



Below-ground ectomycorrhizal community structure in the postfire successional *Pinus koraiensis* forests in the central Sikhote-Alin (the Russian Far East)

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ABSTRACT

This study focuses at the effect of forest fire on the extent of ectomycorrhizal (EcM) colonization of *Pinus koraiensis*. The EcM fungal diversity was estimated directly from mycorrhizas using molecular techniques. The revealed EcM fungal community was highly diverse, with 110 operational taxonomic units detected. The members of Russulaceae and Thelephoraceae were among the most dominant species in both the fire and control sites. The most diverse basidiomycete EcM genera at the burned sites were *Tomentella*, *Russula*, *Piloderma*, *Inocybe*, *Suillus*, *Sebacina* and *Lactarius*. Mycorrhizal colonization was found to be high for seedlings grown at the burned and the unburned sites. However, there was a rather significant shift between sites in terms of the taxonomic composition of EcM symbionts as well as the dominant fungal species. A vertical stratification of EcM fungal diversity at the control site and the sites of later succession stages was found to be more leveled. The results of the study indicate that EcM fungi apparently play an important role in the processes of regeneration of natural forest stands after fire at the studied area.

Key words: ectomycorrhiza, fungal diversity, *mITS*, Korean pine, fire, Primorye Territory

РЕЗЮМЕ

Мальшева Е.Ф., Мальшева В.Ф., Коваленко А.Е., Пименова Е.А., Громько М.Н., Бондарчук С.Н., Воронина Е.Ю. Структура сообществ эктомикоризных грибов в почве кедровых лесов разных стадий послепожарной сукцессии в Центральном Сихотэ-Алине (российский Дальний Восток). Целью исследования было изучение эффекта воздействия пожара на степень эктомикоризной (ЭМ) колонизации корней *Pinus koraiensis*. Идентификация ЭМ компонента производилась непосредственно из микоризных окончаний с использованием молекулярных методов. Сообщества ЭМ грибов, ассоциированные с корнями *P. koraiensis*, были весьма разнообразны. Всего было обнаружено 110 операционных таксономических единиц (ОТЕ). Преобладающими по числу видов семействами во всех изученных сообществах, включая контроль, оказались Russulaceae и Thelephoraceae. Наиболее богатыми по видовой представленности родами были *Tomentella*, *Russula*, *Piloderma*, *Inocybe*, *Suillus*, *Sebacina* и *Lactarius*. Было установлено, что степень микоризной колонизации семянцев в сообществах, подвергшихся пожару, и в негоревших участках была высокой. Выявлена разница между изученными сообществами в таксономическом составе и в составе доминирующих видов ЭМ симбионтов, образующих микоризную связь с сеянцами. Было оценено вертикальное распределение мицелия ЭМ грибов в горизонтах почвы. Показано, что это распределение выглядит более выровненным в ненарушенных лесах и на более поздних стадиях сукцессии. Результаты проведенного исследования показывают, что ЭМ грибы играют важную роль в процессах регенерации природных древостоев после пожаров.

Ключевые слова: эктомикориза, разнообразие грибов, *mITS*, кедр корейский, пожар, Приморский край

Nomenclature: Kharkevich 1985-1996 (for vascular plants)

The growth and development of tree stand in boreal and temperate ecosystems are directly dependent on root associations with mycorrhizal fungi (Trappe 1987, Smith & Read 2008, Brundrett 2009). For more than 85 % of terrestrial plant species the acquisition of water and inorganic nutrition from soil as well as their resistance to environmen-

tal stresses are strongly influenced by mycorrhizal symbiosis (Smith & Read 2008, Brundrett 2009). Inversely, the mycorrhizal fungal communities may be greatly affected by fluctuations in abiotic factors, plant community composition and possible scheme of the regeneration of vegetation after disturbance events.

Fire is one of the most important disturbance factors influencing both ectomycorrhizal (EcM) community dynamics and coniferous forests structure causing radical ecological effects in terms of diversity of EcM fungi, spatial distribution of mycelial networks, the success of mycorrhizal colonization of seedlings, as well as the sequential alteration of the phytocoenosis structure and beginning the determined forest succession (Pietikainen & Fritze 1995, Jonsson et al. 1999, Stendell et al. 1999, Grogan et al. 2000, Buscardo et al. 2010, Kipfer et al. 2011). In the Central Sikhote-Alin, the severe fire caused by either natural reasons or by human activity has always been the main source of ecosystem disturbance (Astafiev et al. 2010). Previous investigations of succession patterns of forest communities at this territory have shown the regeneration failure of Korean pine at some sites after fire (Gromyko et al. 2010), but the special studies on the ectomycorrhiza developing in stands regenerating, the EcM community structure changes and its effect on seedlings growth have never been conducted.

Korean pine (*Pinus koraiensis* Siebold et Zucc.) is dominant tree species in the coniferous-broadleaved forests covering approximately one-fourth of the land area in the Sikhote-Alin mountain range (Krestov et al. 2006). Outside the Russian Far East, *P. koraiensis* occurs in northeast China, North Korea and Japan (Nakamura & Krestov 2005), being a part of pure pine forests but more frequently of mixed pine-broadleaved, pine-spruce or pine-larch forests, in which it also dominates. All these forests are species rich, have a complex pattern and consists of mostly nemoral plants, the representatives of the Manchurian flora (Krestov 2003). They often act as a core ecosystem linking large number of rare and endemic species of fungi, plants and animals. The importance of Korean pine forests as valuable and unique ecosystems defines the needs to study of mechanisms of their succession, its course and speed after natural or human disturbances including fire.

Pinaceae is considered to be the one of the oldest extant plant families that has permanent symbiosis with EcM fungi (Hibbett & Matheny 2009). All *Pinus* species, like most tree species in the temperate and boreal ecosystems, was shown to have obligate symbiosis with EcM fungi required for their normal growth and functioning (Read 1998, Smith & Read 2008). *P. koraiensis*, a five-needle pine of subgenus

Strobis (Price et al. 1998), is no exception, and its mycorrhizal status has been reliably confirmed by previous studies (Zengpu et al. 1995, Kikuchi & Futai 2003, Choi et al. 2005, Yamada et al. 2014). However, all the papers quoted have focused only on narrow issues relating to antagonism between ectomycorrhizal symbionts and fungal pathogens, fruiting bodies of certain species biomass estimation, or the chemicals' effects on the activity of mycorrhiza. Until now little is known about diversity of EcM fungi natively associated with *P. koraiensis*, about the fire-resistance of these EcM species and their special role in post-fire regeneration of forests. This is the first study presenting the EcM community structure of mountain Korean pine forests.

This research was initiated to determine: (i) the degree of EcM species diversity reduction after fire disturbance; (ii) the extent of EcM colonization of *P. koraiensis*' roots in naturally regenerating stands depending on age and stage of plant community following fire event; (iii) the species composition and structure of EcM fungal communities obligatory associated with *P. koraiensis* during stand development; (iv) the source of EcM inoculum for post-fire sites; (v) the EcM fungal community potential for restoring its pre-fire composition during the forest regeneration; (vi) soil depth and tree age impact on the EcM species diversity. The results obtained from the study will provide primary information on the ecological role of EcM fungi associated with *P. koraiensis* in the dynamics and formation of coniferbroadleaved forests in the Far East region.

MATERIAL AND METHODS

Study sites

The research was conducted in conifer or conifer-broadleaved (dominated by *Pinus koraiensis*) forests located on the eastern slopes of the Sikhote-Alin Mountain Range within the Sikhote-Alin Biosphere Nature Reserve, in the north of Primorye Territory (44°49'13"–45°41'25"N, 135°48'46"–136°34'23"E, 500–1200 m above sea level) (Fig. 1). This region is affected by monsoon climate and has mean annual precipitation of 700 mm (with 78–85 % rain falling in April–November), mean temperatures ranging from 15° to 18°C in June to August and from -13° to -24°C in December to February, and a frost-free period of 150 days (Smirnova & Gromyko 2006). The soil cover of the territory was formed in

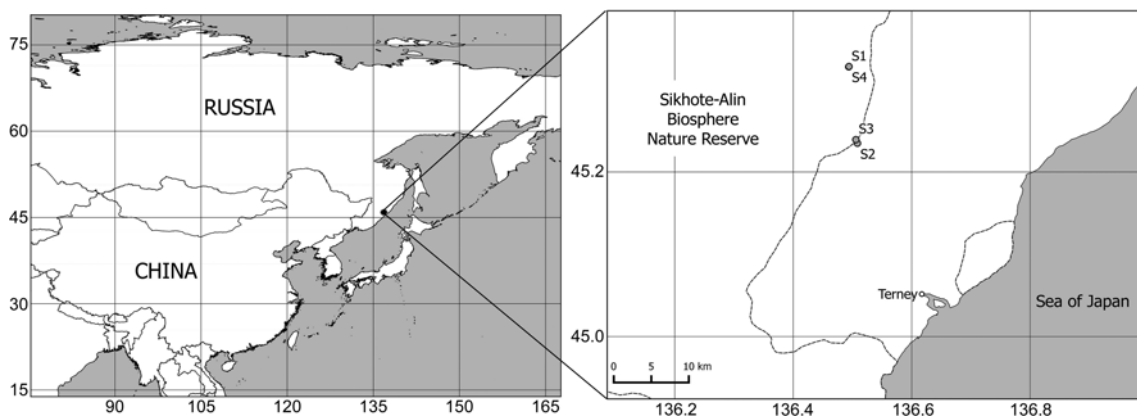


Figure 1 Map showing general study area in the Primorye Territory and sampling sites location in the Sikhote-Alin Mountains

situation of a large variety of plant associations, climatic and geomorphological conditions, diversity of petrographic and chemical composition of the bedrock (Gracheva & Utenkova 2006). For the Reserve territory 20 types and 12 subtypes of soils are defined (Gracheva 2005). Soils in study area are most complex and multicomponent, and aggravated with pyrogenic disturbance of forests. Humus-illuvial burozems is the main soil type in the conifer and conifer-broadleaved forests (Sapozhnikov et al. 2001).

The four sites chosen for the study formed a chronosequence of the valley conifer-broadleaved forest recovering after fire, ranging from early stand development (sapling stage) to old growth phase, where each site represented a certain post-pyrogenic succession stage (Fig. 2). The first site (S1) presented the youngest stage of forest regeneration following the intensive fire which swept about 10 years ago and completely killed almost all mature (more than 150-year-old) trees of *P. koraiensis* as well as other dominant tree species, causing the appearance of large gaps in the forest canopy. Two other sites (S2 and S3) were the succession stages of conifer-broadleaved forest after 60 and 100-year-old wildfire respectively (Table 1). The fourth site (S4) was selected as a control and represented the stand in which the canopy was predominantly old growth Korean pine trees and there were detected no signs of previous fires. Tree ages of *P. koraiensis* in four study sites were: 1–5 year-old, 7–20 year-old, 40–70 year-old, 120–150 year-old and >200 year-old, respectively. At each study site, one plot (at least 400 m² in size) was established for seedlings and soil cores sampling.

Seedlings and roots sampling

Sampling was conducted in August 2013 and in August–September 2014. At each site, on the average 12 (but not less than 5) randomly selected naturally regenerating seedlings were completely removed from the soil with the entire root system, at the same time the 30-cm deep soil cores were sampled with steel tube 5 cm in diameter on the circular plots within one meter around the perimeter of individual trees of different age in their crown projection (at least four for each tree, taken from different sides). Every time before core sampling, undecomposed litter (if present) was removed. In

most cases, the average depth of the organic horizon was 20–25 cm. Seedlings and soil cores were carefully wrapped with polyethylene film or aluminum foil and placed into sealed plastic bags for transporting to field station and then were processed within 72 h. In total, 47 seedlings and 154 soil cores associated with trees of different age classes were collected. Seedlings were rinsed in running water to release their root system, while each soil core was divided at first into soil layers, and roots from each layer then were washed free of soil. As the roots were cleaned, they were examined under a binocular microscope in order to check tips for EcM mantle presence, to separate live Korean pine roots from dead roots and other tree species roots, and to classify pine roots into morphotypes for further molecular investigation. We had no purpose to categorize and to determine the EcM morphotypes (following Agerer 1987–2002) to identify the fungal partner. Each "ad hoc morphotype" selected based on shape, type of ramification, colour and presence of rhizomorphs was then pooled in identical groups which were treated separately in a subsequent molecular typing to avoid mixing different taxa of EcM fungi in one test tube. After morphotyping the samples of tips were stored in 2 % cetyltrimethylammonium bromide (CTAB) buffer in 1.5 ml tubes for further analysis.

Molecular analysis and EcM fungi identification

DNA was extracted from the root tips using the Axy-Prep™ Multisource Genomic DNA Miniprep Kit (Axygen Biosciences) or NucleoSpin® Plant II Genomic DNA Extraction Kit (Macherey-Nagel GmbH and Co. KG) according to the manufacturer's protocols, and the specific DNA region (ITS1-5.8S-ITS2) was then PCR amplified followed Gardes & Bruns (1993) using either the fungal-specific primer pair ITS-1F/ITS-4 or the basidiomycete-specific pair ITS-1F/ITS-4B (Gardes & Bruns 1993, White et al. 1990). Successful amplifications confirmed visually with agarose gel electrophoresis were then cleaned using the Fermentas Genomic DNA Purification Kit (Thermo Scientific) and quantified using the NanoPhotometer® P-300 (Implen GmbH, Germany). The prepared PCR product was then sequenced with the same primers pairs. Cycle

Table 1. Location and forest stand characteristics of the four study sites

Site	Location name	Latitude (N) / longitude (S) / elevation (m asl)	Time since fire (yrs)	Dominant tree species	Dominant shrub species	Dominant herb species	Canopy cover (%)	<i>P. koraiensis</i> age class *
S1	Ust'-Shanduy	45°19.642' / 136°29.629' / 267	≈ 10	–	<i>Rubus sachalinensis</i> , <i>Philadelphus tenuifolius</i>	<i>Carex campylobina</i> , <i>C. lancibracteata</i> , <i>Pseudocystopteris spinulosa</i>	–	(1), (2)
S2	Yasnaya	45°14.088' / 136°30.508' / 154	50–60	<i>Betula platyphylla</i>	<i>Corylus mandshurica</i> , <i>Euonymus pauciflora</i>	<i>Carex lancibracteata</i> , <i>Maianthemum dilatatum</i> , <i>Pseudocystopteris spinulosa</i>	75%	(1), (2), (3), (4)
S3	Yasnaya	45°14.350' / 136°30.350' / 158	> 100	<i>Larix cajanderi</i> , <i>Betula platyphylla</i>	<i>Lonicera chrysantha</i> , <i>Spiraea flexuosa</i>	<i>Carex lancibracteata</i> , <i>C. campylobina</i> , <i>C. siderosticta</i>	50%	(2), (3)
S4	Ust'-Shanduy	45°19.666' / 136°29.650' / 264	–	<i>Pinus koraiensis</i>	<i>Philadelphus tenuifolius</i> , <i>Ribes maximoviczianum</i>	<i>Carex campylobina</i> , <i>C. quadriflora</i> , <i>Dryopteris crassirhizoma</i> , <i>Athyrium sinense</i> , <i>Maianthemum bifolium</i> , <i>Mitella nuda</i>	85%	(1), (2), (3), (4), (5)

* (1) *Pinus koraiensis* age classes: (1) – 1–5 year-old, (2) – 7–20 year-old, (3) – 40–70 year-old, (4) – 120–150 year-old and (5) – >200 year-old



Figure 2 Studied sites representing different post-pyrogenic succession stages of Korean pine-broadleaved forest (S1–S3) and control stand (S4)

sequencing was done by the reaction termination method using the Terminator Ready Reaction Mix according to the protocol of Applied Biosystems (ABI BigDye® terminator v 1.1 cycle sequencing kit protocol). Products were purified by ethanol precipitation method (Applied Biosystems 2009) and sequenced using ABI model 3130 Genetic Analyzer (Applied Biosystems). Sequencing Analysis 5.3.1 (Applied Biosystems) was used for processing the raw data.

Obtained sequences with high quality and degree of similarity (cutoff of 97 %) were clustered into groups and were manually processing and optimized using the MEGA 6 (Tamura et al. 2013). Chimeric sequences assessed by reference-based checking using GenBank were removed from further analyses. We regarded a sequence as a chimera when its ITS1 and ITS2 regions had 98–100 % similarity to different species or > 90 % similarity to different genera. The remaining consensus sequences were then analyzed and clustered into “Operational Taxonomic Units” (OTUs) using the BLASTn search algorithm in NCBI GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) or UNITE sequence databases (<http://unite.ut.ee/>, Kõljalg et al. 2005). The degree of similarity was accepted: for species level $\geq 97\%$ (Kõljalg et al. 2013, Smith et al. 2013), for genus level 95–97 % and for family to order level < 95 %. When two or more sequences or sequence groups differed to each other but matched the same entry in databases, a number was added to the name to mark the differences (e.g. *Russula* sp. 1 and *Russula* sp. 2). A list with the taxa names and the accession numbers of the corresponding database entry of the best match is given in Table 2. Fifteen OTUs,

viz. *Armillaria gemina* known having pathogenic or saprotrophic lifestyle (Anderson 1986, Banik et al. 1996), *Illyonectria robusta*, *I. radicicola* (Agustí-Brisach & Armengol 2013), *Laetium* sp. and *Tinctoporellus* cf. *epimiltinus* being endophytic fungi, saprotrophic species from the genera *Mycena*, *Clitocybe* and *Marasmius*, yeast from the genus *Cryptococcus*, as well as *Nectria lugdunensis* usually behaving as saprotrophic or pathogenic fungi (Chaverri et al. 2011), were excluded from further analyses because they are not strictly considered to be EcM fungi (Tedersoo et al. 2010). Their detection in the soil samples was probably due to the presence of either free mycelium of saprotrophic fungi near ectomycorrhizal mantle, or pathogenic/endophytic fungi hyphae in the inner tissues of the root.

All newly generated sequences have been deposited in GenBank with corresponding accession numbers.

Statistical analysis

For this analysis, all OTUs represented taxa successfully identified to species level or to generic, family and order level only, were included. We considered the groups of EcM root tips of identical morphotype from a certain soil layer of a single core as independent units, but we did not assessed root tips abundance within one soil layer. Thus, diversity of EcM fungi we calculated was based on frequency but not abundance. Comparison of study sites, tree age classes and soil layers based on species composition of EcM fungi was performed. Hierarchical cluster analysis creating groups from multivariate data using a dissimilarity matrix was employed to categorize study sites and tree age

classes based on taxonomic diversity of EcM fungi. It was performed with Euclidean distance measure using Statistica version 10 (StatSoft Inc. 2011).

RESULTS

Sequence data and taxonomic assessments

During two consecutive years (2013–2014), 499 EcM root tips of *P. koraiensis* were sampled from 47 seedlings and 154 soil cores. The molecular technique was used to screen phylogroups resulting from the sequencing of fungal DNA from the EcM mantle. A total of 283 non-chimaerical *m*ITS sequences were obtained. The detected genotypes were grouped into 110 distinct OTUs of EcM fungi. We were able to analyze successfully about 57 % of the selected morphotypes of *P. koraiensis* seedlings and soil core samples. The number of OTUs identified to the species level was 67, to the generic level – 43, and 3 taxa were determined to the order level. Of these, overwhelming majority of OTUs (98) was represented by basidiomycete EcM taxa and only 12 OTUs were ascomycete EcM fungi (Table 2). As shown in Table 3, Russulaceae was the most commonly detected family almost in all forest sites, followed by Thelephoraceae, Inocybaceae and Atheliaceae.

Of the 110 OTUs in total, about 37 % were previously unsequenced lineages that found for the first time in soil of studied area and are not represented in public databases (Table 2). The majority of undetected species belonged to the genera *Tomentella* and *Inocybe*, most diverse groups worldwide, as well as the genus *Piloderma*.

Fire effect on diversity and composition of OTUs

The number of OTUs associated with Korean pine roots were generally somewhat lower on burned sites (S1–S3) than in unburned forest stand (S4). However, we did not reveal a clear trend of OTUs numbers increasing with time period since fire increase, as it was shown, for example, for EcM succession patterns in *Pinus sylvestris* forests after fire (Kipfer et al. 2011).

Most of OTUs were identified for the first time as symbionts of *P. koraiensis*. In general, only a few EcM fungi had frequent occurrence in soil samples while most species occurred sporadically or only once (Table 4). Ectomycorrhizal

communities of all studied forest sites differed in species composition as demonstrated by hierarchical cluster analysis (Fig. 3). 13 species were found at both the control and one or more fire plots. The species composition at burned and unburned sites is correlated in some extent with the age of the forest stands. It is evident that two sites represented succession stages of >100-yr-old (S3) and 50–60-yr-old (S2) after wildfire are closer to the control site (S4) than to the youngest stage of stand regeneration (S1) with significantly more stand structure disturbance and, as a consequence,

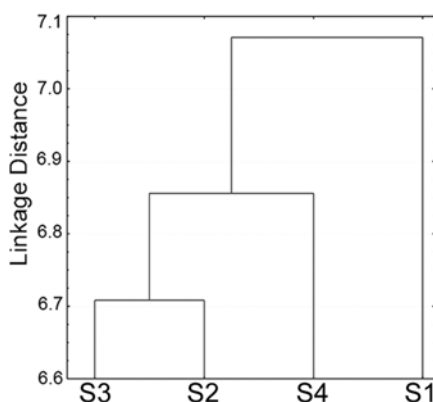


Figure 3 The dendrogram (Euclidean distance, single linkage) of studied sites grouped by EcM fungi taxonomic composition similarity

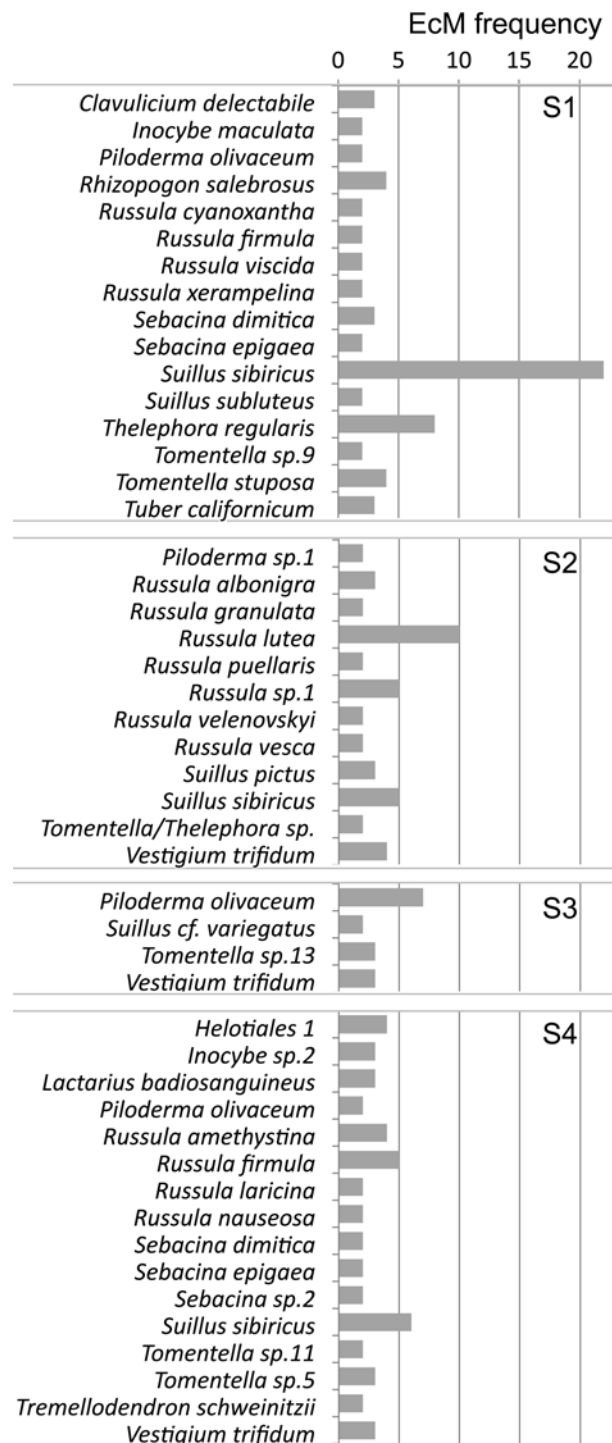


Figure 4 EcM fungi frequency (number of samples in which OTU occurred if > 1) from burned sites (S1–S3) and unburned site (S4)

Table 2. Ectomycorrhizal fungi detected on the roots of *Pinus koraiensis*

Taxa	No. of samples with a taxon revealed	Soil horizon or seedling age	Sample plot	GenBank accession number	BLAST (GenBank, UNITE) result	Similarity (%)
<i>Albatrellus</i> sp.	1	AB	2	KJ769263	<i>Albatrellus ovinus</i> (UDB018057)	482/532 (90)
<i>Amanita spissa</i>	1	Ad	1	KJ769264	<i>Albatrellus skamianus</i> (EU669253)	656/740 (89)
<i>Amanita regalis</i>	1	O3	1	KJ769265	<i>Amanita spissa</i> (AJ889924)	703/703 (100)
<i>Amanita vaginata</i>	1	A1	1	KP783429	<i>Amanita regalis</i> (UDB015178)	621/625 (99)
<i>Amphinema byssoides</i>	3	Ad, A1, AB	1, 3, 4	KP783430	<i>Amanita vaginata</i> (JF907756)	506/516 (98)
<i>Amphinema</i> sp. 1	1	A1	3	KJ769267	<i>Amphinema byssoides</i> (AY838271)	614/623 (99)
<i>Amphinema</i> sp. 2	1	AB	3	KP783431	<i>Amphinema</i> sp. (JX907810)	612/667 (92)
<i>Boletus ferrugineus</i>	1	AB	1	KP783432	<i>Amphinema</i> sp. (JX907810)	701/705 (99)
<i>Cenococcum geophilum</i>	2	B	1, 2	KJ769268	<i>Xerocomus ferrugineus</i> (HQ207698)	685/690 (99)
<i>Ceratobasidium</i> sp.	1	A1	2	KP783433	<i>Cenococcum geophilum</i> (AY394919)	513/540 (95)
<i>Chromelosporium</i> sp.	1	Ad	4	KP783434	<i>Ceratobasidium cornigerum</i> (UDB017026)	328/357 (91)
<i>Clavulicium delectabile</i>	3	A1, AB	1	KP783435	<i>Chromelosporium</i> (JQ318652)	532/540 (99)
<i>Cortinarius</i> sp. 1	1	A1	4	KJ769270	<i>Membranomyces delectabilis</i> (UDB016308)	779/782 (99)
<i>Cortinarius</i> sp. 2	2	Ad	1, 2	KP783436	<i>Cortinarius</i> cf. <i>decepiens</i> (AJ889946)	535/562 (95)
<i>Elaphomyces muricatus</i>	1	AB	2	KP783437	<i>Cortinarius venetus</i> (UDB015960)	179/182 (98)
Helotiales 1 (cf. <i>Dasyyscyphella/Lachnellula</i>)	4	A1, AB	4	KP783438	<i>Elaphomyces muricatus</i> (JF834198)	597/608(98)
Helotiales 2	1	AB	4	KP783439	<i>Dasyyscyphella montana</i> (AB481242)	473/500 (95)
Helotiales 3	1	Ad	3	KP783440	<i>Lachnellula occidentalis</i> (AB481245)	462/500 (92)
<i>Humaria hemisphaerica</i>	1	Ad	4	KJ769271	<i>Bisporella citrina</i> (AF335454)	480/564 (85)
<i>Inocybe geophylla</i>	1	Ad	2	KJ769276	<i>Vestigium trifidum</i> (KC407777)	548/569 (96)
<i>Inocybe langei</i>	1	Ad	1	KP783441	<i>Humaria hemisphaerica</i> (DQ200832)	668/672 (99)
<i>Inocybe maculata</i>	2	Ad	1	KP783442	<i>Inocybe lilacina</i> (HQ604297)	837/857 (98)
<i>Inocybe nitidiuscula</i>	1	AB	1	KJ769277	<i>Inocybe langei</i> (UDB011867)	794/803 (98)
<i>Inocybe sororia</i>	1	AB	3	KP783443	<i>Inocybe maculata</i> (AJ534933)	778/785 (99)
<i>Inocybe</i> sp. 1	1	~ 10 yrs	1	KJ769272	<i>Inocybe nitidiuscula</i> (HQ604086)	696/700 (99)
<i>Inocybe</i> sp. 2	3	Ad+A1	4	KJ769273	<i>Inocybe sororia</i> (HQ604626)	794/801 (99)
<i>Inocybe</i> sp. 3	1	A1	4	KJ769274	<i>Inocybe</i> sp. (FJ936168)	663/724 (92)
<i>Inocybe</i> sp. 4	1	Ad	4	KJ769275	<i>Inocybe appendiculata</i> (FN550926)	705/765 (92)
<i>Laccaria laccata</i> var. <i>pallidifolia</i>	1	Ad	1	KP783444	<i>Inocybe muricellata</i> (AM882915)	746/859 (87)
<i>Lactarius badiosanguineus</i>	3	AB	4	KJ769280	<i>Inocybe quietiodor</i> (FJ936168)	686/772 (89)
<i>Lactarius luculentus</i> var. <i>laetus</i>	1	Ad	1	KP783445	<i>Laccaria laccata</i> var. <i>pallidifolia</i> (DQ149853)	497/502 (99)
<i>Lactarius tabidus</i>	1	AB	2	KP783446	<i>Lactarius badiosanguineus</i> (UDB015865)	777/786 (98)
<i>Lactarius</i> sp. 1	1	7-8 лет	2	KJ769278	<i>Lactarius luculentus</i> var. <i>laetus</i> (FJ845419)	876/884 (99)
<i>Lactarius</i> sp. 2	1	Ad	2	KJ769279	<i>Lactarius tabidus</i> (HM189828)	689/703 (98)
<i>Leotiomycetes</i>	1	AB	2	KP783448	<i>Lactarius fennoscandicus</i> (UDB011462)	570/642 (88)
* <i>Oidiodendron maius</i>	1	AB	4	KP783449	<i>Lactarius alpinus</i> (HQ714789)	717/751 (95)
* <i>Phialocephala</i> cf. <i>fortinii</i>	1	Ad	4	KJ769326	<i>Leotiomycetes</i> (HM044587)	479/491 (98)
<i>Phlebiella</i> sp.	1	Ad	4	KP783450	<i>Oidiodendron maius</i> (KF850371)	529/532 (99)
<i>Piloderma</i> cf. <i>byssinum</i>	1	B	2	KP783451	<i>Phialocephala fortinii</i> (AY394915)	478/493 (97)
<i>Piloderma</i> cf. <i>lanatum</i>	1	Ad	1	KP783452	<i>Phlebiella ardosiaea</i> (UDB016408)	436/535 (81)
<i>Piloderma olivaceum</i>	11	Ad, A1, AB	1, 2, 3, 4	KJ769281	<i>Piloderma byssinum</i> (DQ365682)	187/195 (96)
<i>Piloderma bicolor</i>	1	4-5 yrs	3	KJ769282	<i>Piloderma lanatum</i> (DQ469288)	639/667 (96)
<i>Piloderma</i> sp. 1	2	Ad, B	2	KJ769283	<i>Piloderma olivaceum</i> (JQ711809)	738/749 (99)
<i>Piloderma</i> sp. 2	1	Ad	2	KJ769284	<i>Piloderma jallax</i> (UDB016354)	745/755 (98)
<i>Piloderma</i> sp. 3	1	Ad	1	KP783453	<i>Piloderma olivaceum</i> (JQ711802)	728/795 (92)
<i>Pseudotomentella mucidula</i>	1	A1	4	KP783454	<i>Piloderma sphaerosporum</i> (JQ711866)	764/806 (95)
<i>Pseudotomentella</i> sp. 1	1	AB	1	KJ769285	<i>Piloderma</i> sp. (AJ534902)	712/719 (99)
<i>Pseudotomentella</i> sp. 2	2	A1, B	3, 4	KP783455	<i>Pseudotomentella mucidula</i> (AF274769)	594/598 (99)
<i>Rhizopogon</i> cf. <i>salebrosus</i>	4	A1, AB	1	KJ769300	<i>Pseudotomentella tristis</i> (UDB011636)	552/602 (91)
<i>Russula albonigra</i>	3	B	2	KJ769287	<i>Pseudotomentella tristis</i> (UDB011636)	577/600 (96)
<i>Russula amethystina</i>	4	A1, AB	4	KP783456	<i>Rhizopogon salebrosus</i> (HQ914333)	762/784 (97)
<i>Russula brunneoviolacea</i>	1	AB	2	KJ769296	<i>Russula albonigra</i> (DQ422029)	802/815 (98)
<i>Russula chloroides</i>	1	B	2	KJ769288	<i>Russula amethystina</i> (KF850402)	615/618 (99)
<i>Russula cyanoxantha</i>	2	AB	1	KJ769289	<i>Russula brunneoviolacea</i> (UDB015985)	799/816 (97)
<i>Russula firmula</i>	7	A1, Ad, AB	1, 4	KJ769290	<i>Russula chloroides</i> (UDB018794)	799/809 (98)
<i>Russula granulata</i>	2	5-8 yrs	2	KJ769291	<i>Russula cyanoxantha</i> (UDB018007)	558/571 (97)
<i>Russula integriformis</i>	1	Ad	4	KP783458	<i>Russula firmula</i> (DQ422017)	545/558 (98)
					<i>Russula granulata</i> (JQ272365)	650/658 (99)
					<i>Russula integriformis</i> (AY061684)	712/717 (99)

with shifts in balance and composition of EcM community. Thereby, a certain tendency for EcM community composition of burned sites later succession stages to converge to that of unburned ones can be traced.

The members of Russulaceae and Thelephoraceae were among the most dominant species in both the fire and control sites. The most diverse basidiomycete EcM genera at the burned sites were *Tomentella* (16 OTUs/24 occurrences), *Russula* (14/39), *Piloderma* (7/16), *Inocybe* (6/9), *Suillus*

(5/35), *Sebacina* (4/8) and *Lactarius* (4/4) (Fig. 4). Other genera represented by less than four species but more than one were *Amanita* (3/3), *Amphinema* (2/3), *Cortinarius* (2/2), *Pseudotomentella* (2/2), *Thelephora* (2/9) and *Tylospora* (2/2). Among EcM fungi occurred at the burned sites, several taxa were shown to be clearly dominant in our samples: *Suillus sibiricus*, *Russula firmula*, *Russula* sp. 1, *Russula lutea*, *Sebacina dimitica*, *Tomentella stuposa*, *Thelephora regularis*, *Piloderma olivaceum*, *Rhizopogon* cf. *salebrosus* and ascomycete species *Ves-*

Table 2. Continued

Taxa	No. of samples with a taxon revealed	Soil horizon or seedling age	Sample plot	GenBank accession number	BLAST (GenBank, UNITE) result	Similarity (%)
<i>Russula laricina</i>	2	AB	4	KP783459	<i>Russula laricina</i> (KF850405)	551/555 (99)
<i>Russula lutea</i>	10	A1, AB, B	2	KJ769292	<i>Russula lutea</i> (HQ604848)	842/853 (99)
<i>Russula nauseosa</i>	2	A1, AB	4	KJ769293 KP783460	<i>Russula nauseosa</i> (UDB011239)	780/786 (99)
<i>Russula nigricans</i>	1	AB	4	KP783457	<i>Russula nigricans</i> (DQ367915)	785/793 (99)
<i>Russula puellaris</i>	2	B	2	KP783461	<i>Russula puellaris</i> (HM189941)	665/672 (99)
<i>Russula</i> cf. <i>sanguinea</i>	1	A1	4	KP783463	<i>Russula sanguinea</i> (UDB011318)	776/806 (96)
<i>Russula turci</i>	1	AB	4	KP783462	<i>Russula turci</i> (KF002780)	676/682 (99)
<i>Russula velenovskyi</i>	2	AB	2	KJ769294	<i>Russula velenovskyi</i> (AY061721)	693/697 (99)
<i>Russula vesca</i>	2	A1, AB	2	KJ769295	<i>Russula vesca</i> (DQ422018)	765/783 (98)
<i>Russula viscida</i>	2	AB	1	KP783464	<i>Russula viscida</i> (FJ627039)	601/615 (98)
<i>Russula xerampelina</i>	2	AB	1	KP783465	<i>Russula xerampelina</i> (HM240542)	799/802 (99)
<i>Russula</i> sp. 1	6	A1, Ad, AB	2, 4	KJ769297 KP783466	<i>Russula sanguinea</i> (UDB011318)	758/788 (96)
<i>Russula</i> sp. 2	1	B	4	KJ769298	<i>Russula xerampelina</i> (FJ845433)	790/856 (92)
<i>Russula</i> sp. 3	1	AB	3	KJ769299	<i>Russula gracilis</i> (FJ845431)	803/837 (96)
<i>Sebacina candida</i>	2	AB	2, 4	KP783467	<i>Sebacina candida</i> (KF061277)	590/604 (98)
<i>Sebacina dimitica</i>	5	A1, AB	1, 4	KJ769301 KP783469	<i>Sebacina dimitica</i> (UDB016422)	585/593 (98)
<i>Sebacina epigaea</i>	4	A1, 3 yrs	1, 4	KJ769302 KP783468	<i>Sebacina epigaea</i> (JQ665492)	564/588 (96)
<i>Sebacina</i> sp. 1	1	4 yrs	3	KJ769303	<i>Sebacina incrustans</i> (UDB014122)	571/609 (93)
<i>Sebacina</i> sp. 2	2	Ad	4	KP783470	<i>Sebacina</i> sp. (AB831806)	514/539 (95)
<i>Suillus pictus</i>	3	A1, AB	2	KJ769304	<i>Suillus pictus</i> (AB284411)	687/691 (99)
<i>Suillus sibiricus</i>	33	A1, Ad, AB	1, 2, 4	KJ769305	<i>Suillus sibiricus</i> (AF166512)	570/578 (99)
<i>Suillus subluteus</i>	2	6 yrs	1	KJ769306	<i>Suillus subluteus</i> (AB284444)	585/586 (99)
<i>Suillus</i> cf. <i>tomentosus</i>	1	8 yrs	3	KJ769307	<i>Suillus tomentosus</i> (FJ845441)	797/829 (96)
<i>Suillus</i> cf. <i>variegatus</i>	2	4–5 yrs	3	KJ769308	<i>Suillus variegatus</i> (JQ711867)	689/714 (96)
<i>Thelephora regularis</i>	8	AB	1	KJ769309	<i>Thelephora</i> aff. <i>regularis</i> (KC152241)	623/645 (97)
<i>Thelephora</i> sp.	1	A1	2	KP783471	<i>Thelephora caryophyllea</i> (UDB000119)	634/685 (92)
<i>Tomentella botryoides</i>	1	O ₂ –O ₃	2	KJ769311	<i>Tomentella botryoides</i> (UDB000255)	580/582 (99)
<i>Tomentella bryophila</i>	1	O ₃	1	KJ769312	<i>Tomentella bryophila</i> (UDB014252)	394/399 (98)
<i>Tomentella ellisii</i>	1	3–4 yrs	1	KP783473	<i>Tomentella ellisii</i> (AF272913)	533/543 (98)
<i>Tomentella lateritia</i>	2	Ad	1, 4	KP783474	<i>Tomentella lateritia</i> (UDB016439)	784/789 (99)
<i>Tomentella stuposa</i>	5	O ₃ , Ad	1, 4	KJ769313 KP783475	<i>Tomentella stuposa</i> (AF272902)	576/579 (99)
<i>Tomentella subulilacina</i>	2	AB, 4–5 yrs	2, 3	KJ769310 KP783476	<i>Tomentella albomarginata</i> (UDB011601)	720/729 (98)
<i>Tomentella</i> cf. <i>viridula</i>	1	Ad	4	KP783477	<i>Tomentella viridula</i> (UDB016392)	762/791 (96)
<i>Tomentella</i> sp. 1	1	A1	1	KJ769314	<i>Tomentella bryophila</i> (UDB018449)	627/666 (94)
<i>Tomentella</i> sp. 2	1	A1	1	KJ769315	<i>Tomentella coerulea</i> (UDB016432)	609/649 (93)
<i>Tomentella</i> sp. 3	1	17–18 yrs	1	KJ769316	<i>Tomentella viridula</i> (UDB016192)	692/732 (94)
<i>Tomentella</i> sp. 4	1	O ₂ –O ₃	1	KJ769317	<i>Thelephora palmata</i> (UDB015185)	722/780 (92)
<i>Tomentella</i> sp. 5	3	A1, Ad	4	KJ769318	<i>Tomentella coerulea</i> (UDB016493)	733/769 (95)
<i>Tomentella</i> sp. 6	1	A1	2	KJ769319	<i>Tomentella terrestris</i> (UDB016369)	672/700 (96)
<i>Tomentella</i> sp. 7	1	A1	4	KJ769320	<i>Tomentella bryophila</i> (UDB018449)	784/827 (94)
<i>Tomentella</i> sp. 8	1	7–8 yrs	2	KJ769321	<i>Tomentella terrestris</i> (UDB011638)	494/543 (90)
<i>Tomentella</i> sp. 9	2	3–4 yrs	1	KP783478	<i>Tomentella</i> (HQ336691)	670/675 (99)
<i>Tomentella</i> sp.10	2	Ad, 3–4 yrs	1, 2	KP783479	<i>Tomentella</i> (FR852141)	763/771 (99)
<i>Tomentella</i> sp.11	2	Ad, A1	4	KP783480	<i>Tomentella</i> (EU668198)	668/705 (95)
<i>Tomentella</i> sp.12	1	A1, 6 yrs	4	KP783481	<i>Tomentella</i> (FJ816765)	731/756 (97)
<i>Tomentella</i> sp.13	4	Ad, A1	3, 4	KP783482	<i>Tomentella</i> sp. (KM576635)	622/632 (98)
<i>Tomentella</i> / <i>Thelephora</i> sp.	2	A1, AB	2	KP783472	Thelephoraceae (JF519233)	718/773 (93)
<i>Tomentellopsis submollis</i>	1	4 yrs	3	KJ769322	<i>Tomentellopsis submollis</i> (JQ711898)	719/727 (99)
<i>Tremelodendron schweinitzii</i>	2	Ad, AB	4	KP783483	<i>Tremelodendron pallidum</i> (AF384862)	583/598 (97)
<i>Tuber californicum</i>	4	O ₃ , Ad	1, 2	KJ769323 KP783484	<i>Tuber californicum</i> (DQ478657)	246/249 (99)
<i>Tylospora asterophora</i>	1	A1	2	KJ769324	<i>Tylospora asterophora</i> (UDB008244)	519/522 (99)
<i>Tylospora fibrillosa</i>	1	A1	2	KP783485	<i>Tylospora fibrillosa</i> (AF052563)	624/625 (99)
<i>Vestigiium trifidum</i>	10	Ad, A1, AB	2, 3, 4	KJ769325 KP783486	<i>Vestigiium trifidum</i> (KC407777)	538/557 (97)

* - unclear ectomycorrhizal status

trifidum. The first six species were also most frequent species at the control site (S4), thus they can be either resistant to fire depression or be general colonizers with inoculum source at the unburned adjacent forest area.

As earlier colonizers not sampled neither in the control site nor in the late stages of forest succession, we can consider the following taxa: *Amanita spissa*, *A. regalis*, *A. vaginata*, *Boletus ferrugineus*, *Clavulicium delectabile*, *Cortinarius* sp. 2, *Inocybe langii*, *I. maculata*, *I. nitidiuscula*, *Inocybe* sp. 1, *Laccaria lac-*

cata var. *pallidifolia*, *Lactarius luculentus* var. *laetus*, *Piloderma* cf. *lanatum*, *Piloderma* sp. 3, *Pseudotomentella* sp. 1, *Rhizopogon* cf. *salebrosus*, *Russula cyanoxantha*, *R. viscida*, *R. xerampelina*, *Suillus subluteus*, *Thelephora regularis*, *Tomentella bryophila*, *T. ellisii* and other unidentified species of *Tomentella* (sp. 1, sp. 2, sp. 3, sp. 4 and sp. 9). In the 10-yr-old stand, *Suillus sibiricus* and *Thelephora regularis* colonized the highest proportion of root tips, followed by *Rhizopogon* cf. *salebrosus*, *Tomentella stuposa*, *Sebacina dimitica* and *Russula firmula*.

The most common EcM phylotypes, present only in 50–60-yr-old and >100-yr-old stands (S2 and S3 sites respectively), include *Albatrellus* sp., *Amphinema* sp. 2, *Ceratobasidium* sp., *Cortinarius* sp. 2, *Elaphomyces muricatus*, unidentified Helotiales 2 species, *Inocybe geophylla*, *I. sororia*, *Lactarius* spp., *Piloderma* cf. *byssinum*, *P. bicolor* and other unidentified *Piloderma* species (sp. 1 and sp. 2), *Russula albonigra*, *R. brunneoviolacea*, *R. chloroides*, *R. granulata*, *R. lutea*, *R. puellaris*, *R. velenovskyi*, *R. vesca*, *Russula* sp. 3, *Sebacina* sp. 1, *Suillus pictus*, *S.* cf. *tomentosus*, *S.* cf. *variegatus*, *Thelephora* sp., *Tomentella botryoides*, *T. subhilarina*, *Tomentella* sp. 6, *Tomentella* sp. 8, *Tomentellopsis submollis*, *Tylospora asterophora* and *T. fibrillosa* (Fig. 4).

Besides *Amphinema* species, *Chromelosporium* sp., *Cortinarius* sp. 1, and ascomycetes *Humaria hemisphaerica*, *Oidiiodendron mains*, *Phialocephala* cf. *fortinii*, the EcM communities of the unburned forest stand (S4) were dominated by members of the Russulaceae, Inocybaceae, Thelephoraceae, several *Sebacina* species and unidentified species from Helotiales, which were not present in the burned sites. At the same time, most frequent species of fungi forming mycorrhizas in the 10-yr-old stand was shown also to form EcM community in the three older stands, including the control site. However, there was a tendency for frequency of some of these fungi to change with stand age. Thus, relative frequency (as occurrence in root samples) of *Piloderma olivaceum* and *Sebacina epigea* increased with age of stand after fire event, while that of *Suillus sibiricus* and *Tomentella stiposa* decreased significantly with stand age.

Phytocoenosis parameters and EcM community structure

Obviously, many environmental conditions of abiotic and biotic nature, and particularly phytocoenosis parameters, are able to significantly affect the variation in EcM

Table 3. The taxonomic distribution (species number) of the EcM fungi OTUs at different sites

Family of fungi	The number of species on plot			
	S1	S2	S3	S4
Families characteristic of early successional stages				
<i>Amanitaceae</i>	3	-	-	-
<i>Boletaceae</i>	1	-	-	-
<i>Clavulinaceae</i>	1	-	-	-
<i>Hydnangiaceae</i>	1	-	-	-
<i>Rhizogonaceae</i>	1	-	-	-
Families characteristic of late successional stages (first scenario)				
<i>Albatrellaceae</i>	-	1	-	-
<i>Ceratobasidiaceae</i>	-	1	-	-
<i>Elaphomycetaceae</i>	-	1	-	-
Families characteristic of early and late successional stages				
<i>Gloniaceae</i>	1	1	-	-
<i>Tuberaceae</i>	1	1	-	-
Families characteristic of native forest (control)				
<i>Myxotrichaceae</i>	-	-	-	1
<i>Pezizaceae</i>	-	-	-	1
<i>Pyronemataceae</i>	-	-	-	1
<i>Vibrissaceae</i>	-	-	-	1
Families independent of successional stages				
<i>Atheliaceae</i>	4	6	4	3
<i>Inocybaceae</i>	4	1	1	3
<i>Russulaceae</i>	5	12	1	10
<i>Sebacinaceae</i>	2	1	1	5
<i>Suillaceae</i>	2	2	2	1
<i>Thelephoraceae</i>	12	7	4	10
<i>Cortinariaceae</i>	1	1	-	1

Table 4. The most commonly detected (occurred more than once) EcM fungi frequency on *P. koraiensis* roots (data from 154 soil cores) and seedlings (at different sites)

Taxa	Number of EM cores (for all plots)	Number of seedlings			
		S1	S2	S3	S4
Taxa characteristic of early successional stages					
<i>Cortinarius</i> sp.2	-	1	-	-	-
<i>Inocybe</i> sp.1	-	1	-	-	-
<i>Russula cyanoxantha</i>	2	1	-	-	-
<i>Suillus subluteus</i>	2	1	-	-	-
<i>Tomentella ellisii</i>	-	1	-	-	-
<i>Tomentella stiposa</i>	5	2	-	-	-
<i>Tomentella</i> sp.9	2	2	-	-	-
<i>Tomentella</i> sp.10	2	1	-	-	-
<i>Tomentella</i> sp.1	-	1	-	-	-
<i>Tomentella</i> sp.2	-	1	-	-	-
<i>Tomentella</i> sp.3	-	1	-	-	-
Taxa characteristic of late successional stages (first scenario)					
<i>Russula granulata</i>	2	-	2	-	-
<i>Lactarius</i> sp. 1	-	-	1	-	-
<i>Tomentella</i> sp.7	-	-	1	-	-
<i>Tomentella</i> sp.8	-	-	1	-	-
<i>Tuber californicum</i>	4	-	1	-	-
Taxa characteristic of late successional stages (second scenario)					
Helotiales 3	-	-	-	1	-
<i>Piloderma bicolor</i>	-	-	-	1	-
<i>Pseudotomentella</i> sp.2	2	-	-	1	-
<i>Sebacina</i> sp.1	-	-	-	1	-
<i>Suillus</i> cf. <i>tomentosus</i>	-	-	-	1	-
<i>Suillus</i> cf. <i>variegatus</i>	2	-	-	1	-
<i>Tomentella subhilarina</i>	2	-	-	1	-
<i>Tomentellopsis submollis</i>	-	-	-	1	-
<i>Vestigium tridum</i>	10	-	-	1	-
Taxa characteristic of native forest (control)					
<i>Russula nauseosa</i>	2	-	-	-	2
<i>Tomentella</i> sp.11	2	-	-	-	2
<i>Chromelosporium</i> sp.	-	-	-	-	1
<i>Oidiiodendron mains</i>	-	-	-	-	1
<i>Pseudotomentella mucidula</i>	-	-	-	-	1
<i>Russula integriformis</i>	-	-	-	-	1
<i>Russula laricina</i>	2	-	-	-	1
<i>Sebacina dimittica</i>	5	-	-	-	1
<i>Sebacina epigea</i>	4	-	-	-	1
<i>Sebacina</i> sp.2	2	-	-	-	1
<i>Tomentella</i> sp.12	-	-	-	-	1
Taxa characteristic of early and middle successional stages					
<i>Cenococcum geophilum</i>	2	1	1	-	-
Taxa characteristic of middle and late successional stages					
<i>Piloderma olivaceum</i>	11	-	-	3	1
Taxa independent of successional stages					
<i>Inocybe</i> sp.2	3	1	-	-	1
<i>Suillus sibiricus</i>	33	5	3	-	2
<i>Inocybe</i> sp.2	3	1	-	-	1
Taxa characteristic of mature trees					
<i>Amphinema byssoides</i>	3	-	-	-	-
<i>Clavulinum delectabile</i>	3	-	-	-	-
Helotiales 1	4	-	-	-	-
<i>Inocybe maculata</i>	2	-	-	-	-
<i>Lactarius badiusanguineus</i>	3	-	-	-	-
<i>Piloderma</i> sp.1	2	-	-	-	-
<i>Rhizogonon salebrosus</i>	4	-	-	-	-
<i>Russula albonigra</i>	3	-	-	-	-
<i>Russula amethystina</i>	4	-	-	-	-
<i>Russula firmula</i>	7	-	-	-	-
<i>Russula lutea</i>	10	-	-	-	-
<i>Russula puellaris</i>	2	-	-	-	-
<i>Russula velenovskyi</i>	2	-	-	-	-
<i>Russula vesca</i>	2	-	-	-	-
<i>Russula viscida</i>	2	-	-	-	-
<i>Russula xerampelina</i>	2	-	-	-	-
<i>Russula</i> sp.1	6	-	-	-	-
<i>Sebacina candida</i>	2	-	-	-	-
<i>Suillus pictus</i>	3	-	-	-	-
<i>Thelephora regularis</i>	8	-	-	-	-
<i>Tomentella lateritia</i>	2	-	-	-	-
<i>Tomentella</i> sp.5	3	-	-	-	-
<i>Tomentella</i> sp.13	4	-	-	-	-
<i>Tomentella</i> / <i>Thelephora</i> sp.	2	-	-	-	-
<i>Tremellodendron schweinitzii</i>	2	-	-	-	-

species diversity. At the same time, it is assumed that differences in fungal community structure have physiological implications for regeneration and structuring the forest ecosystems, since EcM fungi vary in benefits to seedlings and mature trees. In our study among numerous environmental variables we assessed the changes in the EcM fungal richness before and after fire in connection with *P. koraiensis* age classes and the pattern of vertical distribution of mycorrhizal colonization within soil horizons.

Mycorrhizal colonization was found to be high for seedlings grown at the burned and the unburned sites, since the mantles of EcM fungi were observed on more than 95 % seedlings harvested. There were small differences in the diversity of EcM fungi between the studied sites (ranged between 6 and 9 OTUs per site) unless the reduction of the number of OTUs in *Betula platyphylla* forest succession stage – S2 (3 OTUs). However, there was a rather significant shift between sites in terms of the taxonomic composition of EcM symbionts as well as the dominant fungal species formed mycorrhizal root tips on seedlings. Natural seedlings in the unburned forest hosted mainly *Russula* spp., *Tomentella* spp., *Suillus sibiricus*, *Sebacina* spp., *Piloderma olivaceum*, and some other taxa. Seedlings at the burned sites (S1–S3) were colonized predominantly by *Suillus sibiricus*, *Tomentella* spp. (different from taxa in the control site), russuloid taxa, *Cenococcium geophilum* and *Piloderma olivaceum* (Table 4).

Higher taxonomic richness of EcM fungi was found on the old trees (max. 26 taxa) and on the mature trees belonging to the middle age classes (40–70 and 120–150 year-old – 30 and 29 taxa respectively) regardless of the succession stage of forest. Accordingly, a significant increase in the number of EcM species with increasing the trees age has not been observed. These results can be explained by the known fact that the structure and species composition of the EcM fungal community stabilize in the period when the trees canopy closes and the root system fully forms (Visser 1995, Kranabetter et al. 2005, Twieg et al. 2007). Thus, we realize that EcM species richness on mature trees was apparently underestimated because of our technique of sampling, in which we could not collect the whole root system with soil cores. The distribution pattern of EcM diversity by age of trees and soil horizons is shown in Figure 5.

The vertical distribution of mycorrhizal colonization indicated that most of the EcM fungi were present throughout the soil profile to a depth of 20–25 cm with the exception of *Tomentella* spp., which tended to form mycorrhizas with roots in the upper organic layer (including litter), and russuloid fungi forming EcM connections in deeper mineral horizons. Interestingly, we did not observe any decreasing of ectomycorrhizal biomass and diversity in the top layer of the soil cores after the recent fire – site S1 (Fig. 5); besides no significant differences were detected for the middle and bottom layers of the soil cores in this site. This is contrary to usually stated outcome of fire impact on the forest ecosystem (Jonsson et al. 1999). A vertical stratification of EcM fungal diversity at the control site and the sites of later succession stages (S2, S3) was found to be more leveled, with some tendency of proliferation to the mineral soil layer (Fig. 5). Due to the large number of *P. ko-*

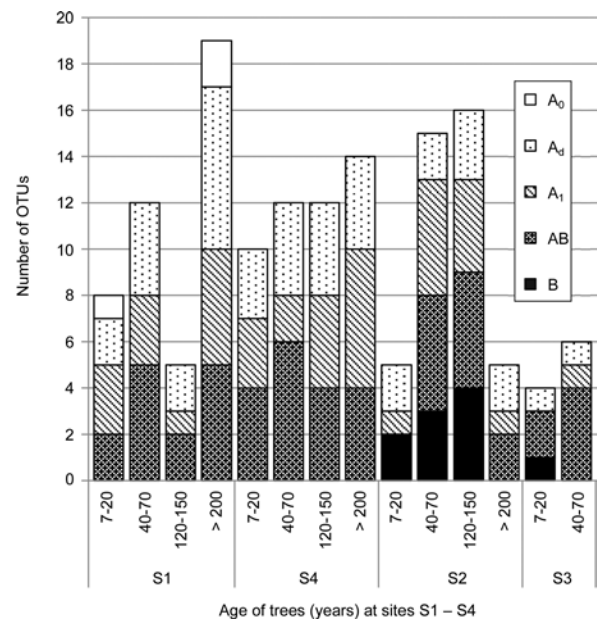


Figure 5 OTUs numbers in relation to soil layers (A₀–AB) and the age of the *Pinus koraiensis* trees at different sites

raiensis mature trees presence in these forest stands, mycorrhizas are apparently present as deep as tree roots are, i.e. in the deepest mineral horizons.

DISCUSSION

The influence of fires on forest vegetation and natural course of the conifer-broadleaved forests recovery in the Central Sikhote-Alin cannot be overestimated. The reforestation process is largely determined by the intensity of the fire and the amount of area burned, and depends on the stand nature preserved after fire and the close presence of seed-producing trees (Komarova et al. 2008). It is well known that mycorrhizal colonization significantly affects both the speed and the direction of any recovery processes in plant associations (Jonsson et al. 2001, Smith & Read 2008), especially under conditions of prolonged and complicated natural regeneration of *P. koraiensis* forests after severe fire (Pimenova et al. 2015). Accordingly, the presence of EcM fungi is vital for the establishment of obligatory mycorrhizal framework in recurring *P. koraiensis* phytocoenoses, where fire-resistant EcM fungi or fungi with rapid re-colonization strategy from available sources of inoculum acquire great importance. To the best of our knowledge, this is the first resumptive study, which generalizes all information of the below-ground EcM community of *P. koraiensis* growing in the Central Sikhote-Alin mountains (Malysheva et al. 2014, Pimenova et al., 2015). At the four study sites we distinguished 110 EcM fungal taxa based on analyzing of *P. koraiensis* mature trees and seedlings root tips. On this basis, it can be argued that the below-ground EcM diversity of *P. koraiensis* is rather high.

Pine regeneration at the study area is variable both in terms of forest structure, plant diversity, density and frequency of *P. koraiensis* seedlings. Analysis of the coenopopulation structure and dynamics showed that the group of initial species, the most active in the early years after the fire,

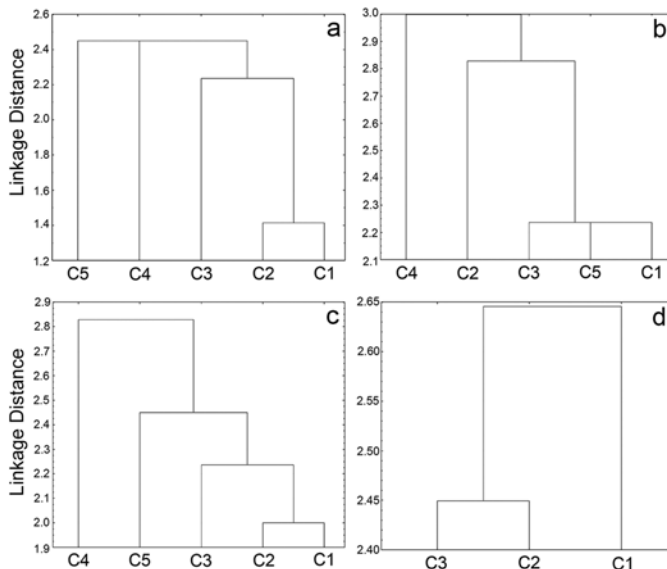


Figure 6 Hierarchical cluster analysis, using the Euclidean distance and 'single linkage' method. The dendrogram of *Pinus koraiensis* tree age classes (C1 – 1–5 year-old, C2 – 7–20 year-old, C3 – 40–70 year-old, C4 – 120–150 year-old and C5 – >200 year-old) grouped by EcM fungi taxonomic composition similarity at different sites: a – S1, b – S2, c – S3, d – S4.

was only 10 % of the total number of species, and serial and climax coenopopulations reached a significant diversity (Pimenova et al. 2015). Initial coenopopulations are represented by annual-biennial herbs and shrubs with a circumpolar, Eurasian and Asian-North American distribution. The ecosystem after fire exposure is open to the resumption of the representatives of all coenopopulation classes, and 10 years of age diversity reaches its highest value. In our case, according to our estimations, there is a possible combination of up to 54 species per 100 m². Therefore, the mycorrhization at the early stages of Korean pine forests succession takes place in a highly competitive environment in terms of both over-ground and below-ground space and a large number of plants in need of EcM component to provide their nutrition. Ten years after fire the closing and thinning undergrowth of vegetation begin, and after 20 years, a large part of the undergrowth of fast-growing species (*Betula platyphylla*, *Populus tremula*, *Salix caprea* propagating by seeds and *Tilia amurensis* reproducing by sprouts) goes into the stand, when, with a total number of shoots in the close shrub layer reaching 67.6 thousand per hectare, most of the species reaches its ultimate abundance (Gromyko et al. 2010). Later, after 50–60 years after fire event the succession process can go in several ways, depending on the degree of burn-out and the presence of adjacent unburned forest stand. In our study, a pattern of plant community development with a completely destroyed native tree stand, which is located at a distance from the unburned forest, is represented by S3 site with *Betula platyphylla* and *Larix cajanderi* predominant in tree stand. At this site, the density of *P. koraiensis* undergrowth is only 600 individuals per ha. These are the least favorable conditions for successful mycorrhization and development of Korean pine (Table 4). We found here the smallest number of EcM fungi is only 15 OTUs.

At places where due to weak ground fire the decay of tree stand was gradual, intensive colonization of *P. koraiensis*, *Picea ajanensis* and *Abies nephrolepis* began during the first years and continued throughout the whole period of succession. In our investigation, this is another line of development of native-born forest stand, corresponding to the S2 site of 90–100-year-old forest with *Betula platyphylla* predominant in the tree layer (Table 1). The formation of a new Korean pine coenopopulation happens quite intensively here, and there is different age undergrowth present, part of which has already become the stand and was capable of producing seeds. In our opinion, this is the most suitable conditions for the development of *P. koraiensis* seedlings.

Thus, the structure, species composition and regeneration variability of EcM fungal communities are largely determined by many factors, not the least of which are the plant community age structure, the presence of certain dominant trees (Ishida et al. 2007, Twieg et al. 2007), soil and climate environmental variables, etc. Our sampling efforts at different forest sites, spatially separated and representing different post-fire succession stages, revealed some peculiarities in community structure of EcM fungi associated in particu-

lar with the processes of initial mycorrhization of *P. koraiensis* seedlings, as well as the mycocoenosis response to the disturbances caused by fire. It was shown at the forest fire sites in the Central Sikhote-Alin that the opportunity for successful growth of conifer seedlings is rather narrow because of severe competition with herbaceous and shrubby species which effectively and promptly colonize the canopy windows at fire sites in the first few years after fire (Pimenova et al. 2015). Under these conditions, the growth of EcM fungi may be significantly limited, and some fungi may not be active. Nevertheless, 39 OTUs have been recorded in the recently burned stand, among which nine formed mycorrhiza with seedlings (Fig. 7), implying considerable number of EcM species survived the fire or re-colonized the root tips rapidly after fire.

In the study conducted we were particularly interested in the question of the EcM inoculum source for pine seedlings regenerating after fire. In some works authors have clearly demonstrated the importance of spores as the dominant form of inoculum in post-fire pine communities (Baar et al. 1999, Grogan et al. 2000). It was shown that pine seedlings of early age, germinating at the burned forest site, where all mature trees were destroyed by fire, were usually colonized exclusively by suilloid fungi, while the seedlings of the same age in unburned forest stands formed a symbiosis with many taxa of EcM fungi from different genera, including *Russula* and *Amanita* (Horton et al. 1998). This is because of most of suilloid fungi are capable to form mycorrhiza with not only mycelium but also with spores, which remain viable in the soil even after a severe fire (Smith & Read 2008). In our study we cannot determine reliably which fungal species survived the fire, and which ones colonized the Korean pine trees from the adjacent unburned forest areas, since the most recent burned forest stand (S1) involved in

our study reached the age of 10 years after fire event. However, the presence of several species (*Rhizopogon* cf. *salebrosus*, *Cenococcum geophilum*, *Tuber californicum*, *Suillus subluteus*, *S. sibiricus*, *Tomentella* spp. and some russuloid species) at this site suggests that there is a specific and persistent EcM community structure in coniferous-broadleaved forests as a pledge of possible community development on the stress scenario. Species mentioned are known to survive the fire of varying severity either in the form of variable propagules or as a resident inoculum like mycelium in deeper layers of soil. Soil acts as a relatively good insulator and killing temperatures caused by forest fire typically tend to be restricted to the mineral horizon upper 5 cm layer (Visser 1995, Baar et al. 1999, Taylor & Bruns 1999, Izzo et al. 2006). On the other hand, the EcM community species composition at the site burned of late is also contributed by early colonizers with high re-colonization abilities because of spore dispersal via air or animals or mycelium emergence from the live Korean pine root tips of surrounding unburned forest. Possible first colonizers of pine sampling root systems belong to Thelephoraceae, Atheliaceae, suilloid fungi as well as Russulaceae and Amanitaceae well known for their ability to colonize pine roots immediately after the fire (Baar et al. 1999), of which most of species were found exclusively in S1 studied site. At the same time, some groups of fungi (from the genera *Suillus*, *Piloderma*, *Russula* and *Tomentella*) dominating in the early stage of post-fire colonization over time will dominate again in more old-growth forests representing so-called multi-stage EcM fungi (Fig. 4). The multi-stage fungi are probably more persistent at the variable environmental conditions, suggesting their considerable resistance to fire among the EcM community. It may be indirect evidence that mycorrhization of seedlings at the earlier stages of forest succession can occur from the mature donor trees (“nurse trees”) facilitating seedling establishment, and success of EcM re-colonization may be strongly determined by EcM community composition in the adjacent forest. *Suillus sibiricus* was the most dominant species at all studied sites (Table 4). A specialized symbiont of a limited number of tree species from Pinaceae and a permanent member of pine forests natural EcM community throughout the lifetime it can act also as an aggressive colonizer of young Korean pine seedlings in burned stands. It provides seedlings with nitrogen and phosphorus and gives them a competitive advantage under harsh conditions. While the multi-stage fungal communities were rather rich in species at burned sites and in unburned forest, there was tendency for OTUs composition to differ qualitatively in different age classes of *P. koraiensis* trees at all studied sites (Fig. 6). Along with the changes in the species composition, a tendency of complication was observed also in terms of the taxonomic structure of EcM community associated with obvious increase of EcM fungi genera number (from 7 to 30) with tree age increase. On the basis of tree age, many EcM fungi OTUs observed in the root tips of seedlings or young trees (in our case first two age classes) may be considered as early-stage EcM fungi. In the present study these include *Suillus* cf. *tomentosus*, *S. variegatus*, *S. subluteus*, *Piloderma bicolor*, *Cenococcum geophilum*, *Sebacina* sp. 2, *Tomentellopsis*

submollis, *Pseudotomentella mucidula*, *Inocybe* sp. 2, *Oidiodendron maius*, *Tomentella* spp. and *Russula* spp. Some of these taxa are actually considered as typical early-stage fungi occurring primarily in young coniferous forests (Visser 1995, Grogan et al. 2000, Aučina et al. 2011, Kipfer et al. 2011). For the 120–150 and >200 year-old trees the EcM species composition was replenished with late-stage fungi not occurring with young trees, mainly such as *Amanita vaginata*, *A. spissa*, *Russula viscida*, *R. nigricans*, *R. amethystina*, *Lactarius tabidus*, *Piloderma* cf. *lanatum*, *Boletus ferrugineus*, *Cortinarius* sp. 2, *Humarina hemisphaerica*, *Rhizopogon salebrosus*, *Elaphomyces muricatus*, *Helotiales* 1. It is noteworthy, that in addition to basidiomycete component the proportion of ascomycete increased, bringing the contribution to the diversity of EcM community connected with mature and old trees.

These groups of fungi (early-stage and late-stage) differ from each other not only in connection with different age of host-tree, but also the ability to extract nitrogen from one or another substrate. The late-stage EcM fungi emerge as a major component in the older fragmented litter and humus, i.e. in the older organic matter and deeper soil horizons, while early-stage fungi can assimilate litter in the initial stages of its decomposition (Lindahl et al. 2007). Thus, the pattern of the dominating early-stage fungi in S1 site, which represents the early stage of post-fire community succession and characterized by re-emerging organic horizon after replacement-severity fire, is in accordance with the known properties of the group.

Our study on burned and unburned stands of conifer-broadleaved forests in the Central Sikhote-Alin showed that *P. koraiensis* was associated with a large number of EcM fungi, many of which may be its specific symbionts. Evidently, all of these taxa of EcM fungi play an important role in the regeneration of natural forest stands after fire at the studied area. Further studies should focus on revealing the entire EcM symbionts diversity, the species specialization and functional significance in plant community, as well as on determination of the EcM fungi effect on the forest succession direction and speed.

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