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Succession and Carbon Source Utilization of Fungi Associated With *Hylocomium splendens* on a Subalpine Forest Floor

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ABSTRACT

Little is known about the relationship between succession and carbon source utilization of fungi associated with moss profiles consisting of live, senescent, and dead tissues at different stages of decomposition in cold regions. Fungal succession and carbon source utilization within the profiles of the forest floor moss *Hylocomium splendens* were investigated to identify the metabolic traits of fungi associated with their successional status. Microfungi were isolated from moss segments collected from a subalpine forest floor in central Japan to examine fungal succession and were tested for their physiological capacity to utilize the 31 carbon compounds assayed using Biolog EcoPlates. A total of 244 fungal isolates were obtained from 120 moss segments and grouped into 44 operational taxonomic units belonging to Ascomycota, Mucoromycota, and Basidiomycota at a 97% similarity threshold. These fungi exhibited the potential to utilize an array of 31 substrates in Biolog EcoPlate and could be differentiated based on their patterns of carbon source utilization. The successional status of the fungi was significantly correlated with their ability to utilize α-ketobutyric acid and D-malic acid. These results demonstrated that the metabolic traits of fungi were closely associated with their successional patterns in decomposing moss tissues on the subalpine forest floor.

1 | Introduction

Fungi are eukaryotic microorganisms that play critical roles in the decomposition of dead residues of terrestrial plants, including mosses (Lindo and Gonzalez 2010; van der Wal et al. 2013). A diverse array of fungi takes part in decomposition by excreting extracellular enzymes that attack organic constituents, leading to the chemical transformation of plant residues and the subsequent colonization, replacement, and succession of fungal species (Eichlerová et al. 2015; Leifheit et al. 2024). Previous studies have demonstrated that different fungal taxa dominate different stages of decomposition during fungal succession (Hudson 1968; Osono 2007), but much remains unknown about how fungal traits related to carbon source utilization are linked to successional patterns on decomposing residues.

Mosses represent a significant proportion of biomass production, contribute to litter in boreal ecosystems, and form a major component of the terrestrial carbon pool in cold regions (Uchida et al. 2001). Their tissues are rich in recalcitrant substrates, making decomposition a critical but slow process in global carbon cycling (Dorrepaal et al. 2005; Lindo and Gonzalez 2010; Turetsky et al. 2012). Exploring the functional link between carbon utilization traits and fungal successional patterns will help improve understanding of the ecology of fungi associated with moss decomposition.

Yuki Hatano and Yudai Nagata should be considered joint co-first authors.

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The purposes of the present study were to examine the succession and carbon source utilization of fungi associated with the profiles of *Hylocomium splendens*, a dominant moss species in central Japan, and to identify the metabolic traits associated with their successional status. We tested the hypothesis that the potential ability to utilize specific carbon compounds was linked to the successional patterns of fungi in decomposing moss tissues on the subalpine forest floor.

2 | Materials and Methods

2.1 | Study Sites and Sample Collection

Samples were collected from a subalpine coniferous forest stand near Shirakomaike Pond, Sakuho, Nagano, central Japan (36.05° N, 138.36° E; 2115 m a.s.l.). The forest stand was composed mainly of *Tsuga diversifolia*, *Abies veitchii*, and *Pinus koraiensis*, with *Rhododendron fauriei* as a major understory species. A dense mat of live and dead tissues of *Hylocomium splendens* covers the forest floor. The mean annual temperature of the forest stand is estimated to be 2.7°C based on observations recorded over a 44-year period (1979–2023) at Haramura (1017 m a.s.l.), approximately 15 km southwest of the study site (Japan Meteorological Agency). The mean annual precipitation over a 15-year period (2008–2023) at Shirakaba Lake (1440 m a.s.l.), approximately 13 km northwest of the study site, is 1810 mm (Japan Meteorological Agency). The forest floor is typically covered with snow from November to April. Five blocks (15 × 15 cm in area and 8–10 cm in depth) of *H. splendens* were arbitrarily collected from the forest floor surface on August 23, 2020. The distance between the blocks was at least 2 m. The moss blocks were stored in plastic bags at 4°C before transport to the laboratory for analysis.

Moss shoots in the blocks exhibited sympodial branching (Uchida et al. 2001), which produces a new and distinct architectural module (i.e., a moss shoot segment) each year. Six shoots comprising at least four segment orders were arbitrarily selected from each block. Each shoot was divided into four segments based on the structural order of these annual modules (designated in the present study as Segments 1 to 4 from the tip to the base) rather than on visual appearance. However, as a natural consequence of aging and consistent with previous observations of *Hylocomium splendens* (Uchida et al. 2001), these structurally separated segments exhibited differences in color and texture: Segment 1 was the current-year shoot with green leaves; Segment 2 was the first-year shoot with green to yellowish leaves; Segment 3 was the second-year shoot with most brownish leaves still attached to the stem; and Segment 4 was a blackish decomposing shoot mostly detached from leaves. Therefore, a total of 120 moss segments (five blocks × six shoots × four segments) were used for fungal isolation, as described below.

2.2 | Fungal Isolation, OTU Determination, and Taxonomic Assignment

Fungi were isolated from moss segments using a modified washing method described by Hirose et al. (2016). For fungal isolation, 1-cm-long moss segments were placed on modified lignocellulose agar (glucose 0.1%, KH_2PO_4 0.1%, $MgSO_4.7H_2O$ 0.02%, KCl 0.02%, $NaNO_3$ 0.2%, yeast extract 0.02%, and agar 1.3% [w/v]) and incubated at 20°C for 8 weeks. An incubation temperature of 20°C was adopted because the estimated maximum air temperature exceeds 20°C at the study site during the growing season, when biological activity occurs (Japan Meteorological Agency). Fungal isolates were examined microscopically for vegetative and reproductive structures at 400× magnification and were taxonomically identified when fruiting structures developed, according to Domsch et al. (2007). The DNA sequences of the fungal isolates were then analyzed. DNA extraction, PCR, and sequencing reactions were performed according to the methods described by Hatano et al. (2022). The rDNA internal transcribed spacer (ITS) region was amplified using the primers ITS1F (Gardes and Bruns 1993) and LR3 (Vilgalys and Hester 1990). The ITS2 region of each sequence was extracted using ITSx version 1.0.11 (Bengtsson-Palme et al. 2013). The ITS2 sequences obtained from isolates were grouped into operational taxonomic units (OTUs) according to a 97% similarity criterion and were then assembled using VSEARCH, as implemented in the Claident pipeline v0.2.2018.05.29 (software available online: https://www.claident.org/). For each OTUs, taxonomic identification was conducted using the query-centric auto-k-nearest-neighbor (QCauto) method (Tanabe and Toju 2013). The ITS sequences were also compared with rDNA sequences available in the GenBank database using BLAST+ (Camacho et al. 2009). The results of Claident and BLAST+ for the taxonomic assignment of fungal OTUs are summarized in Table S1. The ITS sequences determined in the present study were deposited in the DNA Data Bank of Japan (DDBJ) under accession numbers LC904841–LC904880 (Table S1). One fungal isolate of each OTU per moss segment was retained, even when two or more isolates of the same OTU were obtained.

2.3 | Carbon Source Utilization

Carbon source utilization by fungal isolates was evaluated using Biolog EcoPlate (Biolog Inc., Hayward, CA, USA), which contains 31 different carbon sources (Table S1), according to the method described by Tabuchi et al. (2022), using a 10^2 dilution of homogenized mycelia and incubation at 20°C for 14 days. Three replicate wells within a single plate were used for each fungal isolate. The color development measured at 595 nm in the negative control well using a plate reader (Infinite F50R, Tecan Co., Kanagawa, Japan) was subtracted from that measured in each of the 31 carbon source wells to obtain the optical density (OD) for each carbon source. OD values below 0.0001, which was the detection limit of the plate reader, were regarded as negative substrate utilization results. The ability of fungal isolates to utilize carbon sources was quantitatively summarized using average well-color development (AWCD), calculated as follows: $AWCD = \Sigma\ OD_i/31$, where OD_i represents the OD value in the well containing the ith substrate (Nagata et al. 2023). The same fungal isolates used for DNA analysis were used to measure carbon source utilization, with one isolate representing each OTU. The raw OD data for the 31 carbon sources and AWCD values are presented in Table S1.

2.4 | Statistical Analyses

A data sheet was constructed to show the presence or absence of individual fungal OTUs on the 120 moss segments. Singleton

OTUs were defined as those occurring on only one moss segment, and non-singleton OTUs were defined as those occurring on more than one moss segment. The successional trends of individual OTUs were quantified using the succession index (M) using the formula of Hasegawa (1997): $M = \Sigma\, t_i n_i / N$, where t_i is the segment order (i.e., $i = 1–4$), n_i is the number of moss segments on which a given OTU occurred in the ith segment, and N is the total number of moss segments on which the OTU occurred. A generalized linear model (GLM) was used to compare the succession indices of fungal OTUs among fungal phyla. The glm function in R software was used for the analysis, using RStudio for Macintosh version 1.4.1717. The error structure of the GLM was Gaussian. Data from non-singleton OTUs were used in the GLM after excluding the succession index values of singleton OTUs.

Principal component analysis was used to ordinate fungal OTUs based on their patterns of utilization of the 31 carbon sources. The data matrix of OD values for 44 OTUs × 31 carbon sources was analyzed using R software, with the prcomp function. A GLM was used to compare the first (PC1) and second (PC2) principal components of fungal OTUs among fungal phyla, according to the procedure described above.

Pearson's correlation coefficients were calculated to evaluate the relationship between the succession index and the OD values of the 31 carbon sources for 19 non-singleton OTUs. Then, the relationship among the succession index, fungal phyla, and the OD values of 31 carbon sources for 19 non-singleton OTUs was analyzed using a GLM. The error structure of the GLM was Gaussian. The best model explaining variation in succession index was selected using forward model selection based on the Akaike information criterion (AIC).

3 | Results

3.1 | Taxonomic Composition, Occurrence, and Succession

A total of 244 fungal isolates were obtained from 120 moss segments, with 0–5 isolates per segment with a mean of 2 isolates per segment. These isolates were grouped into 44 OTUs at a 97% similarity threshold and were assigned to Ascomycota (35 OTUs, 80% of the 44 OTUs), Mucoromycota (8 OTUs, 18%), and Basidiomycota (1 OTU, 2%) (Table 1). Of the 44 OTUs, 25

TABLE 1 | Taxon and the number of operational taxonomic units (OTUs) of non-singleton and singleton OTUs.

Phylum	Genus	Non-singleton OTU	Singleton OTU	Total
Ascomycota	*Cladosporium*	1	0	1
	Clonostachys	0	1	1
	Coniochaeta	0	1	1
	Coniothyrium	0	1	1
	Cordyceps	1	1	2
	Cylindrodendrum	1	0	1
	Fusarium	0	1	1
	Keithomyces	0	1	1
	Lecanicillium	0	1	1
	Metapochonia	1	0	1
	Penicillium	3	7	10
	Pestalotiopsis	0	2	2
	Phoma	0	1	1
	Pseudopithomyces	1	0	1
	Talaromyces	0	1	1
	Trichoderma	6	2	8
	Xenosphaeropsis	0	1	1
Mucoromycota	*Entomortierella*	1	0	1
	Mortierella	1	1	2
	Mucor	1	1	2
	Podila	2	0	2
	Umbelopsis	0	1	1
Basidiomycota	White sterile	0	1	1
Total		19	25	44

(57%) occurred on only one moss segment and were regarded as singletons, and the remaining 19 OTUs (43%) were classified as non-singletons. Of the 19 non-singleton OTUs, 74% (14 OTUs) belonged to Ascomycota and 26% (5 OTUs) belonged to Mucoromycota. The most OTU-rich genus was *Penicillium* (10 OTUs), followed by *Trichoderma* (8 OTUs) and *Cordyceps*, *Pestalotiopsis*, *Mortierella*, *Mucor*, and *Podia* (2 OTUs each).

Trichoderma OTU_04 was the most frequent OTU, accounting for 23% (55 moss segments) of the 244 total OTU occurrences observed across all moss segments, followed by *Cladosporium* OTU_35 (20%, 50 moss segments); *Mucor* OTU_10, *Trichoderma* OTU_16, and *Penicillium* OTU_38 (each 5%, 13 moss segments); *Trichoderma* OTU_30 (5%, 12 moss segments); and *Trichoderma* OTU_03 (4%, 10 moss segments). The number of moss segments on which the other 12 non-singleton OTUs occurred ranged from 2 to 8. The succession index of the 44 OTUs ranged from 1.0 to 4.0, and that of the 19 non-singleton OTUs ranged from 1.7 to 3.5 (Figure 1). The mean succession index did not differ significantly between Ascomycota and Mucoromycota among the 19 non-singleton OTUs (GLM, deviance = 0.0643, $p = 0.67$).

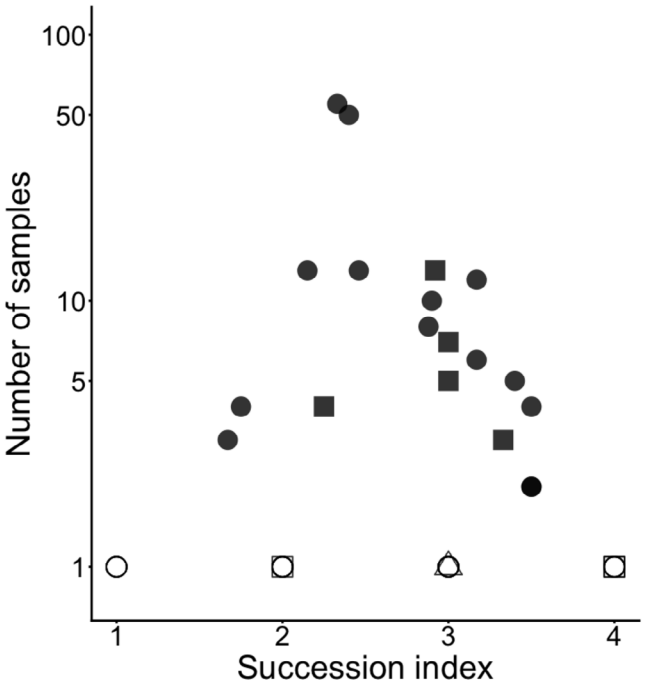


FIGURE 1 | Number of samples from which fungal operational taxonomic units (OTUs) were isolated plotted against the succession index. The OTU categories are represented by symbols: Non-singleton OTUs in Ascomycota (filled circle), non-singleton OTUs in Mucoromycota (filled square), singleton OTUs in Ascomycota (open circle), singleton OTUs in Mucoromycota (open square), and singleton OTUs in Basidiomycota (open triangle). Note that the *Y*-axis is presented on a logarithmic scale and the symbols for singleton OTUs were overlapping.

3.2 | Carbon Source Utilization

The 44 OTUs exhibited the potentials to utilize a range of 31 substrates in Biolog EcoPlate, with the greatest mean OD values observed for Tween 80 and Tween 40 and the lowest mean OD values for glucose-1-phosphate and α-ketobutyric acid (Table S1). Among the 44 OTUs, the greatest AWCD value was observed for *Metapochonia* OTU_25, followed by *Cladosporium* OTU_35, *Trichoderma* OTU_29, *Penicillium* OTU_42, *Trichoderma* OTU_04, and *Penicillium* OTU_38.

Principal component analysis differentiated the 44 OTUs according to their patterns of carbon source utilization (Figure 2). The first two principal components (PC1 and PC2) together accounted for 64% of the total variance. PC1 (eigenvalue = 2.73) accounted for 52% of the total variance and was positively associated with the OD values of Tween 80, D-mannitol, and L-asparagine. PC2 (eigenvalue = 0.63) accounted for 12% of the total variance and was positively associated with the OD values of D-mannitol and negatively associated with those of Tween 40. PC1 did not differ significantly between Ascomycota and Mucoromycota both for the non-singleton OTUs (GLM, deviance = 1.49, $p = 0.54$) and for all OTUs (GLM, deviance = 0.619, $p = 0.64$). In contrast, PC2 was significantly greater in Ascomycota than in Mucoromycota for both the non-singleton OTUs (GLM, deviance = 9.66, $p < 0.001$) and all OTUs (GLM, deviance = 8.81, $p < 0.001$).

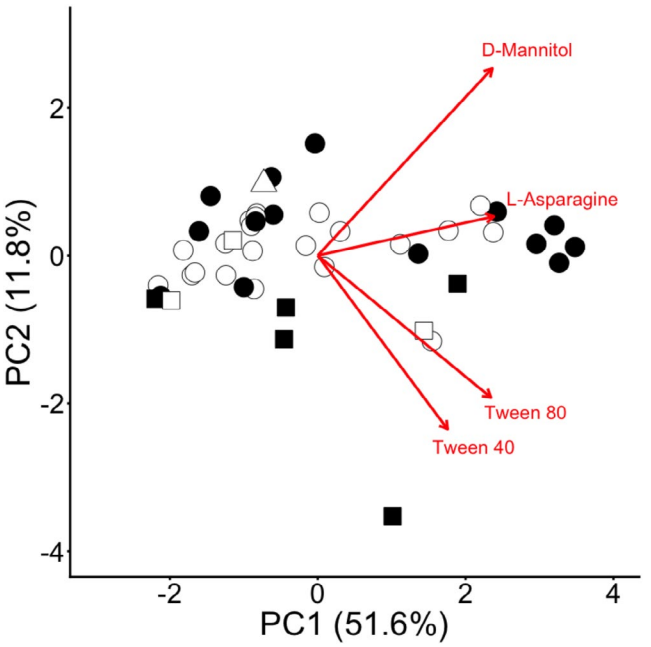


FIGURE 2 | Principal components for utilization of 31 carbon sources in the Biolog EcoPlate for 44 fungal operational taxonomic units (OTUs). The first and second principal components (PC1 and PC2) account for 52% and 12% of the total variance, respectively. PC1 is positively associated with the utilization of Tween 80, D-mannitol, and L-asparagine, whereas PC2 is positively associated with D-mannitol and negatively associated with Tween 40. Symbols are as in Figure 1.

3.3 | Relationship Between Succession and Carbon Source Utilization

Model selection of the GLMs based on the AIC indicated that the model including six carbon sources (α-ketobutyric acid, L-serine, 4-hydroxybenzoic acid, D-malic acid, D-galacturonic acid, and L-phenylalanine) best explained the succession index of the 19 non-singleton OTUs (AIC = −2.56) (Table 2). Variables such as α-ketobutyric acid and L-serine were consistently retained across the top five models, indicating the robustness of

TABLE 2 | Results of forward model selection.

Model	AIC	Intercept	Coefficient					
			D-galacturonic acid	L-phenylalanine	4-hydroxybenzoic acid	L-serine	α-ketobutyric acid	D-malic acid
A	−2.56	2.97	−0.64	−0.98	1.37	−1.13	1.92	0.78
B	10.79	2.83	−0.46	—	0.83	−0.92	1.68	0.60
C	11.87	2.88	—	−0.67	1.14	−1.37	1.97	0.43
D	14.41	2.79	—	—	0.79	−1.16	1.78	0.37
E	15.76	2.99	—	−0.55	1.21	−1.48	2.16	—

Note: Top five generalized linear models selected by the Akaike information criterion (AIC) are shown. Hyphens (–) indicate that the variable was not included in the respective model.

TABLE 3 | Summarized results of the generalized linear model for the relationship between the succession index and the optical densities (ODs) of six carbon sources for 19 non-singleton operational taxonomic units (OTUs).

	Coefficient	*t* value	Probability
α-ketobutyric acid[a]	1.915	7.343	0.000***
4-hydroxy benzoicacid[a]	1.369	6.706	0.000***
D-malic acid[a]	0.776	4.909	0.000***
L-serine[b]	−1.130	−6.318	0.000***
D-galacturonic acid[a]	−0.638	−4.060	0.001**
L-phenylalanine[b]	−0.982	−3.861	0.002**

Note: These six carbon sources were selected as predictor variables in the model selection.
[a]Chemical group: Carboxylic acid.
[b]Chemical group: Amino acid.
***$p < 0.001$.
**$p < 0.01$.

the selected variables (Table 2). The best model showed that the fungal succession index was significantly and positively related to the OD values of α-ketobutyric acid, 4-hydroxybenzoic acid, and D-malic acid and significantly and negatively related to those of L-serine, D-galacturonic acid, and L-phenylalanine (Table 3). The fungal phyla and the OD values of the other 25 carbon sources were not included in the best model.

4 | Discussion

The taxonomic composition of fungi isolated from moss segments of *H. splendens* in the present study (Table 1) was generally consistent with that reported previously. For example, the frequent occurrence of species of *Penicillium* and *Trichoderma*, as well as Mucoromycota genera such as *Mortierella* and *Mucor*, is a common feature of microfungal mycobiota of temperate and arctic mosses (Thormann and Rice 2007; Osono and Trofymow 2012; Osono et al. 2012). Similarly, the pattern of fungal succession in decomposing moss tissues (Table S1; Figure 1) was similar to that reviewed by Hudson (1968) for decomposing plant litter in soil. That is, *Pestalotiopsis* and *Cladosporium* were early-successional taxa whose successional index is less than 2.5 and are regarded as "primary saprophytes" sensu Hudson (1968). In contrast, most OTUs of *Penicillium* and *Trichoderma* were late-successional, with successional indices of greater than 2.5; Hudson (1968) referred to these as "secondary fungi." Osono et al. (2012) isolated microfungi from *H. splendens* shoots collected in Arctic tundra in Canada and reported the frequent occurrence of *Cladosporium herbarum* in current-year shoot tips with green leaves, and of *Penicillium* species in blackened and decomposed shoots. Fungi in the Mucoromycota are generally known as late-colonizers of decomposing plant litter (Hudson 1968); however, no significant difference was found for successional indices of non-singleton OTUs between Ascomycota and Mucoromycota in the present study. It should be noted, however, that our culture-dependent approach assesses metabolic potential and captures only a subset of the fungal assemblage. Previous studies using amplicon sequencing have revealed fungal diversity associated with *H. splendens* (Davey et al. 2013, 2014), including taxa such as Helotiales and basidiomycetous yeasts, which may act as potential decomposers or symbionts. Therefore, further research is needed to integrate functional data with the broader taxonomic landscape to understand nutrient cycling in bryosphere ecosystems.

Tests using the Biolog EcoPlate revealed diverse carbon source utilization by microfungi associated with mosses (Figure 2), suggesting that these fungi may be responsible for the metabolism of these compounds in dead moss tissues. The ability of these fungi to utilize carbohydrates, amino acids/amines, carboxylic acids, and polymers was generally consistent with previous findings (summarized in Domsch et al. 2007). For example, growth and activity of *Penicillium* and *Trichoderma* species occur in the presence of D-mannitol and Tween surfactants (Zeng et al. 2006; Domsch et al. 2007; Khandelwal et al. 2023). We also found that mucoromycetous OTUs tended to utilize D-mannitol less and Tween 40 more actively than the ascomycetous OTUs, as indicated by the significant difference in PC2. Caution is required, however, as this difference was mainly driven by an outlier, *Entomortierella* OTU_32 (Mucoromycota), which showed no activity of D-mannitol

and the highest OD for Tween 40, resulting in the lowest PC2 value. In fact, the ability to utilize D-mannitol, Tween surfactants, and other carbon sources is highly variable among species in Mucoromycota (Pawłowska et al. 2019). It should be noted, however, that *Entomortierella* is a newly proposed genus of Mortierellaceae (Vandepol et al. 2020), and the ability of *Entomortierella* species to utilize various carbon sources, including polymeric compounds, is in most cases still unexplored (Domsch et al. 2007). Therefore, it remains uncertain whether patterns of carbon source utilization differ between moss-associated fungi in Ascomycota and Mucoromycota, and this should be investigated further.

The present study showed that the successional status of microfungi in decomposing tissues of *H. splendens* was influenced not by the taxonomic group but by their potential ability to utilize four carboxylic acids and two amino acids (Table 2). That is, our data indicated that early-successional fungi tended to utilize α-ketobutyric acid, 4-hydroxybenzoic acid, and D-malic acid more actively, whereas the late-successional fungi tended to utilize D-galacturonic acid, L-serine, and L-phenylalanine more actively. Previous studies have shown that mosses, as well as microbes including fungi, produce organic acids (Carter and Arocena 2000; Adeleke et al. 2017). Moreover, mosses contain galacturonic acid in their cell walls (Peña et al. 2008), and the fraction of amino acids in moss tissues declines during decomposition (Philben et al. 2018). These findings suggest that carboxylic acids and amino acids could serve as carbon and nutrient sources for fungi, and that fungal succession in decomposing moss tissues is attributable to differences in fungal metabolic abilities to utilize these compounds. Future studies are needed to examine the pattern of changes in the contents of these carbon sources in decomposing moss tissues, to confirm our conclusions.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Sequencing data were available in the DNA Data Bank of Japan (DDBJ) (accession number LC904841–LC904880). All other data are available upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** List of fungal operational taxonomic units (OTUs), their taxonomic assignments by Claident and Blast, occurrence, and succession index. Standard errors in parentheses.