



The dominance of *Suillus* species in ectomycorrhizal fungal communities on *Larix gmelinii* in a post-fire forest in the Russian Far East

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Abstract

Wildfires can negatively affect ectomycorrhizal (EM) fungal communities. However, potential shifts in community structures due to wildfires have rarely been evaluated in the forests of eastern Eurasia, where surface fires are frequent. We investigated EM fungal communities in a *Larix gmelinii*-dominated forest that burned in 2003 in Zeya, in the Russian Far East. A total of 120 soil samples were collected from burned and adjacent unburned forest sites. The EM fungal root tips were morphotyped and internal transcribed spacer (ITS) sequences were obtained for fungal identification. We detected 147 EM fungal operational taxonomic units, and EM fungal richness was 25% lower at the burned site than at the unburned site. EM fungal composition was characterized by the occurrence of disturbance-adapted fungi (*Amphinema* and *Wilcoxina*) at the burned site and late-successional fungi (*Lactarius*, *Russula* and *Cortinarius*) at the unburned site. These findings suggest that the EM fungal communities did not recover to pre-fire levels 16 years after the fire. *Suillus* species were the dominant EM fungi on *L. gmelinii*, with greater richness and frequency at the burned site. Both *Larix* and *Suillus* exhibit adaptive traits to quickly colonize fire-disturbed habitats. Frequent surface fires common to eastern Eurasia are likely to play important roles in maintaining *Larix* forests, concomitantly with their closely associated EM fungi.

Keywords Diversity · Host specificity · Suilloid · Symbiosis · Wildfire

Introduction

Many dominant trees in boreal forests are obligatory associated with ectomycorrhizal (EM) fungi. EM fungi improve the transfer and uptake of nutrients and water to their host plants, and in turn, receive photosynthetic carbon from their hosts (Smith and Read 2008). Field evidence has shown that limited access to EM fungi can reduce seedling survival and growth (Nara 2006a; Teste and Simard 2008) and forest expansions may fail without compatible EM fungi (Briscoe 1959; Nuñez et al. 2009). Therefore, the presence of EM fungal inocula is essential in disturbed habitats to facilitate

the establishment of seedlings and for subsequent forest development.

Forest fires are natural disturbance agents that can affect soil fungal communities (Cairney and Bastias 2007; Pressler et al. 2019; Yang et al. 2020). EM fungi may be physically removed by a direct transfer of heat and the combustion of surface organic matter during a fire (Smith et al. 2004; Cairney and Bastias 2007). Fires may also indirectly affect EM fungal communities by altering the host plant communities, the physical and chemical properties of soil, and the microclimate (Certini. 2005; Hart et al. 2005). EM fungal richness is reported to decrease immediately after fires but may recover quickly in the early stages of forest development (Treseder et al. 2004; Twieg et al. 2007; LeDuc et al. 2013; Kipfer et al. 2011). In addition, the post-fire community composition of EM fungi generally shifts with stand age (Twieg et al. 2007; LeDuc et al. 2013; Yang et al. 2020). The responses of EM fungal communities to fire vary according to the intensity and severity of the fire events (Jonsson et al. 1999; Reazin et al. 2016; Owen et al. 2019), the fire return interval of an ecosystem (Buscardo et al. 2010; 2012) and

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local environmental factors (e.g., vegetation and topography) (Rincón and Pueyo 2010; Buscardo et al. 2011). For example, high-intensity fires that remove the organic layer may dramatically affect EM fungal composition (Visser 1995; Dahlberg et al. 2001), while low-intensity fires that leave organic layers undamaged may not alter EM fungal composition (Jonsson et al. 1999). The effect of fire on the EM fungal community is region- and context-dependent.

Predicting the effects of fires on ecosystem processes is increasingly important in high-latitude boreal forests, where fires are frequent. Changing fire regimes due to human land use and climate change can have significant impacts on carbon emissions from the vast forests of Eurasia (Rogers et al. 2015; Shuman et al. 2017). In this region, Siberian *Larix* forests cover approximately 263 million ha, forming the world's most extensive coniferous forests (Abaimov 2010). The estimated annual burned area in eastern Eurasia is about 1.4–2.0 Mha year⁻¹ with high interannual variability (Rogers et al. 2015), and the current fire return interval is estimated to range from 53 to 80 years in the south to 200–300 years in the Arctic regions (de Groot et al. 2013; Ponomarev et al. 2016). Historically, high-frequency surface fires are common in Eurasia (de Groot et al. 2013; Rogers et al. 2015). *Larix* trees can survive during surface fires by having thick bark and high leaf moisture content (Shuman et al. 2017). However, the number and extent of wildfires have been increasing and stand-replacing fires are becoming more frequent in eastern Eurasia because of climate warming (Ponomarev et al. 2016; Schaphoff et al. 2016). Some fire-adapted *Pinus* species (e.g., *P. contorta* and *P. banksiana*) in North America produce serotinous cones that open with heat, which enable rapid regeneration after stand-replacing fires. By contrast, *Larix* species produce wind-dispersed seeds annually, and nearby seed sources are necessary for post-fire recruitment if the existing trees are heavily damaged. Changes in fire regimes from frequent surface fires to more intense crown fires in eastern Eurasia may influence post-fire forest recovery processes. Despite the global importance of *Larix* forests, the potential effects of fires on EM fungal communities remain largely understudied compared with the boreal forests of North America and Europe (Dove and Hart 2017; Taudière et al. 2017).

Larix species are associated with suilloid fungi (i.e., *Suillus* and *Rhizopogon*), which exhibit strong specificity to Pinaceae hosts (Molina et al. 1999; Nguyen et al. 2016; Miyamoto et al. 2019). Suilloid fungi are often detected in the roots of *Pinus* and *Pseudotsuga* in fire-disturbed forests, reflecting their pioneer strategy in relation to fires (Baar et al. 1999; Barker et al. 2013; Cowan et al. 2016; Glassman et al. 2016). Suilloid fungi are effective spore dispersers by producing a large number of spores that can be transported over long distances by wind and animals (Ashkannejhad and Horton 2006; Peay et al. 2012). Some suilloid fungi also

produce heat-resistant or heat-activated spores that remain viable in deeper soils after a fire, enabling them to quickly colonize fire-disturbed habitats (Izzo et al. 2006; Peay et al. 2009; Bruns et al. 2019). The above traits of suilloid fungi imply that they are an important component of the EM fungal community in the post-fire *Larix* forests of Eurasia. By contrast, *Larix* species are also associated with many broad host range EM fungal taxa (Leski and Rudawska 2012; Han et al. 2017; Kennedy et al. 2018). The high compatibility of EM fungi between *Larix* and other neighboring trees can occur in early- to late-successional forests, where trees may potentially benefit from the establishment of common mycorrhizal networks (Nara 2006b; Rog et al. 2020). The level of EM fungal specificity and compatibility may shift with forest development following fire disturbances; however, this remains to be elucidated.

In this study, we evaluated the EM fungal communities of *Larix* forests in the Russian Far East, where a large forest fire occurred in 2003. The objective of this study was to characterize the EM fungal community structures of a forest that burned 16 years ago. We investigated (1) whether the EM fungal richness and composition differed between a burned forest and a nearby unburned mature forest, and (2) whether *Larix*-associated EM fungal communities were dominated by narrow host range fungal taxa (i.e., suilloid), and whether their dominance increases in the fire-disturbed forest. Furthermore, we investigated the relative importance of the fire event, host identity, and soil properties in explaining the variation in EM fungal composition.

Methods

Study site

The study area was located in the Zeysky State Nature Reserve (53° 50' N, 127° 10' E), about 500 km north of Blagoveshchensk in Amur Oblast, Russia. The area is characterized by a cold and dry continental climate with discontinuous permafrost soils. The mean annual, January and July temperatures are – 0.7 °C, – 19.3 °C and 19.1 °C, respectively, with a mean annual precipitation of 526.8 mm, of which 77% falls from July to September (Amur Center for Hydrometeorology and Environmental Monitoring 2015). Frequent surface fires of low to medium severity are common in this region.

A wildfire burned ca. 24,500 ha of the forest in the summer of 2003. It was a long-lasting ground fire, which damaged root systems, causing trees to gradually die and fall several years after the fire. In 2016, two permanent plots (50 × 50 m) were established, the first in a burned area (treatment) and the second in an unburned area (control), with a distance of 800 m separating the two plots. In the

burned area, the fire killed 72% of *Larix gmelinii* (Rupr.) Rupr. and 87% of *Betula platyphylla* Suk. The burned site was characterized by a young open-canopy stand, dominated by *L. gmelinii* (88.4%) mixed with *B. platyphylla* (9.9%, Table 1). *Picea obovata* Ledeb. was also present at a low density. Understory vegetation included *Populus tremula* L., *Salix caprea* L., *Sorbus sibirica* Hedl., *Alnus fruticosa* Rupr., *Sambucus sibirica* Nakai, *Padus asiatica* Kom., *Ribes pauciflorum* Turcz. ex Pojark., *Rosa acicularis* Lindl., *Sorbaria sorbifolia* (L.) A. Br., *Rubus idaeus* L. and *Spiraea media* F. Schmidt. The unburned site was approximately 124 years old (no major fire disturbance within 80 years). The forest was dominated by *L. gmelinii* (64.7%), followed by *B. platyphylla* (32.5%) and *P. tremula* (2.6%). Seedlings of *Pinus pumila* (Pall.) Regel and *P. obovata* were also present, and *Rhododendron dauricum* L. dominated the shrub layer. Understory vegetation included *Maianthemum intermedium* Worosch., *Vaccinium vitis-idea* L., *Calamagrostis* sp. and *Carex globularis* L.

Field sampling

In August 2019, 60 soil cubes (5 × 5 cm × 10 cm depth, after removing litter) were collected using a hand trowel from a 1-ha area within and around the permanent plot at each forest stand. Sampling points were randomly chosen but were separated by ≥ 5 m to avoid spatial autocorrelations (Lilleskov et al. 2004; Pickles et al. 2012). All plant roots were collected from each soil sample, and EM roots were morphologically differentiated based on color, branching patterns, textures, and the characteristics of emanating hyphae and rhizomorphs (Agerer 2001) under a dissecting microscope. Three EM root tips, if available, per morphotype per soil sample were collected for molecular analyses. Morphological separation was conducted within 3 weeks of

soil collection. The root tip samples were stored in cetyl trimethyl ammonium bromide (CTAB) solution at 4 °C until processing. EM roots were found in 119 soil samples.

Molecular analyses

Total DNA was extracted from 1519 root tips using the CTAB method described by Nara et al. (2003). Molecular identification of fungal taxa was performed as described by Miyamoto et al. (2015) with some modifications. The internal transcribed spacer (ITS) region (ITS1-5.8S-ITS2) was amplified primarily using the ITS5 and ITS4 primers (White et al. 1990). Additionally, the ITS0F forward primer (Tedersoo et al. 2008) and several reverse primer pairs (LA-W, LB-W, ITS4B, LR22, and ITS4CG) (Gardes and Bruns 1993; Hopple and Vilgalys 1994; Tedersoo et al. 2008; Bahram et al. 2011) were used when the aforementioned primer pair failed to amplify the fungal ITS region. Polymerase chain reaction (PCR) was performed with the EmeraldAmp PCR Master Mix (TAKARA), following the manufacturer's instructions. Amplified products were checked using gel electrophoresis in 1.2% agarose gels (0.5× TAE buffer). A total of 1469 root tips (96.7%) were successfully amplified by PCR. Amplicons were purified using ExoSAP-IT Express (Thermo Fisher Scientific) and sequenced using ITS1 and/or ITS4 primers on an Applied Biosystems 3730xl DNA Analyzer (Applied Biosystems, Foster City, CA, USA), following the manufacturer's instructions. The obtained sequences were manually corrected using chromatograms with ATGC ver. 8 (Genetyx, Tokyo, Japan). Clean and long sequences (> 350 bp) were clustered into operational taxonomic units (OTUs) at a 97% similarity cutoff using the ATGC software, which produced 160 OTUs. BLAST searches were conducted to determine the fungal identity using known sequences in the NCBI databases. We additionally used the

Table 1 Site descriptions

	Burned site				Unburned site			
	<i>Larix gmelinii</i>	<i>Betula platyphylla</i>	<i>Picea obovata</i>	Total	<i>Larix gmelinii</i>	<i>Betula platyphylla</i>	<i>Populus tremula</i>	Total
Composition (%)	88.4	9.9	1.7		64.7	32.5	2.6	
Basal area (m ² ha ⁻¹)	12.9	1.4	0.3	14.6	15.0	7.6	0.6	23.2
Density (count ha ⁻¹)	128	300	24	452	436	484	28	948
DBH (cm)	35.8	7.8	11.5		18.7	14.1	16.7	
Soil parameters								
Total carbon (%)				27.64 ± 1.21				26.57 ± 1.13
Total nitrogen (%)				1.16 ± 0.06				1.03 ± 0.04
pH				5.31 ± 0.06				4.68 ± 0.03

The soil parameter values are the mean ± SE
DBH diameter at breast height

usearch_global tool in vsearch to assign fungal nomenclature with a $\geq 97\%$ match to UNITE ver. 8.2 species hypotheses (Abarenkov et al. 2020). EM fungal guild was defined based on Tedersoo et al. (2010), Tedersoo and Smith (2013) and the UNITE database (Koljalg et al. 2013). Thirteen OTUs were saprotrophs, endophytes or fungi with unknown functional guilds, and were excluded from statistical analyses (Table S1).

Host root identification was primarily confirmed by restriction fragment length patterns (RFLPs). First, *Larix*, *Picea*, and angiosperms were distinguished by RFLPs of the *trnS*-G intergenic spacers of the chloroplast DNA region amplified using the *trnS* and *trnG* primers (Hamilton 1999). The RFLPs of the *trnS*-G region separated target conifer hosts, while the pattern was identical among angiosperm hosts (*Betula*, *Populus* and *Salix*). Therefore, angiosperm hosts were secondly differentiated by RFLPs of the chloroplast *trnL* region amplified using the *trnL_c* and *trnL_d* primers (Taberlet et al. 1991). The PCR products for both regions were digested using the restriction enzyme *HinfI*, and RFLPs were compared to reference patterns generated from sequenced samples by electrophoresis in 2.5% agarose gels. Samples with unclear RFLP patterns were subjected to direct sequencing. The plant *trnL* regions (*trnL_c* and *trnL_d*, *trnL_e* and *trnL_f* primer pairs; Taberlet et al. 1991) or the ITS region (17SE and 26SE primer pair; Sun et al. 1994) were amplified and sequenced depending on amplification and reading success. These molecular analyses enabled unequivocal identification of the host genera. The host species were assigned according to the tree composition information.

Soil analysis

Total carbon (C), total nitrogen (N) and pH were measured for each soil sample (to a depth of 10 cm) after removing plant roots for morphotyping. Soil samples were oven-dried at 60 °C for 24 h and passed through a 2-mm mesh sieve. Soil pH was measured in a 1:5 soil to water ratio using a glass electrode (HI 2215, HANNA Instruments, Germany). The total C and N concentrations were measured using the combustion method coupled with gas chromatography/thermal conductivity detection using a TOC-L analyzer (Shimadzu, Japan). Each soil sample was homogenized using a mortar and less than 100 mg of soil was encased in tin foil for combustion.

Statistical analyses

Statistical analyses were conducted using R ver. 3.2.3. (R Core Team 2015) with a statistical significance of $\alpha < 0.05$, unless otherwise noted. The frequency of each EM fungal OTU was defined as the number of soil samples

containing that OTU (i.e., its presence or absence in each sample). Species rarefaction curves and Chao2 estimated richness were generated using EstimateS software version 9.1.0. (Colwell 2019). Fisher's exact test was used to determine whether the frequencies of each OTU were different between the burned and unburned sites.

The EM fungal composition with different fire events (burned vs. unburned), host genus and soil properties, was treated as a community unit. Soil samples were assigned to four levels of C concentrations (quantiles of Q1–Q4 from low to high). A preliminary analysis revealed that the C and N concentrations in the soil were strongly positively correlated ($P < 0.001$), with no significant differences between the burned and unburned sites ($P > 0.09$). Thus, the soil groupings (Q1–Q4) were constructed from low to high C and N concentrations independent of the fire event (Table S2). We excluded OTUs that occurred only in one sample from the community analyses. The dissimilarity among the EM fungal composition was visualized using a non-metric dimensional scaling (NMDS) procedure with the Bray–Curtis distance and 999 permutations. The effects of fire, host and soil C and N concentrations on EM fungal composition were tested using the perMANOVA (permutation multivariate analysis of variance) in the *adonis* function and variation partitioning in the *varpart* function implemented in the “vegan” package of R. The soil pH was significantly higher at the burned than the unburned site ($P < 0.001$; Table 1). Therefore, the soil pH was considered a part of the fire effect on the fungal composition and was not included in the community analyses. Instead, the potential influence of soil pH on the occurrence (incidence) of individual fungal OTUs was tested using a logistic regression model with a binomial error distribution (the *glm* function in the “stats” package). Individual fungal OTUs that occurred at both sites and in > 4 samples were tested.

Results

Molecular analysis results

A total of 147 EM fungal OTUs were detected, of which 13 and 134 OTUs were Ascomycota and Basidiomycota, respectively (Table S1). The four most OTU-rich genera were *Tomentella* (32 OTUs), *Cortinarius* (31), *Russula* (11) and *Piloderma* (9). The Chao2 estimated OTU richness of this area was 225.1 ± 26.3 (SD). The host genus was identified in 1459 root tips (96.1%). The majority of root tips were *Larix* (43.9%) and *Betula* (31.8%), followed by *Populus* (22.1%), *Picea* (2.0%) and *Salix* (0.2%).

Richness

The observed EM fungal richness was significantly lower at the burned site than at the unburned site, based on the non-overlap of the 95% confidence interval of the rarefaction curves (Fig. 1, Table 2). The observed richness at the burned site was 75.0%, 77.2% and 14.5% of that at the unburned site for *L. gmelinii*, *B. platyphylla* and *P. tremula*, respectively. The 95% confidence intervals of the rarefaction curves between the burned and unburned sites overlapped for *L. gmelinii* and *B. platyphylla*, indicating no significant decrease in OTU richness after the fire (Fig. S1). *Populus tremula* roots were scarce and the EM fungal richness was significantly lower at the burned site than at the unburned site.

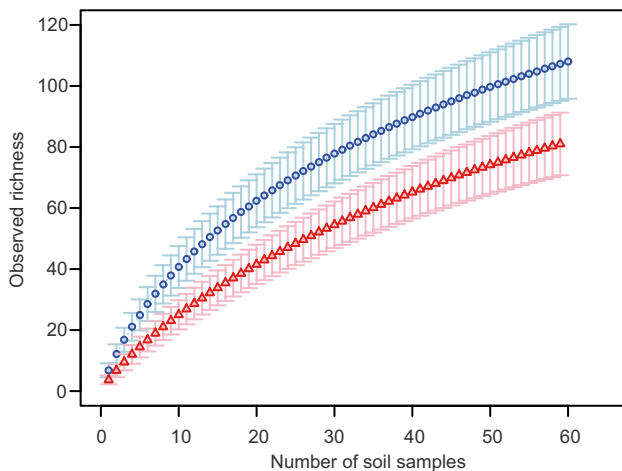


Fig. 1 Species rarefaction curves for ectomycorrhizal fungal OTU richness at the burned (red, triangle) and unburned (blue, circle) sites. The 95% confidence interval is based on 100 resamples without replacement

Table 2 Summary of ectomycorrhizal fungal diversity

Site	Host	No. of samples containing EMF	Observed richness	Chao2 estimated richness (\pm SD)	Richness per sample (\pm SE)	Shannon indices H'	Simpson indices (1/D)
Burned	Total	59	81	122.3 \pm 16.9	3.68 \pm 0.22	3.68	18.68
	<i>Larix</i>	44	42	67.9 \pm 14.5	2.41 \pm 0.18	3.24	15.31
	<i>Betula</i>	33	44	69.4 \pm 13.8	2.97 \pm 0.27	3.33	15.00
	<i>Populus</i>	6	9	26.5 \pm 14.4	2.17 \pm 0.60	2.06	6.76
Unburned	Total	60	108	168.3 \pm 23.9	6.85 \pm 0.31	4.04	28.86
	<i>Larix</i>	46	56	114.8 \pm 30.6	4.09 \pm 0.31	3.40	17.71
	<i>Betula</i>	36	57	92.9 \pm 17.4	3.83 \pm 0.29	3.56	20.09
	<i>Populus</i>	43	62	108.0 \pm 21.2	3.95 \pm 0.29	3.52	17.64

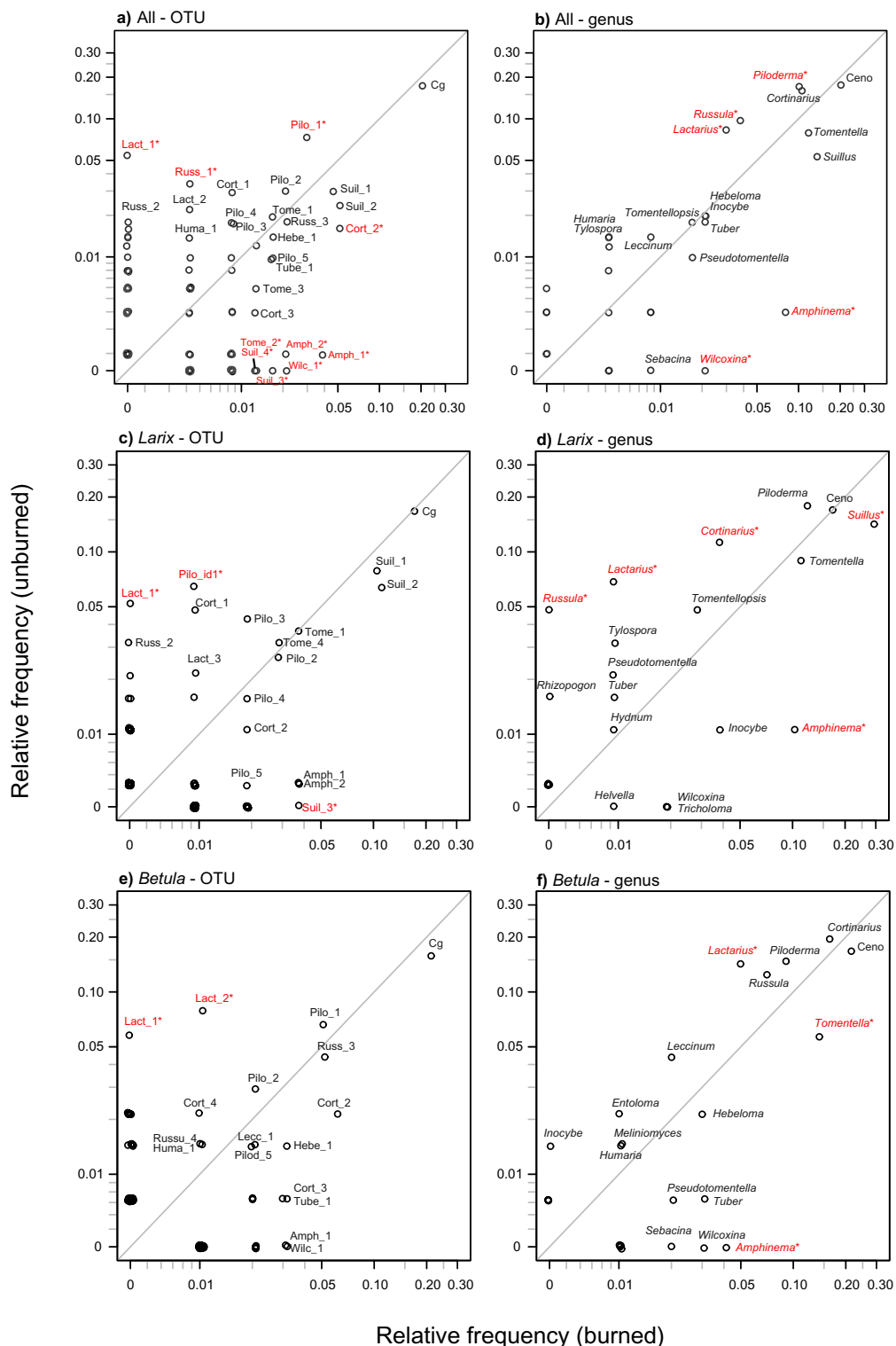
Hosts with low frequencies (*Picea* and *Salix*) are not shown
EMF ectomycorrhizal fungi

Composition

Seven OTUs occurred more frequently at the burned site, while 3 OTUs occurred more frequently at the unburned site (Fig. 2a). The genus-level analysis revealed that *Amphinema* and *Wilcoxina* had high frequencies at the burned site, while *Russula*, *Lactarius* and *Piloderma* occurred more frequently at the unburned site (Fig. 2b). EM fungi that were specific to *L. gmelinii* included six *Suillus* species and *Rhizopogon laricinus*. *Suillus cavipes* and *S. spectabilis* were the second- and third-most frequent taxa after *Cenococcum geophilum* OTU1. The frequency of *S. grevillei* ($P = 0.016$) at the burned site was significantly different from zero. *Lactarius uvidus* ($P = 0.016$) and *Piloderma bicolor* OTU1 ($P = 0.036$) occurred more frequently at the unburned site (Fig. 2c). At the genus level, *Suillus* ($P = 0.003$) and *Amphinema* ($P < 0.001$) occurred more frequently at the burned site, whereas *Cortinarius* ($P = 0.030$), *Lactarius* ($P = 0.021$) and *Russula* ($P = 0.029$) occurred more frequently at the unburned site (Fig. 2d). *Cenococcum geophilum* OTU1, *P. bicolor* OTU1, *Lactarius vietus* and *Russula versicolor* were the four most frequently occurring taxa for *B. platyphylla*. *Lactarius uvidus* ($P = 0.022$) and *L. vietus* ($P = 0.016$) were found more frequently at the unburned site than at the burned site (Fig. 2e). At the genus level, *Lactarius* ($P = 0.030$) occurred more frequently at the unburned site, while *Tomentella* ($P = 0.039$) and *Amphinema* ($P = 0.028$) were more frequent at the burned site (Fig. 2f).

Putative factors influencing fungal composition

The NMDS result indicated that the EM fungal community composition was differentiated by fire event and host identity (Fig. 3). The potential effects of putative factors on the variation in EM fungal composition were tested for *L. gmelinii* and *B. platyphylla* as they were the dominant host species at



both sites with sufficient amounts of fungal community data for comparison. The EM fungal composition was significantly differentiated by the fire event ($F_{1, 14} = 3.324$, $R^2_{\text{adj}} = 0.192$, $P = 0.0038$) and the host ($F_{1, 14} = 5.582$, $R^2_{\text{adj}} = 0.285$, $P < 0.0001$); however, soil C and N concentrations did not significantly explain variations in the composition ($F_{3, 12} = 0.935$,

$R^2_{\text{adj}} = 0.189$, $P = 0.53$). Variation partitioning revealed that the host alone ($R^2 = 0.257$) explained more of the variation in the EM fungal composition than the fire event ($R^2 = 0.147$) or soil C and N concentrations ($R^2 = 0.009$). The mean pairwise community distances (Bray–Curtis) between the burned and

Fig. 2 The relative frequencies of ectomycorrhizal fungal taxa at the burned (x-axis) and unburned (y-axis) sites for operational taxonomic units (OTUs; **a, c, e**) and genus (**b, d, f**). The diagonal line indicates equal frequencies at both sites. Fungal taxa below the line occurred more frequently at the burned site, while those above the line occurred more frequently at the unburned site. Asterisks following the taxa (red-colored) indicate significantly higher frequencies or frequencies significantly different from zero either at the burned or unburned site (Fisher's exact test). A small amount of jitter (i.e., random noise) is added to the plot to prevent overlapping data points. Taxonomic identifiers are Amph_1 (*Amphinema byssoides*), Amph_2 (*Amphinema* aff. *byssoides* OTU1), Cg (*Cenococcum geophilum* OTU1), Cort_1 (*Cortinarius comptulus*), Cort_2 (*Cortinarius casimiri*), Cort_3 (*Cortinarius* OTU1), Cort_4 (*Cortinarius decipiens*), Hebe_1 (*Hebeloma* cf. *leucosarx*), Huma_1 (*Humaria hemisphaerica*), Lact_1 (*Lactarius uvidus*), Lact_2 (*Lactarius vietus*), Lact_3 (*Lactarius porninsis*), Lecc_1 (*Leccinum scabrum* OTU1), Pilo_1 (*Piloderma bicolor* OTU1), Pilo_2 (*Piloderma bicolor* OTU3), Pilo_3 (*Piloderma olivaceum* OTU1), Pilo_4 (*Piloderma bicolor* OTU2), Pilo_5 (*Piloderma byssinum*), Russ_1 (*Russula emetica*), Russ_2 (*Russula griseascens*), Russ_3 (*Russula versicolor*), Russ_4 (*Russula robertii*), Suil_1 (*Suillus spectabilis*), Suil_2 (*Suillus cavipes*), Suil_3 (*Suillus grevillei*), Suil_4 (*Suillus asiaticus*), Tome_1 (*Tomentella terrestris* OTU1), Tome_2 (*Tomentella lateritia*), Tome_3 (*Tomentella subclavigera*), Tome_4 (*Tomentellopsis* cf. *submollis*), Tube_1 (*Tuber* OTU2) and Ceno (*Cenococcum*). Taxonomic identifiers are not shown for taxa with low frequencies for clarity.

unburned sites were significantly larger for *B. platyphylla* than *L. gmelinii* ($t = 2.601$, $P = 0.014$).

Compatibility between *L. gmelinii* and *B. platyphylla*

We considered suilloid (Molina et al. 1999; Nguyen et al. 2016) and *Leccinum* (den Bakker et al. 2004) as narrow host range fungi and the remaining OTUs as broad host range fungi (Fig. 4). The proportion of shared EM fungal OTUs between *L. gmelinii* and *B. platyphylla* increased from the burned (14.7% in richness) to the unburned (28.4%) site (Fig. 4). Fisher's exact test revealed that the differences were significant for richness ($P = 0.038$) and frequency ($P < 0.001$).

Fungal occurrence along the soil pH gradient

The change in fungal occurrence (incidence) along a soil pH gradient was tested for 26 fungal OTUs. Binomial tests showed that the soil pH was negatively associated with the occurrence of 6 OTUs (*P. bicolor* OTU1, *T. terrestris* OTU1, *C. geophilum* OTU1, *Cortinarius comptulus*, *L. vietus* and *Russula emetica*), and positively associated with the occurrence of *Amphinema byssoides* (Fig. S2).

Discussion

We found that the EM fungal diversity was lower at the burned site than at the unburned site, and the fungal composition was significantly different between the two sites.

These results suggest that the EM fungal community did not recover to its pre-fire levels 16 years after a fire in the *L. gmelinii*-dominated forest of Zeya in the Russian Far East. Previous chronosequence studies have reported that the recovery of EM fungal richness to the pre-fire levels can take < 20 years (Kipfer et al. 2011; LeDuc et al. 2013; Rincon et al. 2014) or longer (41–65 years) (Visser 1995; Twieg et al. 2007). Although large variations exist between studies, most studies have indicated dramatic increases in fungal diversity within two decades after a fire (Twieg et al. 2007; Kipfer et al. 2011; LeDuc et al. 2013; Dove and Hart 2017). We found that post-fire EM fungal richness was 75% of the nearby unburned forest. This value was similar to a prediction from a study on *Pinus sylvestris* forests in the central Alps (Kipfer et al. 2011) and slightly lower than a prediction from a global meta-analysis (Dove and Hart 2017). Considering the high variability among previous reports, our results are comparable to those of other boreal forests. We also found apparent differences in the EM fungal composition between the burned and unburned sites (Fig. 3). The burned site was characterized by the occurrence of disturbance-adapted fungi (*Suillus*, *Amphinema* and *Wilcoxina*), while the unburned site was characterized by the dominance of late-successional fungi (*Lactarius*, *Russula* and *Cortinarius*). These results were similar to those of previous studies in boreal forests. For example, *Amphinema* and *Wilcoxina* are highly competitive early colonizers commonly found in fire-disturbed habitats (Mah et al. 2001; Smith et al. 2004; Barker et al. 2013). By contrast, the frequencies of *Lactarius*, *Russula* and *Cortinarius* species often increase with time after a fire (Visser 1995; Smith et al. 2004; Twieg et al. 2007; Holden et al. 2013). Thus, the EM fungal composition at our burned site is considered to be in the early- to mid-successional stages.

Suillus was the dominant genus on *L. gmelinii* roots, with higher richness and relative frequency at the burned site compared to the unburned site. *Suillus asiaticus*, *S. cf. aurihymenius*, *S. viscidus* and *S. grevillei* were recorded only at the burned site, and the frequency of *S. grevillei* was significantly reduced to zero at the unburned site (Fig. 2c). These results suggest that *Suillus* species may be important in the recovery of *Larix* forests after fire events. Some *Suillus* species exhibit adaptive strategies to quickly colonize disturbed habitats. They produce abundant fruit bodies and spores that are effectively dispersed by wind and mycophagous mammals (Ashkannejhad and Horton 2006; Peay et al. 2012; Urcelay et al. 2017; Vasutova et al. 2019). Their spores have high germination rates in response to host roots (Theodorou and Bowen 1987), but also remain viable for an extended time with high desiccation resistance (Ashkannejhad and Horton 2006; Bruns et al. 2019). *Suillus* EM roots are often found in fields immediately and within several years after fire events (Bruns et al. 2002; Smith

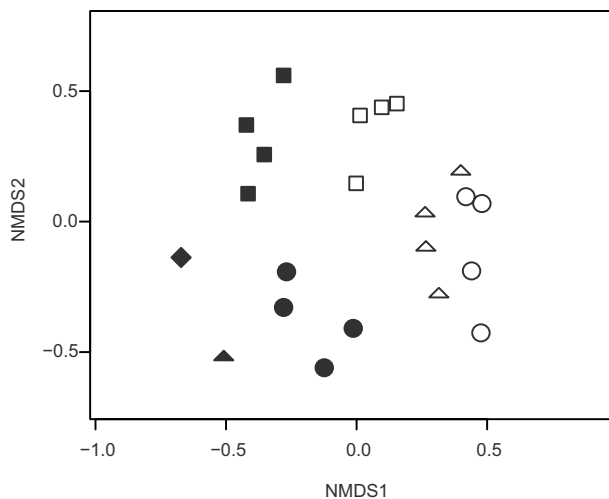


Fig. 3 Dissimilarity in the ectomycorrhizal fungal composition shown by non-metric multidimensional scaling (NMDS) with the Bray–Curtis distance. Filled and open symbols denote burned and unburned sites, respectively. The square, circle, triangle and diamond symbols indicate *Larix gmelinii*, *Betula platyphylla*, *Populus tremula* and *Picea ovobata*, respectively

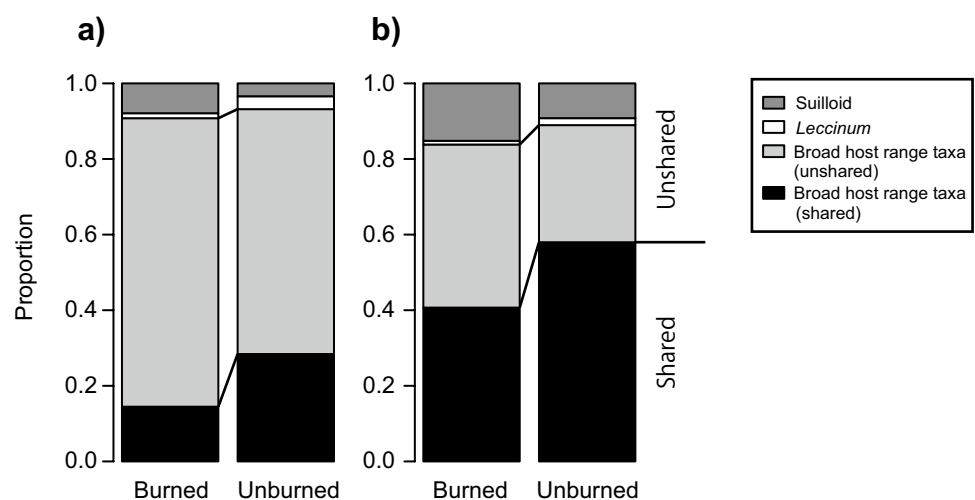
et al. 2004; LeDuc et al. 2013), inferring their resilience to fire disturbances. Moreover, the above traits may increase the competitiveness of *Suillus* over late-successional EM fungi, partly due to strong priority effects (Kennedy and Bruns 2005). For example, *Suillus* forms long rhizomorphs (Agerer 2001) and can expand vegetatively over broad areas (Bonello et al. 1998; Bruns et al. 2002), which enables effective colonization of new roots in habitats where root density is low (Peay et al. 2011). Although *Rhizopogon* species are an important component of post-fire EM fungal communities on *Pinus* and *Pseudotsuga* (Baar et al. 1999; Twieg et al. 2007; Cowan et al. 2016; Glassman et al. 2016), *R. laricinus* was only detected at the unburned site at low

frequency (0.0073%). This species was recently discovered to be associated with *Larix* in northeastern Siberia (Miyamoto et al. 2019). Our results imply that the species may be less common in this area, but more studies are required to better understand the ecological roles of this species in relation to fire disturbances.

Although the overall frequency of the genus *Suillus* decreased at the unburned site, *S. cavipes* and *S. spectabilis* were the second- and third-most dominant taxa on *L. gmelinii* at both sites. This finding implies that some *Suillus* species may be important for *Larix* growth throughout forest development. *Larix* forests are historically linked and well-adapted to fire disturbances in eastern Eurasia. Frequent fires may enhance seed germination and growth of shade-intolerant *Larix* seedlings by improving seedbed conditions and reducing the canopy of competing trees (Alexander et al. 2018). Without fires, *Larix* may be replaced by late-successional, shade-tolerant trees, such as *Picea* (Schulze et al. 2012; Shuman et al. 2017). Subsequently, *Suillus* may be replaced by other broad host range fungi with decreasing dominance of the compatible host in the absence of fire disturbances. The highly specialized symbiosis between *Larix* and *Suillus* is assumed to be genetically regulated through a long history of plant-fungal coevolution (Liao et al. 2016). Frequent surface fires common in eastern Eurasia may be important in maintaining *Larix* forests (de Groot et al. 2013; Rogers et al. 2015) and are likely to be concomitant with tightly linked *Suillus* species.

The EM fungal composition was distinct between *L. gmelinii* and *B. platyphylla*. *Betula platyphylla* was mainly associated with broad host range taxa, such as *Lactarius*, *Piloderma* and *Tomentella*, while narrow host range taxa on *Betula* (i.e., *Leccinum* spp.; den Bakker et al. 2004) were relatively uncommon. The fungal composition was more differentiated between the burned and unburned sites for *B. platyphylla* than for *L. gmelinii* (Fig. 3), indicating a

Fig. 4 The proportion of ectomycorrhizal fungal operational taxonomic units with reference to their host overlap and specificity between *Larix gmelinii* and *Betula platyphylla*. **a** Richness and **b** frequency



high variability in the EM fungal composition for *B. platyphylla*. However, the EM fungal richness at the burned site was 75–77% of that at the unburned site for both hosts, implying similar recovery rates for fungal richness after the fire. We also found that the proportion of shared EM fungi between the two hosts increased in the mature forest (28.4% in richness) compared with the burned site (14.7%). This pattern agrees with a previous study that showed that the relative abundance of compatible fungi between *Pseudotsuga menziesii* and *B. papyrifera* increased with time in Canadian boreal forests (Twieg et al. 2007). Moreover, Buscardo et al. (2012) reported that the EM fungal compatibility between *Pinus pinaster* and understory shrubs was reduced at sites with short fire intervals, whereas it was maintained at sites with long fire intervals. These observations imply that the fungal compatibility between pioneer Pinaceae hosts and coexisting angiosperms may increase over time after fires.

In this study, the EM fungal inoculum potential was expected to be high at the burned site for several reasons. Firstly, because 28% of *L. gmelinii* trees survived the 2003 fire, some of the EM roots and mycelia probably survived, thereby acting as a primary source for the rapid colonization of new roots at the burned site. Secondly, some EM fungi produce heat-resistant propagules and form “propagule banks” in deeper soils, which remain viable after fire disturbances (Izzo et al. 2006; Peay et al. 2009). Propagule banks were likely present in the studied forest because they often function as inoculum sources for regenerating seedlings in fire-disturbed habitats (Baar et al. 1999; Stendell et al. 1999; Glassman et al. 2016). Lastly, the burned and unburned sites in this study were only 800 m apart; thus, the spores of late-successional EM fungi could have readily dispersed from nearby forests. These settings imply that EM fungal inocula may not be a limiting factor for fungal colonization at the burned site. Rather, the specific site conditions, including the host community and soil properties, may explain the differences in the EM fungal community structure between the two sites. For example, we found a substantial reduction in EM fungal richness for *P. tremula*, which was less abundant after the fire (Table 1, Fig. S1). Moreover, the post-fire tree density was less than half (i.e., 47.7%) of the unburned site, indicating reduced host root densities and habitat spaces for EM fungal colonization. Our burned site was characterized as a young open-canopy stand, while EM fungal diversity has been reported to increase with canopy closure (LeDuc et al. 2013). EM fungal composition is also affected by various soil properties (Jonsson et al. 1999; Kranabetter et al. 2009; Cox et al. 2010). Thus, despite a high inoculum potential, altered habitat conditions after a fire may restrict late-successional EM fungi from dominating in burned forests.

Soil pH is an important factor influencing EM fungal community structure (Cox et al. 2010; van der Linde et al.

2018). EM fungal richness generally increases in slightly acidic soils (Tederloo et al. 2014), which can be influenced by competition with bacteria and saprotrophic fungi that prefer a high soil pH (Yamanaka 2003; Barcenas-Moreno et al. 2011). Thus, the decreased EM fungal richness at our burned site may be partly attributed to increased soil pH, which might have been influenced by ash and charcoal depositions following the fire (Bryanin and Sorokina 2019). We noted that the occurrence of some EM fungal OTUs was associated with soil pH conditions (Fig. S2). We found that three fungal OTUs (*C. comptulus*, *L. vietus* and *R. emetica*) appeared to prefer low pH conditions, but they were also abundant at the unburned site; thus, their occurrence may be attributed to soil pH or other unmeasured factors that covaried with the fire event. By contrast, two OTUs (*P. bicolor* OTU1 and *T. terrestris* OTU1) appeared to prefer low soil pH independently from the fire event (Fig. S2). These fungi might specifically prefer microhabitats with low soil pH at the burned site.

Our burned and unburned sites were only 800 m apart along a continuous forest on a uniform topography, indicating that the observed contrasting pattern in EM fungal community structure between the two sites was likely attributable to fire effects. However, our sampling was limited to a single comparison of burned and unburned forest sites, which limits our ability to distinguish site-specific patterns from local or regional patterns. Thus, the observed patterns should be considered with caution when generalizing the pattern of the post-fire EM fungal community structure in this region. However, our findings are consistent with those of previous studies in boreal forests that reported reduced EM fungal richness and the dominance of disturbance-adapted fungi following fires (Mah et al. 2001; Smith et al. 2004; Kipfer et al. 2011; Barker et al. 2013; LeDuc et al. 2013; Yang et al. 2020). Thus, the present study provides valuable information on the EM fungal community structure of a post-fire forest in the Russian Far East, one of the regions where such information is scarce (Dove and Hart 2017; Taudière et al. 2017). More studies are needed to improve our understanding of the effect of fire on forest biota, particularly for specialized host-fungus symbiotic partners in ecological and evolutionary contexts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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