



OLD-GROWTH SPRUCE-FIR FORESTS IN THE PLAIN AREA OF THE KOMI REPUBLIC

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СТАРОВОЗРАСТНЫЕ ЕЛОВО-ПИХТОВЫЕ ЛЕСА НА РАВНИННОЙ ЧАСТИ РЕСПУБЛИКИ КОМИ

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Abstract. Old-growth spruce and spruce-fir forests can be extremely variable in the composition and diversity of their ground layer of vegetation, sometimes with over 10 times difference in diversity between various forests. What is the reason for such a big difference? Here we propose a hypothesis that the ground layer of vegetation is most strongly affected by fire history of boreal forest ecosystems. We estimated composition, structure and diversity of vascular plant and bryophyte species in seven forest types in old-growth forests dominated by either *Picea obovate* or *Picea obovate* together with *Abies sibirica*, which were located in the plains of the Komi Republic. All the study areas were either at elevated or hilly plains with good and moderate drainage, or in valleys of small rivers and streams, away from wets and bogs. We analyzed Landolt's species ecological values, coverage of vegetation layers and deadwoods at different stages of decay, bedrock parameters, and soil charcoals in order to explain differences in the plant species composition and diversity. We showed that there are weak but statistically significant correlations between the coverage of deadwoods at different decay stages and vascular species composition and a positive correlation between the total deadwood coverage and bryophyte species diversity. Among the studied forests, those that are dominated by boreal and nitrophilous tall herbs (located in watersheds and in river valleys respectively), have no fire scars on stems of *Pinus spp.* and almost no charcoal in the soil and demonstrate the highest species diversity. We estimated that these forests have not experienced fires for over 400 years. In contrast, the diversity of vascular plants in the forests dominated by green mosses, dwarf shrubs, small boreal herbs and large ferns was low; we evaluated that the last time when these forests suffered intense multiple fires was at least 150 years ago.

Key words: spruce-fir forests, tall herb forests, vascular plants, bryophytes, deadwood, charcoal, fire.

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Аннотация. Старовозрастные еловые и елово-пихтовые леса очень разнообразны по составу и структуре напочвенного покрова: число видов растений на 100 м² может различаться в 10 и более раз. Какова причина такой большой разницы? Наша гипотеза состоит в том, что напочвенный ярус растительности наиболее сильно подвержен пожарам в экосистемах бореальных лесов. Мы оценили состав, структуру и разнообразие сосудистых растений и мохообразных в семи типах леса, выделенных среди старовозрастных лесов, где преобладают либо *Picea obovata*, либо *Picea obovate* и *Abies sibirica*, расположенных в равнинных районах республики Коми. Все исследуемые леса находятся вне болот и затопленных участков – на слегка поднятых или холмистых равнинах с хорошим или умеренным дренажом, либо в долинах малых рек и ручьев. Экологические шкалы Ландольта, покрытие различных ярусов растительности и валежа на разных стадиях разложения, параметры подстилающих пород, характеристики углей в почвах были проанализированы с целью объяснения разницы в составе и разнообразии растительности. Мы выявили слабые, но статистически значимые корреляции между покрытием валежа разной степени разложения и видовым составом сосудистых растений, а также положительную корреляцию между общим покрытием валежа и разнообразием мохообразных видов. Среди изученных районов елово-пихтовые леса с преобладающими бореальными и нитрофильными высокими травами (расположенные на водоразделах и в долинах рек соответственно) отличаются самыми высокими показателями видового разнообразия, и именно в этих лесах не было пожарных подсушин на стволах сосны и практически не было угля в почве. По нашим оценкам, эти леса не подвергались пожарам более 400 лет. Разнообразие сосудистых растений в лесах с доминированием зеленых мхов, бореальных кустарничков и мелкотравья, а также крупных папоротников было низким; мы оценили, что последний раз, когда эти леса испытывали многократные пожарные воздействия, был, по крайней мере, 150 лет назад.

Ключевые слова: елово-пихтовые леса, высокотравные леса, сосудистые растения, мохообразные, сухой, уголь, пожар.

Introduction

Old-growth dark coniferous forests dominated by *Picea spp.* (spruce) and *Abies spp.* (fir) have been studied extensively in Europe and North America. The main characteristics of their stand structure and dynamics, their relationships with site parameters and regional features are well investigated [1–10, etc.]. However the ground level of vegetation remains a poorly examined component of boreal ecosystems although more studies on this topic appear [11–24]. Ground vegetation has been mainly investigated in widespread spruce and spruce-fir forests dominated by dwarf shrubs, small boreal herbs and green mosses, which are characterized by relatively low vascular plant di-

versity [16–18, 21–26]. Species-rich tall herb spruce-fir forests have also been investigated, but most of them are swamp or riparian forests, which are characterized by continuous or periodic waterlogging and a varying degree of running water [27–31]. Despite that there are studies that describe tall herb forests located on watersheds with good and moderate drainage [11–14, 19, 20, 32, 33]; these forests are rare and information about them is scarce, while the structure and composition of such tall herb forests is important for forecasting and modelling of vegetation diversity under different forest management and global change scenarios [34, 35]. Here we focus on old-growth *Picea abies* – *Abies sibirica* forests growing in well-drained areas in the plain part of the Komi Republic, classify

them and analyze the relationships between composition and diversity of the ground vegetation and environmental parameters of the study areas.

Methods

Study areas

Seven areas, located within the plain part of the Komi Republic in the basins of the Northern Dvina, the Mezen and the Pechora Rivers were taken as the

study areas (Fig. 1). The choice of the study areas was defined by their location within the region of the intact forest landscapes (IFL) where old-growth *Picea obovata* – *Abies sibirica* forests were found. The IFL were mapped on the basis of high-resolution satellite imagery data [36, 37] and data of field expeditions [4]. All the study areas are hard to access and are very remote from roads and settlements.

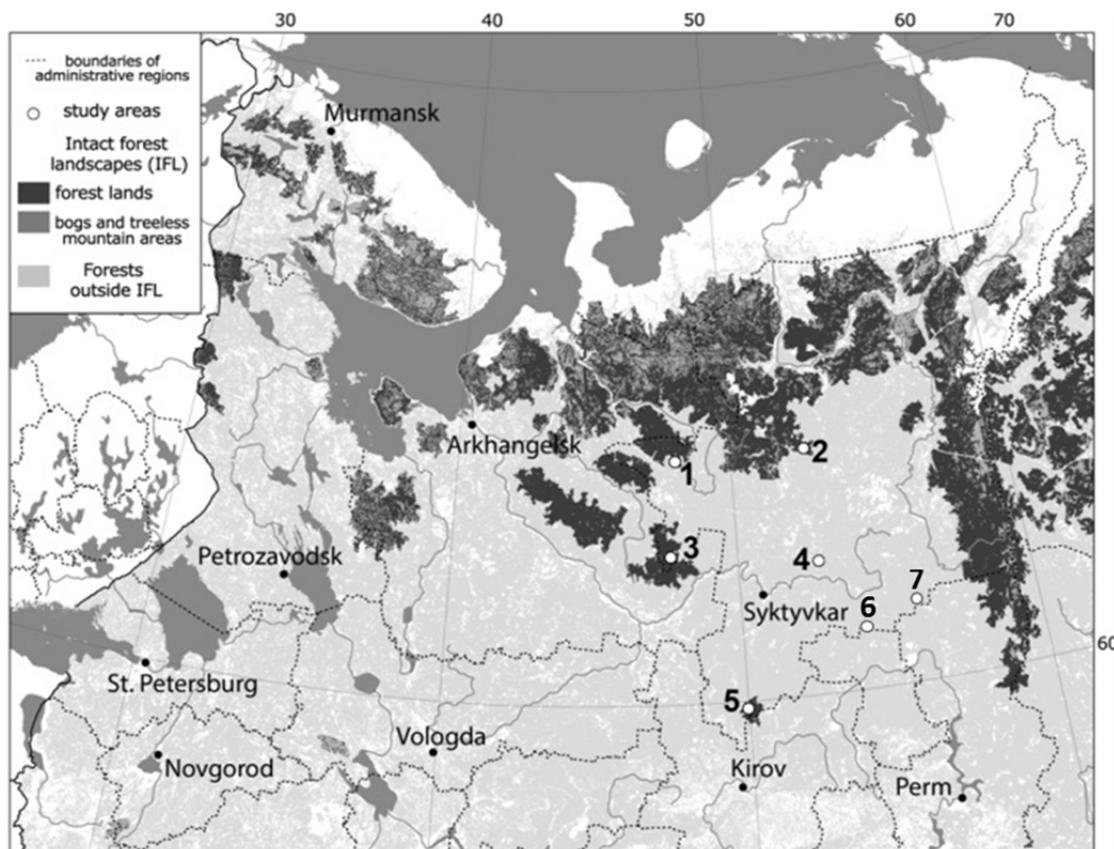


Fig. 1. Map of the intact forest landscapes in the boreal European Russian region (according to Yaroshenko et al., 2001) with localities of the study areas: 1 – the watershed between the Mezen and the Vashka Rivers; 2 – Middle Timan Ridge, the basin of the Ukhta River; 3 – the upper reaches of the Vashka River; 4 – Southern Timan Ridge, the upper reaches of the Vol River; 5 – the upper reaches of the Sedka and the Suran Rivers; 6 – the eastern part of the Northern Ridge, the basin of the Vol River; 7 – the upper reaches of the Nem River

The climate of the region is temperate continental. The average January temperature ranges from minus 15 to minus 18 °C and the average July temperature – from 15 to 17 °C [38]. The average annual precipitation varies from 680 to 730 mm. The study areas are situated on the elevated and/or somewhat hilly plains, 180–250 m asl.

All plots included into analysis are located away from wetlands and bogs: either on watersheds or mild slopes with good and moderate drainage on moraine, silty, and sandy loams, or in valleys of small rivers and streams on alluvial sediments [39]. Two study areas (numbers 1 and 2 in Fig. 1) are attributed to the northern taiga; the other areas are attributed to the middle taiga [40].

Data sampling

Data on vegetation and soil in old-growth Siberian spruce (*Picea obovata*) and Siberian fir (*Abies sibirica*) forests was collected in 1998 and 1999. Vegetation was sampled at square plots of 10 × 10 m. GPS coordinates of all plots were recorded. The absolute age of some individuals of *Picea obovata*, *Pinus sylvestris* and *P. sibirica* was calculated based on their tree cores. The stems of *Pinus sylvestris* and *P. sibirica* were examined for the presence of fire scars. Four layers of the forest vegetation were described: (1) overstorey (or tree canopy layer); (2) shrub layer, which includes tree undergrowth and tall shrubs; (3) field layer, comprising herbaceous species (herbs, grasses, sedges, ferns,

etc.) and dwarf shrubs, as well as low shrubs and tree/shrub seedlings, and (4) bottom layer, which includes cryptogamic species. Total vegetation cover ratio of each forest layer was visually assessed; species abundance lists were composed for the vascular plants of the first three layers. Species abundance was assessed using the Braun-Blanquet cover scale [41]. For the plots located in the 3rd and 5th study areas (Fig. 1), a full list of bryophytes was compiled, and the proportion of large dead wood fragments in the ground layer was inventoried in regard to their decay rate. We distinguished five decay stages, ranging from the freshest to the most decayed: (1) hard wood, fresh bark, knife penetrates into the wood at a depth of only a few millimeters; (2) hard wood, most of the bark is still present, knife penetrates into the wood at a depth of 1–2 cm; (3) the cover is partly decayed at the surface or in the centre, large pieces of bark are often detached, knife penetrates into the wood at a depth of 3–5 cm; (4) most of wood is soft, usually without bark, knife penetrates into the wood easily and (5) wood is very soft and crumbles if lifted. The morphology of soil was described on the basis of data from 49 soil profiles (2-m deep) and small soil pits (60–70-cm deep). Soils were classified according to the World Reference Base for Soil Resources [42]; bedrock types were defined according to the Soil Atlas [39]. Soil horizons types and thickness as well as morphological features outside the horizons were profiled. Frequency, shape, and location of charcoal in the soil profiles were identified.

Data analysis

We used 239 phytosociological relevés to classify and describe vegetation of the studied forests. While categorizing vegetation plots we followed Zaugolnova and Martynenko [43] and used ‘synthetic’ dominant ecological-coenotic approach described in [44] (Table 1). Seven basic ECGs (Table 2) and groups of boreal dwarf shrubs, small herbs and ferns, and tall herbs and ferns within the boreal ECG were used to classify the sample plots and to

describe structural diversity of the field layer. Nonmetric Multidimensional Scaling (NMDS) of the plots was used to classify the identity of the disputed plots to a particular forest type. NMDS was performed on species abundance in the field layer using *metaMDS* function of the *vegan* package [45] for the R statistic system [46] with the Bray-Curtis distance measure and the settings recommended by McCune and Grace [47]. To interpret the ordination axes, the correlation vectors with the environmental characteristics of the plots were built using the *envfit* function of the *vegan* package. Landolt’s indicator species values [48] weighted by species cover and averaged for relevés were applied as the main environmental characteristics of the plots. In addition to the Landolt’s scores, coverage of the main vegetation layers and proportion of the large dead wood fragments at different decay stages in the ground layer (deadwood coverage, DWC) were also used as the plots environmental characteristics and their correlation vectors with the ordination axes were also built. Pearson correlations of the environmental variables with the first and second ordination axes were calculated. 999 random permutations of the coverage variables were performed to assess the significance of the coverage vectors. The goodness of fit statistic was R^2 . Their Landolt’s scores were analyzed to outline environmental parameters of the forest types. To characterize the quality and the quantity of deadwood, the boxplots of DWC at different decay stage were built for the forest types. Pearson correlations between the numbers of species in a plot and the values of DWC and the coverage of vegetation layers were also calculated for the forest types. *P*-values for the significance tests were obtained on the base of 999 random permutations of the data. Species diversity was estimated for each forest type for vascular plants and for bryophyte species separately: the mean number of species per plot and the total number of species in the forest types (species richness) were calculated.

Table 1

Studied forest types

Abbreviation	Forest types according to the ecological-coenotic approach	Description	Associations and subassociations according to the Braun-Blanquet approach* (from Zaugolnova & Martynenko, 2014)
1	2	3	4
GM	<i>Piceeta hylocomiosa</i>	Pure green moss spruce forests	<i>Empetro-Piceetum obovatae</i> (Sambuk 1932) Morozova comb. nov. 2008
DwGM	<i>Piceeta (Abieta) fruticoso-hylocomiosa</i>	Dwarf shrub – green moss spruce and spruce-fir forests	<i>Linnaeo borealis-Piceetum abietis</i> (Caj. 1921) K.-Lund 1962 subass. <i>myrtilletosum</i> K.-Lund 1981
BrGM	<i>Piceeta (Abieta) parviherboso-hylocomiosa</i>	Small boreal herb – green moss spruce and spruce-fir forests	<i>Linnaeo borealis-Piceetum abietis</i> (Caj. 1921) K.-Lund 1962 and <i>Melico nutantis-Piceetum abietis</i> (Caj. 1921) K.-Lund 1981

End of Table 1

1	2	3	4
NmBr	<i>Piceeta (Abieta) nemoralo-borealiherbosa</i>	Nemoral-boreal herb spruce and spruce-fir forests	<i>Rhodobryo rosei-Piceetum abietis</i> Korotkov 1986
LF	<i>Piceeta-Abieta magnofilicosum</i>	Large fern <i>Dryopteris dilatata</i> spruce-fir forests	<i>Linnaeo borealis-Piceetum abietis</i> (Caj. 1921) K.-Lund 1962 subass. <i>abietetosum sibiricae</i> Martynenko et al. 2008
BrTH	<i>Piceeta (Abieta) magnoherbosa</i>	Mesophilous boreal tall herbs spruce and spruce-fir forests located on watersheds and slopes	<i>Aconito septentrionalis-Piceetum obovatae</i> Zaugolnova et al. 2009 subass. <i>typicum</i> Zaugolnova et al. 2009
NtTH	<i>Piceeta (Abieta) nitrophilo-magnoherbosa</i>	Nitrophilous tall herb spruce and spruce-fir forests located in the valleys of small rivers and streams (riparian tall herb forests)	<i>Aconito septentrionalis-Piceetum obovatae</i> Zaugolnova et al. 2009 subass. <i>filipenduletosum</i> Zaugolnova et al. 2009

Note. *A detailed hierarchical floristic classification system has not been built for the European Russian forests [43, 44, 49]. Therefore here we mark associations and subassociations which are relatively close to the studied forest types. According to the newest system for the vegetation of Europe [50], the forest types GM, DwGM, BrGM and LF belong to the union *Piceion excelsae* Pawłowski et al. 1928; the forest types BrTH and NtTH belong to the union *Aconito rubicundi-Abietion sibiricae* Anenkhonov et Chytrý 1998; both of the of the class *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939. The forest type NmBr can be referred to the union *Aconito septentrionalis-Piceion obovatae* Solomeshch, Grigoriev, Khaziakhmetov et Baisheva in Martynenko et al. 2008 of the class *Asaro europaei-Abietetea sibiricae* Ermakov, Mucina et Zhitlukhina in Willner et al. 2016 or to the union *Quercu roboris-Tilion cordatae* Solomeshch et Laiviņš ex Bulokhov et Solomeshch in Bulokhov et Semenishchenkov 2015 of the class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968.

Table 2

Basic ecological-coenotic groups* of vascular plant species inhabiting the European Russian forests

Number	Abbreviation	Title	Description
1	Br	Boreal	Species that grow in the understorey of <i>Picea</i> spp. and <i>Abies sibirica</i> forests on soils that may differ in trophic status, but with a mesic moisture regime
2	Nm	Nemoral	Species that grow on rich soils in the understorey of forests of broadleaf trees, such as <i>Quercus robur</i> , <i>Tilia cordata</i> , <i>Ulmus</i> spp., and <i>Fraxinus excelsior</i>
3	Nt	Nitrophilous	Species growing on moist to wet sites with rich soils; they are usually species of flooded forests dominated by <i>Alnus glutinosa</i>
4	Pn	Piny	Species growing in the understorey of pure <i>Pinus sylvestris</i> forests on dry and poor soils
5	Md	Meadow-edge	Species growing on wet to dry soils of different trophic status in non-wooded areas, such as meadows, forest edges, and clear-cut areas
6	Wt	Water-marsh	Species of coastal and water-rich habitats and mesotrophic and eutrophic bogs
7	Olg	Oligotrophic	Plants of oligotrophic bogs and mires

Note. *Following the Russian botanist Nitsenko [51], we defined an ‘ecological-coenotic species group’ (ECG) as a group of species that are similar in ecological features and in constancy of occurrence in vegetation communities of different types. The ecological-coenotic group concept has been often used in Russia, though variation in group specification commonly occurs [52]. We grouped vascular plant species following Smirnova and Zaugolnova [52, 53] and further developed by Smirnov et al. [54, 55]. The composition of these ecological-coenotic groups was first defined by experts and then verified by discriminant analysis and decision tree techniques using Ellenberg’s indicator values [56] and species ordination scores produced by nonmetric multidimensional scaling of several thousands of phytosociological relevés from European Russian forests [54]. About 1000 vascular plants inhabiting forests of European Russia were divided into these seven ECGs [55]. For the boreal forest region, we additionally distinguish groups of boreal dwarf shrubs, small herbs and ferns and tall herbs and ferns within the boreal ECG.

The affinity of vascular plant species to forest types was evaluated by the indicator species analy-

sis IndVal [57]: the arrays of species abundance data were analyzed with the *indval* function of the

labdsv package for the R statistics system. The constancy of bryophyte species in different forest types was also calculated. The list of the vascular plants with the ECGs and the list of bryophyte species, both encountered in the analyzed plots can be found in Supplementary Materials (Tables S1 and S2). The used nomenclature follows Cherepanov [58] for vascular plants, Ignatov and Ignatova [59] and Ignatov et al. [60] for mosses and Konstantinova [61] for liverworts.

Relative frequency of the occurrence of different forest types on different bedrocks was calculated in order to analyze the correlation of the forest types with the bedrock variants. Soil types were described for the forest types. Frequency, shape, and location of charcoal pieces in the soil profiles together with the presence of *Pinus* spp. in the overstorey were used as signs for reconstruction of forest fire history. For this, we applied the concept of ecosystem history, which was firstly developed by Ponomarenko [62] on the basis of the soil morphological approach and then improved by Bobrovsky [63]. The following principles are used for the fire historical reconstruction.

1. During the forest fires, lamellar charcoal is usually formed. Over time, charcoal pieces gradually decrease in size and become rounded as a result of their long exposure at the soil surface, where they are broken or grinded by mineral particles of the soil during rainfalls [63]. As the charcoal pieces become covered with organic litter, the transformation of lamellar to rounded charcoal is ended. Therefore, the presence of the rounded charcoal in the soil indicates that the soil surface was exposed for a fairly long period of time and the renewal of the vegetation after the fire was slow at the particular site. On the contrary, the prevalence of the lamellar charcoal in the soil indicates relatively rapid renewal of the vegetation and relatively rapid formation of the organic litter after the fire.

2. The presence of the charcoal directly under the litter or in the upper part of the mineral soil means that the charcoal was only covered by the litter and was not transferred to the deeper soil layers as it happens when trees fall with uprooting. The most common cause of trees not being uprooted is that the time elapsed since the last fire is not long enough and the trees did not have time to fall and to turn the soil over by their roots. It means that the first generation of *Picea obovata* or *Abies sibirica* trees is growing after the last fire. In the studied region, the average life durations of the *Pinus sylvestris*, *Pinus sibirica* and *Picea obovata* are approximately 200, 400 and 250 years, respectively [64]. Therefore, we can conclude, the presence of *Pinus sylvestris* individuals in the overstorey and the presence of charcoal under the litter mean

that at least 150–200 years have been passed since the last fire. In other cases the time elapsed from the last fire is more than 200 years.

3. Small number of charcoal fragments inside the mineral soil horizon (and only there), the absence of *Pinus sylvestris*, and the presence of *Picea abies* deadwood at different stages of decay testifies to the fact that the time elapsed since the last fire can be estimated as no less than 400 years.

4. Generally, the frequency of the charcoal in the soil is directly related to the frequency of the forest fires.

Results

Vegetation and soil

Seven forest types were defined in the plain area of the Komi Republic (Table 1). All studied forests were characterized by a similar composition and structure of their tree layer, whereas the ground layer showed a much greater variety. The overstorey of all forests was dominated by *Picea obovata*, often together with *Abies sibirica*. Most *Picea obovata* individuals were from 100 to 180 years old; the previous generation was 250 years old; and the oldest *Picea obovata* individuals were found occasionally, reaching an age 380 years old. *Betula pubescens* also regularly occurred in the stands. *Pinus sylvestris* was common in the overstorey of *Piceeta hylocomiosa*. *Pinus sylvestris* together with *Pinus sibirica* also appeared in *Piceeta (Abieta) fruticoso-hylocomiosa* and both were rarely found in the other forest types. *Populus tremula* occurred in all forest types, but mainly in the southern areas, and *Tilia cordata* grew only in the south (numbers 5–7 in Fig. 1). Only two tree species (*Alnus incana* and *Salix caprea*) showed the forest-type specificity in their distribution: in the overstorey, both of these species were found only in tall herb forests (BrTH and NtTH) while *Salix caprea* also occurred in nemoral-boreal forests (Table S1). Tree stands were usually sparse, and their crown coverage varied from 20 to 60 % (Fig. 2). Gaps in the canopy caused by tree falls, coarse deadwood, and pit-and-mound topography caused by tree falls with uprooting were abundant in all forest types. Stems of *Picea obovata* individuals were often broken in *Piceeta hylocomiosa* and sometimes in *P.(A.) fruticoso-hylocomiosa*. In *P. hylocomiosa* most *Picea obovata* individuals were relatively low and their size did not correlate with their age; crowns were also small and often contained dead branches. The undergrowth mainly consisted of *Picea obovata* and *Abies sibirica* in all forest types.

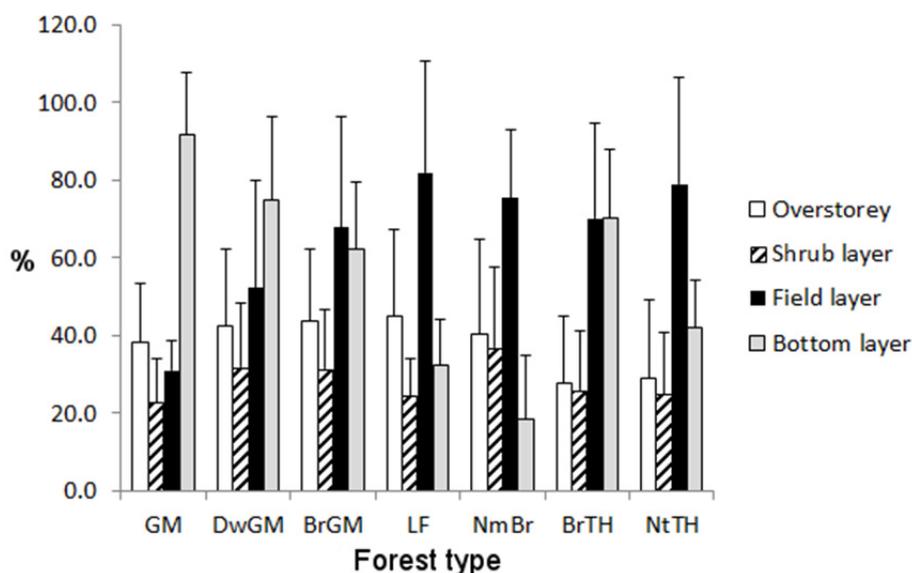


Fig. 2. Means and standard deviations of the coverage of the vegetation layers in the studied forest types. Forest types are the same as in Table 1

Only tall herb spruce-fir forests were studied in the valleys of small rivers and streams; therefore all the vegetation plots sampled in these areas were referred to the riparian tall herb forests, which were named as the nitrophilous tall herb spruce-fir

forests. All other investigated forest types were located on watersheds or slopes with good and moderate drainage and the vegetation plots sampled there were classified into the forest types according to the composition of the field layer (Fig. 3).

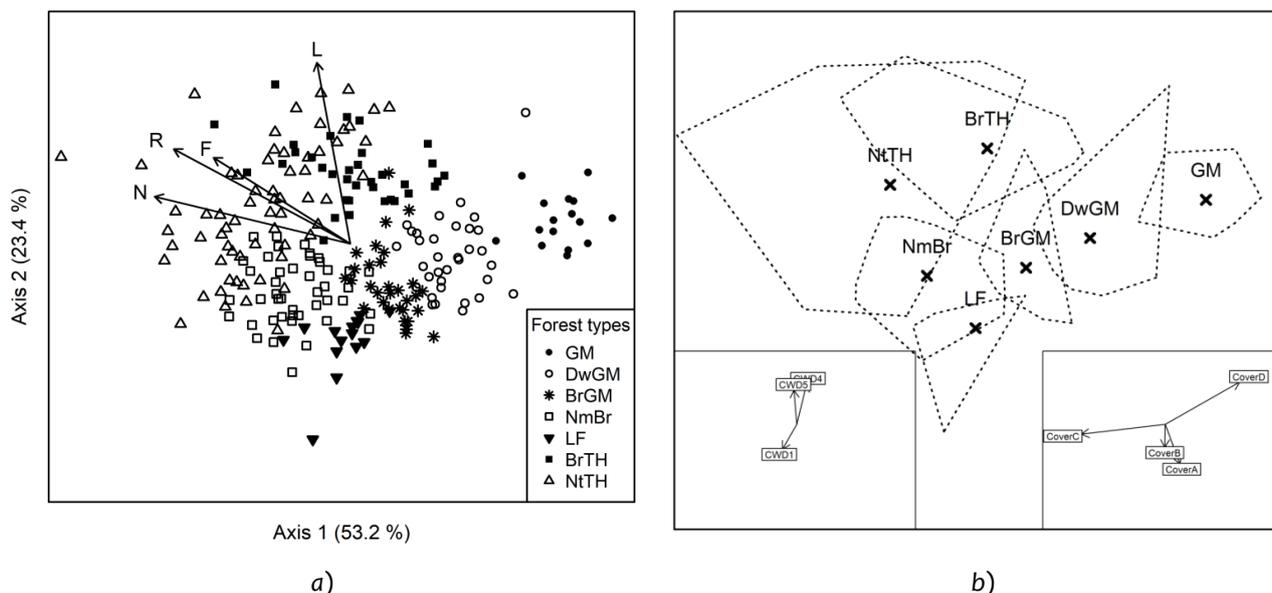


Fig. 3. NMDS ordination of the vegetation plots sampled in old-growth *Picea obovata* (*-Abies sibirica*) forests located in the study areas: a – arrows are vectors of Landolt's ecological values with the highest Pearson correlation: L light, F soil moisture, R reaction, and N nutrients. The axes jointly represent 76.6 % of total variation. The percentages were calculated by the method of McCune and Grace [47]; b – convex hulls and centroids for the forest types. Insets show significant vectors of deadwood coverage (in the bottom left corner) and layers coverage (in the bottom right corner). CWD1, CWD4 and CWD5 are the coverage of deadwoods at the first, fourth and fifth stages of decay. CoverA, CoverB, CoverC and CoverD are coverage of the overstorey, the shrub, the field, and the bottom layers, respectively. Forest types are the same as in Table 1

Ordination of 239 vegetation plots showed that the main ecological gradients were soil nutrients, reaction, and light: correlations with the first axis amounted to -0.91 for soil nutrients and -0.86 for

soil reaction; correlations with the second axis amounted to 0.82 for light availability. Along the first NMDS axis, vegetation varied from the tall herb and nemoral-boreal herb forest types on mod-

erately fertile and weakly neutral soils to the green moss – dwarf shrub and pure green moss forests on infertile and acid soils (Fig. 4). The second NMDS axis was correlated to the greatest degree with the light availability: boreal tall herb forests and a part of the riparian forests were the best illuminated; pure green moss forests were also rather light (Fig. 4). Soil

moisture also correlated well with the first NMDS axis: correlation amounted to -0.68 , though a noticeable variability in this parameter was found only in pure green moss and riparian forests, from moderately moist to moist soils, whereas rank values of the other forest types were very close (Fig. 4).

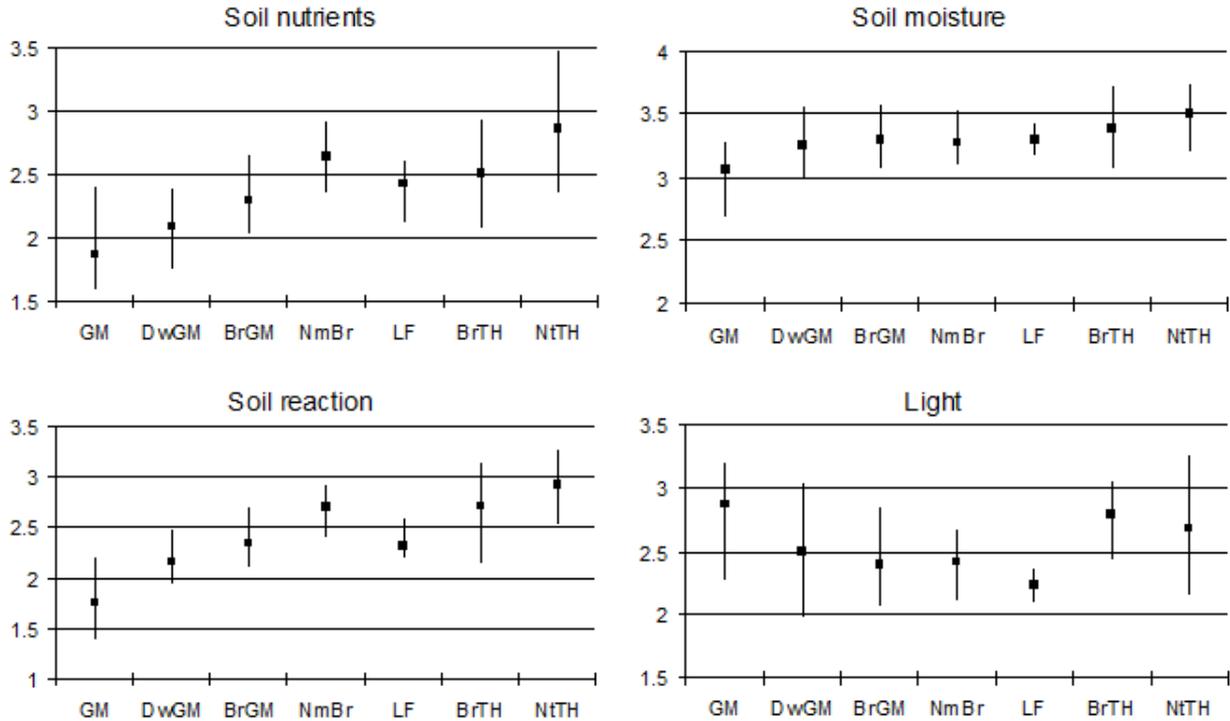


Fig. 4. Ranges and mean ecological values of the forest types calculated on the basis of Landolt's ecological species values. Forest types are the same as in Table 1

Picea hylacomiosa was found in all studied areas except for the southernmost localities in the upper reaches of the Sedka and the Suran Rivers (the 5th study area in Fig. 1). These forests were often found in flat areas, on plateaus and shallow terraces; mainly on sandy loams and sometimes on moraine loams (Table 3). Haplic and Histic Podzols prevailed. The E horizon was 10–25 cm thick. Only *Picea obovata* prevailed in the stands; *Betula pubescens* and *Pinus sylvestris* often occurred; *Abies sibirica* and *Larix sibirica* very rarely occurred; *Pinus sibirica* was absent. Windbreak often prevailed over tree falls with uprooting. The shrub layer was sparse (Fig. 2) and poor in species (Table

S1). *Juniperus communis* and an undergrowth of *Picea obovata* and *Betula pubescens* rarely occurred. Cover of the field layer was minimal among the studied forest types (Fig. 2).

The dwarf shrubs *Vaccinium vitis-idaea*, *V. myrtillus* and *Empetrum nigrum* sometimes dominated in the field layer. Boreal herbaceous species were occasionally found; species of the nemoral, nitrophilous and meadow ECGs were practically absent (Fig. 5). The bottom layer had the highest coverage values among the forest types (Fig. 2), but the species richness of mosses and liverworts was the lowest (Table 4); the green mosses *Hylocomium splendens* and *Pleurozium schreberi* prevailed.

Table 3

Relative frequency (%) of the forest type occurrence on different bedrocks

Bedrock type	Forest types*						
	GM	DwGM	BrGM	NmBr	LF	BrTH	NtTH
Sandy loams	81.2	52.9	16.1	0.0	0.0	71.4	0.0
Moraine loams	18.8	41.2	67.7	9.1	21.4	28.6	0.0
Silty loams	0.0	5.9	16.1	90.9	78.6	0.0	0.0
Alluvial sediments	0.0	0.0	0.0	0.0	0.0	0.0	100.0

Note. *Forest types are the same as in Table 1.

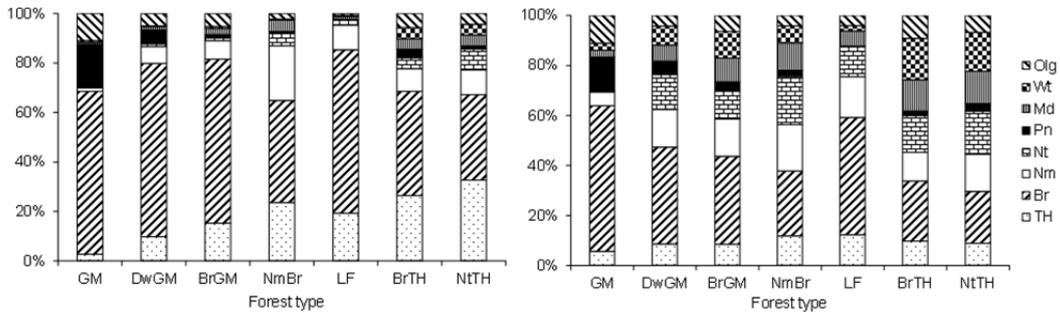


Fig. 5. Proportion of species of different ecological-coenotic groups in the forest types. Left – mean number of species per plot and right - total number of species in the forest types. Forest types are the same as in Table 1. Ecological-coenotic groups: TH tall boreal herbs and ferns, Br all other boreal species, Pn piny, Nm nemoral, Nt nitrophilous, Md meadow-edge, Wt water-marsh and Olg oligotrophic plants.

Table 4

Species diversity of the studied forest types

Forest types	Vascular plants			Bryophyte species		
	Mean species number per plot	Species richness	Number of plots	Mean species number per plot	Species richness	Number of plots
<i>P. hylocomiosa</i>	10.3±4.11*	36	16	6.0±1.83	27	11
<i>P.(A.) fruticoso-hylocomiosa</i>	20.3±6.81	94	34	5.8±2.67	38	13
<i>P.(A.) parviherboso-hylocomiosa</i>	22.9±7.27	102	31	5.9±2.21	28	6
<i>P.-A. magnofilicosum</i>	20.2±3.97	50	15	9.0±3.21	31	10
<i>P.(A.) nemoralo-borealiherbosa</i>	36.4±6.42	120	44	7.9±2.98	63	34
<i>P.(A.) magnoherbosa</i>	40.2±7.91	174	35	7.7±4.30	76	21
<i>P.(A.) nitrophilo-magnoherbosa</i>	40.1±9.12	194	64	8.2±3.77	96	52
Totally		232	239		132	147

Note. *standard deviation.

Piceeta (Abieta) fruticoso-hylocomiosa (Fig. 6) was widely distributed over the all study areas as well as throughout the entire boreal forest region. These forests mainly occupied relatively well-drained flat tops, terraces and terraced slopes; they were equally common on sandy loams and moraine loams and sometimes occurred on silty loams (Table 3). Podzols, mainly Haplic Podzols, were common (Fig. 7,a); Albeluvisols also occurred (Fig. 7,b). The E horizon was 10–25 cm thick; the same as it was in the pure green moss spruce forests. *Picea obovata* dominated more frequently than *Abies sibirica* in the overstorey and in the undergrowth as well. *Betula pubescens*, *Populus tremula*, *Pinus sibirica* and more rarely *P. sylvestris* also occurred in the overstorey. *Larix sibirica* was occasionally found. *Sorbus aucuparia* and *Rosa acicularis* often occurred in the understory. Cover of the field layer was higher compared to that in *P. hylocomiosa* (Fig. 2); *Vaccinium myrtillus* prevailed; the small boreal herbaceous species *Equisetum sylvaticum*, *Gymnocarpium dryopteris*, and *Lycopodium annotinum* sometimes co-dominated. These species together with *Trientalis europaea*, *Linnaea borealis*, *Oxalis acetosella* and *Maianthemum bifolium* often appeared as well as the oligotrophic sedge *Carex globularis* and the piny dwarf shrub *V. vitis-idaea*. The tall herbs and

ferns *Chamaenerion angustifolium*, *Rubus idaeus*, *Cirsium heterophyllum* and *Dryopteris dilatata* sometimes occurred with a small abundance. Cover of the bottom layer was rather high (Fig. 2); *Pleurozium schreberi* and *Hylocomium splendens* often prevailed; *Polytrichum commune* and *Ptilium crista-castrensis* often co-dominated; *Dicranum polysetum* was common.

Piceeta (Abieta) parviherboso-hylocomiosa was found in all the study areas. These forests more often occurred in the middle and lower parts of slopes and river terraces; mainly on moraine loams (Table 3). Podzols were common soils in these forests. Haplic Podzols with the E horizon of 20 cm thick prevailed. Structure and composition of the overstorey and the shrub layer were similar to those observed in *P.(A.) fruticoso-hylocomiosa*, but cover of the field layer amounted to 70–90 %. The small boreal herbs and ferns *Gymnocarpium dryopteris*, *Maianthemum bifolium*, and *Oxalis acetosella* dominated (Fig. 8). Boreal species, such as *Trientalis europaea*, *Linnaea borealis*, *Equisetum sylvaticum*, *Vaccinium myrtillus*, *Rubus idaeus*, *Dryopteris dilatata* and *Lycopodium annotinum* often occurred with less abundance. The tall herbs *Chamaenerion angustifolium*, *Aconitum septentrionale* and *Cirsium heterophyllum* were rarely found. Cover of the bottom layer was rather high,

but lower than in the previous forest types; *Pleurozium schreberi* and *Hylocomium splendens* often prevailed; *Polytrichum commune*, *Ptilium crista-*

castrensis, *Dicranum polysetum*, and *Rhytidiadelphus triquetrus* often appeared.



Fig. 6. *Piceeta (Abieta) fruticoso-hylocomiosa* in the plain part of the Komi Republic (photos by M. Bobrovsky)



a)



b)

Fig. 7. Soil profiles (a – Podzol and b – Albeluvisol) in the *Piceeta-Abieta fruticoso-hylocomiosa* in the 3rd and 5th study areas, respectively (photos by M. Bobrovsky)



Fig. 8. *Piceeta parviherboso-hylocomiosa* in the upper reaches of the Vashka River (3rd study area; photo by M. Bobrovsky)

Piceeta (Abieta) nemoralo-borealiherbosa was found in the southern study areas (numbers 5–7 in Fig. 1). These forests grew on terrains of diverse relief, mainly on silty loams and sometimes on moraine loams (Table 3). Albeluvisols with the E horizon of 7–15 cm thick were common; Albeluvisols with second humus horizon were also found. In the overstorey, *Picea obovata* dominated more frequently than *Abies sibirica*; in the undergrowth both these species prevailed. *Betula pubescens* and *B. pendula* were common in the overstorey. *Populus tremula* often occurred in all the layers and sometimes co-dominated in the overstorey. *Tilia cordata* often occurred in the overstorey and in the undergrowth as well. *Pinus sibirica* and *P. sylvestris* rarely occurred in the stands. There were large gaps in the canopy caused by tree falls; practically all fallen large trees were in their initial stage of the decay and there were no old deadwoods at late stages of decay. Fallen trees were mainly uprooted and they were located in groups rather than singly (Fig. 9,a). The understory was rich in species; cover of the shrub layer was the highest among the studied forest types (Fig. 2).

Sorbus aucuparia and *Rosa acicularis* prevailed; *Lonicera xylosteum*, *Padus avium* and *Ribes hispidulum* were common; *R. rubrum*, *R. nigrum* and *Daphne mezereum* occurred. Cover of the field layer was 80–100 %. Boreal and nemoral species of the middle and small size dominated in the ground layer and defined the aspect of these forests (Fig. 5). Tall herbs also occurred in small patches, but they did not form a separate layer (Fig. 9,b). *Gymnocarpium dryopteris*, *Aegopodium podagraria*, *Equisetum sylvaticum*, *Calamagrostis arundinacea*, *Pulmonaria obscura*, *Diplazium sibiricum*, *Aconitum septentrionale*, *Dryopteris dilatata*, *Rubus idaeus*, etc. often prevailed. The nemoral herbs and grasses *Stellaria holostea*, *Paris quadrifolia*, *Milium effusum* and *Melica nutans* also often occurred. Cover of the bottom layer was no more than 10–20 %, but bryophyte species richness was high (Table 4). *Pleurozium schreberi*, *Hylocomium splendens* and *Rhytidiadelphus triquetrus* dominated. *Sanionia uncinata* and *Dicranum scoparium* were common. *Plagiomnium medium*, *D. polysetum*, *Ptilium crista-castrensis*, *Brachythecium starkei*, etc. occurred.



a)



b)

Fig. 9. *Piceeta-Abieta nemoralo-borealiherbosa* in the upper reaches of the Suran River (the 5th study area): a – group treefall; b – *Atragene sibirica* (photos by M. Bobrovsky)

Piceeta-Abieta magnofilicosum were found in several small areas in the Southern Timan Ridge and in the upper reaches of the Sedka and the Suran Rivers (Nos 4 and 5 in Fig. 1) on silty and, sometimes, moraine loams. Albeluvisols with the E horizon of 10–20 cm thick prevailed there. Strongly eroded soils on drained sites were common in these forests. *Picea obovata* prevailed and *Abies sibirica* often co-dominated; *Betula pubescens* usually appeared; *Pinus sibirica* and *P. sylvestris* rarely occurred. The shrub layer was

poor. The large fern *Dryopteris dilatata* prevailed the field layer, covering up to 80–100 % of a plot (Fig. 10). Small boreal herbs, ferns and tall herbs (such as *Rubus idaeus* and *Cinna latifolia*) often occurred with a small abundance; species of other ECGs are very rare (Fig. 5). Mosses did not cover much of the soil but mainly occupied deadwoods at different stages of decay; *Pleurozium schreberi* dominated; *Hylocomium splendens*, *Dicranum fuscescens* and *Brachythecium reflexum* often appeared.



Fig. 10. *Piceeto-Abieta magnofilicosum* with *Dryopteris dilatata* in the 5th study area (photo by M. Bobrovsky)

Piceeta (Abieta) boreo-magnoherbosa (Fig. 11) was found in all the study areas except the upper reaches of the Sedka and Suran rivers (number 5 in Fig. 1). The areas covered by these forests varied greatly in a size: from hundredths of a hectare to tens of hectares. These forests were located on watersheds and on slopes, on sandy loams and less often on moraine loams (Table 3). The feature of the soils was their well-expressed mosaic structure, which was formed as a result of numerous tree falls with uprooting. Soils of various types occurred there: combinations of Haplic and Entic

Podzols prevailed in the upper reaches of the Vashka River and on the Middle Timan Ridge; Histosols and Gleysols occurred in depressions. The thickness of the litter layer in Podzols was 5–10 cm; the E horizon was about 10 cm thick; the Ah or H horizons in peaty soils were up to 50 cm thick. Haplic Albeluvisols prevailed in the south of the region; soils with buried moder or mull humus horizons often occurred. The Albic horizon was 15–25 cm thick. Dystric Cambisols and Histosols also occurred.

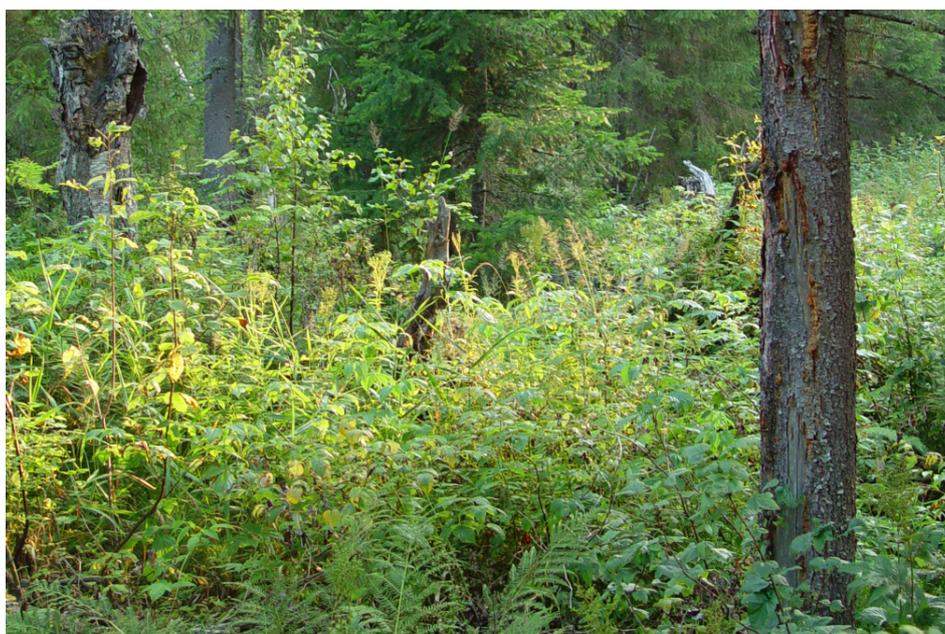


Fig. 11. *Piceeto-Abieta magnoherbosa* with *Athyrium filix-femina*, *Calamagrostis arundinacea*, *Chamaenerion angustifolium*, *Filipendula ulmaria*, *Rubus idaeus*, etc. in the plain part of the Komi Republic (photo by N. Alatyrtseva)

There were a lot of gaps in the canopy caused by tree falls and a lot of deadwoods at different

stages of decay; the fallen trees were mainly uprooted. *Picea obovata* dominated in the overstorey

with an admixture of *Betula pubescens*. *Abies sibirica* also occurred. *Pinus sibirica* could be occasionally found. Undergrowth of *Picea obovata* prevailed. *Betula pubescens*, *Abies sibirica*, *Sorbus aucuparia*, *Alnus incana* and *Salix caprea* often occurred in the understory. Cover of the shrub layer was small, but its diversity was high. *Rosa acicularis*, *Juniperus communis*, *Spiraea media* and *Daphne mezereum* were common. Species of the genus *Lonicera* (*L. altaica*, *L. pallasii* and *L. xylostemum*) and *Ribes* (*R. hispidulum*, *R. rubrum* and *R. nigrum*) also occurred. In the ground layer, patches of different composition with the dominance of plants from different ECGs were distinguished (Fig. 5). The tall herbs *Aconitum septentrionale*, *Cirsium oleraceum*, *Filipendula ulmaria* and *Diplazium sibiricum* dominated in the upper herbaceous sublayer; the tall herbs *Chamaenerion angustifolium*, *Geranium sylvaticum*, *Geum rivale*, *Calamagrostis canescens*, *Cirsium heterophyllum*, *Aragene sibirica*, *Angelica sylvestris*, *Delphinium elatum* and others were common. The tall herbs defined the aspect of these forests; they grew on patches between tree crown projections in the upper herbaceous sublayer. Nemoral species such as *Lathyrus vernus*, *Milium effusum* and *Paris quadrifolia* often grew in the second herbaceous sublayer; the small boreal herbs and ferns *Gymnocarpium dryopteris*, *Rubus saxatilis* and *Trientalis europaea* grew under them and often dominated; *Oxalis acetosella*, *Maianthemum bifolium*, *Equisetum sylvaticum*, etc. also occurred with a high frequency in the lower sublayer of the field layer. Dwarf shrubs such as *Vaccinium myrtillus*, *V. vitis-idaea* and *Linnaea borealis* often occurred together with bo-

real mosses and sometimes bushy lichens on the deadwood and at the base of large standing trees. Nitrophilous species such as *Chrysosplenium alternifolium* and *Stellaria nemorum* grew together with the water-marsh species *Calamagrostis canescens*, *Equisetum palustre* and *Veronica longifolia* in the pits formed after tree falls with uprooting; meadow species such as *Vicia sepium* and *Ranunculus propinquus* could be found on the mounds formed by tree falls and the oligotrophic species *Viola epipsila*, *Carex globularis*, *Rubus chamaemorus*, etc. often occurred in the waterlogged depressions also formed after tree falls. In the bottom layer a high diversity of mosses was remarkable. *Pleurozium schreberi*, *Hylocomium splendens*, *Rhytidiadelphus triquetrus* and *Sphagnum warnstorffii* often occurred and sometimes prevailed.

Piceeta (Abieta) nitrophilo-magnoherbosa (Fig. 12) occurred in the valleys of rivers and streams in all the study areas. Generally, riverine floodplains with linear fluvial levees and hollows are common in the plain part of the Komi Republic, and nitrophilous tall herb spruce and spruce-fir forests often occupy well-drained areas, while forests dominated by sphagnum mosses or water-marsh hygrophilous plants occupy adjacent poorly drained areas. The width of the studied riparian spruce-fir forests was usually tens of meters but sometimes reached hundreds of meters. Dystric Fluvisols (Fig. 13,a) with a very thick soil profile prevailed; different Histosols and Gleysols (Fig. 13,b) also occurred frequently on alluvial sediments.



Fig. 12. ***Piceeta-Abieta nitrophilo-magnoherbosa*** in the Suran River (the 5th study area) at the beginning of summer (photo by M. Bobrovsky)

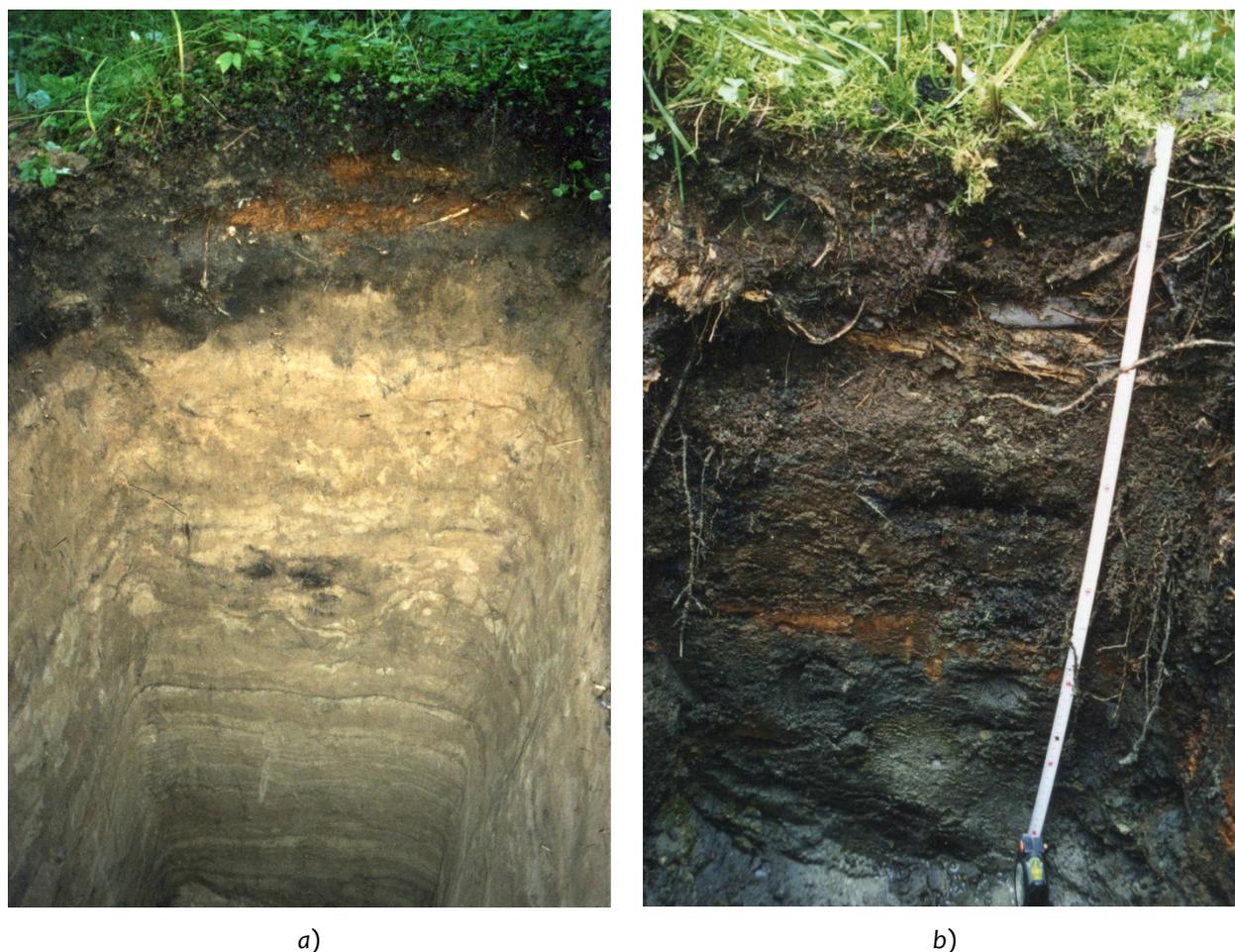


Fig. 13. Soil profiles (a – Dystric Fluvisol and b – Gleysol) in the ***Piceeta-Abieta nitrophilo-magnoherbosa*** in the 3rd and 5th study areas, respectively (photos by M. Bobrovsky)

Gaps in the canopy caused by treefalls often occurred; deadwoods at different decay stages and uprooted fallen trees were common. *Picea obovata* dominated in the overstorey with an admixture of *Betula pubescens*; *Abies sibirica* occurred in a half of the plots. *Alnus incana* often occurred in the understorey, where *Picea obovata* prevailed and *Sorbus aucuparia*, *Salix caprea*, *Padus avium* and *Abies sibirica* also occurred. The shrub layer was not dense, but relatively rich in species: not only boreal shrubs, such as *Rosa acicularis*, *Lonicera altaica* and *L. pallasii*, but also nitrophilous species, such as *Ribes nigrum*, *R. hispidulum*, *R. rubrum* and nemoral *Spiraea media* and *Daphne mezereum*, often occurred. The field layer was the richest in species (Table 4) and the cover was high (Fig. 2). The nitrophilous tall herb *Filipendula ulmaria* often dominated and defined the aspect of these forests. Common tall herbs, such as *Aconitum septentrionale*, *Diplazium sibiricum* and *Rubus idaeus* were also abundant. Nitrophilous and boreal tall herbs, such as *Cacalia hastata*, *Urtica dioica*, *Atragene sibiica*, *Veratrum lobelianum*, *Chamaenerion angustifolium*, *Geranium sylvaticum*, etc.

frequently occurred. The small boreal herbs and ferns *Oxalis acetosella*, *Trientalis europaea*, *Maianthemum bifolium*, *Gymnocarpium dryopteris*, *Equisetum sylvaticum* and *E. pratense* occurred very frequently with a high abundance. Nemoral species, such as *Aegopodium podagraria*, *Adoxa moschatellina*, *Milium effusum*, *Paris quadrifolia*, *Stellaria holostea*, etc. and light-demand meadow species, such as *Vicia sepium*, *Ranunculus propinquus*, *Fragaria vesca*, *Lathyrus pratensis*, *Artemisia vulgaris*, etc. were also found in the floodplains. Cover of the bottom layer was low (Fig. 2), but the number of species was high: *Pleurozium schreberi*, *Sanionia uncinata*, *Rhytidiadelphus triquetrus*, *Hylocomium splendens*, *Rhodobryum roseum* and *Plagiomnium ellipticum* prevailed.

Thus, the studied forest types showed the high variation in the field layer of vegetation. It was confirmed by the results of the ordination analysis and by the results of the indicator species (IndVal) analysis as well: from 232 vascular plant species, which were totally found, 119 (51.3 %) showed significant affinities to certain forest types (Table 5).

Table 5

**Vascular plants species with significant (indicator species analysis) affinity
to forest types sorted by decreasing indicator value**

ECG*	Species	Indicator value (%)	P
1	2	3	4
<i>Piceeta hylocomiosa</i>			
Pn	<i>Vaccinium vitis-idaea</i>	38.2	0.001
Br	<i>Avenella flexuosa</i>	30.8	0.001
Pn	<i>Festuca ovina</i>	13.4	0.006
Olg	<i>Empetrum nigrum</i>	11.6	0.006
Pn	<i>Pinus sylvestris</i>	10.1	0.023
Br	<i>Melampyrum sylvaticum</i>	9.5	0.041
<i>Piceeta (Abieta) fruticoso-hylocomiosa</i>			
Br	<i>Vaccinium myrtillus</i>	30.6	0.001
Olg	<i>Carex globularis</i>	22.4	0.001
Br	<i>Listera cordata</i>	18.8	0.001
Br	<i>Melampyrum pratense</i>	14.8	0.006
Pn	<i>Diphasiastrum complanatum</i>	12.1	0.009
<i>Piceeta (Abieta) parviherboso-hylocomiosa</i>			
Br	<i>Gymnocarpium dryopteris</i>	28.5	0.001
Br	<i>Linnaea borealis</i>	24.2	0.001
Br	<i>Oxalis acetosella</i>	21.4	0.001
Br	<i>Lycopodium annotinum</i>	21.1	0.002
Br	<i>Maianthemum bifolium</i>	21.0	0.005
Br	<i>Trientalis europaea</i>	20.6	0.003
Br	<i>Abies sibirica</i>	19.0	0.011
Br	<i>Sorbus aucuparia</i>	18.2	0.013
<i>Piceeta-Abieta magnofilicosum</i>			
TH	<i>Dryopteris dilatata</i>	52.6	0.001
Br	<i>Phegopteris connectilis</i>	40.6	0.001
TH	<i>Cinna latifolia</i>	37.5	0.001
TH	<i>Rubus idaeus</i>	29.7	0.001
Br	<i>Circaea alpina</i>	23.7	0.001
Br	<i>Equisetum sylvaticum</i>	21.4	0.001
TH	<i>Diplazium sibiricum</i>	16.2	0.01
<i>Piceeta (Abieta) nemoralo-borealiherbosa</i>			
Nm	<i>Pulmonaria obscura</i>	69.4	0.001
Nm	<i>Aegopodium podagraria</i>	52.2	0.001
Br	<i>Calamagrostis arundinacea</i>	44.0	0.001
Nm	<i>Stellaria holostea</i>	39.7	0.001
Nt	<i>Aconitum septentrionale</i>	31.3	0.001
Nm	<i>Ajuga reptans</i>	29.5	0.001
Nm	<i>Paris quadrifolia</i>	27.3	0.001
Md	<i>Fragaria vesca</i>	26.7	0.002
Md	<i>Galium mollugo</i>	25.6	0.001
Br	<i>Rubus saxatilis</i>	25.1	0.001
Br	<i>Viola selkirkii</i>	24.4	0.001
Nm	<i>Tilia cordata</i>	23.9	0.001
Nt	<i>Athyrium filix-femina</i>	22.2	0.001
Nm	<i>Melica nutans</i>	22.0	0.003
Br	<i>Lonicera caerulea</i>	21.4	0.001
Nm	<i>Asarum europaeum</i>	18.1	0.001
Nm	<i>Milium effusum</i>	18.0	0.011
Nm	<i>Populus tremula</i>	16.1	0.003
Nm	<i>Carex digitata</i>	15.2	0.003
Nt	<i>Ribes hispidulum</i>	12.8	0.024
TH	<i>Actaea erythrocarpa</i>	9.4	0.027
Nt	<i>Galium aparine</i>	6.8	0.034

Continuation of table 5

1	2	3	4
<i>Piceeta (Abieta) magnoherbosa</i>			
Br	<i>Orthilia secunda</i>	34.1	0.001
Nt	<i>Geum rivale</i>	33.7	0.001
Md	<i>Galium boreale</i>	32.4	0.001
Wt	<i>Bistorta major</i>	29.7	0.001
Wt	<i>Equisetum palustre</i>	29.2	0.001
Pn	<i>Juniperus communis</i>	28.1	0.001
Nm	<i>Spiraea media</i>	26.2	0.001
TH	<i>Saussurea alpina</i>	24.5	0.001
Wt	<i>Calamagrostis canescens</i>	24.4	0.001
Nm	<i>Lathyrus vernus</i>	23.4	0.001
TH	<i>Geranium sylvaticum</i>	22.4	0.002
Nt	<i>Cirsium oleraceum</i>	22.1	0.002
Md	<i>Vicia sepium</i>	22.1	0.001
Nt	<i>Cirsium heterophyllum</i>	20.8	0.003
TH	<i>Chamaenerion angustifolium</i>	20.3	0.006
Br	<i>Rosa acicularis</i>	20.0	0.006
Md	<i>Ranunculus propinquus</i>	19.5	0.003
Br	<i>Solidago virgaurea</i>	18.3	0.003
TH	<i>Trollius europaeus</i>	17.9	0.003
Nt	<i>Crepis paludosa</i>	15.7	0.013
TH	<i>Delphinium elatum</i>	15.6	0.001
Br	<i>Moneses uniflora</i>	14.3	0.012
Br	<i>Carex vaginata</i>	14.1	0.015
Nm	<i>Daphne mezereum</i>	14.0	0.005
Olg	<i>Rubus chamaemorus</i>	13.2	0.011
Wt	<i>Carex cespitosa</i>	12.9	0.008
Md	<i>Thalictrum minus</i>	12.9	0.008
Nt	<i>Ribes rubrum</i>	11.9	0.016
Wt	<i>Equisetum scirpoides</i>	11.7	0.008
Br	<i>Rhizomatopteris sudetica</i>	11.4	0.006
Olg	<i>Epilobium palustre</i>	9.0	0.007
<i>Piceeta (Abieta) nitrophilo-magnoherbosa</i>			
TH	<i>Cacalia hastata</i>	42.5	0.001
Nt	<i>Filipendula ulmaria</i>	41.5	0.001
Wt	<i>Valeriana officinalis</i>	34.5	0.001
Nm	<i>Elymus caninus</i>	30.8	0.001
Nt	<i>Urtica dioica</i>	30.3	0.001
Nt	<i>Thalictrum aquilegifolium</i>	29.3	0.001
Nt	<i>Stellaria nemorum</i>	25.1	0.001
TH	<i>Senecio nemorensis</i>	23.7	0.002
TH	<i>Atragene sibirica</i>	23.1	0.001
Nt	<i>Veratrum lobelianum</i>	19.6	0.004
Br	<i>Lonicera altaica</i>	19.1	0.001
Nt	<i>Ribes nigrum</i>	18.6	0.001
Wt	<i>Veronica longifolia</i>	17.8	0.004
Olg	<i>Viola epipsila</i>	17.4	0.012
Nm	<i>Adoxa moschatellina</i>	17.3	0.004
Wt	<i>Thalictrum flavum</i>	17.2	0.003
Nt	<i>Galium palustre</i>	17.1	0.002
Nt	<i>Alnus incana</i>	16.5	0.004
Br	<i>Equisetum pratense</i>	16.5	0.025
Nt	<i>Ranunculus repens</i>	15.6	0.009
Nt	<i>Chrysosplenium alternifolium</i>	14.6	0.011
Olg	<i>Comarum palustre</i>	12.9	0.007

End of table 5

1	2	3	4
Wt	<i>Caltha palustris</i>	12.7	0.011
Wt	<i>Thalictrum lucidum</i>	12.5	0.004
Nt	<i>Padus avium</i>	12.0	0.018
Nm	<i>Brachypodium pinnatum</i>	11.2	0.01
Wt	<i>Carex vesicaria</i>	11.2	0.014
Md	<i>Artemisia vulgaris</i>	10.9	0.017
Nt	<i>Scirpus sylvaticus</i>	10.9	0.007
Wt	<i>Galium uliginosum</i>	10.4	0.016
Nt	<i>Matteuccia struthiopteris</i>	10.2	0.015
Nm	<i>Poa nemoralis</i>	10.2	0.026
Wt	<i>Carex nigra</i>	9.4	0.023
Br	<i>Pyrola media</i>	9.4	0.019
Md	<i>Vicia cracca</i>	9.2	0.034
Wt	<i>Phalaroides arundinacea</i>	9.0	0.035
Wt	<i>Scutellaria galericulata</i>	8.7	0.027
Nt	<i>Cardamine amara</i>	8.3	0.047
Nt	<i>Salix fragilis</i>	8.2	0.021
Md	<i>Kadenia dubia</i>	7.2	0.045

Note. *ECG (ecological-coenotic groups): TH boreal tall herbs and ferns, Br all other boreal plants, Pn piny, Nm nemoral, Nt nitrophilous, Md meadow-edge, Wt water-marsh and Olg oligotrophic plants.

Totally 232 vascular plants (including 14 trees, 16 shrubs and 202 herbaceous species) and 132 bryophyte species (including 113 mosses and 19 liverworts) were found in 239 and 147 vegetation plots, respectively (Table 4; it should be reminded that full lists of bryophytes were composed only for plots located in the study areas 3 and 5 in the Fig. 1). Diversity of vascular plant species was the highest in the boreal and the nitrophilous tall herb spruce-fir forests and in the nemoral-boreal spruce-fir forests as well (Table 4). For bryophyte species, the mean number of species per plot was close to each other in different forest types, but species richness was the highest in the tall herb spruce-fir forests. As shown by the IndVal analysis (Table 5), the each forest type that was poor in species diversity had from 5 to 8 affiliated species and the each “rich” forest type had from 22 to 40 affiliated species; this indicates that the richest forest types contributed significantly to the overall plant species diversity. Note that only among species affiliated to the boreal tall herb forests were the species of the all ECGs. On the whole, along to increase of species diversity of the forest types, the average ecological-coenotic structure of vascular plants in a plot was changing by the following way (Fig. 5, left): (i) proportion of tall herbs and ferns increased, (ii) proportion of the other boreal plants decreased and (iii) plants of different ECGs began to attend constantly in a plot. Along to increase of species richness, structure of vascular plants was changing by the following (Fig. 5, right): (i) proportion of tall herbs and ferns remained almost

constant and (ii) proportion of the other boreal plants was constantly reduced by the increasing proportion of species of the other ECGs.

Environmental parameters

Aiming to estimate effects of environmental parameters on species composition and diversity, we analyzed the coverage of vegetation layers and the coverage of deadwoods in regard to their correlations with the ordination axes and with a number of species in plots.

We found significant correlations between the ordination axes and the coverage of different vegetation layers (Fig. 3, b; Table 6). Correlation values calculated for the field and the bottom layers were higher than the values calculated for the tree and shrub layers. There were also significant correlations (at the 0.001 permutation threshold) between the number of vascular plant species in a plot and the coverage of the field layer ($r = 0.49$), the coverage of the tree and the bottom layers ($r = -0.19$ and -0.35 , respectively). In contrast, no significant correlations between the number of bryophytes in a plot and the coverages of any vegetation layer were found. These results indicate that vascular plant species composition and diversity depends on the coverage of the main vegetation layers, and especially on the coverage of the field layer. In turn, diversity of bryophyte species depends neither on their coverage nor on coverage of other vegetation layers.

Table 6

Pearson correlations of the environmental variables with the first and second NMDS axes and the statistics (R^2) to assess the statistical significance

Variable*	Axis 1	Axis 2	R^2	$p (>r^2)$
CoverA	0.156	-0.333	0.135	0.001
CoverB	-0.004	-0.202	0.041	0.014
CoverC	-0.65	-0.06	0.426	0.001
CoverD	0.625	0.279	0.469	0.001
DWC totally	-0.027	0.162	0.028	0.123
DWC1	-0.163	-0.203	0.062	0.011
DWC2	-0.015	-0.096	0.009	0.488
DWC3	-0.052	-0.028	0.003	0.779
DWC4	0.147	0.349	0.134	0.001
DWC5	0.001	0.304	0.094	0.001

Note. CoverA, CoverB, CoverC and CoverD are coverages of the overstorey, the shrub, the field, and the bottom layers of vegetation, respectively. DWC totally is the total coverage of deadwoods at different decay stages. DWC from 1 to 5 are the coverages of deadwoods from the first to the fifth stages of their decay, respectively.

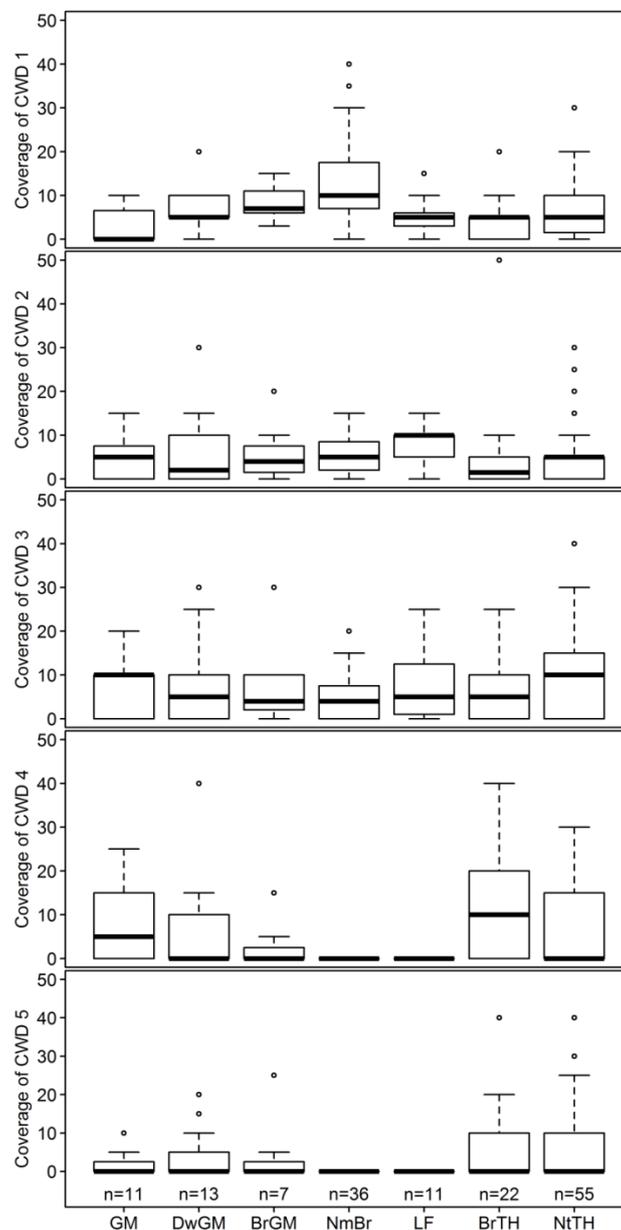


Fig. 14. Boxplots of the coverage of deadwoods at different stages of their decay (from 1 to 5) for the studied forest types. The forest types are the same as in Table 1

We tested another environmental variable as a potential driver of species composition and diversity was the coverage of deadwoods at different stages of their decay. On average, deadwoods covered 31.2 ± 20.7 % of the ground in plots. Correlation of the ordination axes with the total DWC was weak and insignificant, whereas weak, but significant for the coverage of deadwoods at the first, fourth, and fifth stages of their decay (Fig. 3,b; Table 6). DWC at different decay stages varied in different forest types (Fig. 14). In pure green moss forests, the highest coverage values were observed for the deadwoods at the 3rd and 4th decay stages. In nemoral-boreal herb forests, deadwoods at the 1st decay stage prevailed and deadwoods at the 4th and 5th decay stages were absent. Deadwoods at the 4th and 5th stages had the highest coverage values in the boreal and nitrophilous tall herb forests. The coverages of deadwoods at the 2nd and 3rd decay stages were close in different forest types. There were no significant correlations between the diversity of vascular plants and the values of DWC at different decay stages, but there was a significant correlation between the number of bryophytes in a plot and values of the total deadwood coverage ($r = 0.20$). Thus, the composition of the field layer had the weak correlations with the coverage of deadwoods at the 1st, 4th and 5th stages of their decay, and a diversity of

bryophyte species had a positive correlation with the total deadwood coverage.

Fire signs

In addition to environmental factors, fire history might have a strong impact on plant species composition and diversity in boreal forests. We analyzed the signs of past fires in vegetation and soils of each studied forest type.

Piceeta hylocomiosa, *P.(A.) fruticoso-hylocomiosa* and *P.(A.) parviherboso-hylocomiosa* were very similar to each other in terms of fire signs in the vegetation and characteristics of charcoal in soils. Stems of *Pinus* spp. individuals usually had fire scars. Analysis of tree fire cores showed that these trees were affected by fires 150–340 years ago. Agglomerations of charcoal pieces were found in all soil profiles: lamellar and rounded charcoal fragments occurred at the border of the litter and mineral soil horizons; lamellar charcoal also occurred inside the mineral soil, in the material of old pits caused by treefalls with uprooting (Table 7). In pure green moss and dwarf shrub – green moss forests, lamellar charcoal often occurred as a layer or several layers under the litter. All these signs indicate that fire regime of these forests was very severe: there were several large fires in the past and at least 150 years passed since the last fire.

Table 7

Charcoal in the soil profile in the studied old-growth *Picea obovata* (*Abies sibirica*) forests

	Forest types				
	<i>Piceeta hylocomiosa</i> , <i>P.(A.) fruticoso-hylocomiosa</i> and <i>P.(A.) parviherboso-hylocomiosa</i>	<i>P.-A. magno-filicosum</i>	<i>P.(A.) nemoralo-boreali-herbosa</i>	<i>P.(A.) magno-herbosa</i>	<i>P.(A.) nitrophilo-magnoherbosa</i>
Charcoal frequency	Agglomerations or layers (up to 7 layers)	Single or agglomerations	Single	Single	Single or agglomerations (up to 4 layers)
Charcoal form	Lamellar, rounded	Rounded	Lamellar	Lamellar	Lamellar
Charcoal location	On the border of the litter and the mineral soil and in the mineral soil horizon	On the border of the litter and in the mineral soil horizon	In the mineral soil horizon	In the mineral soil horizon	In the mineral soil horizon

In small areas, which were occupied by *P.-A. magnofilicosum*, we found only a few individuals of *Pinus* spp.; all they were with fire scars. Charcoal in the soil was common, and most of charcoal pieces were rounded and small (less than 2 mm in diameter). They occurred singly or in clusters, usually at the litter/mineral soil border or in the upper part of the mineral soil horizon. We assume intense fires in the past and slow recovery of vegetation after fires in areas currently occupied by the large

fern spruce-fir forests. The time elapsed since the last fire is, according to our estimate, 150–400 years. Unfortunately, it is practically impossible to reveal the traces of fires of a more distant past in large fern spruce-fir forests, since most of the soils there are eroded, and no buried coal can be found.

In *P.(A.) nemoralo-borealiherbosa*, *Pinus sibirica* and *P. sylvestris* rarely occurred and they did not have fire scars on their stems. Solitary lamellar charcoal pieces were common in the miner-

al soil horizon. We concluded that more than 400 years passed since the last fire in areas occupied by this forest type now. However, deadwoods at the 4th and 5th stages of their decay were completely absent in those forests and, on the contrary, there was a lot of deadwoods at the 1st decay stage. This indicates some external impact on these forests in the past, possibly cuttings which occurred in the region in 18th and 19th centuries [4].

P.(A.) magnoherbosa and *P.(A.) nitrophilomagnoherbosa* occupied a relatively large area in the study region, but only a few individuals of *Pinus* spp. were found there. All these individuals had no fire scars. In the boreal tall-herb forests that grow on watersheds, charcoal in the soil occurred much rarer compared to all other forest types: only single lamellar pieces were found in the mineral soil horizon. In riparian spruce-fir forests, in addition to single pieces of charcoal, thin multiple (up to four) layers of charcoal in old pits were also present. The pits were formed at different moments of forest history, as a result of windfalls on thick alluvial soils. This charcoal material may have originated from rare crown fires in the adjacent watersheds, from where it was transported. A remarkably large area of these forests was covered by deadwoods at the last stages of their decay, indicating the absence of recent fires. Based on the fire signs in vegetation and soils, we estimate that the last fire occurred in these forests more than 400 years.

Discussion

The old-growth forests dominated by *Picea obovata* and *P. obovata* with *Abies sibirica* located on well-drained areas in the plain part of the Komi Republic demonstrate a great variability in species composition and diversity of plants in the ground layer of vegetation. Especially large variability was found in the species composition of vascular plants growing in the field layer: more than a half of these species showed a significant affinity to specific forest types. The diversity of vascular plants revealed strong forest-type specificity, while composition and diversity of bryophyte species seemed to be less specific in regard to the forest types.

Our goal was to assess what environmental parameters affect plant species composition and diversity in the studied old-growth spruce-fir forests. According to Landolt's values, the main environmental gradients along which the forest vegetation varied were soil nutrients, soil reaction and light availability (Figs. 3 and 4). Soil nutrients and reaction are undoubtedly the main drivers of vegetation composition and diversity in the boreal region [65–67]. However, there is a strong feedback between

soil properties and vegetation: the litter of tall herbs is rich in nutrients and has large values of the annual biomass [20, 68–70], thus increasing fertility of soil and improving the soil structure [63, 66, 67, 71]. Therefore, it is likely that the soil properties have changed drastically during successional development of the founded forest ecosystem and were controlled by the type of vegetation, which would explain the good correlation we observe.

In contrast to the soil characteristics, bedrock type is a variable independent of vegetation and therefore it could be considered as a driver of species composition and diversity. However, only riparian forests located on alluvial sediments and nemoral-boreal herb forests located in the south of the region, where silty loams prevail, showed the conjunction of the forest type and the type of bedrock (Table 3). All the other forest types occurred on bedrocks of various types and showed no correlations between the bedrock type and the plant species composition/diversity.

Light availability is a very important environmental factor, and dark coniferous forests have well-illuminated spots owing to gap mosaic in the forest canopy or mesorelief heterogeneity, which is often evident in floodplains. In such cases, high illumination directly affects the species composition and plant diversity of forest communities. However, in the studied forests both the richest tall herb forests and the poorest green moss forests occupied plots with similar light values (Fig. 4). Our calculations also showed that the nemoral-boreal herb forests, which were rich in species, were illuminated rather poorly. Therefore, though important, light availability cannot be considered as a universal factor affected the composition and diversity of the studied forest types.

A high biodiversity of riparian forests can essentially arise from a high variability of microsites that they grow upon. The patchy nature of the microsites can be caused by rivers and streams that provide opportunities for coexistence of species with different ecological properties [12, 13, 28, 30, 33]. Another important factor that increases diversity of microsites in old-growth forests is the pit-and-mound topography caused by treefalls with uprooting [4, 11, 19, 20, 68]. Earlier, this factor was shown to affect the species diversity and plant biomass of the old-growth boreal tall-herb forests located in the mountain part of the Komi Republic [68, 69, 72]. In the present work, we did not test direct relationships between elements of pit-and-mound topography and plant species diversity and composition. However, we checked the relationships between these plant species variables and coverage of deadwoods. Our results showed that there are weak but statistically significant (i) a pos-

itive correlation between the total DWC and bryophyte species diversity and (ii) correlations between DWC at different decay stages and vascular species composition. The results of IndVal analysis also indirectly confirmed our assumption about the importance of microsite structure of community in the maintenance of species diversity. According to the IndVal analysis, species from one to three ECGs showed a significant affinity to the poorest forest types, whereas species affiliated to the species-rich forest types were the species of five and even eight ECGs (Table 5). Species of different ECGs grow at different patches (microsites) therefore the diverse ecological-coenotic structure of vegetation testifies the high microsite diversity of the communities.

Analysis of correlations between the coverage of vegetation layers and species composition/diversity showed that characteristics of vascular plants depended on the coverage of the main layers of vegetation. The dependences, albeit statistically significant, were very low: only the cover of the field layer was quite well correlated (positively) with the vascular plant diversity. This indicates that an increase of the field layer coverage was not simply due to increasing abundance of one or several species, but was also accompanied by a rise in number of species in a plot. An interesting fact is also that the diversity of bryophyte species did not correlate with the area they covered, or with the area covered by the vegetation of any other layer. This result needs to be checked by additional studies and in the other forests and regions.

On the whole, we concluded that the analyzed environmental variables showed too weak correlations with the species composition and plant diversity to be the main factor that controls their variability. However, there is one more factor that broadly separates the “poor” and “rich” communities, and it is their past fire regimes. The plant communities that had the largest differences in their species composition and diversity also mostly varies in the frequency of fires on their territory and in the estimated time elapsed since the last fire.

The forests that were dominated by green mosses, dwarf shrubs and small boreal herbs were formed after multiple fires, with the estimated times since the last fires of 150 years or more. This is consistent with previous studies on modern dark coniferous forests in North-Eastern Fennoscandia that indicate that the majority of these forests experienced recent fires. For example, Uotila et al. [73] showed that, according to historical records, 89 % of 79 boreal forest sites dominated by *Picea abies* and *Vaccinium myrtillus* experienced fires in the 19th or 20th century. In contrast, the time since the last fire in species-rich tall-herb and nemoral-

boreal forests is estimated to exceed 400 years. These forests seem to be better preserved from (or had a better recovery after) fires in comparison with other forest types. Thus, in future studies on plant composition and diversity of old-growth coniferous forests, their fire history has to be taken into account and studied in detail (e.g. with charcoal radiocarbon dating), as it has strong effects on these characteristics.

Conclusions

In this work, we have distinguished seven types of old-growth *Picea obovata* and *Picea obovata/Abies sibirica* forests located in the plain area of the Komi Republic. These forest types vary in composition of their ground vegetation and diversity of vascular plant and bryophyte species. We explain the variability between these forests by differences in their fire history. The ground layer of species-poor dark coniferous forests is dominated by green mosses, dwarf shrubs, small boreal herbs and large ferns. All these forests were formed after multiple fires, and we estimated the last time when they experienced intense fires as 150–400 years ago. The richest spruce-fir forests are tall-herb forests growing either in valleys of rivers and streams or on watersheds and small hills/slopes. These species-rich forests also experienced fires, but much earlier than the forests dominated by green mosses, dwarf shrubs, small boreal herbs and large ferns; we estimated the time since the last fire in these forests to be more than 400 years. The detailed study of regional and local history of those fires is a matter of the future. We believe species-rich dark coniferous forests are very valuable: their study will contribute to our understanding of the theory of forest biodiversity conservation and will help us to define conditions for the nature-based forest management.

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