent, endodynamic processes are interrupted from time to time, pine forests regenerate in burnt areas which are rid of spruce undergrowth. Such forest areas are dominated by relatively uneven-aged spruce stands, which fail to reach the climax before the next fire occurs.

In retrospective fire studies practically all researchers use the method of dating fire scars on trees. In this case, however, retrospective analysis is limited to the past 300–350 years (maximum age of trees with fire scars). More rarely archival and historical data have been used to reveal the patterns in the fire regime, but this method is rather general. Only very large fires were recorded without accurate referencing of burned areas to certain territory and ecotopes.

Gromtsev (1993, 1996, 2000) carried out a study of landscape-specific patterns of the natural fire regimes in Eastern Fennoscandia that developed in the second half of the Holocene. He used data from mass palaeoecological analyses of peat deposits in the profiles established in different types of the geographic landscape. Ash and charcoal layers were recorded in the peat and they were then roughly dated using the average peat accumulation rate. The overall conclusion was that the Holocene pristine forests had a large variety of fire regimes. The occurrence of fires ranged from 1–2 times in a millennium to 1–2 times in a century in different landscapes (the mean area of the landscape contour was about 100000 ha). The author states that, with very

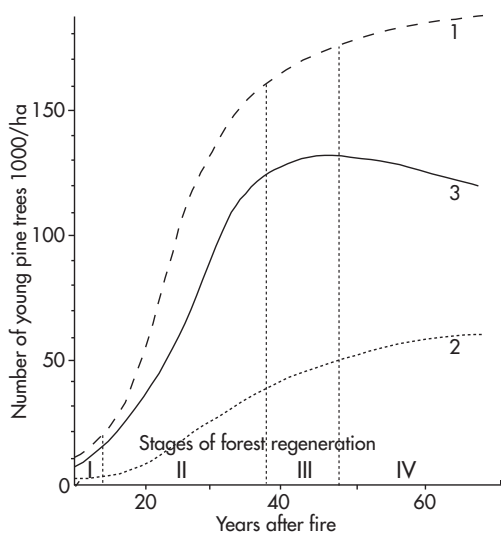


Fig. 2. The process of natural regeneration under the canopy of fire disturbed lichen and cowberry pine forest in the Kola peninsula (Tsvetkov 1968). Cumulative numbers of (1) all seedlings, (2) dead seedlings, (3) living seedlings.

few exceptions, all forest communities represent widely ranging stages of pyrogenic succession series, from young on the open burnt areas to the climax (Gromtsev 1993, 1996, 2000).

2.6 Fires and Pine Regeneration

With a few exceptions fire is regarded as a mandatory pre-condition for natural regeneration of pine. According to the data by Levin (1959) pine regeneration in burnt areas usually occurs within 20 years. In the Kola peninsula Tsvetkov (1968) remarks that these forests regenerate successfully after surface fires and distinguishes several stages in the regeneration under the canopy of fire-disturbed lichen and cowberry pine forests. Thus, in a cowberry pine stand regeneration is the most intensive 10–15 to 25–30 years after the fire (Fig. 2).

Detailed descriptions of regeneration under pine forest canopy after surface fires are provided also by many other researchers (Pushkina 1938, Vilikainen et al. 1974, Zyabchenko 1984 and many others). They give evidence of massive pine

regeneration in such stands, while regeneration in similar communities not affected by fire is relatively low.

Essential factors influencing regeneration in burnt areas are the tree species composition, the distance to the survived forests, and the presence of seed trees or tree groups (Korchagin 1954). Generally speaking, almost all authors stress the successful natural post-fire regeneration of pine stands, as well as regeneration of spruce stands that proceeds through the deciduous forest stage.

2.7 Fires and Spruce Regeneration

A classic paper by Melekhov (1944) describes various patterns of burnt area colonization from the unburned wet valleys of spruce forests, which are very fire-resistant (Fig. 3).

Spruce spreads successfully from these moist fire-free refugia both under the canopy of fire-thinned pine stands, and to open burnt areas generated by severe fires. Even-aged spruce stands may develop as a result of burnt area colonization by spruce either via species replacement or directly. According to Voropanov (1950), the formation of an even-aged stand requires 1) a forest-free area; 2) the preliminary formation of deciduous species on heavy soils; 3) the subsequent formation of spruce under the canopy of young deciduous stands; and 4) the formation of both deciduous and coniferous species on light soils.

In the Archangels region Gusev (1978) describes different options of spruce-stand formation in post-fire gaps and states that even-aged spruce stands formed in the burnt areas having sufficient seed sources and suitable temperature regimes. The process of burnt area regeneration by spruce lasts 20–40 years. The following fires in even-aged stands result in their complete destruction and formation of a second even-aged generation of spruce (Gusev 1978).

Different variants of uneven-aged spruce forests develop under similar conditions, but via replacement of deciduous species by spruce. Bakhtin (1997) shows that spruce appears in burnt areas within 1–3 years after the fire, and the total regeneration period ranges from 6 to 40 years. In

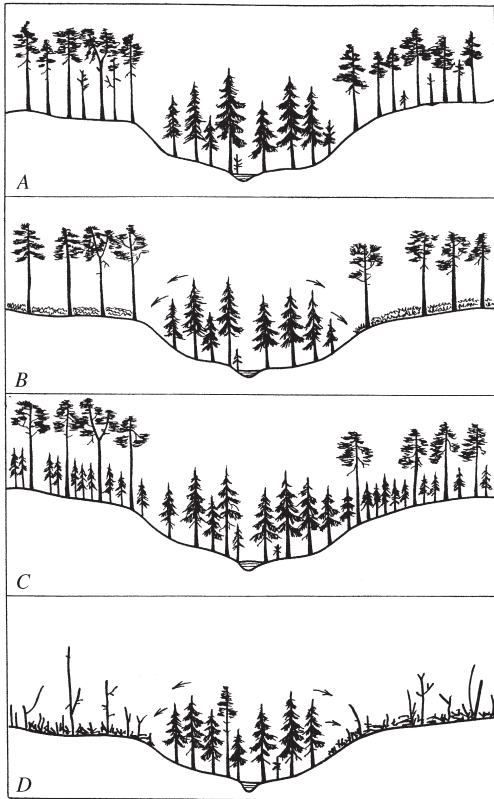


Fig. 3. Replacement of pine by spruce in connection with forest fire (Melekhov 1944). *A*) Pine forest surrounds a moist depression of spruce forest. *B*) With time since last fire, spruce invades the surrounding pine understory. *C*) A thick spruce understory develops in the pine forest. *D*) A severe crown fire devastates the pine forest, but the moist spruce forest escapes the fire. Spruce regenerates in the area surrounding the moist depression.

most cases, however, mass regeneration occurs during 3–5 years after the fire and lasts 6–7 years. Simultaneously regeneration of deciduous species starts, and already within 5–10 years their abundance reaches densities of 30 000–50 000/ha or more. Deciduous canopy creates a favorable microclimate for spruce survival. According to Korchagin (1954) spruce seedlings on clay and loamy soils can only survive under a deciduous canopy.

Pure spruce stands are known to develop in burnt areas with large amounts of woody debris

(Melekhov 1948 and others). Wood residues in open burnt areas provide protection and shelter similar to that offered by a deciduous canopy, which protect the spruce seedlings from the late spring and early autumn frosts. An essential factor is the degree to which forest litter is burnt. With the increase of one centimeter of litter thickness, the number of seedlings in most cases drops 2–3 times in the Archangels region (Molchanov 1934, Table 1).

In the north-taiga low mountain landscapes of the Murmansk region it may happen that the organic horizon is completely burnt and persistent treeless post-fire wastelands may form (Pushkina 1938).

2.8 Natural Fire Regimes and Age Structure of Forest Communities

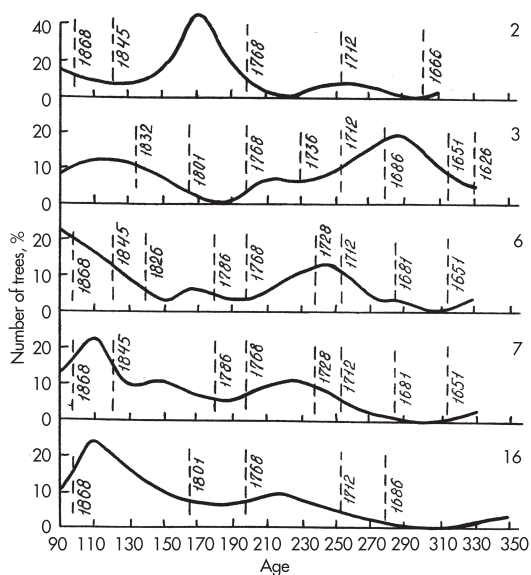
The age structure of pine forests is largely dependent on fires (Valyaev 1968, Levin 1959, Listov 1980, Zybchenko 1984, Gromtsev 1993, 2000). For example, Levin (1959) carried out an extensive survey of the dynamics of pine forests in the Archangels region and concluded that almost all studied pine stands (even in paludified habitats) were of post-fire origin. Zybchenko (1984) showed the peculiarities of age structure of pine stands in connection with fire periodicity in Northern Karelia (Fig. 4).

The same was reported by Kolesnikov (1985) for the Vychegda river basin: all pine forest areas either had emerged on a burnt area, or were several times disturbed (approximately 5–6 times) by fire during their life history. Gromtsev (2000) summarized the results of the reviewed studies as follows.

Pine-dominated forest. In pine-dominated landscapes with high fire frequency pine, forests were destroyed either totally or partially by fires depending on fire intensity. Where the stand was totally destroyed, mass regeneration of the species followed and an even-aged pine stand developed. In the stands partially destroyed by fire, pine regeneration was concentrated in the newly formed gaps. These regenerated trees gradually penetrated into the dominant tree story. As older trees died and new pine generations regenerated after surface fires (in the newly formed gaps) a

Table 1. Dependency of the number of tree seedlings on the type of forest and degree of burning of the forest litter in Arkhangelsk province. Data of Molchanov (1934) from: Korchagin (1954)

Type of pine forest	Degree of the the burning of the forest litter	Pine	Spruce	Number of tree seedlings			In total	Studied area m ²
				Larch	Birch	Aspen		
Lichen-green moss	Not damaged	44700	700	400	–	–	45800	400
	Middle	27750	–	1250	1250	750	31000	120
	Heavy	19650	–	90	1572	864	22176	320
Lingonberry	Not damaged	387	113	5	212	16	733	620
	Middle	4700	1350	175	2750	750	9725	800
	Heavy	17900	2150	1300	6500	1200	29040	610
Blueberry	Not damaged	200	480	–	200	–	880	260
	Middle	3780	1000	90	3800	420	9090	280
	Heavy	16700	1660	630	10840	2960	32790	220
Sphagnum	Not damaged	1100	–	–	180	–	1290	100
	Damaged	30483	83	–	2083	–	32649	120

**Fig. 4.** Examples of age distribution of trees in uneven aged pine stands and the occurrence of fires in Northern Karelia (fire years are marked by touch line). 2, 3, 6, 7, 16 are No of sample plots (Zjabchenko 1984). Vertical, dotted lines indicate the year of fire as detected from fire scars in trees. Measured in 1965–1970.

fully uneven-aged pine stand developed. Thus, a range of tree stands with the most varied age-structure patterns, from fully even-aged to fully uneven-aged, was present within the most easily flammable landscapes.

In landscapes with low fire frequency pine stands could only form in severely burnt areas. These were even-aged stands present as fragments within the spruce-dominated landscape matrix. Dense spruce undergrowth developed under the pine stand and pine was gradually replaced by spruce. Thus a monodominant spruce forest formed, and that could only be destroyed by the next devastating fire (Gromtsev 2000).

There existed also intermediate variants that combined the features of both extreme patterns of pyrogenic succession series in pine forests. These extreme patterns represented, however, the two major trends in the age structure dynamics in pine phytocenoses.

Spruce-dominated forest. Spruce stands on mineral soils are usually almost completely destroyed by fire. Even-aged spruce stands develop in the burnt areas (usually via a deciduous forest stage). This first spruce generation starts to fall apart gradually after 200 years. Spruce undergrowth appears in the emerging gaps, and gradually penetrates into the dominant tree story. The process of die-back of older trees and their substitution by new ones becomes continuous. About 400–500 years after the fire, an absolutely uneven-aged (climax) spruce forest is formed. At this stage the mortality and growth processes are balanced (Kazimirov 1973, Gusev 1978 and others). Without external disturbances a spruce stand can maintain such a dynamic equilibrium state for an indefinite period of time.

The proportion of spruce forest area of different age structure, or the distribution of different stages of pyrogenic successions, in different boreal regions and geographic landscapes of the Russian European part depends on the duration of the fire-free period. The longer it is, the more widespread uneven-aged spruce forests are, climax stands included, and vice versa. If the process of uneven-age structure formation in the spruce community is interrupted by a new fire, an even-aged stand redevelops in the burnt area (Gromtsev 2000).

2.9 Fires and Relationships between the Pine and Spruce Formations

There are three major theories in Russia regarding the role of fires in the relationships between the pine and spruce formations. A majority of researchers postulate that the existence of pine forests on mineral soils under natural conditions is dependent on fires. Fires periodically destroy spruce stands and spruce undergrowth under pine stands, thus preventing the otherwise inevitable replacement of pine by spruce (Valyaev 1971, Listov 1980, Vilikainen et al. 1974, Zhabchenko 1984, Kolesnikov 1985, Gromtsev 2000 and many others). Melekhov (1944, 1980) expressively concluded “an unending war is going on in the taiga between the pine and spruce armies”. Particular emphasis in this context is placed on the role of spruce forests in moist valleys. They are practically unburnable, surviving even in large catastrophic fires. These communities act as important natural fire barriers that limit spontaneous fire spread. From these fire-free refugia spruce spreads into the surrounding burnt areas.

On the other hand, Morozov (1949, p. 363), a classic of the Russian sylviculturists, stated that “... the outcome of the species change will depend primarily on the soil conditions”. This means basically that certain rich soils (clay, loamy, etc.) always have been, and will be, occupied by the shade-tolerant spruce, while other poorer soils (sandy, etc.) are occupied by pine. However, the possibility of pine regeneration in secondary spruce stands may be provided by fire, storm or some other disturbance. This view however has not so far been supported by experimental proof.

On the other hand, spruce stands may replace pine stands even in dry lichen sites, given several fire-free centuries (Korchagin 1954). This situation happens in nature very rarely, because in lichen-type forests fires usually occur 1–2 times in a century.

Sukachev (1975 p. 239) believed that “... most pine associations are essentially not pristine, but rather, in a sense, temporary, like birch or aspen stands”. He argued that owing to human-induced fires pine stands have spread widely and replaced pristine spruce forests. “If it was not for human influence, pine in the North would have only been found in the driest sites and mires” (Sukachev 1975).

All these views apparently reflect the fundamental role of fire as a natural ecological factor regulating the relationship between the pine and spruce formations and controlling the spontaneous dynamics of pristine forests in most mineral lands. On the other hand, fires can be seen as a stochastic factor. In this case, however, one will have to admit also that prior to the anthropogenic impact the predominant part of pristine taiga was not in fact pristine. This idea is groundless, for fires are already known to have been a leading ecological factor during the prehistoric era. Taiga was then a mosaic of forest communities at different stages of pyrogenic successions.

2.10 Ecological Consequences and Role of Fires

In the following the effect of fires on different components of forest communities are discussed.

Soil cover. The number of studies on the role of fires in this aspect is rather limited. Some authors speak of the process of pyrogenic “depaludification” as a consequence of hydrophilic vegetation and the peat horizon being burnt up (Melekhov 1948, Kolesnikov 1985). An improvement in the growth of pine and spruce is observed on moderately burnt sandy loam and loamy soils, which is attributed to intensified nitrification (Sushkina 1933: cited from Vakurov 1975). However, if the soil is heavily burnt this process is suppressed. Generally speaking, the impact of fire varies considerably depending on the fire intensity, soil

texture, forest litter thickness and other factors. For example, intensive fires on dry sandy soils may result in complete burn-up of organic matter and produce a horizon comprised of caked mineral particles impermeable for water, air and roots (Korchagin 1954). On loamy soils, however, these changes may be small. The chemical composition of soil water also changes after fires, because acidity is reduced due to combustion of organic acids and release of exchange bases.

Live ground cover. Melekhov (1947) was one of the first to study susceptibility and post-fire regeneration capacity of individual species of ground vegetation. In a more detailed study by Korchagin (1954) all species were divided into two groups: 1) species that are temporarily abundant in burnt areas and 2) general forest species typical of forests not disturbed by fire (both groups divided into subgroups). Korchagin (1954) suggested that three types of regeneration processes can be distinguished in the lower vegetation layers of burnt areas: 1) regeneration of the species that were dominant prior to the fire ("cowberry burns"), 2) regeneration of the same species that were dominant prior to the fire, but with one clearly dominating species (heath burns), 3) total alternation of species (e.g., burns with *Chamaenerion angustifolium* (L.)).

Gorshkov et al. (1995) used stand chronosequences to study the regeneration of the lower vegetation layers in north-taiga lichen pine stands in the Kola Peninsula from 0 to 210 years after a fire. The authors state that the time required for complete stabilization of the percent cover and species composition occurs 120–140 years after a fire. The corresponding recovery period in green moss pine stands is 60–90 years (Gorshkov 1995). In burnt spruce forests in mid-taiga the early development of the ground cover is peculiarly dominated by the abundance of *Chamaenerion angustifolium* (L.) (Orlov 1947).

Stand structures. Melekhov (1948) gave a detailed description of the types of pyrogenic damage to pine, including the rates of fire scar healing, changes in the timber increment, annual ring structure and wood anatomy. He has shown that the character and size of fire scars predetermine the share of the following dieback. Fire-induced wounds gradually heal. The healing rate ranges from 1–2 to 200 years, though

some wounds may not disappear at all (Korchagin 1954). Findings of 300–350-year-old pine trees with distinct fire scars that were formed in fires over 200 years ago are not rare (Gromtsev 2000).

The burns inflicted on spruce or birch are usually lethal because of their thin bark and superficial root system. Spruce and fir forests usually either die completely or turn into irregularly stocked open woodland after surface fires. In mixed pine-dominated forests birch and spruce die completely, and the stands turn into pure pine forests (Korchagin 1954, Vyalykh 1987). Konovalov and Semenov (1990, p.157) remark that in north-taiga lichen pine stands "relatively healthy trees intensify physiological processes during the post-fire period, which results in a 20–25% increase in the diameter increment" and further: "stem damage by fire impairs metabolic processes in pine and larch, and their normal levels may not be achieved even within 8 years after the fire". Authors do not explain the reasons of this phenomenon. In general, however, a temporary deterioration of tree growth is observed after fires (Melekhov 1948). Another noteworthy fact is that tree viability and resistance to the impact of fire diminishes with age (Korchagin 1954). On the other hand, as pine trees age they grow more resistant to fire owing to the thicker bark, and their deep and strong root system.

Mammals and birds. There are only a few scattered studies of influence of fires on mammals and birds. L.V. Kuleshova et al. (1996) studied the effect of forest fires on the soil mesofauna and birds, and calculated the biota species richness at different stages of pyrogenic successions in the "Kostomukshsky" reserve (Republic of Karelia). The same authors postulate that a decrease in fire occurrence in boreal areas dramatically deteriorates the feeding conditions for elk and results in mass migrations of the this animal from the region in question (1981).

3 Windthrows and Gap-phase Forest Mosaic

Strong winds play a significant part in the dynamics of pristine forests. It is common to distinguish windthrow (with uprooting) and windbreak (with stem breaking). The largest review devoted to the ecological role of windthrow in Russian European forests is the paper by Skvortsova et al. (1983).

3.1 Scope and Ecological Role of Windthrows

Skvortsova et al. (1983, p. 169) claim that “Windthrow has been one of the key factors of forest community disturbances. Windthrows of varying scope and intensity occur in forests.” They show that coniferous stands experience windthrow (in an area over half a hectare) at a wind velocity of 20–25 m/sec. On average windthrow occurs in the same area once in 150–300 years. At lower wind velocities groups or single, primarily weak, trees are uprooted. It is one of the ways of the forest-forming species life-cycle completion.

According to Skvortsova et al. (1983) every region has a constant ratio of different windfall areas. Thus, gap regeneration in primary south-taiga spruce forests usually proceeds via replacement by deciduous species (rowan, birch). The specific soil complexes with vegetation microsuccessions occur at uprooting spots. The vegetation composition becomes stable only in 80–100 years after uprooting, and the windthrow-induced microrelief disappears only after 300–500 years. Accordingly, uprootings create a mosaic pattern, which increases the floristic diversity in the phytocenosis and tree age diversity of communities.

It has been estimated that a complete mixing throughout the “forest biogeocenosis (community)” area would take from 2–3 thousand to 5 thousand years (Karpachevsky et al. 1980). This means that almost every point in a phytocenosis undergoes a radical change of the soil and vegetation due to such disturbances at least once in 2 to 5 thousand years. A detailed description of the effect of uprooting on the soil cover was made by Basevich and Dmitriev (1979) who state that windthrows are a powerful soil-mixing factor.

3.2 Windthrows in Pristine Forests in Different Boreal Regions of the Russian European Zone

Pugachevsky’s (1989) observations in the Central forest reserve (south-taiga subzone, Tver region) show that spruce forests periodically experience tree uprooting. The storm, which was studied, damaged all of the forest area (windfall and windbreak in different habitat types made up 12–35% of the total tree stock), the largest trees being most susceptible to damage. Practically no wind-related disturbances were recorded in swamp spruce stands. Pugachevsky (1989) attributes this fact to the low wind-catching capacity of small spruce crowns. However, other researchers contradicted this latter finding that the mortality in spruce stands, due to windthrow and windbreak, was higher in paludal habitats in the Central forest reserve at the south-taiga subzone in the Tver region (Gueorgievsky 1995 a, b).

In Gueorgievsky’s (1995 a, b) opinion south-taiga climax spruce forests live in dynamic equilibrium caused by continuous die-back and destruction of old trees under the effect of strong winds. In some years massive windthrow mortality is observed up to 30% of total tree stock. Pristine spruce forests contain gaps with different regeneration stages, from newly regenerated to those with completely regenerated spruce cover. As a whole this gap disturbance regime ensures a continuous rejuvenation of the community and maintains the uneven-aged structure.

The gap-phase dynamics was examined using aerial photos from 1981–1991 in an area of pristine mid-taiga spruce forests in the “Vepssky les” nature park in the Leningrad region (Fedortchuk et al. 1999, Table 2). The size of the gaps, ranging on average within 0.015–0.06 ha (in some cases up to 0.144 ha), was determined. Their area in the forest land with well-drained soils reached 0.76%. The largest gaps (up to 3 ha) were formed after hurricane winds. Spruce dominated the gaps; these trees were part of the undergrowth that survived in the windthrow. Birch appears immediately after the gap formation. Rowan is common, and a few aspen trees are present. Fjodorchuk et al. (1998) state that periodically repeated intensive stand destruction over considerable areas are the main factors affecting observed structure of

Table 2. Area and dimensions of gaps in various forest types in the “Vepssky les” nature park, Leningrad region as observed at 1970, 1981 and 1991 (Fedortchyk et al.1999).

Year of observation	Type of forest	Gap area, ha (%) of various dimensions			In total	Gap area (% of total stand area)
		0.015–0.06	0.07–0.25	>0.25		
1970	Blueberry, fresh	1.44 (64)	0.81 (36)	–	2.25	0.76
	Blueberry, moist	0.02 (100)	–	–	0.02	0.06
	Green moss	0.18 (100)	–	–	0.18	0.11
	<i>In total</i>	1.64 (67)	0.81 (33)	–	2.45	0.5
1981	Blueberry, fresh	0.49 (35)	0.90 (65)	–	1.39	0.46
	Blueberry, moist	–	–	–	–	–
	Green moss	0.14 (63)	0.08 (37)	–	0.23	0.14
	<i>In total</i>	0.63 (39)	0.98 (61)	–	1.62	0.3
1991	Blueberry, fresh	2.89 (7)	8.48 (21)	29.76 (72)	41.13	13.8
	Blueberry, moist	0.14 (11)	0.63 (52)	0.45 (37)	1.22	3.4
	Green moss	1.11 (17)	2.43 (36)	3.13 (47)	6.67	4.1
	<i>In total</i>	4.14 (8)	11.54 (24)	33.34 (68)	49.02	9.8

natural spruce forest areas. This spruce forest is dominated by relatively uneven-aged stands.

Observations in the largest area of pristine mid-taiga spruce forests in the west of the Eurasian boreal zone (Vodlozersky National Park) lead us to similar conclusions (Gromtsev 1999). According to the latest data (V.A. Ananyev, personal communication) hurricane winds which in May 2000, blew over various areas in the southwest of the park (Lake Vodlozero area) produced continuous windfall areas of 800 ha. It is obvious that continuous formation of varying-sized gaps is typical for primary spruce forests. For a general review of this topic, see Ulanova (2000).

4 Outbreaks of Insects and Fungal Diseases

Uskov (1959) and Krutov (1989) show that wood-attacking fungi usually attack dying or weak trees (e.g., those with fire scars). Fungal diseases may be an important reason for the dieback of old pine trees. These are diseases such as *Biaterella* canker (*Biaterella difformis*), resin-top disease (*Cronartium flaccidium* and *Peridermium pini*), as well as stem rots caused by white pocket rot (*Phellinus pini*). Development of heartrot (*Onnia leporina*) in the lower part of the trunk make spruce stands more susceptible to windthrow. Uneven-aged spruce forests are usually infected

by annosus root rot (*Fomes annosus* (Fr Chc. *Fomitopsis annosa* (Fr.) Bod et Sing.). No data could be found in the literature about large-scale damage by fungal, bacterial, virus infections or insects to pristine forest areas that would cause significant deviations in their natural dynamics (Chertovskoi 1978, Materials of the inventory ... 1998).

According to Gusev (1978, p. 125) nearly 40% of the 261–300-year-old spruce generation in the Archangels region are infected with annosus root rot. Moreover, the oldest and largest trees were those infected. According to Gusev (1978, p. 125) “annosus root disease infects clusters of spruce trees, which die back or are uprooted exposing the roots of the neighboring trees and thus facilitating their infection... The resulting gap promotes more intensive propagation of spores”. Yezhov (2000) reported massive outbreaks of spruce needle rust (*Chrysomyxa ledi* and *Chrysomyxa abietis*) in the Archangelsk region in 1985 and 1990. In general, the pattern is that singular trees are attacked which then reach the average natural dieback age.

Yakovlev (1996) found that some stem insect species are able to settle in viable trees and cause their death. They are primarily bark beetles (*Tomicus piniperda*, *T. minor*, *Dendroctonus micans*) and buprestid beetles (*Melanophila cyanea*) for pine, bark beetles *Ips typographus* and *Pityogenes chalcographus*, and longhorn beetles of the genus *Tetropium* for spruce. In Eastern Fennoscandia no large-scale outbreaks of the insects' abun-

dance have been (were) recorded. Only foliage-grazing insects are capable of such outbreaks, which undermine spruce stand health without causing their dieback. The most important among these pests are pine sawflies (*Diprion pini* and *Neodiprion sertifer*), butterflies, pine looper moth (*Bupalus piniarius*) and pine beauty (*Panolis flammea*). The survey of forests in the regions however revealed no entomological invasions (Yakovlev et al. 2000). In spite of the significant age of the surveyed forests, lack of management, frequent fires and a relatively high abundance of potentially damaging species, stem pests mainly attack already dead and dying trees, the die-back of which was induced by other reasons.

There are some fragmentary data that the foci of infection with the sawfly *Neodiprion sertifer* and green-winged spruce-pine chermes *Chermes (Adelges) virgis* were found in the Archangels region (Yezhov 2000). The author, however, offers no evidence of considerable die-back in the areas.

5 Other Disturbance Factors

Some reports can be found on the destructive effect of weather abnormalities on forest communities. For example, mass die-back during droughts was observed in the 1870s–1970s in spruce forests of the Russian plains, including the stands growing under the climatic optimum of the species (Maslov 1972). Periodic spruce dieback (withering), however, was recorded only within the coniferous-broad-leaved (mixed) forest zone. Excess water may become a disturbance factor, eliminating mature trees from paludified habitats, in the years with increased precipitation (Abrazhko 1988). The probability of several consecutive years with increased precipitation is very low. No documents of such catastrophic destruction could be found in the literature. Another potential disturbance factor is snowbreak, but its scope is quite negligible, not usually exceeding 2–3% of the total number of trees in uneven-aged pristine forests (Pugachevsky 1989).

6 Discussion and Conclusions

To conclude the brief review of the special literature it appears relevant to assess the coverage by studies of pristine boreal forest dynamics as related to various natural disturbances. The European part of the Russian boreal zone has been covered by large-scale studies of fires. The reviewed studies show that lightning strikes were the only natural source of fires in taiga. The frequency of fires varied in various types of pristine landscape from 1–2 per century to 1–2 per millennium. The pyrogenic factor maintained a dynamic equilibrium between compositionally different forest communities or their certain ratio and areal arrangement. Fires favored the regeneration and recovery of pine stands and prevented the replacement of shade-intolerant species (e.g. pine) by shade-tolerant ones (e.g. spruce). Taiga forests generally displayed a mosaic pattern of different successional phases, varying from pioneer plant communities, growing in open burns, to climax communities extremely seldom affected by fire. The results of the reviewed studies suggest that fires were a powerful ecological factor. They were largely responsible for the structure and spontaneous dynamics of forest communities.

However, the time-scale of these studies is limited and there are no data on fire regimes in pristine forests in the remote past (going back in time more than 500 years) for this region (except for Karelia). This fact is due to the demand for the latest techniques for identification and dating of fire traces. For example, one of the most promising techniques is fixation and dating (radiocarbon dating) of ash and charcoal layers in peat deposits and upper soil horizons. It is in fact the only method that could provide us with an insight into natural fire regimes and the role of fire in the boreal ecosystem dynamics during the Holocene.

In European Russia there have, so far, been no multidisciplinary investigations on the ecological role of fires. The consequences of elimination of fires from the forest ecosystem have not been addressed. First of all this concerns the role of fire in soil formation and the population dynamics of forest dwelling animals. There are few, if any, data on the changes in the soil cover structure,

populations of soil organisms, mammals, birds, insects, etc., in different stages of post-fire successions. The problem is important from both scientific and practical points of view. However, it is obvious that the conservation of pristine boreal landscapes within protected areas is only possible if natural fire regimes, that prevailed through the last millennia, are maintained. For example, an important question is whether naturally emerging fires should be permitted to proceed in protected areas.

Data on windthrow-related gap dynamics in pristine forest areas are still rather fragmentary. Windfalls were also common in pristine taiga landscapes. They regulated spontaneous dynamics in a gap-mosaic regime. Such dynamics is most characteristic of spruce stands. We lack understanding of the succession series of vegetation associations developing in the gaps in various forest areas.

The study of forests in the region has revealed no evidence of a large-scale effect of fungal diseases, bacterial and viral infections or insects on the spontaneous dynamics of pristine forests. At the moment a principal task is to carry out multidisciplinary research on the dynamics of pristine forest areas under various natural disturbances.

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