Mycorrhiza (2025) 35:27
https://doi.org/10.1007/s00572-025-01201-y

RESEARCH

Reduction of the α and β diversity of ectomycorrhizal fungal community under snowmelt: highlights from a common garden trial using *Abies sachalinensis* with differing host origins and light condition

Yoriko Sugiyama[1] · **Shunsuke Matsuoka**[1] · **Wataru Ishizuka**[2] · **Tetsuto Sugai**[3]

Received: 25 April 2024 / Accepted: 18 March 2025 / Published online: 3 April 2025

Abstract

The community structure of ectomycorrhizal (ECM) fungi typically displays temporal dynamics. However, heavy snow cover hinders belowground investigations in temperate-to-boreal forests where ECM trees dominate, and the dynamics of the ECM fungal community structure during winter have not been fully elucidated. Given that boreal conifer species start root production in response to snowmelt, studies on the response of the ECM fungal community to snowmelt are needed. In the present study, to infer the community dynamics during the snowmelt season and their susceptibility to host tree conditions, we investigated ECM fungi associated with saplings of the evergreen conifer *Abies sachalinensis* immediately after the start and end of snowmelt in a common garden experiment. Saplings derived from two sources of contrasting snowfall conditions (heavy vs. little) were grown under two different light conditions (open vs. shaded), and the ECM fungal community dynamics patterns were compared across these combinations. The response of the ECM fungal community structure varied across treatments; although significant loss of ECM fungal operational taxonomic units (OTUs) was observed when saplings from the heavy snowfall region were grown under shade conditions, no change in community structure across the snowmelt season was observed for the other combinations. The stability of community composition despite the change in abiotic conditions with snowmelt, together with the effects of host origin and light conditions on community dynamics patterns, would imply the importance of host-mediated community dynamics of ECM fungi during the snowmelt season.

Keywords *Abies sachalinensis* · Community composition · Ectomycorrhiza · Snowmelt season · Temporal dynamics

Introduction

In temperate-to-boreal forests, many of the dominant tree species form mutualistic associations with ectomycorrhizal (ECM) fungi (Taylor and Alexander 2005; Brundrett and Tedersoo 2020). As these tree species largely depend on ECM fungi for soil nutrient acquisition (Smith and Read 2008), with different fungal taxa having different abilities for soil nutrient acquisition (Pena et al. 2013; Van Nuland and Peay 2020; Jörgensen et al. 2023; Khokon et al. 2023), information on the ECM fungal community composition is useful for understanding nutrient cycling and plant community dynamics in temperate-to-boreal forests. Thus, many studies have been conducted to reveal the community composition of ECM fungi and its spatial and/or temporal dynamics (Lilleskov et al. 2004; Izzo et al. 2005; Tedersoo et al. 2008; Pickles et al. 2010; Jarvis et al. 2013; Bahram et al. 2015; Matsuoka et al. 2016; Sugiyama et al. 2020).

Despite these efforts to describe the temporal dynamics of ECM fungal communities, little is known about their dynamics outside the growing season. The temporal dynamics of the ECM fungal community structure have been described at various resolutions, from across years (Izzo et

✉ Yoriko Sugiyama
sugiyama.yoriko.3f@kyoto-u.ac.jp

[1] Field Science Education and Research Center, Kyoto University, Kyoto, Japan

[2] Hokkaido Research Organization, Sapporo, Japan

[3] Forestry and Forest Products Research Institute, Hokkaido Research Center, Sapporo, Japan

al. 2005; Pickles et al. 2010), seasons (Buée et al. 2005; Walker et al. 2008; Richard et al. 2011) to months (Koide et al. 2007; Courty et al. 2008; Mundra et al. 2015; Sugiyama et al. 2020). However, these studies were mainly conducted during the growing season. Reports on community dynamics during the nongrowing season are still limited, possibly due to the thick snow cover, especially in temperate-to-boreal forests where ECM tree species dominate.

The response of host roots to snowmelt would make it worthwhile to investigate the dynamics of the ECM fungal community structure from winter to early spring. In fact, boreal tree species often stop fine-root production in winter and resume it gradually in early spring (Fukuzawa et al. 2021; Radville et al. 2016; Wang et al. 2018), mainly utilizing the stored starch in roots (Hansen et al. 1996; Endrulat et al. 2010). Particularly in temperate and boreal coniferous species, spring root elongation occurs in response to snowmelt (Sugai et al. 2024) and the increase in soil temperature (Wang et al. 2018). As these newly produced fine roots can serve as the recruiting ground for new ECM fungal species, community dynamics under snowmelt are partially responsible for the formation of the ECM fungal community in the growing season.

The root production pattern in the snowmelt season can change depending on the genetic variation in the host plants and the growing conditions. Inter- (McCormack et al. 2014) and intraspecific (Sugai et al. 2024) variations in root production patterns have been revealed, and abiotic factors can also change root production patterns (e.g., nutrient availability and light condition, Nadelhoffer 2000; Poorter et al. 2019). These variations in root production patterns during the snowmelt season may affect the ECM fungal community structure. Thus, studies that consider the variation in host condition will further enhance our understanding of the temporal dynamics of the ECM fungal community structure during the snowmelt season.

In the present study, to infer the response of the ECM fungal community to snowmelt and its susceptibility to host tree conditions, we investigated the ECM fungal community composition immediately after the start and end of the snowmelt season in a common garden experiment. *Abies sachalinensis* (Sakhalin fir) saplings from two different geographic origins were grown under two different light conditions. Sakhalin fir is an evergreen conifer and the most dominant component of boreal to subarctic forests on the northernmost island of Japan. In this species, intraspecific ecological variation in growth and survival traits (Ishizuka et al. 2021) and differences in root elongation patterns during the snowmelt season (Sugai et al. 2024) among different origins with contrasting snowfall conditions (heavy vs. little) have been reported. In addition, shading is known to change host carbon allocation and root elongation (Poorter et al. 2012, 2019). With this common garden experimental setting, we aimed to clarify (1) how the ECM fungal community structure changes during the snowmelt season and (2) whether the dynamic pattern of the ECM fungal community structure changes with host conditions.

Materials and methods

Study design

The root samples were obtained from a common garden experiment reported by Sugai et al. (2024). Sakhalin fir (*Abies sachalinensis*) saplings was established at the nursery of the Forestry Research Institute, Hokkaido Research Organization, located in western Hokkaido (43°29 N, 141°85 E, 50 m a.s.l.), the northernmost island in Japan. Saplings studied were obtained from multiple seedlots collected in the autumn of 2014 from a commercial seed orchard, sown at the nursery described above in the spring of 2015, and transplanted to the established plots of our experimental site in the spring of 2019. In this experiment, saplings derived from eight locations of two different regions with contrasting climatic conditions were selected: four locations from eastern Hokkaido (43°07 ± 0.01 N, 145°03 ± 0.01 E) and four from northern Hokkaido (44°35 ± 0.08 N, 142°32 ± 0.01 E). Eastern Hokkaido is characterized by cool temperatures with little snowfall in winter, whereas northern Hokkaido is characterized by heavy snowfall. The climatic conditions in winter were similar between northern Hokkaido where seeds were collected and western Hokkaido where the common garden experiment was conducted. Corresponding to this climatic contrast, the root elongation pattern in early spring differed between Sakhalin firs from eastern Hokkaido and those from northern Hokkaido. Specifically, under heavy snowfall conditions, such as those at our experimental site, root elongation starts earlier in lineages from the heavy snowfall region than in those from the little snowfall region (Sugai et al. 2024).

In the common garden experiment, six plots were established, and in each plot, saplings from two different origins were transplanted via a randomized design. In each plot, approximately 50 saplings were placed at least 50 cm apart from each other. The experiment at the six plots was performed at relatively uniform soil condition; soil was derived from a sedimentary rock formed mainly by clay which was normally found around the experimental field and nearby forests, but was cultivated here for the nursery. The soil was watered twice a day with an automatic irrigation system during the growing season (i.e., May to November) and fertilized with 2 g per litter of soil of Osmocote Exact Standard 15-9-12 (HYPONeX JAPAN CORP., Osaka, Japan) at the

Table 1 The number of samples and retrieved ectomycorrhizal (ECM) fungal OTUs and reads for each treatment category

Month	Host origin	Shading treatment	The number of samples	The number of ECM fungal OTUs*	The number of ECM fungal reads*
April	East	Light	12	9 (4.1 ± 1.1)	407,849 (33987.4 ± 8508.3)
		Shade	12	15 (5.3 ± 1.2)	214,853 (17904.4 ± 6156.8)
	North	Light	11	9 (3.7 ± 0.6)	377,524 (34320.4 ± 11241.6)
		Shade	12	35 (8.5 ± 3.3)	214,381 (17865.1 ± 13779.0)
May	East	Light	12	12 (4.7 ± 1.2)	408,815 (34067.9 ± 11599.5)
		Shade	10	11 (4.7 ± 1.9)	248,209 (24820.9 ± 9644.0)
	North	Light	9	7 (3.6 ± 0.9)	275,088 (30565.3 ± 12573.1)
		Shade	12	14 (4.8 ± 1.3)	290,405 (24200.4 ± 13220.8)

*Outside the parentheses are the total numbers and inside the parentheses are the mean value and standard deviation for each sample

Table 2 The list of treatments and the number of samples and retrieved ectomycorrhizal (ECM) fungal OTUs and reads for each group

Treatment[1]	Group	The number of samples	The number of ECM fungal OTUs[2]	The number of ECM fungal reads[2]
Sampling month	April	47	38 (5.4 ± 2.6)	1,214,607 (25842.7 ± 12914.4)
	May	43	18 (4.5 ± 1.4)	1,222,517 (28430.6 ± 11979.8)
Host origin	East	46	16 (4.7 ± 1.4)	1,279,726 (27820.1 ± 11036.1)
	North	44	38 (5.3 ± 2.8)	1,157,398 (26304.5 ± 13909.0)
Shading treatment	Light	44	14 (4.0 ± 1.1)	1,469,276 (33392.6 ± 10400.9)
	Shade	46	41 (5.9 ± 2.6)	967,848 (21040.2 ± 11320.5)

[1]Treatments with significantly different number of OTUs between groups are shown in bold (GLMM, $p < 0.05$). The detailed statistical values are provided in the text

[2] Outside the parentheses are the total numbers and inside the parentheses are the mean value and standard deviation for each sample

beginning of the growing season in 2019 and 2020. The soil pH and electrical conductivity in KCl and C/N ratio were ca. 4.0-4.5, 66.0–89.0 and 14.7, respectively.

To test the effects of shading on the response of plants and ECM fungal communities, three plots were shaded throughout the growing season by covering the entire plot with black mesh net. 80% of the light intensity was cut off by this shading treatment, which affected the host plants' growth (Ishizuka et al., manuscript preparation). It should be noted that the shading treatment temporarily ceased just before the snowfall (snowpack) until the snow completely melted, as not to change the effect of snowfall on the plant and ECM fungal communities. During the snowing season, saplings were buried in snow. The further information on the experimental settings is provided in Supplementary material 1, including the photos and the data on the detailed soil condition and climatic condition of experimental site, latitude/longitude of each host origin and the change in host biomass between sampling occasions.

Root sampling

To investigate the community dynamics of ECM fungi in early spring, root sampling was conducted twice in 2021; immediately after snowmelt started (April 9–11th, hereafter April sampling) and after the snow completely melted and the soil temperature increased (April 30th to May 2nd, hereafter May sampling). On each sampling occasion, eight saplings (approximately less than 1 m in height, six years old), composed of four eastern and northern Hokkaido individuals, were harvested from each plot, yielding a total of 48 samples. These 48 samples were composed of 24 shade and light samples or 24 eastern and northern-origin samples, respectively. However, in April, one light plot yielded seven (lacking one northern sapling) saplings. In May, two light plots yielded six (lacking two northern saplings) and seven (lacking one eastern sapling) saplings and one shade plot yielded six (lacking two eastern saplings) saplings. Thus, the total number of April samples was 47, which was composed of 24 shade and 23 light samples or 24 eastern- and 23 northern-origin samples, and the total number of May samples was 43, which was composed of 22 shade and 21 light samples or 22 eastern- and 21 northern-origin samples (Table 2). In the sampling, the entire root system was excavated (ca. 40 cm in depth) and, after the shoots and roots were separated, one root system was divided for ECM analyses and morphology analyses (Sugai et al. 2024). The root system for ECM analyses from one sapling was placed into one plastic bag, transported to the laboratory and stored in a plastic bag at -20 °C until further ECM root-tip sampling (Table 1).

In the laboratory, 20 root tips (3–4 mm in length) were collected from each of the 47 April and 43 May saplings. Before the root tip sampling, the root samples were thoroughly checked and morphologically confirmed that ECM diversity would be sufficiently covered with 20 root tips. The root tips from the same sample were pooled into one 1.5 ml tube, serially washed in 70% ethanol (w/v) and 0.005% aerosol OT (di-2-ethylhexyl sodium sulfosuccinate) solution and rinsed with sterile distilled water to remove

adhering soil particles and fungal tissues (e.g. spores). After washing, the samples were stored at -20 °C in cetyltrimethylammonium bromide (CTAB) lysis buffer until DNA extraction.

Molecular identification of ECM fungi

Total DNA was extracted from the root tips of 90 samples using the modified CTAB method (Gardes and Bruns 1993). To analyze the fungal communities colonizing the roots, polymerase chain reaction (PCR) amplification targeting the ribosomal internal transcribed spacer region (ITS15.8 S-ITS2) of the ribosomal DNA was conducted using the ITS1F_KYO2 and ITS2_KYO2 (Toju et al. 2012) primer pair fused with an Illumina sequencing primer and six random bases (N). For PCR, 10 µL of a KOD FX Neo (TOYOBO, Osaka, Japan) buffer system containing 1 × PCR buffer, 0.4 mM deoxynucleoside triphosphates, 3 nmol each of the forward and reverse primers, 0.2 units of KOD FX Neo polymerase, and 1.0 µL of template DNA was used. The PCR conditions were as follows: initial denaturation for 2 min at 94 °C, 40 cycles of 10 s at 98 °C, 30 s at 60 °C, and 30 s at 68 °C, and a final extension for 5 min at 68 °C. To subsequently fuse the 8 bp identifier indices (Hamady et al. 2008) and the MiSeqP5/P7 adapter to the initial PCR amplicons, we conducted an additional PCR using the same PCR mixture and conditions as the initial PCR. The only change to the protocol was that the number of cycles was reduced to 12. The resulting PCR amplicons were pooled and purified using AMPure XP (Beckman Coulter, Brea, CA, United States). The purified library was then excised using E-Gel SizeSelect (Thermo Fisher Scientific, Waltham, MA, United States). The resulting library was subjected to 2 × 250-bp paired-end sequencing on the MiSeq platform (Illumina, San Diego, CA, United States).

Bioinformatics

From the 90 samples, 3041791 fungal reads were obtained via MiSeq sequencing. The retrieved reads were processed using CLAIDENT version 0.2.2018.05.29 (Tanabe and Toju 2013). Reads were first demultiplexed using the "clsplitseq" command. The resulting reads were deposited in the Sequence Read Archive of the DNA Data Bank of Japan (accession numbers: DRR545416-DRR545506). Then, using the "clfilterseq" command, low-quality 3' tails were trimmed, and low-quality reads were filtered based on a minimum quality value of 30. The resulting forward and reverse reads were merged using the "clconcatpair" command. From the resulting merged reads, potentially noisy and chimeric sequences were eliminated using the "clcleanseqv" command. The remaining reads were clustered into operational taxonomic units (OTUs) with similarity thresholds of 0.97 using the "clclasseqv" command. Potentially chimeric OTUs were eliminated using UCHIME (Edgar et al. 2011) without any references. Additionally, cells with reads less than 0.02% of the total reads in each sample (which corresponds to 1–11 reads) were removed because these rare entries could represent contamination. After these processes, 2,992,795 reads from 332 OTUs remained (Table S1). Then, the taxonomic assignment of the retrieved OTUs was conducted using CLAIDENT. The resulting sample × OTU matrix with the taxonomic identities of each OTU is available in Table S1. Based on their taxonomy, the functional groups of the obtained OTUs were inferred using FungalTraits (Põlme et al. 2021). In addition, for ECM fungal OTUs, the exploration type was inferred using FungalTraits. In further analyses, only OTUs that were assigned to ECM fungi were extracted and used.

Statistical analyses

All the analyses were conducted with R ver. 4.3.3 (R Core Team 2024). Before the analyses, we calculated the sequencing read coverage for each of the 90 samples. The coverage was 100% for all the samples, and the rarefaction curves reached a plateau. Therefore, no rarefaction was conducted on the OTU matrix.

First, the overall difference in community composition among sampling occasion × plot × host origin was visualized with nonmetric multidimensional scaling (NMDS) ordination. In this ordination, a community matrix recording the presence/absence of each ECM fungal OTU for each category was constructed and converted into a dissimilarity matrix using the Jaccard index. Here, to illustrate the variation in community structure due to differences in richness and composition, we used the Jaccard index, which reflects both changes in composition and richness (Chase et al. 2011). Then, the variation in ECM fungal OTU richness and composition among the samples was tested. We first checked the relationships between OTU numbers and sampling occasions, host origins and shading treatments by constructing a generalized linear mixed model (GLMM) using 'glmer' command in 'lme4' package. In the GLMM, sampling occasion (April vs. May), host origin (North vs. East) and shading treatment (shade vs. light) were included as fixed effects and plot as a random effect. The error structure and link function were Poisson and log, respectively. Following this GLMM analysis, the categories with significantly different ECM OTU numbers were specified using Tukey's honestly significantly different post hoc test using the 'glht' function of the 'multcomp' package in R (Hothorn et al. 2008). For the analysis of OTU composition, PERMANOVA and betadisper analyses were conducted with the

'adonis2' and 'betadisper' commands, respectively, in the vegan package. In the PERMANOVA, sampling occasion, host origin and shading treatment were included as explanatory variables and plot was included as strata. In the betadisper analysis, eight categories (2 sampling occasions × 2 shading treatments × 2 host origins) were included as the explanatory variables. In these analyses, the Raup–Crick index was used to generate the dissimilarity matrix instead of the Jaccard index. This is because the Raup–Crick index is less susceptible to the difference in OTU number among categories (Chase et al. 2011), and in our analyses, we conducted separate analyses on the difference in OTU number from the composition.

The present study aims to see the effects of host origin and light condition on the ECM fungal community dynamics in snowmelt season. To check these effects, further analyses that divide samples in accordance with the host origin and/or light condition were conducted. If differences in the number of OTUs or the dispersion of OTU composition due to host origin × light condition were detected in the above GLMM and betadisper, the samples were divided into four datasets according to host origin × shading treatment category, and for each of these four datasets, differences in OTU richness and composition between April and May were tested. For the analysis of richness, a GLMM was constructed that included sampling occasion as the fixed effect and plot as the random effect. For the analysis of composition, PERMANOVA and betadisper analyses were conducted, with including sampling occasion as the explanatory variable. In these analyses, the Raup–Crick index was used to generate the dissimilarity matrix. These GLMM, PERMANOVA and betadisper analyses were repeated on the additional four datasets: each of the light and shaded sample datasets (with no discrimination of the host origin) and each of the northern and eastern sample datasets (with no discrimination of the shading treatments). The results for these four additional datasets are provided in Supplementary material 2.

To further estimate how the ECM fungal community composition of each of the host origin × shading treatments changed from April to May, the dissimilarity between the April and May communities was separated into turnover and nestedness components (Baselga 2010). Turnover reflects the replacement of OTUs, and nestedness reflects the loss of OTUs. By calculating these two values, we assessed the contributions of replacement and OTU loss (or gain) to the change in community structure from April to May. In this analysis, the standardized effect size (SES) values of pairwise turnover and nestedness values along with the total Jaccard dissimilarity among samples were calculated. SES was defined as $(B_{obs}–B_{null})/B_{sd}$, where B_{obs} is the observed value of turnover or nestedness, B_{null} is the mean of the null distribution of turnover or nestedness and B_{sd} is the standard deviation of the null distribution. B_{obs} were calculated using the 'beta.pair' function in the 'betapart' package, with the index family 'jaccard'. The null distribution was calculated based on 999 randomizations, preserving the OTU occurrence frequency with the 'randomizeMatrix' command in the 'picante' package. To evaluate the contribution of these two components to the temporal variation in the ECM OTU composition of each host origin × shading treatment, four ECM OTU matrices for each of the host origin × shading treatment categories were generated, and sample-based pairwise total Jaccard/turnover/nestedness SES matrices were calculated. From the resultant dissimilarity matrices, values comparing the April and May samples were extracted, and their means and 95% confidence intervals were calculated. Here, we used the Jaccard index because, unlike the Raup–Crick index, which focuses on the turnover component, the Jaccard index is the sum of nestedness and turnover components.

To check whether the trend changes when the detailed host origins (i.e. four localities within each of East and North regions) were considered, boxplots of the number of ECM OTUs per sample and the degree of the dispersion of OTU composition among samples were depicted. Here, we visually check the trend and no statistical test was conducted, as the sample sizes of each category (sampling occasion × detailed host origin × light condition) can be too small ($n = 1–4$). The results for these analyses are provided in Supplementary material 3.

Results

Community overview

In total, 41 ECM fungal OTUs were detected in the 90 root samples. Among these, 38 and 18 OTUs were detected in April and May, respectively, and 15 OTUs were shared between the two sampling occasions.

Among the 41 ECM OTUs, 37 were Basidiomycota, and four were Ascomycota. The retrieved ECM OTUs were composed of 21 genera, among which *Tomentella* and *Russula* were the most and the second most OTU-rich genera, respectively (*Tomentella*: 7 OTUs, 17% of the total ECM OTUs; and *Russula*: 6 OTUs, 15%). The 38 ECM OTUs detected in the April samples were composed of 15 genera. Within the April community, *Tomentella* and *Russula* were again the most and the second most OTU-rich genera, respectively (*Tomentella*: 6 OTUs, 16%; and *Russula*: 5 OTUs, 13%). On the other hand, 18 ECM OTUs detected from the May samples were composed of nine genera, among which *Tomentella* and *Sebacina* were the OTU-richest (3 OTUs, 17%). When focusing on the exploration type

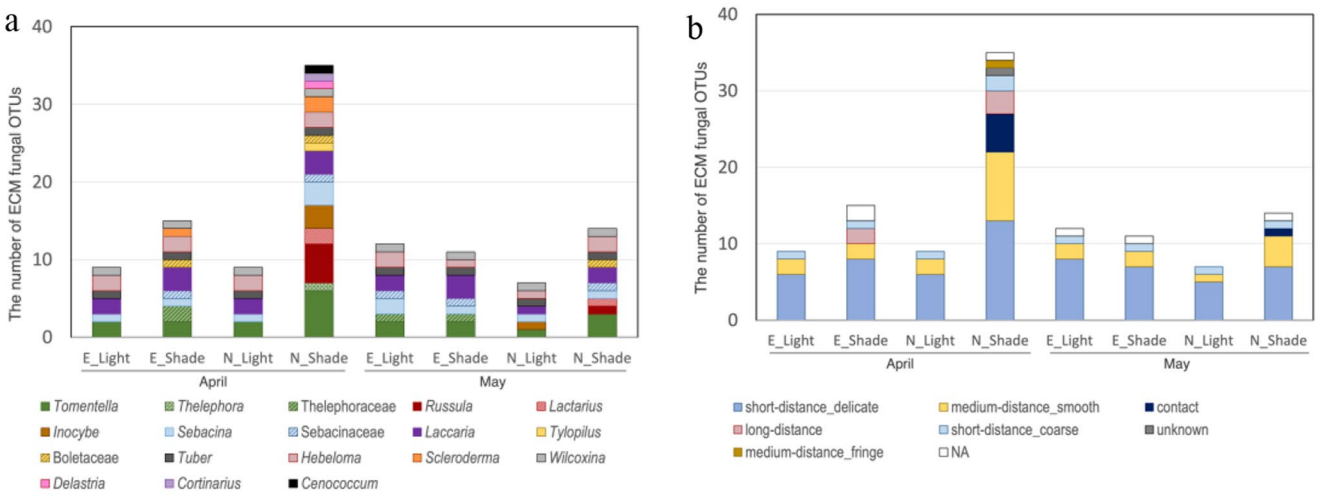

Fig. 1 The number of retrieved ECM fungal OTUs and their genus (**a**) and exploration type (**b**) composition

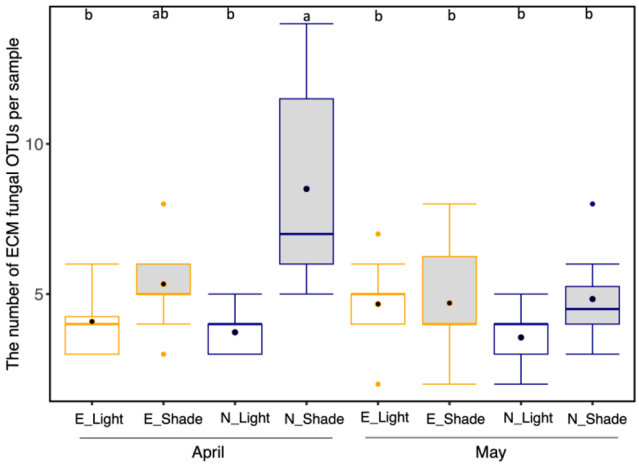

Fig. 2 Boxplot depicting the number of ECM fungal OTUs retrieved from each sapling. The colors of the fill and frame represent the light availability condition (gray: Shade, white: Light) and the host origins (orange: East, blue: North), respectively. The bottom and the top of the boxes represent the first and the third quartiles and the thick line in the box represents the second quartile. The whiskers represent the maximum and minimums values within 1.5 × interquartile value from the third and the first quartile, respectively. The black dots represent the mean value. Different letters indicate significant differences ($p<0.05$) among categories based on Tukey post hoc tests after one-way ANOVA

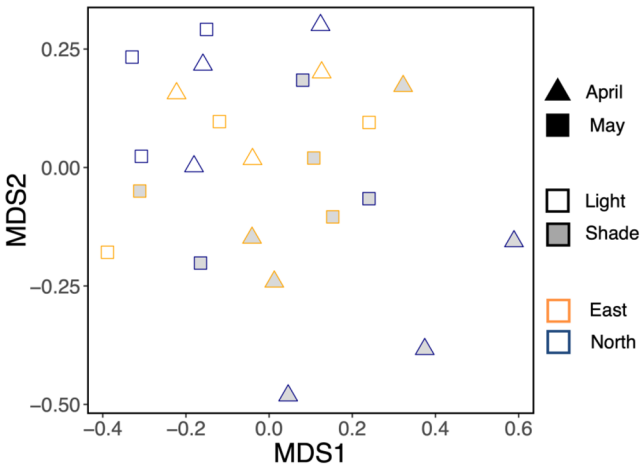

Fig. 3 NMDS ordination results. The shape represents the sampling occasion (triangle: April, square: May). The colors of the fill and frame represent the light availability condition (grey: Shade, white: Light) and the host origins (orange: East, blue: North), respectively. Stress value = 18.2

composition, the short-distance_delicate type and medium-distance_smooth types were the most and the second most dominant, accounting for 59% (24 OTUs) and 42% (17 OTUs) of the total ECM fungal OTUs.

Variation in the ECM fungal community structure among treatments and sampling occasions

The total number of ECM fungal OTUs retrieved from each of the eight categories was approximately 10, except for the April × North × Shade one, which yielded 35 OTUs (Table 1; Figs. 1a and 2). The NMDS ordination indicated that the ECM OTU composition was not clearly separated in accordance with differences in sampling occasions, host origins or shading treatments, but April × North × Shade communities seemed to be slightly different from the others (Fig. 3). From April × North × Shade samples, OTUs with diverse exploration types were obtained. The long-distance type, medium-distance_fringe type, and contact type, which were absent or scarce in other categories, exists in April × North × Shade samples (Fig. 1b).

The number of ECM fungal OTUs per sample significantly changed with sampling occasion (GLMM, Estimate = -0.20, $p=0.04$) and light condition (Estimate = 0.37, $p<0.001$), but not with host origin (Estimate = 0.091, $p=0.34$). The multi-comparison test showed that the

number of OTUs per sample was significantly greater in the April × North × Shade samples than in other samples except for April × East × Shade ones. The number of OTUs in the April × East × Shade samples did not significantly differ from other samples (Fig. 2). The OTU composition significantly differed between sampling occasions ($R^2=0.03$, $p=0.04$), shading treatments ($R^2=0.07$, $p=0.003$) and host origins ($R^2=0.03$, $p=0.03$). The betadisper analysis showed that the dispersion in the OTU composition significantly differed among the categories ($F=9.48$, $p<0.001$; Fig. 4). The greatest dispersion was observed among the April × North × Shade samples, followed by the April × East × Shade and May × East × Shade samples.

The number of ECM fungal OTU tends to be high in April × Shade × each of four northern origins. Also, the dispersion of OTU composition was large in April × Shade × each of four northern origins followed by April × Shade × each of four eastern origins and May × Shade samples, suggesting the consistency of results between localities in North regions (Supplementary material 3).

Temporal changes in the ECM fungal community

Among the four host origin × shading treatment categories, only the North × Shade category showed a significant decrease in OTU richness from April to May (GLMM, Estimate = -0.56, $p<0.001$). In this category, the OTU composition did not significantly differ between sampling occasions (PERMANOVA, $R^2=0.02$, $p=0.63$), but the dispersion of composition was significantly greater in April ($F=5.6$, $p=0.027$). For the remaining three categories, neither OTU richness (North × Light, Estimate = -0.047, $p=0.84$; East × Shade, Estimate = -0.14, $p=0.46$; and East × Light, Estimate = 0.13, $p=0.50$) nor composition showed significant temporal changes (PERMANOVA: North × Light, $R^2=1.72$, $p=0.11$; East × Shade, $R^2=0.05$, $p=0.38$; East × Light, $R^2=0.03$, $p=0.49$; betadisper: North × Light, $F=0.43$, $p=0.52$; East × Shade, $F=3.27$, $p=0.09$; and East × Light, $F=2.97$, $p=0.10$).

The SES value of the Jaccard index did not deviate from the random expectation for all the host origin × shading treatment categories. However, the separation of beta diversity into nestedness and turnover components indicated that the contributions of OTU replacement and loss differed among the host origin × shading treatments. In the North × Shade treatment (Fig. 5), the community showed significantly high nest structure and low turnover, indicating that the change in the OTU composition was attributable to OTU loss rather than to OTU replacement. On the other hand, the North × Light sample showed significantly lower nest structure and high turnover. For the remaining categories, both the nestedness and turnover values did not significantly deviate from the random expectation.

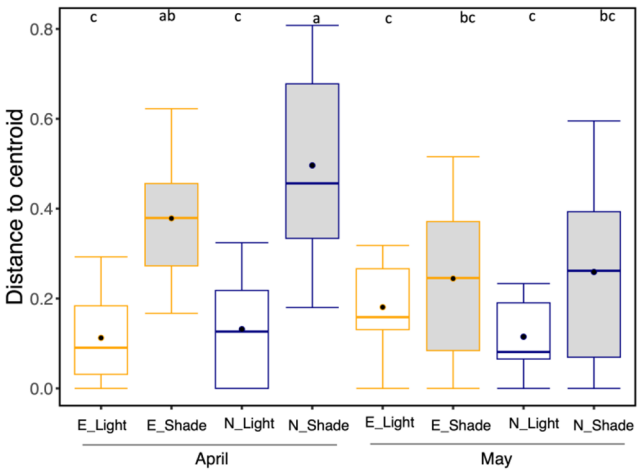

Fig. 4 The result of betadisper analysis. The boxplot depicts the distance of each ECM fungal community from each sapling to the group (sampling occasion × host origin × shading treatment) centroid based on the Raup–Crick dissimilarity index. The colors of the fill and frame represent the light availability condition (gray: Shade, white: Light) and the host origins (orange: East, blue: North), respectively. The bottom and the top of the boxes represent the first and the third quartiles and the thick line in the box represents the second quartile. The whiskers represent the maximum and minimums values within 1.5 × interquartile value from the third and the first quartile, respectively. The black dots represent the mean value. Different letters indicate significant differences ($p<0.05$) among categories based on Tukey post hoc tests

Discussion

The present study described the dynamics of ECM fungal communities across the snowmelt season and the effects of host tree origin and light conditions on those dynamics. Remarkably, the response of ECM community varied depending on the combination of these two treatments, and the turnover of ECM fungal OTUs seemed to be small during this period.

The total number of OTUs decreased from April to May, but this change was mainly driven by North × Shade samples. Among the 26 OTUs that were exclusively observed in April (i.e., those disappeared in May), 21 OTUs were observed only in the North × Shade samples (Table S1). The significant loss of OTUs in the North × Shade samples was supported by the GLMM (Fig. 2) and the large nestedness values between the April and May samples (Fig. 5). The loss of OTU in North × Shade samples was observed in all of four localities within North region when each of four origins within North and East was separately analyzed, supporting the influence of the host origin.

The OTU loss observed in the North × Shade samples provide important insights relevant to the interpretation of

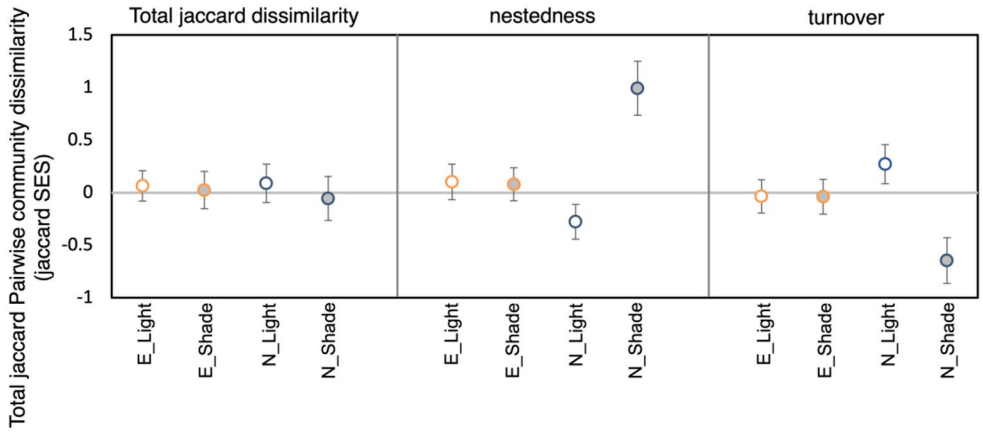

Fig. 5 The composition of Jaccard dissimilarity between the April and May communities. The means and 95% confidence intervals (CI) are indicated. The SES was calculated based on the null distribution obtained from the 999 randomizations of the community matrices. Horizontal gray line represents zero and when CI do not include zero, the dissimilarity value was regarded as significantly large/small. The colors of the fill and frame represent the light availability condition (grey: Shade, white: Light) and the host origins (orange: East, blue: North), respectively

previously reported dynamics patterns. Decreases in ECM fungal richness and soil microbial biomass from winter to the growing season have been previously observed (Lipson et al. 2000; Mundra et al. 2015), but specifically when such decrease occurs is still uncertain. Our results demonstrate that such a decrease in species richness may occur in part during snowmelt season. In addition, the finding that such OTU loss was exclusively observed in the North × Shade samples in our common garden experiment supports the possibility that the change in community composition was attributable to the host response. The possibility of host response-mediated temporal dynamics of ECM fungi has been mentioned (Koide et al. 2007; Pickles et al. 2010; Sugiyama et al. 2020), but rarely demonstrated. Thus, our results based on the common garden experiment provide important insights to advance the discussion of host-mediated dynamics. On the other hand, despite the known effects of temperature or soil conditions on community dynamics in the growing season (Sugiyama et al. 2020), little change in community structure was observed in most samples in the present study from April to May, when temperature and soil conditions clearly changed. This may suggest that the community dynamics during the snowmelt season are driven by a different process than those during other seasons.

Among the two candidate processes that lead to the loss of OTUs, namely, selection and ecological drift (Vellend 2016), selection is suggested to be the process responsible for the response of the North × Shade samples. In the North × Shade samples, the loss of OTUs from April to May decreased the dispersion in the OTU composition among the samples. Considering that ecological drift usually leads to the random loss of OTUs (Vellend 2016), the convergence of OTU composition observed in the North × Shade samples should result from the selective loss of sample-specific OTUs and the selective persistence of common OTUs. In addition, with snowmelt, the OTU composition of the North × Shade samples became closer to those of the other treatment categories (Fig. 3). This would indicate that the North × Shade communities converged towards the communities in the other treatments. From these results, it might be possible that in samples other than the North × Shade samples, the favorable ECM fungal community for spring had already formed in April, but in the North × Shade samples, the formation of spring communities accompanied by the selective loss of OTUs occurred from April to May. The exact pressure for the selective OTU loss is unclear, but the dominance of short-distance exploration type in May, which is known as C cost-efficient in inorganic N rich soil may imply the selection by host towards less carbon demanding fungi in our fertilized soil (Suz et al. 2014; Fernandez et al. 2017). In addition, competition with other microbes (e.g., Bödeker et al. 2016; DeLancey et al. 2024) may also have affected the ECM community, considering that the activity of soil microbes can be also enhanced by the host belowground activities (Broeckling et al. 2008; Huang et al. 2014; Meier et al. 2020) in May.

In samples other than the North × Shade samples, little change in community composition from April to May was observed. As the community dynamics pattern of these samples, two possibilities can be proposed: (1) the community structure changed from winter to spring in these samples, but that change preceded the April sampling (i.e., the response was delayed in the North × Shade samples), and (2) the community structure was stable from winter to May in these samples (i.e., the change in community composition from winter to spring occurred only in the North × Shade samples). As the underlying mechanisms for the first possibility (that the formation of the spring community was

delayed in the North × Shade samples), two mechanisms can be postulated. First, the reduced carbon availability or the delayed root response may have delayed the formation of the spring community in North × Shade samples. Specifically, the reduced carbon allocation to roots by shading (Rosinger et al. 2020) may have led to the lower carbon availability in spring in shaded samples, which may have delayed the response of the ECM fungal communities in these samples. Besides, the possible difference in the timing of root response to snowmelt may have led to the difference in the timing of ECM community response between host origins. A previous study, which investigated the root morphological change under snowmelt using the same saplings as ours, suggested that the root response to spring advances in eastern saplings (Sugai et al. 2024). It is possible that the response of ECM fungi could be also advanced in the eastern samples than in the northern samples. Secondly, there is also a possibility that in North × Shade samples, specific snow condition or temperature was required to form the spring community. By the contributions of either or both of these mechanisms, it is possible that the spring community may have formed from April to May in the North × Shade samples, whereas in the other samples, it had already formed in April.

Based on previous reports, the second possibility that the increase in ECM OTU in winter exclusively occurred in North × Shade samples could also be relevant. Previous studies based on field observations reported higher ECM fungal OTU richness in winter and/or early spring (Mundra et al. 2015; Sugiyama et al. 2020). Considering that the winter conditions in our common garden experiment were mostly similar to the natural conditions of the North × Shade saplings, it is possible that such increase in richness occurred only in the North × Shade saplings. The host tree species is categorized as a shade-tolerant species that usually regenerates under closed forest floors. Additionally, our common garden experiment was conducted in a heavy snowfall region, which has climatic conditions similar to the origin of the North individuals, but not to the East ones. Thus, for light-exposed and eastern individuals, the distinctly different conditions of our common garden experiment from the actual environments for their regeneration may have hindered the formation of an OTU-rich winter community. As another possible explanation, the limited carbon assimilation and allocation to roots in the Shade and North saplings implied from the reduced biomass in Shade and North samples (Supplementary Material 1) may have accelerated the turnover of ECM fungi within each root tip, and the temporary colonization of various OTUs may have led to the higher richness in the North × Shade saplings. The winter reduction in carbon allocation (Zarter et al. 2006) would be more severe in the North saplings, considering that the East saplings are adapted to lower soil temperatures (Ishizuka et al. 2021). The reduced carbon allocation results in more non-colonized root tips (Trocha et al. 2016; Turner et al. 2009), which may provide opportunities for the colonization of new OTUs. Even if a stable association could not form, the repeated death and reinfection of new OTUs would maintain richness. From our study, it cannot be determined which of these possibilities is most relevant, and why such differences in dynamics patterns were observed. Therefore, investigations over longer periods of time and further experiments in other environments are needed.

The finding that community dynamics differ between host light conditions and origins provides insights into the spatiotemporal dynamics of the ECM fungal community in forests. In forests, saplings in the understory are often shaded (Jenkins and Chambers 1989; Lewis et al. 2000; Lieffers et al. 1999; Rodríguez-Calcerrada et al. 2008), whereas trees in gaps or mature trees are exposed to light. Such differences in light availability among habitats or between tree ages may lead to differences in ECM fungal community dynamics. In addition, in plantation forests, trees are sometimes planted at sites with environmental conditions that differ from their origins. In particular, the recent trials in the reconstruction of seed zones and/or assisted migration to mitigate the impacts of ongoing climate change (Etterson et al. 2020; Ying and Yanchuk 2006) will increase the chances of plantation on the foreign region apart from seed source provenances. In these trials, it is possible to predict the suitability of the climatic conditions at the planting site, whereas it is also necessary to know the suitability and incompatibility of the soil conditions in order to ensure excellent performance in the future. The importance of considering ECM fungi to understand transplants' performance has been often discussed (Kranabetter et al. 2012, 2015; Winder et al. 2021), especially focusing on the compatibility between transplanted hosts and local fungal communities (Kranabetter et al. 2015; Pickles et al. 2015; Winder et al. 2021). According to the present study, the ECM community dynamics could differ with the hosts from different origins with different phenology. This suggests the possibility that the introduction of hosts whose phenology differs from the native ones can affect local ECM community dynamics. Further studies on the long-term impact of such introduction on the local ECM fungal communities are required. In addition, it should be noted that there is a possibility that the interaction between light conditions and host origin affects the response or its timing of ECM fungal community to snowmelt, as implied by the unique characteristics of the North × Shade sample (Figs. 1, 2 and 3). It is unclear whether such interaction occurs additively or synergistically, but our results highlight the complexity of the spatiotemporal community dynamics of ECM fungi in

early spring in forests, where host trees with varying light conditions and varying root production patterns are growing in combination.

As another significant result, the recruitment of new OTUs rarely occurred from April to May in all the treatment categories. Little recruitment was obvious from the low turnover values (i.e., simultaneous OTU loss and gain rarely occurred) between April and May, and the result that among the 19 OTUs that were detected in May, only three were newly recruited in May. Such little recruitment is characteristic of our study, as in previous studies, continuous recruitment was observed with a monthly survey during the growing season (Mundra et al. 2015; Sugiyama et al. 2020). From our study, it is unclear whether little recruitment is characteristic to our sampling period or to our site, but for the following two reasons, the sampling season might be more responsible. First, in the North × Shade samples, higher richness was observed in April, suggesting that recruitment to form the April community should have occurred at some point earlier in the year. Second, in the snowmelt season, limitations in the number of non-colonized root tips and spore arrival may limit OTU recruitment. Although some fine-root production may occur in early spring, its peak occurs from summer to autumn (Fukuzawa et al. 2021; Joslin et al. 2001; Konôpka et al. 2005; Sato 1995; Tamura et al. 2022; Wang et al. 2018). Therefore, there should be fewer non-colonized roots just after the snowmelt season, which may have limited the colonization of new ECM fungal species. Furthermore, the limited sporocarp production of ECM fungi in the snowmelt season limits the recruitment of new OTUs from outside the sampling site. Although spores buried in soil can be a source of new OTUs, the reduction in total OTU richness of available spores may have led to the limited recruitment of new OTUs. Nevertheless, the possibility that little recruitment is characteristic of our site cannot be ruled out. Further studies at other sampling sites or repeated surveys over multiple years will confirm whether the snowmelt season is generally associated with limited recruitment.

There are some limitations in our study. First, in the present study, the number of host origins was limited, and the generality of the relatedness between the difference in host root elongation patterns across origins and ECM fungal dynamics needs to be further tested. In the present study, saplings from eight origins were used and the trends were similar among origins, supporting the generality of the results. However, the number of replications was too small to be statistically tested, so this remains a topic for further study. The strength of the present study was the use of saplings from origins where a difference in root elongation patterns has been demonstrated. The current setting enables us to discuss the relationship between root elongation patterns and ECM fungal dynamics, but studies with larger sample sizes or the use of hosts from a wider range of climatic conditions will help confirming the generality of our results and to more robustly relate the host root elongation to community dynamics. Second, in the present study, sampling was only conducted twice. Thus, the relative importance of the dynamics in snowmelt season in determining the community composition in other seasons is uncertain. As the aim of our study was to understand community dynamics under snowmelt, samplings were conducted only twice, before and after snowmelt. However, surveys in other seasons, such as under snow cover or in late spring, would allow for the further discussion on the impact of snowmelt on the ECM fungal community dynamics in snowy regions.

In the present study, we investigated the changes in the ECM fungal community structure associated with Sakhalin fir across the snowmelt season in a common garden experiment and showed that the dynamics pattern of the ECM fungal community composition may change in association with differences in host geographic origins and light conditions. Additionally, we showed that the recruitment of new OTUs may not be prevalent across the snowmelt season. These results may suggest the importance of host-mediated changes in community composition and little response to changes in abiotic environmental conditions with snowmelt. In addition, our results suggest that ECM fungal community dynamics can vary at a fine scale depending on the light conditions and seasonal response of associated host individuals, suggesting the necessity of fine-scale and/or long-term studies to understand fungal dynamics in forests. As our study is based on observations in a nursery and only targets a single host species, further investigation is necessary to verify whether similar results can be observed in natural settings and in other tree species or mature trees. Furthermore, although we observed little compositional change in the ECM fungal community from April to May, how long the composition remained stable is unknown. Since many ECM tree species grow in areas with snow (Steidinger et al. 2019), confirming the generality of our results and enhancing our understanding of the response of the ECM fungal community to snowmelt is essential for understanding the temporal dynamics of ECM fungal communities.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00572-025-01201-y.

Acknowledgements We thank Drs. Makoto Kobayashi, Naoki Makita, Saki Fujita, Jun'ichiro Ide and Izuki Endo, Mr. Taiga Masumoto and the staffs of the Forest Research Institute, Hokkaido Research Organization, for their help in the field experiments.

Author contributions T. S. and W. I. designed the study and set up the common garden experiment. T. S., W. I. and S. M. conducted field

sampling. Y. S. and S. M. performed the molecular analyses and data analyses. Y. S. wrote the initial draft of the manuscript and T. S., W. I. and S. M. critically reviewed the manuscript. All authors read and approved the submitted version.

Data availability Sequence data that support the findings of this study have been deposited in the DDBJ Sequence Read Archive (DRA) under the accession numbers: DRR545416-DRR545506.

Declarations

Competing interests The authors declare no competing interests.

References

Bahram M, Peay KG, Tedersoo L (2014) Local-scale biogeography and Spatiotemporal variability in communities of mycorrhizal fungi. New Phytol 205:1454–1463. https://doi.org/10.1111/nph.13206

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity: partitioning beta diversity. Glob Ecol Biogeogr 19:134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bödeker ITM, Lindahl BD, Olson Å, Clemmensen KE (2016) Mycorrhizal and saprotrophic fungal guilds compete for the same organic substrates but affect decomposition differently. Funct Ecol 30:1967–1978. https://doi.org/10.1111/1365-2435.12677

Broeckling CD, Broz AK, Bergelson J et al (2008) Root exudates regulate soil fungal community composition and diversity. Appl Environ Microbiol 74:738–744. https://doi.org/10.1128/AEM.02188-07

Brundrett MC, Tedersoo L (2020) Resolving the mycorrhizal status of important Northern hemisphere trees. Plant Soil 454:3–34. https://doi.org/10.1007/s11104-020-04627-9

Buée M, Vairelles D, Garbaye J (2005) Year-round monitoring of diversity and potential metabolic activity of the ectomycorrhizal community in a Beech (*Fagus silvatica*) forest subjected to two thinning regimes. Mycorrhiza 15:235–245. https://doi.org/10.1007/s00572-004-0313-6

Chase JM, Kraft NJB, Smith KG et al (2011) Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2:art24. https://doi.org/10.1890/ES10-00117.1

Courty P-E, Franc A, Pierrat J-C, Garbaye J (2008) Temporal changes in the ectomycorrhizal community in two soil horizons of a temperate oak forest. Appl Envir Microbiol 74:5792–5801. https://doi.org/10.1128/AEM.01592-08

DeLancey LC, Maillard F, Hobbie SE, Kennedy PG (2024) Shifting fungal guild abundances are associated with altered temperate forest soil carbon stocks. Ecosystems 27:986–998. https://doi.org/10.1007/s10021-024-00934-9

Edgar RC, Haas BJ, Clemente JC et al (2011) UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27:2194–2200. https://doi.org/10.1093/bioinformatics/btr381

Endrulat T, Saurer M, Buchmann N, Brunner I (2010) Incorporation and remobilization of 13 C within the fine-root systems of individual abies Alba trees in a temperate coniferous stand. Tree Physiol 30:1515–1527. https://doi.org/10.1093/treephys/tpq090

Etterson JR, Cornett MW, White MA, Kavajecz LC (2020) Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species. Ecol Appl 30:e02092. https://doi.org/10.1002/eap.2092

Fernandez CW, Nguyen NH, Stefanski A et al (2017) Ectomycorrhizal fungal response to warming is linked to poor host performance at the boreal-temperate ecotone. Glob Change Biol 23:1598–1609. https://doi.org/10.1111/gcb.13510

Fukuzawa K, Tateno R, Ugawa S et al (2021) Timing of forest fine root production advances with reduced snow cover in Northern Japan: implications for climate-induced change in understory and overstory competition. Oecologia 196:263–273. https://doi.org/10.1007/s00442-021-04914-x

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Hamady M, Walker JJ, Harris JK et al (2008) Error-correcting barcoded primers for pyrosequencing hundreds of samples in multiplex. Nat Methods 5:235–237. https://doi.org/10.1038/nmeth.1184

Hansen J, Vogg G, Beck E (1996) Assimilation, allocation and utilization of carbon by 3-year-old Scots pine (. Trees 11:83. https://doi.org/10.1007/s004680050063

Hothorn T, Bretz F, Westfall P (2008) MULTCOMP: simultaneous inference in general parametric models. Biom J 50:346–363. https://doi.org/10.1002/bimj.200810425

Huang X-F, Chaparro JM, Reardon KF et al (2014) Rhizosphere interactions: root exudates, microbes, and microbial communities. Botany 92:267–275. https://doi.org/10.1139/cjb-2013-0225

Ishizuka W, Kon H, Kita K et al (2021) Local adaptation to contrasting Climatic conditions in Sakhalin Fir (*Abies sachalinensis*) revealed by long-term provenance trials. Ecol Res 36:720–732. https://doi.org/10.1111/1440-1703.12232

Izzo A, Agbowo J, Bruns TD (2005) Detection of plot-level changes in ectomycorrhizal communities across years in an old-growth mixed-conifer forest. New Phytol 166:619–630. https://doi.org/10.1111/j.1469-8137.2005.01354.x

Jarvis S, Woodward S, Alexander IJ, Taylor AFS (2013) Regional scale gradients of climate and nitrogen deposition drive variation in ectomycorrhizal fungal communities associated with native Scots pine. Glob Change Biol 19:1688–1696. https://doi.org/10.1111/gcb.12178

Jenkins MW, Chambers JL (1989) Understory light levels in mature hardwood stands after partial overstory removal. Ecol Manag 26:247–256. https://doi.org/10.1016/0378-1127(89)90085-6

Jörgensen K, Clemmensen KE, Wallander H, Lindahl BD (2023) Do ectomycorrhizal exploration types reflect mycelial foraging strategies? New Phytol 237:576–584. https://doi.org/10.1111/nph.18566

Joslin JD, Wolfe MH, Hanson PJ (2001) Factors controlling the timing of root elongation intensity in a mature upland oak stand. Plant Soil 228:201–212. https://doi.org/10.1023/A:1004866705021

Khokon AM, Janz D, Polle A (2023) Ectomycorrhizal diversity, taxon-specific traits and root N uptake in temperate Beech forests. New Phytol 239:739–751. https://doi.org/10.1111/nph.18978

Koide RT, Shumway DL, Xu B, Sharda JN (2007) On Temporal partitioning of a community of ectomycorrhizal fungi. New Phytol 174:420–429. https://doi.org/10.1111/j.1469-8137.2007.02000.x

Konôpka B, Yuste JC, Janssens IA, Ceulemans R (2005) Comparison of fine root dynamics in Scots pine and pedunculate oak in sandy soil. Plant Soil 276:33–45. https://doi.org/10.1007/s11104-004-2976-3

Kranabetter JM, Stoehr MU, O'Neill GA (2012) Divergence in ectomycorrhizal communities with foreign Douglas-fir populations and implications for assisted migration. Ecol Appl 22:550–560. https://doi.org/10.1890/11-1514.1

Kranabetter JM, Stoehr M, O'Neill GA (2015) Ectomycorrhizal fungal maladaptation and growth reductions associated with assisted migration of D ouglas-fir. New Phytol 206:1135–1144. https://doi.org/10.1111/nph.13287

Lewis JD, McKane RB, Tingey DT, Beedlow PA (2000) Vertical gradients in photosynthetic light response within an old-growth Douglas-fir and Western Hemlock canopy. Tree Physiol 20:447–456. https://doi.org/10.1093/treephys/20.7.447

Lieffers VJ, Messier C, Stadt KJ et al (1999) Predicting and managing light in the understory of boreal forests. Can J Res 29:796–811. https://doi.org/10.1139/x98-165

Lilleskov EA, Bruns TD, Horton TR et al (2004) Detection of forest stand-level Spatial structure in ectomycorrhizal fungal communities. FEMS Microbiol Ecol 49:319–332. https://doi.org/10.1016/j.femsec.2004.04.004

Lipson DA, Schmidt SK, Monson RK (2000) Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. Soil Biol Biochem 32:441–448. https://doi.org/10.1016/S0038-0717(99)00068-1

Matsuoka S, Kawaguchi E, Osono T (2016) Temporal distance decay of similarity of ectomycorrhizal fungal community composition in a subtropical evergreen forest in Japan. FEMS Microbiol Ecol 92:fiw061. https://doi.org/10.1093/femsec/fiw061

McCormack ML, Adams TS, Smithwick EAH et al (2014) Variability in root production, phenology, and turnover rate among 12 temperate tree species. Ecology 95:2224–2235. https://doi.org/10.1890/13-1942.1

Meier IC, Tückmantel T, Heitkötter J et al (2020) Root exudation of mature Beech forests across a nutrient availability gradient: the role of root morphology and fungal activity. New Phytol 226:583–594. https://doi.org/10.1111/nph.16389

Mundra S, Bahram M, Tedersoo L et al (2015) Temporal variation of *Bistorta vivipara* -associated ectomycorrhizal fungal communities in the high Arctic. Mol Ecol 24:6289–6302. https://doi.org/10.1111/mec.13458

Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol 147:131–139. https://doi.org/10.1046/j.1469-8137.2000.00677.x

Pena R, Tejedor J, Zeller B et al (2013) Interspecific Temporal and Spatial differences in the acquisition of litter-derived nitrogen by ectomycorrhizal fungal assemblages. New Phytol 199:520–528. https://doi.org/10.1111/nph.12272

Pickles BJ, Genney DR, Potts JM et al (2010) Spatial and Temporal ecology of Scots pine ectomycorrhizas. New Phytol 186:755–768. https://doi.org/10.1111/j.1469-8137.2010.03204.x

Pickles BJ, Twieg BD, O'Neill GA, et al (2015) Local adaptation in migrated interior Douglas-fir seedlings is mediated by ectomycorrhizas and other soil factors. New Phytologist 207:858–871. https://doi.org/10.1111/nph.13360

Põlme S, Abarenkov K, Henrik Nilsson R et al (2021) FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Divers 105:1–16. https://doi.org/10.1007/s13225-020-00466-2

Poorter H, Niklas KJ, Reich PB et al (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Poorter H, Niinemets Ü, Ntagkas N et al (2019) A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. New Phytol 223:1073–1105. https://doi.org/10.1111/nph.15754

R Core Team (2024) R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Radville L, McCormack ML, Post E, Eissenstat DM (2016) Root phenology in a changing climate. J Exp Bot 67:3617–3628. https://doi.org/10.1093/jxb/erw062

Richard F, Roy M, Shahin O et al (2011) Ectomycorrhizal communities in a mediterranean forest ecosystem dominated by *Quercus ilex*: seasonal dynamics and response to drought in the surface organic horizon. Ann Sci 68:57–68. https://doi.org/10.1007/s13595-010-0007-5

Rodríguez-Calcerrada J, Mutke S, Alonso J et al (2008) Influence of overstory density on understory light, soil moisture, and survival of two underplanted oak species in a mediterranean montane Scots pine forest. Invest Agrar: Sist Recur for 17:31–38. https://doi.org/10.5424/srf/2008171-01021

Rosinger C, Sandén H, Godbold DL (2020) Non-structural carbohydrate concentrations of fagus sylvatica and Pinus sylvestris fine roots are linked to ectomycorrhizal enzymatic activity during spring reactivation. Mycorrhiza 30:197–210. https://doi.org/10.1007/s00572-020-00939-x

Sato T (1995) Fundamental studies on the root growth of trees in Hokkaido. Bull Hokkaido Res Inst 32:1–54

Smith SE, Read D (2008) Mycorrhizal Symbiosis., 3rd edition. Academic Press, New York

Steidinger BS, Crowther TW, Liang J et al (2019) Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. Nature 569:404–408. https://doi.org/10.1038/s41586-019-1128-0

Sugai T, Ishizuka W, Masumoto T et al (2024) Spring growth variation in pioneer and fibrous roots in *Abies sachalinensis* seedlings from provenances with contrasting snow cover environments. IJPS 185:187–197. https://doi.org/10.1086/728188

Sugiyama Y, Matsuoka S, Osono T (2020) Two-years of investigation revealed the inconsistency of seasonal dynamics of an ectomycorrhizal fungal community in Japanese cool-temperate forest across years. FEMS Microbiol Ecol 96:fiaa118. https://doi.org/10.1093/femsec/fiaa118

Suz LM, Barsoum N, Benham S et al (2014) Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests. Mol Ecol 23:5628–5644. https://doi.org/10.1111/mec.12947

Tamura A, Oguma H, Fujimoto R et al (2022) Phenology of fine root and shoot using high frequency Temporal resolution images in a temperate larch forest. Rhizosphere 22:100541. https://doi.org/10.1016/j.rhisph.2022.100541

Tanabe AS, Toju H (2013) Two new computational methods for universal DNA barcoding: a benchmark using barcode sequences of bacteria, archaea, animals, fungi, and land plants. PLoS ONE 8:e76910. https://doi.org/10.1371/journal.pone.0076910

Taylor AFS, Alexander I (2005) The ectomycorrhizal symbiosis: life in the real world. Mycologist 19:102–112. https://doi.org/10.1017/S0269915X05003034

Tedersoo L, Suvi T, Jairus T, Kõljalg U (2008) Forest microsite effects on community composition of ectomycorrhizal fungi on seedlings of *Picea abies* and *Betula pendula*. Environ Microbiol 10:1189–1201. https://doi.org/10.1111/j.1462-2920.2007.01535.x

Toju H, Tanabe AS, Yamamoto S, Sato H (2012) High-Coverage ITS primers for the DNA-Based identification of ascomycetes and basidiomycetes in environmental samples. PLoS ONE 7:e40863. https://doi.org/10.1371/journal.pone.0040863

Trocha LK, Weiser E, Robakowski P (2016) Interactive effects of juvenile defoliation, light conditions, and interspecific competition on growth and ectomycorrhizal colonization of *Fagus sylvatica* and *Pinus sylvestris* seedlings. Mycorrhiza 26:47–56. https://doi.org/10.1007/s00572-015-0645-4

Turner GD, Lewis JD, Mates-Muchin JT et al (2009) Light availability and soil source influence ectomycorrhizal fungal communities on oak seedlings grown in oak- and hemlock-associated soils. Can J Fo Res 39:1247–1258. https://doi.org/10.1139/X09-051

Van Nuland ME, Peay KG (2020) Symbiotic niche mapping reveals functional specialization by two ectomycorrhizal fungi that expands the host plant niche. Fungal Ecol 46:100960. https://doi.org/10.1016/j.funeco.2020.100960

Vellend M (2016) The theory of ecological communities. The theory of ecological communities. Princeton University Press, Princeton

Walker JF, Miller OK Jr., Horton JL (2008) Seasonal dynamics of ectomycorrhizal fungus assemblages on oak seedlings in the southeastern Appalachian mountains. Mycorrhiza 18:123–132. https://doi.org/10.1007/s00572-008-0163-8

Wang Y, Mao Z, Bakker MR et al (2018) Linking conifer root growth and production to soil temperature and carbon supply in temperate forests. Plant Soil 426:33–50. https://doi.org/10.1007/s11104-018-3596-7

Winder RS, Kranabetter JM, Pedlar JH (2021) Adaptive management of landscapes for climate change: how soils influence the assisted migration of plants. Soils and landscape restoration. Elsevier, pp 275–297

Ying CC, Yanchuk AD (2006) The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. For Ecol Manag 227:1–13. https://doi.org/10.1016/j.foreco.2006.02.028

Zarter CR, Adams WW, Ebbert V et al (2006) Winter down-regulation of intrinsic photosynthetic capacity coupled with up-regulation of Elip-like proteins and persistent energy dissipation in a subalpine forest. New Phytol 172:272–282. https://doi.org/10.1111/j.1469-8137.2006.01815.x