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ABSTRACT

Climate change has a major impact on arctic and boreal terrestrial ecosystems as warming leads to northward treeline shifts, inducing consequences for heterotrophic organisms associated with the plant taxa. To unravel ecological dependencies, we address how long-term climatic changes have shaped the co-occurrence of plants and fungi across selected sites in Siberia.

We investigated sedimentary ancient DNA from five lakes spanning the last 47,000 years, using the ITS1 marker for fungi and the chloroplast P6 loop marker for vegetation metabarcoding. We obtained 706 unique fungal operational taxonomic units (OTUs) and 243 taxa for the plants. We show higher OTU numbers in dry forest tundra as well as boreal forests compared to wet southern tundra. The most abundant fungal taxa in our dataset are Pseudeurotiaceae, *Mortierella*, Sordariomyceta, *Exophiala*, *Oidiodendron*, *Protoventuria*, *Candida vartiovaarae*, *Pseudeurotium*, *Gryganskiella fimbricystis*, and *Trichosporiella cerebriformis*. The overall fungal composition is explained by the plant composition as revealed by redundancy analysis. The fungal functional groups show antagonistic relationships in their climate susceptibility. The advance of woody taxa in response to past warming led to an increase in the abundance of mycorrhizae, lichens, and parasites, while yeast and saprotroph distribution declined. We also show co-occurrences between Salicaceae, *Larix*, and *Alnus* and their associated pathogens and detect higher mycorrhizal fungus diversity with the presence of Pinaceae. Under future warming, we can expect feedbacks between fungus composition and plant diversity changes which will affect forest advance, species diversity, and ecosystem stability in arctic regions.

1. Introduction

Permafrost soils comprise almost half of the global soil organic carbon (Tarnocai et al., 2009). The permanently frozen ground enables only the establishment of vegetation with shallow roots (Blume-Werry et al., 2019), most usually, tundra plants. However, global warming is leading to increased shrub-growth on permafrost in arctic regions, particularly at the boundary between the High and Low Arctic (Myers-Smith et al., 2015). Changes in the vegetation cover will subsequently influence the carbon pool as tundra plants growing on permafrost regulate the uptake and release of carbon dioxide and methane (McGuire et al., 2009).

Boreal forests are the world's largest terrestrial biome, covering an area of around 9% of the total land mass between 45° and 70° north (Czimczik et al., 2005). The climate in their distribution area

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is defined by severe winters, warm summers, relatively little precipitation, and an overall short growing season (MacDonald et al., 2008), leading to generally low species diversity in the forests. Boreal ecosystems are highly impacted by global warming as increasing temperatures result in reduced snow cover (Kreyling et al., 2012), loss of permafrost (Fedorov et al., 2017), longer growing seasons (Jarvis and Linder, 2000) or severe droughts and wildfire (Flannigan et al., 2009). As a consequence, the distribution and abundance of boreal plants is altered (Zhang et al., 2011) and local wildlife is endangered (Bradshaw et al., 2009). Furthermore, in Siberia, the migration of evergreen coniferous tree taxa into *Larix* dominated areas after warming has been observed, possibly leading to decreased albedo and further temperature increases (Kharuk et al., 2007, 2009). The composition of underground microorganisms in boreal forests, for example fungi and bacteria, is also impacted as it is shaped by the tree species present (Urbanová et al., 2015), suggesting microbial communities will shift with changing vegetation.

Fungi represent a principal component of soils and sustain a broad variety of ecosystem functions (Frąc et al., 2018). Fungal functional types reflect the strong interactions between plants and fungi but, so far, detailed processes involved in particular temporal changes in their covariation are not understood (Zobel et al., 2018). Grouping fungi according to their roles in the terrestrial ecosystem allows the assessment of compositional shifts. This, however, remains challenging as the ecological functions of many taxa are still not understood. Major ecological functional fungus groups in forest ecosystems are saprotrophs, mycorrhizae, and parasites. Saprotrophic species are decomposers in terrestrial ecosystems (Baldrian and Valášková, 2008). A plant's benefit from mycorrhizal fungi is the enabled acquisition of mineral nutrients in solution (e.g. phosphate), while the fungus in return receives carbohydrates from the plants (Finlay, 2008), making them indispensable for the plants' establishment and survival. Mycorrhizal fungi-plant associations include arbuscular mycorrhizae, ectomycorrhizae, ericoid mycorrhizae, and orchid mycorrhizae (Brundrett and Tedersoo, 2018). Parasitic fungi, such as *Heterobasidion,* infecting conifer tree taxa (Garbelotto and Gonthier, 2013), are important for eliminating weak trees to maintain the functioning of healthy forest ecosystems. While biotrophic plant parasites feed from living tissue, necrotrophic fungi penetrate the plant, destroy the tissue, and subsequently provoke plant death (Naranjo-Ortiz and Gabaldón, 2019).

Experimental warming led to an increase in ectomycorrhizal fungi and free-living filamentous fungi, while a decrease in yeast was observed (Treseder et al., 2016). It also showed an increase in the evenness of fungal tundra communities, including ectomycorrhizal fungi, in relation to rising temperature (Deslippe et al., 2012). Furthermore, under warming, saprotrophs shifted their metabolism from wood-decaying to self-maintenance and subsequent spore-production (Romero-Olivares et al., 2015, 2019). Warming also leads to an increase in specific plant pathogens (Otrosina and Cobb, 1989). Next generation sequencing studies of soil fungi in arctic Alaska revealed that warming does not affect overall fungus richness but leads to changes in the community composition. The results of these studies revealed that decreases in ectomycorrhizae, ericoid mycorrhizae, and lichens in the tundra accompany increases of saprotrophic, pathogenic, and root endophytic fungal richness (Geml et al., 2015; Mundra et al., 2016). Almost all information on fungal compositional turnover originates from short-term warming experiments (from one season up to a few years; e.g. Heinemeyer et al., 2003; Geml et al., 2015). Accordingly, time-series of compositional changes in fungal communities during past climate changes are highly desirable to assess potential shifts of ecosystem functioning in a rapidly warming world. Time-series are also an asset when testing whether lab experiments reflect real natural developments on long geological timescales.

Compositional changes of vegetation and associated fungal communities are slow. They occur on decadal, centennial, or even millennial time-scales not being covered by short observational time-series and thus the exploitation of palaeoecological archives is required. As large parts of Siberia were not covered by glaciers during the Last Glacial Maximum (LGM; Svendsen et al., 2004), lakes from this region provide sedimentary archives which continuously cover the rather warm marine isotopic stage (MIS) 3 (50–30 thousand years (ka)), the cold MIS 2 (30–15.5 ka), and warm Holocene (MIS 1) (the last 11.6 ka) (Kreveld et al., 2000; Swann et al., 2005), thereby encompassing tremendous vegetation changes. Lake sediments represent natural archives of terrestrial environmental change (e.g. Epp et al., 2015; Alsos et al., 2018; Courtin et al., 2021). As northern Russia is warming faster than the global average (Biskaborn et al., 2019b), lake sediments can provide valuable information on associated terrestrial ecosystem changes. While many sedimentary pollen records focus on vegetation change, there is only limited information about fungi (e.g. from non-pollen palynomorphs; Van Geel, 2001) as their fossil remains are limited (Loughlin et al., 2018; Quamar and Stivrinsz, 2021).

Sedimentary ancient DNA metabarcoding (sedaDNA) is a promising palaeoecological proxy using specific genetic marker regions to study past biodiversity (Sønstebø et al., 2010). So far, many sedaDNA studies have investigated plant metabarcoding, mostly applying the trnL P6 loop marker (Parducci et al., 2017; Alsos et al., 2018; Liu et al., 2020), but only a few studies focus on fungal aDNA from sedimentary deposits (Lydolph et al., 2005; Bellemain et al., 2013; Talas et al., 2021), working on Siberian permafrost sediments (Bellemain et al., 2013) and lake sediments (Talas et al., 2021). For fungal metabarcoding, the internal transcribed spacer (ITS) region is the most commonly used DNA barcoding region (Seifert, 2009), but the primers used in early studies caused quite some amplification biases (Bellemain et al., 2010). Subsequently, primers specifically targeting ancient and degraded DNA were designed and used on permafrost deposits (Epp et al., 2012; Bellemain et al., 2013). These have been refined according to the current status of reference databases by Seeber et al. (2022), providing a primer pair that is highly suitable to amplify sedaDNA, targeting short amplicons of a mean length of 183 bp and highly specific towards fungi. This primer combination enables studies using sedaDNA to trace fungus-plant interactions over time and their adaptation mechanisms towards warming even up to species level. The advantage of targeting lake sediment samples as ancient DNA records over permafrost is that during the sedimentation processes, environmental DNA is continuously deposited in the lake, allowing a chronological community reconstruction. A recent investigation of lake sediments showed clear variations in fungal community compositions: while saprotrophs remained stable over time, host-specific fungi such as plankton parasites and mycorrhizae shifted in relation to human impact and changing climate (Talas et al., 2021).

This study analyses lake sediments from five sites in Siberia spanning MIS 3, 2, and 1 for their fungal composition using sedaDNA metabarcoding with the ITS1 marker as well as their vegetation composition applying the trnL P6 loop marker. We address the following questions: (1) How does fungal and plant alpha diversity change with varying climatic and environmental conditions? (2) How do fungal taxonomic composition and function change relative to vegetation transition? Based on the answers, we draw conclusions on fungus-plant covariation under climatic changes over long timescales and its impact on biodiversity alteration in Arctic terrestrial environments. As exemplified by the response of fungus-plant interactions, our results help to predict

more accurately the impact of future warming on biodiversity shifts.

2. Geographic setting and study sites

All study sites are located within Siberia, central eastern Russia (Fig. 1), and are characterised by permafrost soils (Brown et al., 1997; Tchebakova et al., 2009). The climate in the area is rather continental with hot summers and long, severe winters (Atlas Arktiki, 1985). The most prevalent vegetation is boreal forest with spruce, pine, fir, and larch in the western and southern parts and pure larch forest in the east. Arctic regions along the coast and on the Taymyr Peninsula are covered by tundra. The main characteristics of the sampling locations are displayed in Table 1. The climate data are taken from the Russian Institute of Hydrometeorological Information: World Data Center (2021) unless indicated differently.

3. Materials and methods

3.1. Sampling

After coring, all sediment was stored at 4 °C to remain cool until sampling and further processing to preserve the cores under conditions similar to those on the lakebed. A parallel study (Seeber et al., 2022) on the fungal metabarcoding marker addressed whether the time of the coring and the subsequent long-term storage conditions influenced the metabarcoding results, for example by promoting mould. The study demonstrated that there is no direct impact on the results. SedaDNA samples were taken from 1 m sub-core segments that were cut in half lengthwise. Subsampling was undertaken in the climate chamber of the Helmholtz Centre Potsdam – German Research Centre for Geosciences (GFZ) at 10 °C. The chamber is located in the cellar where no molecular genetic studies are conducted. Before subsampling, all surfaces were cleaned with DNA Exitus Plus™ (VWR, Germany) and demineralised water. All tools were cleaned according to the recommendations of Champlot et al. (2010) to avoid contamination with modern DNA and between the samples themselves. All materials were taken from the palaeogenetic DNA laboratory at the Alfred-Wegener-Institute (AWI) in Potsdam where they had been treated to remove DNA.

During sampling, protective clothing as well as face masks were worn. The surfaces of the core halves were scraped off twice with sterile scalpel blades and samples were taken using four knives and then placed in sterile 8 mL Sarstedt tubes. All samples were taken under the same conditions. The core from Levinson Lessing was similarly sampled in the laboratories of the Institute of Geology and Mineralogy at the University of Cologne. After sampling, the aDNA samples were frozen at −20 °C until DNA extraction and amplification.

Samples for DNA analyses were taken according to their estimated ages, at intervals of about 5 cal kyr (calibrated kiloyears), leading to 15 samples from Lama, 9 samples from Levinson Lessing, 10 samples from Kyutyunda, and 8 samples from Bolshoe Toko. For CH12, 28 samples were taken, at a higher temporal resolution of intervals of about every 100–250 years.

3.2. DNA extraction and amplification

SedaDNA was extracted using the DNeasy PowerMax Soil DNA Isolation Kit (Qiagen, Germany) according to the manufacturer's instructions. Before adding 3–7 g of wet sediment material for each sample, the PowerBead solution was mixed with buffer C1 and additionally Proteinase K (2 mg mL^{-1}) and DTT (5 M) to break up remaining small pieces of tissue and yield higher DNA concentration. The Proteinase K was added to the bead beating tubes before vortexing to reduce the risk of cross-contamination. We placed the tubes on a vortexer for 10 min and included an additional incubation step at 56 °C in a rotation oven overnight. All further steps were conducted according to the manufacturer's instructions. The final elution was conducted using 2 mL of solution C6. Each extraction batch was processed on a different day to avoid contamination between batches. 0.5 mL of the CH12 extracts were purified and concentrated to 50 μL with a GeneJET PCR purification

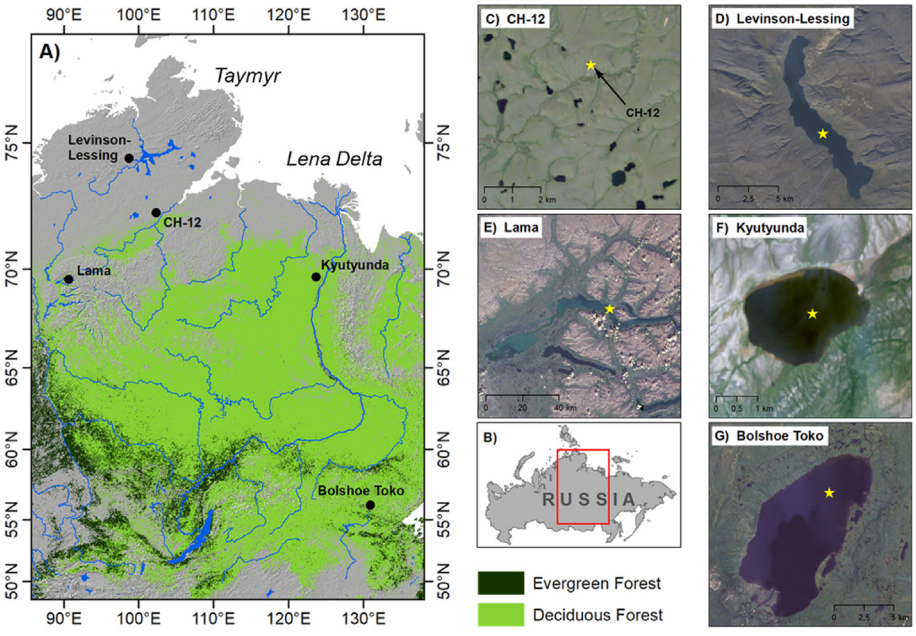

Fig. 1. Map of central Russia showing the location of the study sites (A+B). (C) to (G) satellite images of the lakes with their surroundings. The locations of the cores are marked with a star. The "distribution of deciduous and evergreen forests" is taken from the ESA CCI Land Cover time-series v2.0.7 (1992–2015)- data set (https://www.esa-landcover-cci.org/). For the illustration, the land cover classes "70" ("Tree cover, needleleaved, evergreen") and "80" ("Tree cover, needleleaved, deciduous") were extracted.

Table 1
Main characteristics of the sampled lakes.

Lake	Coordinates	Type of vegetation	Mean temperature	Dimension	Coring
Levinson Lessing	74.27°N, 98.39°E; 48 m a.s.l. (Taymyr peninsula)	sparse lichen-herb, moss-forb, dry sedge-forb tundra with dominant *Dryas octopetala*, *Salix polaris,* and *Cassiope tetragona* (Anisimov and Pospelov, 1999)	July: 12.5 °C January: 31.5 °C Hatanga weather station; 71.98 °N, 102.47 °E; distance to the lake: 289 km	15 km × 2.5 km, maximum depth: 120 m (Lebas et al., 2019)	year: 2017 length: 46 m (Co1401; Fig. 1D) at a depth of 112 m age: 62 cal ka BP (Scheidt et al., 2021)
CH12	72.4°N, 102.29°E; 60 m a.s.l. (southern Taymyr Peninsula north of the Putorana Plateau)	shrub tundra dominated by *Sphagnum*, *Hylocomium, Aulacomnium, Dicranum,* and *Polytrichum* as well as *Empetrum nigrum, Betula nana,* and *Vaccinium uliginosum;* stands of *Larix gmelinii* (Klemm et al., 2016; Niemeyer et al., 2017)	July: 12.5 °C January: 31.5 °C Hatanga weather station; 71.98 °N, 102.47 °E; distance to the lake: 60 km	elliptically shaped, mean radius: 100 m, maximum depth: 14.3 m	year: 2011 length: 1.21 m (Fig. 1C) age: 7.1 cal ka BP (Stoof-Leichsenring et al., 2015; Klemm et al., 2016)
Kyutyunda	69.38 °N, 123.38°E; 66 m a.s.l. (northern Siberia on the central Siberian Plateau)	tundra-taiga transition zone, formed of a mosaic of *Larix* forest and shrub tundra with Poaceae, *Dryas,* and *Saxifraga* species	July: 13 °C January: 35.3 °C Kjusjur weather station; 70.68 °N, 127.4 °E; distance to the lake: 210 km	roughly circular at 2.2 km by 3 km, maximum depth: 3.5 m	year: 2010 length: 7 m (PG 2023; Fig. 1F) age: 38.8 cal ka BP (Supplement 1 and 2)
Lama	69.32°N, 90.12°E; 53 m a.s.l. (Putorana Plateau)	dense taiga with *Picea*, *Larix*, and *Betula*, shrubs such as *Alnus fruticosa*, *Salix,* and *Juniperus communis*, and dwarf shrubs (Andreev et al., 2004)	July: 13.8 °C January: 28.8 °C Volochanka weather station; 70.97 °N, 94.5 °E; distance to the lake: 247 km	area: 318 km^2; 80 km × 7 km; maximum depth: 254 m	year: 1997 length: 18.85 m (depth 66 m; PG1341, Fig. 1E) age: 23 kal ca BP (Supplement 3 and 4)
Bolshoe Toko	56.15° N, 130.30 °E; 903 m a.s.l. (northern slope of eastern Stanovoy Mountain Range in southern central Yakutia)	deciduous boreal forests formed by *Larix cajanderi* and *L. gmelinii* with occurrences of *Picea obovata*, *P. jezoensis,* and *Pinus sylvestris* (Konstantinov, 2000)	July: 34 °C January: 65 °C Toko weather station; 56.1 °N, 131.01 °E; distance to the lake: 44 km (Konstantinov, 2000)	area: 15.4 km × 7.5 km, maximum depth: 72.5 m	year: 2013 length: 3.8 m (at 26 m depth; PG2133; Fig. 1G) age: 33.8 cal ka BP (Courtin et al., 2021)

Kit (Thermo Fisher Scientific, Germany). For all other lakes, 1 mL DNA extract was used for the purification. Afterwards, the concentration was measured with a Qubit Fluorometer (Qubit dsDNA BR assay kit, Qubit 4.0 Fluorometer, Thermo Fisher Scientific, USA) and the DNA diluted to 3 ng μL^{-1} which balanced out the differently processed volumes. Small aliquots were prepared to avoid freeze-thaw cycles. DNA extraction blanks were not concentrated, but used directly for subsequent PCR analyses.

For the amplification of fungal DNA, the tagged forward primer ITS67 and reverse primer 5.8 S were used (Seeber et al., 2022). The amplified region has a size of approximately 183 bp (without the primers). The use of tagged primers is essential to enable the assignment of the DNA sequences to original samples after next generation sequencing. For each batch, six replicates were conducted independently from each other.

For the reconstruction of the palaeovegetation, we used the chloroplast trnL P6 loop marker region with the tagged primer trnL g as the forward and trnL h as the reverse primer (Taberlet et al., 2007). For each batch, three replicates were conducted independently from each other.

A PCR reaction contained in total 25 μL consisting of 3 μL DNA at a concentration of 3 ng μL^{-1}, 0.2 μM of each primer, 10× HiFi buffer, 2 mM MgSO4, 0.1 mM dNTPs, 0.8 mg mL^{-1} BSA, and 1.25 U Platinum Taq High Fidelity DNA Polymerase (Invitrogen, United States), which can replicate through Uracil and is thus suitable for PCRs on damaged DNA (Rasmussen et al., 2010). Each PCR batch also contained 3 μL of the corresponding DNA extraction blank and a PCR negative control with 3 μL of DEPC-water instead of the DNA sample. All steps were conducted in the palaeogenetic laboratories at AWI Potsdam.

The PCR reaction itself was conducted in the Post-PCR laboratories at AWI Potsdam, which are located in a separate building to avoid contamination of ancient DNA samples with amplified DNA. Initially, lake CH12 was conducted as a separate project itself for the establishment of the metabarcoding primers (Seeber et al., 2022). To support the study of the marker establishment as well as this study, the results were merged after sequencing which led to small differences in the PCR protocol as described as follows. The fungal ITS marker amplification for the CH12 samples was conducted in a thermocycler (Biometra, Germany) following the protocol for voucher samples (Seeber et al., 2022) while the other fungal samples were amplified using the following protocol: initial denaturation at 94 °C for 2 min, 40 cycles of 30 s denaturation at 94 °C, 30 s annealing at 54 °C, and 30 s elongation at 72 °C, final elongation of 10 min at 72 °C. The thermocycler protocol for plant trnL P6 loop amplification followed the protocol of Epp et al. (2018).

All PCR products were checked by gel electrophoresis (2% agarose gels). Only products showing expected gene bands were used for purification and subsequent sequencing. Purification was done with the MinElute PCR Purification Kit (Qiagen, Germany) with the elution in 50 μL of the elution buffer. Each PCR product was used entirely for purification and treated independently. DNA concentration was measured with a Qubit 4.0 Fluorometer, measuring dsDNA using the broad-sensitivity kit. For sequencing, 40 ng of each purified PCR product were pooled. If the concentration was not measurable, the total purified volume was added to the pool. All PCR replicates were used for the final pools (6 for the ITS1 metabarcoding, 3 for the chloroplast P6 loop metabarcoding). For extraction blanks and PCR no-template controls, 5 μL of each PCR product was added to avoid diluting the concentration of the

final sequencing pool too much. The final pool was purified again with MinElute and adjusted to a final concentration of 33 ng μL^{-1} in 30 μL. Three fungal sequencing pools with 175–187 samples each (Pool 1: 187 samples (3 replicates of each lake besides CH12 and 18 samples of a different project), Pool 2: 187 samples (all CH-12 samples), Pool 3: 175 samples (3 more replicates for the other lakes)) were sent to Fasteris SA sequencing service (Switzerland). The service included library preparation using a specified protocol (Metafast library; a PCR-free library preparation method), quality control and sequencing on an Illumina MiSeq platform (2 × 250 bp, V3 chemistry with an expected output of 20 million paired-end reads).

The plant PCR products were treated equally to the fungal PCR products. We sequenced two pools for the plant metabarcoding. These pools were sequenced on an Illumina NextSeq500 device (2 × 150 bp, 120 million paired-end reads). In addition, plant trnL P6 loop data from the lake CH12 were used from Epp et al. (2018).

3.3. Bioinformatic analysis

For the quality-check, filtering and taxonomic assignment of the sequencing results, we used the open source OBITools pipeline (Boyer et al., 2016). First, *illuminapairedend* was conducted to pair sequence ends, followed by *obigrep* which filters out all unpaired reads. Afterwards, *ngsfilter* was used to demultiplex the file into unique samples and *obiuniq* was applied to dereplicate sequence reads. All sequences shorter than 10 bp and with fewer than 10 reads were deleted applying *obigrep*. A detailed description of all filtering steps is attached (Supplement 5).

After filtering, *ecotag* was applied to the vegetation dataset to perform taxonomic classification of the sequences against the sequence database. For the taxonomic assignments in the metabarcoding community, different approaches can be used. One approach is to work with each assigned sequence variant (ASV) present in the sample (after filtering out sequencing errors) and compare them to a reference database. In the case of the vegetation dataset, we are working on the level of ASVs. For taxonomic classification of the vegetation dataset, we used the ArctBorBryo database based on quality-checked and curated Arctic and Boreal vascular plant and bryophyte reference libraries (Sønstebø et al., 2010; Willerslev et al., 2014; Soininen et al., 2015). Only those ASVs that have a 100% match to the database were kept in the plant dataset. The taxonomic names (either family, genus or species level) of the plant ASVs were checked on https://www.gbif.org/ for their occurrence in the study area. To simplify the dataset, all reads assigned to the ASVs with the same scientific name are merged into one taxon.

A different approach to analyse metabarcoding data is to work with operational taxonomic units (OTUs). When working on the OTU level, the sequence types are clustered together according to a specific threshold of sequence identity. For fungal metabarcoding, working on ASV level instead of OTUs might lead to an overestimation of the richness of common fungal species due to their haplotype variation (Estensmo et al., 2021; Tedersoo et al., 2022), but might also result in an underestimation of the richness of rare species. As the common fungi drive the main composition of the datasets, we therefore chose to work on an OTU level for this study. Additionally, clustering fungal OTUs is, in general, commonly used by the community, following the guideline of Tedersoo et al. (2022), and makes a comparison to other studies easier. For the fungal dataset, the open source *sumaclust* algorithm (Mercier et al., 2013) was applied to cluster sequences with an identity threshold of 0.97, generating operational taxonomic units (OTUs) before applying *ecotag*.

An analysis comparing ASVs and OTUs for the fungal data showed only small differences in the results, which did not change the overall pattern. Only absolute numbers of assigned sequences differed (5684 ASVs and 5411 OTUs). Nonetheless, we tested the distribution of the fungal taxa based on OTUs as well as on ASVs in a PCA. A fairly similar distribution of the samples is found (Supplements 6 and 7). The richness analysis revealed very similar trends when using ASVs or OTUs. We compared the ordinations by applying the functions procrustes () and protest () in the R package vegan (Oksanen et al., 2020). The Procrustes comparison of the first two PCA axis scores of the datasets with OTUs and ASVs yielded a sum of squares of 1.44 while the Protest comparison with 999 permutations showed the sum of squares to be 0.7213 with a significance level of 0.001.

After filtering, *ecotag* was applied to perform taxonomic classification of the OTUs against the embl142 (based on the EMBL nucleotide sequence database, release 142; Kanz et al., 2005) and the UNITE database release for fungal metabarcoding (Nilsson et al., 2019). The UNITE database is a curated fungus database where detection of false positive reads might be lower than in the broader EMBL release. Using only the UNITE database for the assignment, however, might preclude identification of certain taxa. Therefore, the final assignment for each fungal OTU is based on the assignment from the database with the higher identity. When both databases match the same identity but differ in their specific species assignment, the UNITE database is used for final taxonomic classification.

All databases were built to be applicable for the *ecotag* algorithm as following: the sequences of the databases and NCBI taxonomy files were formatted in the ecoPCR format and ecoPCR was run to simulate *in silico* amplification of database sequences with the subsequent primers (allowing 5 mismatches in each primer sequence). The putatively amplified sequences were used as the reference databases and taxonomy information was added.

Fungal OTUs with identity levels equal to or higher than 98% were used for further analyses to keep only well-annotated sequences. All contaminants (non-fungal reads; OTUs occurring only in no-template controls/extraction blanks) and aquatic fungi as well as OTUs with total read counts lower than 10 have been excluded from further analysis. Seeber et al. (2022) describe these reads in more detail and show that they make up only a small part of the dataset, validating the reliability of the primer pair. For the vegetation data, the identity cut-off was at 100%. The taxa were checked on https://www.gbif.org/ for their occurrence in the study area. Taxa which do not occur in the area were filtered out from the dataset. Further excluded ASVs are algae which are also amplified by the marker, but are not part of the terrestrial vegetation being assessed in this study. We resampled both datasets to normalise the count data following the script of Kruse (2020; https://github.com/StefanKruse/R_Rarefaction) while using the lowest overall count of a sample as the base count. The vegetation data were resampled to a base count of 12,489, resulting in an exclusion of the samples from 9.9 cal ka BP (calibrated kiloanni before 1950 CE) of Kyutyunda and 7 cal ka BP from CH12 due to too low counts. The fungus data were resampled to a base count of 5,284, resulting in the exclusion of the sample from 5 cal ka BP from Kyutyunda and the sample from 18.8 cal ka BP from Lama.

3.4. Assessment of negative controls and contamination

For the plant dataset, we ran in total 29 extraction blanks (EBs) and 29 no-template controls (NTCs) along with the 189 samples. 100% of EBs and 90% of NTCs are clean and show no or a negligible

proportion of contamination (lower than 0.01% of total reads). In 10% of NTCs we detected between 0.014 and 0.035% of the total reads (Supplement 8). We also checked the blanks for their contained ASVs and the percentage of the reads in the blanks vs. the samples. We identified 12 different ASVs which are present at more than 10% of their abundance (samples + blanks) in the blanks (Supplement 9).

We ran a total of 58 EBs and 45 NTCs along with the 384 samples for the fungal metabarcoding. 81% of EBs and 82.2% of NTCs are clean and show no or a negligible proportion (lower than 0.01%) of total reads. In 19% of EBs we detected 0.01–0.49% of the total reads, and in 17.8% of NTCs we detected 0.01–0.44% of the total reads (Supplement 10). We identified 13 different OTUs which are present at more than 10% of their abundance (samples + blanks) in the blanks (Supplement 11). We excluded these OTUs from the analysis and ran the RDA again. The RDA with the excluded OTUs is displayed in Supplements 13 and 14. The results are very similar to the RDA in Fig. 4 (RDA1: 11.95% and RDA2: 2.83%; with excluded OTUs: RDA 1: 12.15% and RDA2: 2.84%). Also, the distribution of the samples and the taxa is robust. Those OTUs which we found in the controls are mostly highly dominant in the samples which therefore can easily lead to cross-contamination during the laboratory work. As this happened in only a very few controls, we kept the OTUs in the dataset. Nonetheless, we cannot rule out entirely that the OTUs which do occur in the controls are partially contamination as these are mostly taxa which can be found ubiquitously (e.g. *Malassezia* can be found in soil but also on human skin).

3.5. Statistical analysis and visualisation

We filtered the fungus dataset following Schiro et al. (2019) and assigned identified taxa to functional types according to their most probable role in the ecosystem (Schulze and Mooney, 2012). Mycorrhizal fungi include arbuscular mycorrhizae, ectomycorrhiza, and ericoid mycorrhizae. Other groups are saprotrophs, parasites, lichens, yeasts, and symbionts. A large number remained as "unknown" if their role in the ecosystem is not well understood. Identified plant taxa were assigned to either woody or herbaceous taxa.

For the statistical analysis, all data have been double-square rooted to better account for low-abundant taxa. All statistical analyses were implemented on percentage data using R, version 4.0.3 (R Core Team, 2020). Taxa were plotted colour-coded after their assigned functions. Plotting was done using the tidyverse package and ggplot2 (Wickham, 2016). To analyse differences in species diversity amongst the samples and locations, we calculated the alpha diversity using specnumber () of each sample from the resampled fungus and plant dataset.

To investigate relationships between fungi and vegetation, we used the functions cor.test () and cor (). First, we assessed whether there is a correlation between fungal OTU and ASV richness and plant taxon richness. Second, we related the fungal richness to the most significant vegetation PCA axis scores which were extracted from the PCA performed on the vegetation dataset. Finally, we applied the significant vegetation PCA axes as constraining variables in a redundancy analysis (RDA) performed on fungal compositional data using the function rda (). The scores of the vegetation PC axes were combined in a data frame using the function as.data.frame () to be used as the explanatory variable. For each axis, only taxa making up most of the separation of the axes were plotted with their names in the final RDA to not overload the plot. The significance of the vegetation PC axes was identified using PCAsignificance (). We used 10 samples from CH12 which are evenly distributed over the sediment record for the RDA to balance the weight of all lakes in the ordination. All ordination analyses were performed on double square-rooted data.

4. Results

4.1. Fungi: sedaDNA sequencing results and overall patterns of alpha diversity and taxonomic composition

In total, we obtained 52, 213, 129 paired read counts in the fungal dataset. After applying the OBItools pipeline, we retained 25,751 unique sequences with 32, 027, 606 counts. Clustering at a similarity threshold of 97% with *sumaclust* resulted in 5411 OTUs. Excluding OTUs with a similarity lower than 98% against the databases led to 716 remaining OTUs for the embl142 database, whereas the UNITE database returned 268 OTUs. After resampling to a base count of 5284 and subsequent filtering steps, 118 OTUs remained, covering 95.25% of the initial reads obtained after applying the OBItools pipeline. The filtered OTUs are regarded as "rare" and are not further assessed.

The highest OTU numbers before subsequent filtering of taxa are detected for CH12 (209 OTUs). This is followed by forested Bolshoe Toko (146 OTUs), Levinson Lessing (137 OTUs), and Lama (135 OTUs). The lowest OTU number is detected for the northern lake Kyutyunda (78 OTUs). The OTU richness of single samples ranges from 3 OTUs (Kyutyunda, 30 cal ka BP) to 82 OTUs (CH12, 5.5 cal ka BP) with a mean of 23.53 OTUs. Samples from the Holocene show higher richness in comparison to samples from MIS2 and MIS3 in most lakes, while for Bolshoe Toko the overall OTU richness follows a decreasing trend.

The 10 most dominant taxa, summing up to 71% of the entire fungal dataset, are Pseudeurotiaceae (20%; 30 samples), *Mortierella* (13%; 63 samples), Sordariomyceta (11%; 26 samples), *Exophiala* (5.8%; 6 samples), *Oidiodendron* (5.6%; 10 samples), *Protoventuria* (5.5%; 14 samples), *Candida vartiovaarae* (3.1%; 7 samples), *Pseudeurotium* (2.7%; 9 samples), *Gryganskiella fimbricystis* (2.6%; 32 samples), and *Trichosporiella cerebriformis* (2.4%; 11 samples).

The most dominant functional type in the dataset are saprotrophs (40%; 38 OTUs), while yeasts are present at 10% (23 OTUs). Parasites (9.05%; 13 OTUs) and mycorrhizae (4.5%; 14 OTUs) are relatively rare. Least abundant are other symbionts (1.07%; 5 OTUs), lichens (0.2%; 4 OTUs), and mould (0.2%; 1 OTU). Fungi of unknown function comprise 24.2% (21 OTUs) of the dataset.

4.2. Vegetation: sedaDNA sequencing results and overall patterns of alpha diversity and taxonomic composition

In total, we obtained 48, 939, 032 reads for the vegetation data. Assembling of paired-end reads, demultiplexing into samples, and cleaning resulted in 152,194 unique sequence types with 20, 063, 932 counts. A total of 243 distinct taxa were obtained with 100% similarity to the database (Sønstebø et al., 2010; Willerslev et al., 2014; Soininen et al., 2015).

The comparison of taxa richness between the lakes reveals the highest number for Lama (163), followed by Bolshoe Toko (152) and Levinson Lessing (146). CH12 (138) and Kyutyunda (133) have the lowest numbers. The taxon richness of single samples varies between 9 (7 cal ka BP, CH12) and 112 (35 cal ka BP, Bolshoe Toko).

The most common plant taxa are Salicaceae (37.4%; 69 samples), *Dryas* (20.4%; 69 samples), *Larix* (5.94%; 44 samples), *Alnus alnobetula* (5.88%; 67 samples), *Papaver* (3.86%; 59 samples), *Menyanthes trifoliata* (3.83%; 45 samples), *Bistorta vivipara* (2.72%, 63 samples), Asteraceae (2.43%; 66 samples), *Betula* (1.6%; 67 samples), and *Anemone patens* (1.4%; 18 samples). These taxa constitute 85.5% of the dataset.

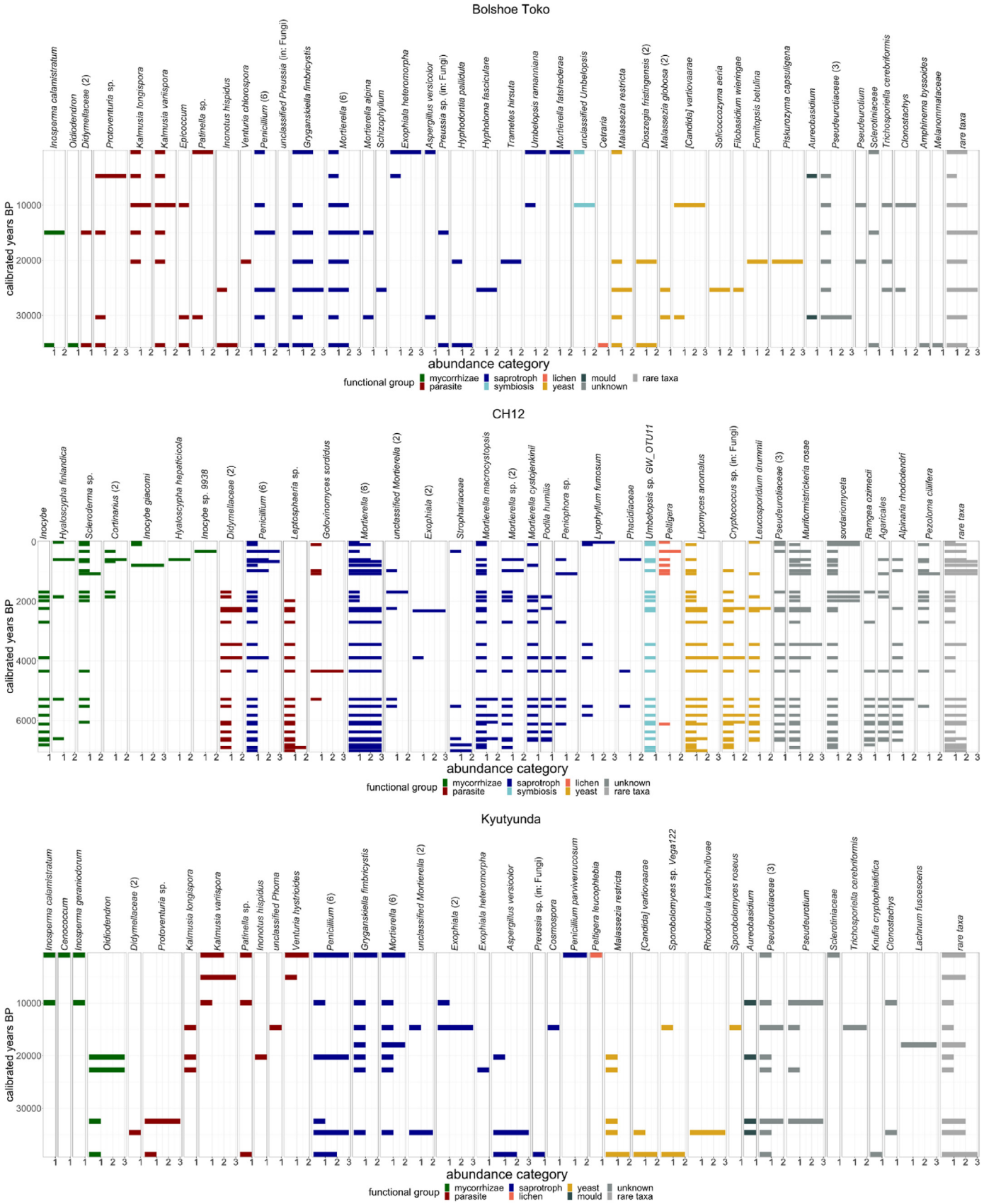

Fig. 2. Site-specific fungus abundance displayed in abundance categories according to relative percentages. Fungi of the same functional type are colour-coded. The numbers in brackets give the OTUs detected for the specific taxon. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.3. Site-specific plant-fungus covariation

4.3.1. Fungus and plant covariation in arctic Siberia from MIS3 to the Holocene

In Levinson Lessing (northern Taymyr Peninsula, tundra, 40–0 cal ka BP), the Pseudeurotiaceae (unknown function) as well as *Mortierella* and *Gryganskiella fimbricystis* (both saprotrophs) are highly abundant during MIS3 (Fig. 2). Around 38 cal ka BP, the Didymellaceae (parasites) also occur. At the end of MIS3, *Thamnolia vemicularis* (lichen) occurs. The most abundant plant taxa at this time are Salicaceae, *Dryas,* and *Papaver*. The most abundant fungus taxa in MIS2 are also Pseudeurotiaceae and *Mortierella*, but *Trichosporiella cerebriformis* (unknown function) also occurs often. For plants, the most dominant taxa are Salicaceae and *Papaver*, followed by *Dryas* at the end of MIS2 (Fig. 3). During the Holocene, *Mortierella* remains the most frequent fungal taxon but mycorrhizal OTUs (*Inosperma calamistratum, I. geraniodorum, Mallocybe fuscomarginata, Oidiodendron*) and parasites (Didymellaceae, *Kalmusia variispora*) become abundant as well. In the Holocene, there is a drastic decline in *Papaver* while *Alnus alnobetula* becomes highly abundant. *Dryas* as well as Salicaceae remain mostly abundant.

CH12 (southern Taymyr Peninsula, tundra, 7–0 cal ka BP) only spans the mid to late Holocene. Around 7 cal ka BP, *Inocybe* (mycorrhizae) as well as *Golovinomyces sordidus* and Didymellaceae (parasites) are highly abundant. *Mortierella* is present throughout the whole record but shows strong declines when mycorrhizae and parasites are abundant around 5 cal ka BP (Fig. 2). Until 5.5 cal ka BP, *Alnus alnobetula* and Salicaceae are highly abundant. Woody taxa such as *Alnus alnobetula*, *Larix*, *Betula,* and *Rhododendron* have their highest abundances around 5 cal ka BP (Fig. 3). After 5 cal ka BP, an increase in yeast taxa (e.g. *Lipomyces anomalus, Cryptococcus*) is detected. This coincides with a decline in the aforementioned

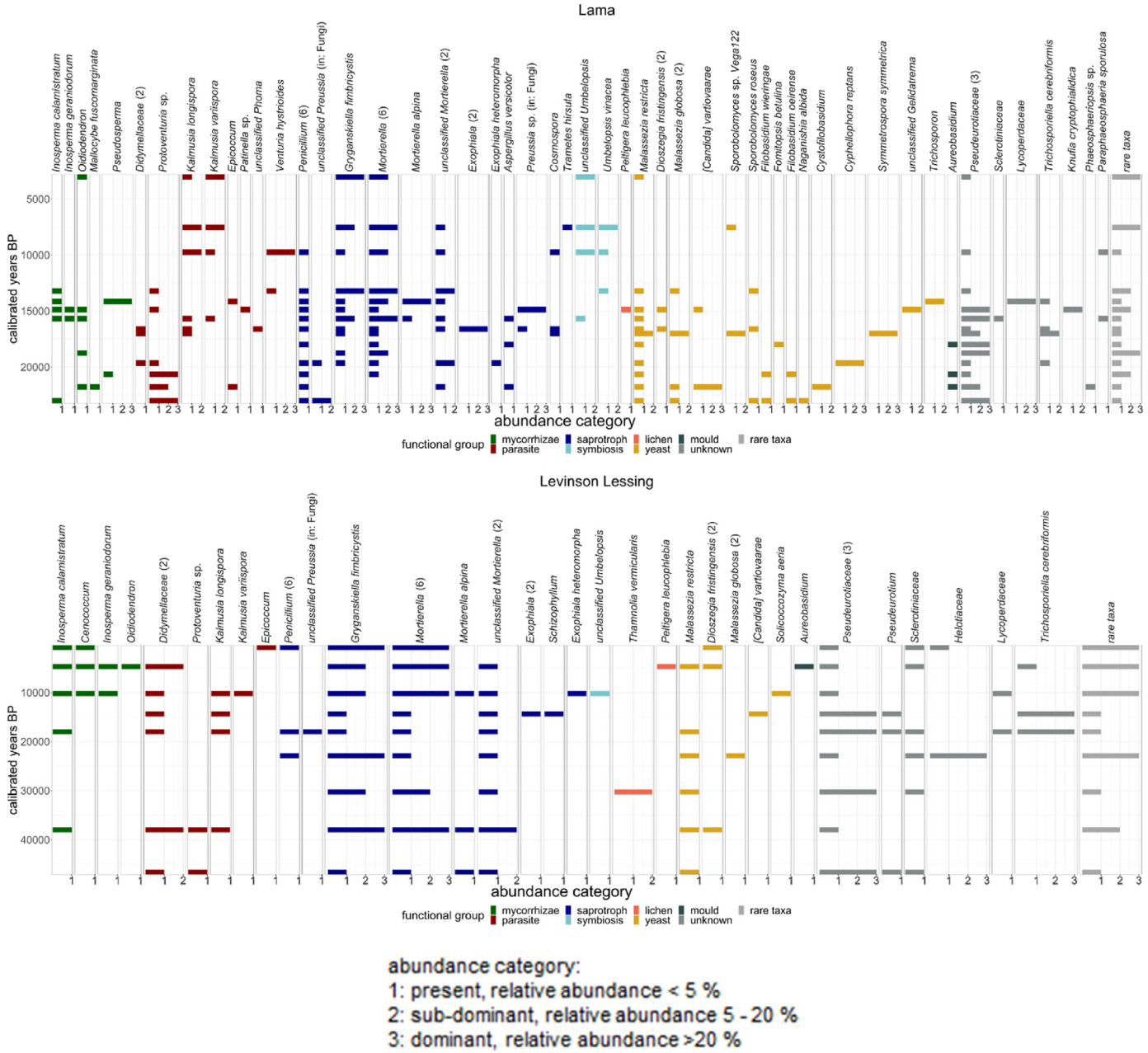

Fig. 2. (*continued*).

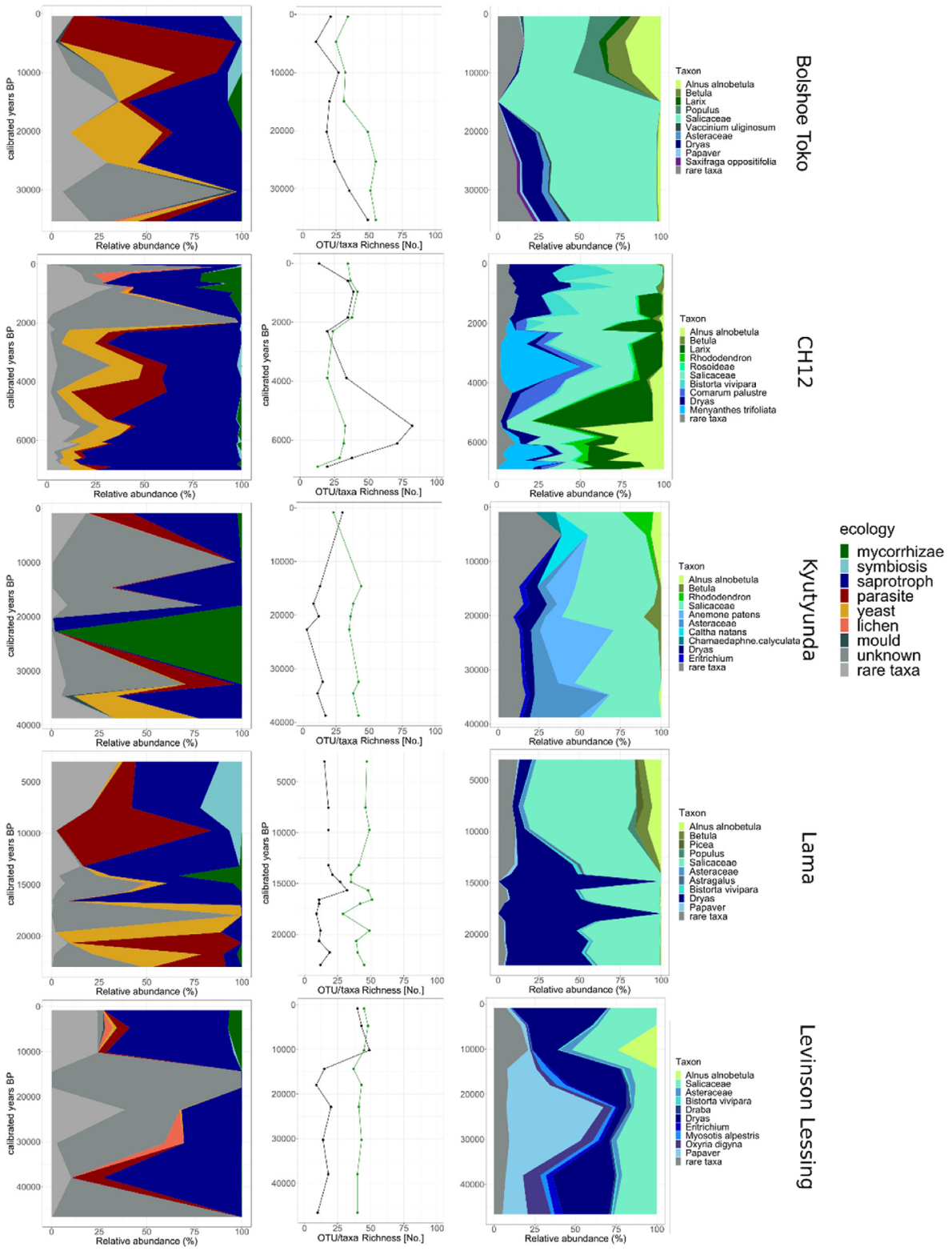

Fig. 3. Fungal functional types in relation to fungal OTU richness and dominant plant taxa. Left column: distribution of fungal functional types for each lake. Middle column: fungal OTU richness of each lake (total OTU numbers), with the black line representing the fungal taxa while the green line marks the vegetation taxa for comparison. Right column: ten most dominant plant taxa of each lake. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

woody taxa. The lichen genus *Peltigera* is abundant in more recent times when the variety of mycorrhizal taxa also increases and *Inocybe*, *Hyaloscypha finlandica, Scleroderma, Cortinarius, Inocybe giacomi,* and *Hyaloscypha hepaticola* occur. Saprotrophic taxa such as *Mortierella* species, *Lyophyllum fumosum*, *Penicillium,* and *Exophiala* are present throughout the whole record.

Lama (northern Siberia, tundra-taiga transition zones, 24–0 cal ka BP) covers MIS2 and the Holocene. The most abundant fungal

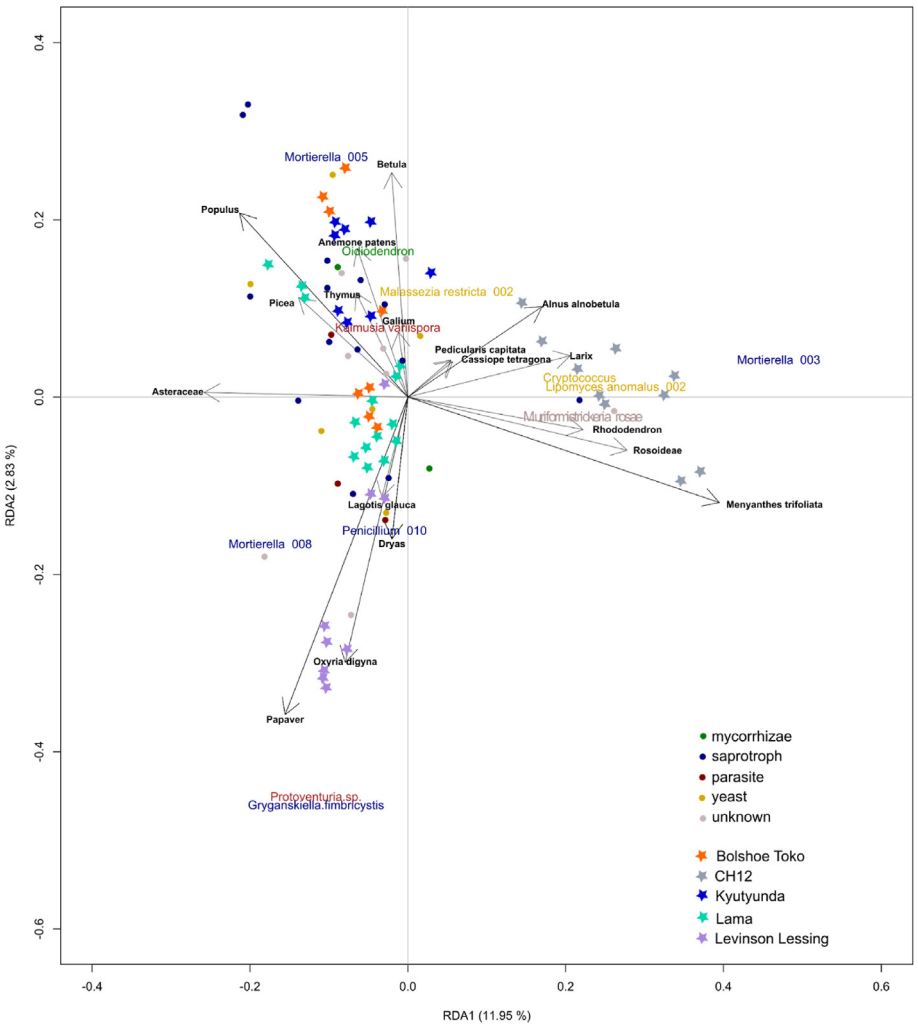

Fig. 4. Fungal and plant co-variation displayed in a redundancy analysis (RDA). The most relevant principal component axes of the vegetation were determined, the scores extracted and then integrated into the RDA. The fungal taxa are displayed either with their names or as a dot colour-coded according to their functional group (see Fig. 2 and 3). The plant taxa are marked with black arrows. The numbers after the taxa names indicate the specific OTU. The samples are displayed as stars and colour-coded according to their lake origin. The vegetation explains 20% of the fungus distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

taxa during MIS2 are Pseudeurotiaceae, *Protoventuria* (parasite), *Mortierella*, and *Cyphellophora reptans* (yeast) (Fig. 2). *Dryas* as well as Salicaceae dominate the vegetation. Around the beginning of the Bølling/Allerød (15 cal ka BP), *Pseudosperma* and *Inosperma* species (mycorrhizae) become abundant. A little later, *Venturia hystrioides* and *Kalmusia* species (all parasites) start to occur. Salicaceae is still the most dominant plant taxon, but *Alnus alnobetula*, *Picea*, *Betula,* and *Populus* also frequently occur after 15 cal ka BP. Additionally, a drastic decline in *Dryas* took place after 15 cal ka BP (Fig. 3).

Kyutyunda covers the late MIS3 to the Holocene (northern Siberia, tundra-taiga transition zones, 38.8–0 cal ka BP). The most dominant fungal taxa during the late MIS3 are *Oidiodendron*, *Pseudeurotium* (unknown function), and *Penicillium* (saprotroph) (Fig. 2). During this time, Salicaceae and Asteraceae are the most abundant plant taxa but *Alnus alnobetula* also occurs (Fig. 3). *Oidiodendron* is mainly present at the end of MIS3. Shortly after, a large increase in *Betula* is detectable. In MIS2, the fungal taxa *Oidiodendron* and *Penicillium* are still highly prevalent and the taxon *Lachnum fuscescens* (unknown function) becomes common (Fig. 2). Salicaceae remains the most dominant plant taxon and *Betula* starts to occur more frequently. High abundance of *Dryas* as well as the first instances of *Alnus alnobetula* are detectable in the late MIS2 (Fig. 3). During the Holocene, *Pseudeurotium* (unknown function) and *Kalmusia variispora* became the most abundant fungal taxa. Salicaceae maintained its broad distribution while other woody taxa such as *Alnus alnobetula* and *Rhododendron* increased in their abundances.

Bolshoe Toko also spans the late MIS3 to the Holocene (central Yakutia, taiga, 35–0 cal ka BP). During the late MIS3, Pseudeurotiaceae are the most abundant fungal family but parasitic species (e.g. *Kalmusia* species, *Inonotus hispidus*) and saprotrophs (e.g. *Mortierella, Grykanskiella fimbricystis*) also occur (Fig. 2). At this time, Salicaceae is the most abundant plant taxon with *Dryas* occurring frequently. *Alnus alnobetula* and *Betula* are also present but at low abundance (Fig. 3). In MIS2, *Gryganskiella fimbricystis* and *Mortierella* are highly abundant fungi and a few yeast taxa (e.g. *Dioszegia fristringensis, Piskurozyma capsuligena*) start to occur. In late MIS2, *Inosperma calamistratum* (mycorrhizae) also occurs. Vegetation is still dominated by Salicaceae until the end of MIS2 with scarce abundances of *Alnus alnobetula* and *Betula*. In the Holocene, *Protoventuria* (parasite) is the most abundant fungal taxon but also *Kalmusia* species (parasite), *Exophiala heteromorpha* (saprotroph), and *Candida vartiovaarea* (yeast) are commonly found. A large increase in more diverse woody taxa is detected with more

occurrences of Salicaceae as well as *Alnus alnobetula*, *Betula*, *Larix,* and *Populus*.

4.3.2. Quantitative relationships between fungi and plant richness and composition

In all records, we found only a weak borderline-significant correlation between fungi OTU and plant taxa richness (r 0.2394, p-value 0.098). For the fungal ASVs and plant taxa richness, the correlation is similar (r 0.2351, p-value 0.1039) Fungal richness is positively correlated to the sample scores of the first plant PCA axis (PC1: r 0.3863, p-value 0.006; ASVs: PC1 r 0.387, p-value 0.006) and negatively correlated to the sample scores of the second plant PCA axis (PC2: r −0.41, p-value 0.003; ASVs: PC2 r −0.424, p-value 0.002). The first axis reflects the differences between samples characterised by woody taxa including *Larix* and *Alnus alnobetula* and typical tundra taxa. On the second axis, we detected herbaceous plant taxa such as *Anemone patens* and *Thymus* positively correlating alongside other taxa preferring wetter habitats. Taxa such as *Oxyria digyna* and *Dryas*, which are associated with rather dry sites, show a negative correlation.

Sample scores of plant PCA axes 1–5 explain 20% of fungi composition (p 0.001) as revealed by RDA (Fig. 4 and Supplement 12). Woody taxa such as *Alnus alnobetula*, *Larix,* and *Rhododendron* appear in the upper right quadrant of the RDA plot together with the fungal taxa *Mortierella*_003, *Cryptococcus*, and *Muriformistrickeria rosae* (unknown function) (Fig. 3) and samples from CH12 aged 5.5 and 1.8 cal ka BP. The RDA also shows that parasitic fungi, such as Didymellaceae, and yeast, such as *Lipomyces anomalus* and *Cryptococcus*, tend to occur in the presence of woody taxa. Lichens occur predominantly in samples of Holocene age. *Papaver* and *Dryas* together with the fungal taxa Pseudeurotiaceae, *Grykanskiella fimbricystis* (saprotroph), and *Mortierella* species occur in the lower left quadrant together with all samples from Levinson Lessing. *Populus* and *Ranunculus* in the upper left quadrant appear together with *Lipomyces anomalus* (yeast), *Cryptococcus* (yeast), and *Mortierella*. Samples here mostly originate from Bolshoe Toko although there are some from Lama (around the Bølling/Allerød period) and Kyutyunda (Holocene). Samples from the Holocene all occur in the upper half of the RDA where woody plant taxa are found and a broader fungal species richness is detected. In general, Lake CH12 shows a unique fungal composition in comparison to the other lakes. The samples can be found in the right quadrants of the RDA while the samples of the other lakes are located in the left quadrants or centred (Fig. 4 and Supplement 6).

5. Discussion

5.1. Fungus and plant diversity along a spatiotemporal gradient in Siberia

Assessing the species richness in an environment enables the determination of community diversity and can be an indicator for ecosystem turnover (Hillebrand et al., 2018). After applying metabarcoding on 70 samples from five lakes across Siberia, we detected high fungal richness (706 OTUs) while the analyses of plant richness yielded 243 distinct taxa. In comparison to Liu et al. (2020) who investigated plant species richness in lake sediments in north-eastern Siberia, we detected slightly higher plant diversity (their study: 90 to 120 taxa in a single lake, this study: 133 to 163 taxa in a single lake) which might be explained by the sediments from the present study covering a longer time span and therefore more diverse climate scenarios. To assess fungal richness, we used OTU clusters instead of sequence variants, which might lead to under- or overestimation in comparison to species assessment (Frøslev et al., 2017). Underestimation may also originate from missing reference material of local taxa in databases (Goodwin et al., 2016; Quince et al., 2009). Comparably, a modern species assessment from the western Ural yielded 376 observed fungal species (Palamarchuk and Kirillov, 2019), which supports the conclusion of Seeber et al. (2022) that their marker is suitable to assess diversity even on long time-scales. Nonetheless, higher OTU richness (1125 OTUs in 55 samples) was obtained by Talas et al. (2021) in their study of a Holocene lake sediment core from eastern Latvia. Their discovery of higher overall diversity is explained by inclusion and detection of aquatic fungi (23%, terrestrial 40%), which are mostly lacking in our data. Additionally, they kept very short reads and included reads with fewer counts (4 instead of 10 in our study).

Bolshoe Toko (146 OTUs) and Lama (135 OTUs) are in forested areas and show higher fungal OTU richness compared to Kyutyunda (78 OTUs) from the northern tundra (Fig. 3). A relationship between fungal richness and vegetation composition has been shown by multiple studies (e.g. Tedersoo et al., 2013; Geml et al., 2017), however data from the Siberian treeline are lacking. Our data concur that ectomycorrhizal fungal richness is highest with forest cover (Geml et al., 2017). Spatial fungal richness is confirmed by the temporal relationship: we observed co-occurrences of high fungal richness and woody vegetation. Levinson Lessing shows a large increase in fungal OTU richness and woody taxa dominance during the warm Holocene compared to the late Glacial although experimental warming did not result in higher fungal diversity (Geml et al., 2015; Mundra et al., 2016). Talas et al. (2021) show high richness as well as community turnover with increases in plankton parasitic species and mycorrhiza after 4 cal ka BP, suggesting that fungi with more specific hosts or substrates (e.g. ectomycorrhizae) are more susceptible to ecosystem changes than taxa with wide preferences. CH12 shows higher OTU richness than the other lakes, even when considering similar sample numbers, supporting the hypothesis that fungal communities from the warmer Holocene might be more species rich. Potentially, warming-induced vegetation responses rather than direct warming shape the diversity in fungal communities, suggesting a broadening diversity of fungi species alongside future treeline migration.

Metabarcoding on arctic tundra communities reveals that each specific tundra type has a unique community of associated fungi (Wallenstein et al., 2007; Geml et al., 2021). This might explain the overall highest fungal OTU richness originating from CH12 (dry forest tundra), while Kyutyunda (wet southern tundra) shows a rather low richness. Furthermore, our analysis shows a negative correlation between fungal richness and the second vegetation PC axis, covering a wetness gradient from species related to drier areas (high PC scores) to species rather related to wetter areas.

A modern spatial study on the Tibetan plateau showed that fungal richness is positively correlated with plant richness (Yang et al., 2017). Interestingly, through statistical analyses, we find only a weak positive correlation between fungal and plant richness. Most probably, this indicates a quite complex relationship between plant richness and vegetation composition. It is also known that other biotic or abiotic factors such as the bacterial composition or soil N and C content influence the fungal and plant communities (Singh et al., 2009). Besides, the shorter amplicon length of the plant compared to the fungal marker can cause biases when amplifying highly fragmented DNA, resulting in a weak statistical relationship. Incomplete databases for arctic fungi might also lead to underestimation of taxa richness. For plants, it is known that the catchment influences the record quality if the plants are growing closer to the soil surface (Giguet-Covex et al., 2019). Potentially, some fungi are also more likely to end up in the sediment of the lake if they are growing in the upper soil horizons with their DNA transported to the lake either via animals or rainfall. At the broad

scale, plant richness decreases with latitude (Kerkhoff et al., 2014). However, a modern study from Kamchatka, Russian Far East, reports highest plant species richness in alpine tundra and snowbed communities (Doležal et al., 2013). Recent sedaDNA studies from the treeline in Chukotka, Russian Far East, and from Bolshoe Toko showed highest terrestrial plant richness in the late Pleistocene in steppe-tundra areas and lowest in the forested Holocene (Huang et al., 2020; Courtin et al., 2021). This indicates that a high correlation between fungus and plant alpha diversity cannot be expected.

5.2. Changes in ecosystem functioning over a spatiotemporal gradient

To date, molecular analyses of ecosystem functioning that trace fungus-plant covariation have been addressed by multiple modern studies. These studies mainly focus on the organisms required for modern plant establishment, that is, over spatial (Merges et al., 2018) and short temporal gradients (Zhang et al., 2016) or under varying growing conditions (Mohamed and Martiny, 2011). In palaeo-research, plant communities have been subject to molecular analysis such as metabarcoding studies (Liu et al., 2020), shotgun sequencing (Parducci et al., 2019) or target capture (Murchie et al., 2021). So far, the turnover of entire ecosystems tracing not only the plant constituent but also their associated fungal symbionts has not yet been studied. Our data form not only one of the first molecular biological studies revealing fungus community changes over a large temporal gradient but also allow conclusions to be drawn on their long-term impact on forest establishment. The following examples highlight the impact of vegetation changes alongside climate change on fungus ecological functionality and subsequent whole ecosystem turnover.

5.2.1. Long-term mutualism in arctic environments inevitable for plant establishment

Most mycorrhizal taxa detected are from the families Cortinariaceae and Inocybaceae and some from Myxotrichaceae and Hyaloscyphaceae (Fig. 2), in agreement with previous metabarcoding studies (Nilsson et al., 2005; McGuire et al., 2013; Botnen et al., 2014). We retrieved *Inocybe* (including the subgenus *Inosperma* (Matheny et al., 2020)) and *Cortinarius,* both known from high latitudes (Timling et al., 2012). They represent ectomycorrhizal associates of arctic tundra and shrubs including *Salix* and *Dryas integrifolia* (Ryberg et al., 2009; Botnen et al., 2014), both being common taxa in our plant data. Our data also support previous studies from boreal forests (McGuire et al., 2013), including a study from the Russian Far East detecting *Cortinarius*, in addition to *Lactarius* and *Russula*, as important ectomycorrhizal of *Larix gmelinii* (Miyamoto et al., 2021). *Cortinarius* also associates with shrubs of Salicaceae and Rosaceae as well as herbaceous Cyperaceae (Garnica et al., 2005), which frequently occur in our plant dataset, indicating a broad variety of host taxa for these fungi, from which we can infer high adaptability towards warming and changing overall environmental conditions.

After the Last Glacial, vegetation species richness decreased as well as arbuscular mycorrhizal taxa while ectomycorrhiza associated with woody taxa and non-mycorrhizal fungi increased (Zobel et al., 2018). This resulted in changes in the mutualist trait structure after the Last Glacial Maximum, making mycorrhizal associations important factors when predicting ecosystem responses to changing environmental conditions. We also observe increasing fungal richness in Holocene samples (Fig. 3). This underlines the suitability of sedaDNA fungal metabarcoding studies for appropriate ecosystem reconstructions and when considering adaptation mechanisms alongside ecosystem turnover.

Interestingly, we observed highest values of Pinaceae only after the presence of mycorrhizal taxa (e.g. *Cortinarius*, *Inosperma calamistratum*) (Figs. 2 and 3), although this might be due to low sample numbers. Without mycorrhizal fungi, Pinaceae growth is restrained or establishment is inhibited as nutrient uptake is impossible (Marschner and Dell, 1994). Studies from Japan (Ishida et al., 2007) and temperate areas in the Himalaya (Pande et al., 2004) revealed Cortinariaceae as the main ectomycorrhizal associates of Pinaceae, strengthening the precision of our dataset and its ability to correctly recover fungal-plant covariation over long time scales and its possibility to assess ecosystem dynamics. Our analysis also highlights the longevity of the dependency of Pinaceae on these particular fungi.

5.2.2. Wood-decaying species highly impacted by warming

We found *Mortierella*, *Penicillium,* and *Exophiala* as the main biomass-decaying taxa (Fig. 2). These are common soil fungi in high-latitude ecosystems (Treseder et al., 2007; Allison et al., 2009) and are reported amongst the main soil fungi in arctic tundra soils (Kurek et al., 2007; Zhang et al., 2016) due to their cold tolerance. *Mortierella* associates with *Vaccinium uliginosum*, *Betula nana*, *Salix glauca*, *Empetrum nigrum*, and *Cassiope tetragona* (Voříšková et al., 2019), which are typical taxa in our study. Rhizosphere samples from *Larix sibirica* and *Betula pendula* from Krasnoyarsk, Siberia revealed *Penicillium* as one of the main constituents (Boyandin et al., 2012). *Larix* forests growing on permafrost show broad host spectra towards saprotrophs (Leski and Rudawska, 2012) as a response to changing environment, for example after wildfires (Miyamoto et al., 2021), which explains the overall broad distribution of saprotrophs after warming in the area.

Saprotrophs are generally highly abundant throughout all records. Their significant decrease around 10 cal ka BP (Figs. 2 and 3) demonstrates that the climate change during the Pleistocene/Holocene transition (Biskaborn et al., 2016, 2019a) also affected soil communities alongside vegetation. This finding agrees with results from experimental warming studies in boreal ecosystems, indicating that relative saprotroph abundance declines with warming, while the abundance of mycorrhizal fungi and lichens increases, underlining long-scale ecosystem turnover as a response to warming (Deslippe et al., 2012; Geml et al., 2015; Mundra et al., 2016).

5.2.3. Host-specific parasites show strong co-occurrence with woody taxa

We detected parasitic OTUs mostly in samples from the warm Holocene (Fig. 2), confirming early findings that experimental warming leads to increases in parasitic and virulent fungi (Geml et al., 2015) along with woody taxa expansion. The most abundant parasitic species from our dataset are *Protoventuria*, *Kalmusia variispora, K. longispora,* and Didymellaceae which co-occur with Salicaceae, *Larix,* and *Alnus alnobetula* (Figs. 2 and 3). In shrubby tundra in Greenland with *Salix* occurrences, *Venturia* species are amongst the highest abundant fungi (Voříšková et al., 2019), indicating a strong covariation between these taxa. Interestingly, we observe a decline in Salicaceae after *Protoventuria* abundance around 20 cal ka BP (Figs. 2 and 3), supporting previously noted fungal parasite abundances in permafrost during the LGM (Lydolph et al., 2005). Venturiaceae has been assigned to Salicaceae as pathogens in northern latitudes (Hosseini-Nasabnia et al., 2016), while *Kalmusia* has been detected in *Alnus* forests (Iznova and Rukšėnienė, 2012). Didymellaceae co-occurs with a broad range of host plants such as *Larix decidua* (Chen et al., 2017). The RDA reveals that *Kalmusia* species preferentially occur in forested areas alongside saprotrophic and mycorrhizal species (Fig. 4), supporting the value of our data and the feasibility of co-occurrence analysis in

sedaDNA studies and their potential when assessing ecosystem dynamics up to species level. Plant-parasite interplay in relation to climate change is not fully understood (Burdon and Zhan, 2020) but it is assumed that parasitic fungi are more specific in their hosts than mycorrhizal taxa, making them a great target when assessing ecosystem dynamics and turnover (Põlme et al., 2018).

5.2.4. Lichens influence soil carbon dynamics and local fauna

The recovered lichen OTUs belong to 16 families with the highest richness in Peltigeraceae and Parmeliaceae. The most abundant genera are *Thamnolia*, *Peltigera,* and *Cetraria,* all of them being common in northern Siberian communities (Zhurbenko and Yakovchenko, 2014) and permafrost (Lydolph et al., 2005). *Thamnolia* species often occur in arctic tundra (Sheard, 1977), showing low specificity concerning their photobiont while associating with various *Trebouxia* species (Nelsen and Gargas, 2009). *Peltigera* preferentially grows in temperate regions on soils and among mosses over rocks, but also on tree trunks (Nash, 2002) and in boreal forests (Asplund and Wardle, 2015), explaining their abundance in the forested Holocene in CH12 (Fig. 2).

Our analyses are among the few palaeoecological studies detecting lichens (Fig. 2). Lichens are commonly missing from fossil records (Taylor and Osborn, 1996) despite being an important component of boreal forest and tundra biomass (Asplund and Wardle, 2017; Shevtsova et al., 2020). However, we could only detect a few reads, belonging to 48 OTUs (<1% of the whole dataset).

Unexpectedly, most lichens are recorded from warm periods with well-developed vegetation (late MIS3 and Holocene). Lichens are a prominent feature of arctic landscapes and short-term experimental warming in the Canadian arctic led to their decline (Fraser et al., 2014). For Siberia, lichens have been recovered along a broad latitudinal gradient with high diversity and biomass (Safronova and Yurkovsksya, 2019). Lichen cover on permafrost produces a cooling effect, making lichens of great importance when considering thawing effects (Porada et al., 2016). Reduced or no lichen cover during the glacial might be relevant for past soil carbon dynamics. Lichens tolerate high percentages of CO_2 (Badger et al., 1993), but studies about the impact of low CO_2 supply are missing. Possibly, they suffer more than other fungi from reduced atmospheric CO_2 content as lichens also have to supply their algal or cyanobacterial symbionts.

Lichen distribution also impacts the occurrence of animals such as *Moschus moschiferus*, which preferentially settle in lichen-rich habitats for their food supply (Slaght et al., 2019). Increased lichen coverage during the Holocene may have supported the compositional turnover in the megaherbivore fauna. Reindeer mostly feed on lichen but changing environmental conditions might impact their distribution and diet to include less lichen (Drucker et al., 2011) or to vary seasonally (Bocherens et al., 2015), giving them higher survival advantage. Changing fungus communities will thus not only impact the boreal forest, but also its fauna.

5.2.5. Habitat-loss of fungal species due to warming resulting in feedback on whole ecosystem

The most abundant yeast taxa in our dataset are *Candida vartiovaarae*, *Malassezia restricta*, *Cyphellophora reptans*, *Cryptococcus*, and *Lipomyces anomalus* (Fig. 2), which are widely distributed in Siberian soils (Polyakova and Chernov, 2001). *Candida vartiovaarae* is broadly present in forest as well as in grassland soils (Yurkov et al., 2012), while *Cryptococcus* is associated with peatland (Thormann, 2006) and boreal swamps (Kachalkin and Yurkov, 2012). A correlation between *Malassezia* species and nematodes in central European forests was discovered, suggesting that nematodes act as vectors for the fungi (Renker et al., 2003). To investigate these zoophilic relationships and their contribution to ecosystem stability, further metabarcoding data on small soil organisms could be an asset.

Whenever yeasts are highly abundant in the records, especially in colder time periods like the LGM, mycorrhizae decrease (Figs. 2 and 3). Most yeasts show adaptive responses when temperatures drop to maintain their survival (Kandror et al., 2004). Experimental warming also shows yeast decline with rising temperatures (Treseder et al., 2016), indicating that some species will lose their habitats with ongoing warming, resulting in a major feedback to the ecosystem, potentially leading to shifts in the entire ecosystem and subsequent turnover from, for example, tundra to taiga.

From our data, it is not possible to determine the role of yeast in soil. Generally, they serve both as biotoxins (Santos et al., 2004; Compant et al., 2005) or growth promoters for plants (Nassar et al., 2005; El-Tarabily and Sivasithamparam, 2006). In Siberia, yeasts might either function as plant parasites (Hernández-Fernández et al., 2021) or as biodegraders, as after a period of high yeast abundance, we detect decreasing woody taxa. Further research on modern mutualistic and parasitic interactions in the area will help to solve this research gap and to understand yeast impact on long-term ecosystem stability.

5.3. Implications of our results for ecosystem functioning and future research avenues

The interplay between climate, vegetation, fungi, and microorganisms in the boreal forest ecosystem is not yet understood. As fungi are a key component of ecosystem functioning, a major impact on future ecosystem-climate feedback is expected alongside compositional change and varying soil microbiome (McCalley et al., 2014). To our knowledge, we conducted the first study on fungus-plant interactions and co-occurrences in the palaeo context, assessing community shifts in boreal forests as well as tundra ecosystems. However, our results are only a first proxy on future community changes as the magnitude of warming differs strongly between our samples and present warming and any relationship may incorporate lagged responses over large time-scales (Biskaborn et al., 2021).

To our knowledge, this is the first long-term dataset showing antagonistic relationships among fungal functional types as well as warming-related vegetation change related to fungus diversity and composition changes. By analogy to the past, future woody taxa advance into arctic regions might result in higher fungus diversity and a relative increase in mycorrhizae, parasites, and potentially lichens at the cost of saprotroph and yeast abundance.

Our study design does not allow a definite conclusion to be drawn on whether future treeline advances will rely on the presence of specific fungal communities. As ectomycorrhizal communities in sub-arctic tundra are generally species-rich and do not show high host preferences (Ryberg et al., 2009, 2011), major changes may not ensue. However, the investigated soils in the sub-arctic already have long histories of soil development, unlike the northern tundra sites and upper mountain areas. Temperature wise, these are potential habitats for forest establishment but might not be favourable for diverse soil fungus composition due to a lack of nutrients.

Lichens do not generally suffer from warming but are affected by the vegetation. The observed decline in lichens with denser canopy cover (Cornelissen et al., 2001) may only be relevant to the more southerly forests. As our study only returned a few lichen OTUs, it is not possible to draw a robust conclusion here. High CO_2-concentrations during experimental darkening leads to generally quick CO_2 uptake by the genus *Peltigera* and subsequently relatively slow release (Badger et al., 1993), making lichens potentially valuable for

the storage of future warming-induced CO_2 from soil. Further research into lichens is promising to delve into mechanisms supporting ecosystem adaptation towards changing environments.

Besides the limitation in temporal resolution, our study suffers from limited taxonomic resolution and complex abundance patterns. SedaDNA metabarcoding is highly susceptible to damage and degradation, leading to biases in PCR products as taxa might be dismissed due to short lengths (Coissac et al., 2012; Taberlet et al., 2012). Sometimes, reference genomes are missing and identification at the relevant taxonomic resolution is not possible (Sønstebø et al., 2010). Also, different taxa possess varying amounts of genome copy numbers per cell which might lead to over-representation of taxa with high copy numbers while rare taxa can be missed (Behnke et al., 2011). To strengthen the metabarcoding data, a further comparison to target capture similar to Murchie et al. (2021) but on the fungal DNA of the same samples would be an asset to validate the recovered abundances and diversity.

6. Conclusions

This is the first study showing spatial and temporal changes in palaeo fungus-plant covariation. Knowing which fungi influenced the growth of specific plant communities in the past will help to predict future community turnover due to varying climate. To understand palaeo community turnover in more detail, it is necessary to consider a plant's associated heterotrophic organisms in present times. This will help to place knowledge gained in this study into a better context. Additionally, our data are a great asset to existing knowledge about boreal forests as they help to shed light on adaptation mechanisms of plants towards warming and their subsequent northward migration. Nevertheless, there are still many ecological interactions that are unknown which need to be addressed in future research, such as which organisms contribute to the rhizospheres of specific plants and whether or how these associations change with varying climate or how the fauna is impacted by a changing habitat and food source. This might help the development of future afforestation and silviculture strategies. Despite this, our findings will already help the assessment of future tipping points in boreal forest stability.

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Availability of data and material

The data are available under Dryad and Pangaea and will be publicly available after the acceptance of the manuscript.

Pangaea: Metadata of the cores and links to existing Pangaea entries. doi: 10.1594/PANGAEA.948180

Dryad: Fungal and Plant DNA Datasets (Raw data and scripts). doi:10.5061/dryad.05qfttf3x

Author contribution

The study was designed by BvH, KSL, UH; KSL supervised and BvH conducted the experimental lab work; BvH analysed the data under supervision of UH and KSL; LS sampled the cores and supervised the DNA extractions; PS and LE performed the bioinformatic evaluation of the marker; MM retrieved the sediment core of Lake Lama; BD led the projects on Kyutyunda and Bolshoe Toko; BB retrieved and dated the sediment cores including age depth modelling of Bolshoe Toko, Kyutyunda and CH12; BvH dated Lama and performed the age modelling; BvH supervised by UH wrote a first version of the manuscript; all authors commented on the first and revised version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data will be publicly available after acceptance.

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Appendix A. Supplementary data

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