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Arctic driftwood reveals unexpectedly rich fungal diversity

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ABSTRACT

Arctic driftwood can provide unique insight into the diversity of colonizing and decaying fungi at the interface of extremely cold terrestrial and marine environments. Entering the Arctic Ocean via large boreal river systems and being transported by currents and sea ice, driftwood is finally deposited along shallow coastlines. Here, we sequence 177 fungal cultures in driftwood from Iceland, Greenland and the Siberian Lena Delta. Although some fungi may survive during ice drift, most species are not shared among the different sampling sites. Many indigenous Arctic fungi are generalists in their ability to colonize and decompose organic substrata, with massive effects on carbon cycling. *Cadophora* species are the most frequent Ascomycota, and soft rot is the most prevalent form of decay. Few Basidiomycota were found, with many of them having poor sequence matches to known species. Future research is warranted with a focus on the biology, ecology and taxonomy of Arctic driftwood inhabiting fungi.

1. Introduction

Driftwood deposits along Arctic coastlines where trees do not grow have been utilized in the past by indigenous people for cultural purposes (Alix and Brewster, 2004; Alix, 2005), and their origin has been a topic of interest since early Arctic explorers reported their occurrence (Graah, 1828; Agardh, 1869; Hellmann et al., 2013) Currently, the massive amount of Arctic driftwood is considered an extremely valuable resource for dendrochronological studies to better understand paleo-environmental changes over the past centuries to millennia (Eggertsson, 1994; Hellmann et al., 2015), and ideally even over the entire Holocene (Dyke et al., 1997; Funder et al., 2011). Arctic driftwood has been documented from archaeological sites in Greenland where it has survived with excellent preservation underground in permafrost (Matthiesen et al., 2014). Thawing of permafrost, however, in some Arctic areas due to climate change is accompanied by microbial degradation of this ancient material and concerns are mounting that increasing temperatures and thawing will accelerate the decay of these important archaeological remains (Matthiesen et al., 2014). Recent investigations utilizing Arctic driftwood for tree-ring analyses reported microbial decay in many of the samples studied (Hellmann et al., 2013). The decomposition complicates anatomical assessment for studying the origin of the material and interferes with any kind of dendrochronological and wood anatomical assessments. Although polar regions have extreme environments that may limit the rate of microbial decomposition, studies of relict driftwood and other woods brought into the Arctic or Antarctic by early explorers have shown that fungi in these cold ecosystems can cause considerable wood degradation over time (Blanchette et al., 2004, 2008, 2010; Matthiesen et al., 2014).

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The origin of the driftwood in Greenland and Iceland has long been suggested to come from the boreal forests of Siberia arriving by circumpolar currents (Graah, 1828; Johansen and Hytteborn, 2001). Recently, Hellmann et al. (2013, 2015), using a large number of driftwood samples from East Greenland, Iceland and Svalbard, showed that species specific wood anatomical characteristics could be used to trace the origin of most driftwood to Siberia. The wood enters the Arctic Ocean through the large boreal river systems, moves out to the sea and freezes into the ice pack (Hellmann et al., 2015). The wood drifts in the ice following Arctic sea surface currents and as thawing occurs the wood is deposited along Arctic coastlines. The rafting of wood has been previously proposed as a mechanism for long distance dispersal of fungi in the Arctic (Stenlid, 2008), but detailed study of the fungi that colonize driftwood and their origin has not yet been carried out. A study of marine fungi in submerged driftwood along the northern coast of Norway was recently completed, showing diverse fungal communities to be present in waterlogged woods (Rämä et al., 2014). Differences in fungal taxa between the eastern and western regions of the northern Norwegian coast were found, and the type of substrate as well as origin of the logs were suggested as key factors that influenced different microbial communities.

Information about fungi occurring in Greenland and Iceland has been presented in checklists of macrofungi which include several taxa of wood colonizing fungi (Cavaliere, 1968; Elburne and Knudsen, 1990; Hallgrimsson and Hauersley, 1995; Jensen, 2003; Hallgrimsson and Eyjolfsdottir, 2004; Borgen et al., 2006). It was thought, however, that many of these fungi were introduced by planted conifers, birch and other trees, as well as imported timber. Although relatively little research has been completed on the organisms responsible for microbial decomposition across the Arctic, there is currently a need to better understand microbial diversity and decomposition in Arctic ecosystems. Fungal activity in the Arctic has been suggested to be exceedingly important to the future of the biosphere (Timling and Taylor, 2012). The Arctic stores large amounts of organic carbon and considerable microbial activity occurs in Arctic soils under snow packs (Sturm et al., 2005; Timling and Taylor, 2012). As climate changes and the Arctic warms, microbial decomposition of organic carbon is expected to release greenhouse gases into the atmosphere that could influence the Earth's climate. Although microbial decay is exceedingly important in this process, the microorganisms responsible for decomposition of organic materials in the Arctic are poorly understood (Timling and Taylor, 2012). A recent study of mummified wood from forests that once grew in the high Arctic of Canada has shown this ancient wood being released onto soil surfaces after glacier retreat. Once on the soil surface, indigenous fungi were found to be important pioneer colonists capable of growing in the exposed woody material and decomposing it (Jurgens et al., 2009). The influx of driftwood into Greenland and Iceland over the past millennia has brought and continues to bring large amounts of woody biomass into the Arctic. This material provides a resource to study Arctic fungi diversity and ecology, as well as to get further insights into their possible origin and to obtain new knowledge on the microbial diversity of the region and how these fungi contribute to ecosystem functioning.

Here we explore the diversity of wood inhabiting fungi in Arctic driftwood from East Greenland and Iceland. We also compare these fungi with those found in driftwood from the Lena Delta in northeast Siberia, the world's largest delta that delivers endless amounts of wood into the Arctic Ocean (Büntgen et al., 2014). A culture-based approach was used to obtain study materials from which rDNA was used for sequencing to identify the fungi obtained. The fungal cultures provide opportunities for more in-depth studies on the taxonomy, physiology and ecology of these fungi.

2. Materials and methods

Driftwood from the supralittoral zone and just above this area along terrestrial coastlines in Scoresbysund and Kulusuk, East Greenland; Westfords north of Holmavik, Eyjafjörður and Grimsey Island, Iceland and the Lena Delta in Siberia was sampled (Table 1, Fig. 1). Eighty logs were sampled (25, 43 and 12 from Greenland, Iceland and Siberia respectively) by cutting wood disks from logs and sampling smaller segments from below the surface of the wood or by removing segments of wood directly from the circumference of the driftwood to a depth of 5–10 cm (Fig. 2). One wood disk or partial wood disk was used per log. Wood samples were placed into separate sterile bags and kept cool until processed. Five subsamples were obtained from each of the log samples and small segments were cut from each subsample using aseptic techniques and incubated on four different culture media: 1.5% Difco malt extract agar (MEA), MEA with 2 ml of lactic acid added after autoclaving, a semi-selective media for Basidiomycota that included 15 g of malt extract, 15 g of agar, 2 g of yeast extract, 0.06 g of Benlate with 0.01 g of streptomycin sulfate, and 2 ml of lactic acid added after autoclaving, and a selective media for the isolation of ophiostomatoid fungi that cause blue stain consisting of MEA amended with 0.01 g cyclohexamide and 0.05 g chloramphenicol added after autoclaving. All ingredients for each media type were added to 1 L of deionized water. These types of media were used because of previous success obtaining diverse taxa in other investigations at terrestrial polar sites (Blanchette et al., 2004, 2010; Arenz and Blanchette, 2009; Arenz and Blanchette, 2011). Incubation was at 20 °C–22 °C since previous studies have shown filamentous fungi from polar environments are primarily psychrotrophs or mesotrophs and can grow above 20 °C (Robinson, 2001; Arenz and Blanchette, 2009; Blanchette et al., 2010). Cultures of fungi were transferred to new individual plates, and pure cultures were obtained.

DNA was isolated from pure cultures grown on malt agar (15 g malt extract, 15 g agar and 1 L deinonized water) using a CTAB extraction procedure. Fungal hyphae from approximately ¼ of a Petri dish were scraped from the surface of an actively growing culture and suspended in 500 μl of cetyltrimethylammonium bromide (CTAB) lysis buffer and glass beads and vortexed for 1 min and centrifuged briefly to aggregate hyphal material. Supernatant was transferred to a new microcentrifuge tube and placed in a hot water bath (65 °C) for 20 min. Following the hot water bath, 500 μl of chloroform/phenol/isoamyl alcohol (25:24:1) was added to each tube and mixed vigorously and centrifuged for 5 min at 15,871 rcf. The supernatant was then removed and transferred to a clean microcentrifuge tube and isopropanol (stored at −20 °C) was added (2/3 the amount of supernatant), gently mixed and incubated at room temperature for 5 min. Tubes were then centrifuged for 7 min at 21,130 rcf and isopropanol was carefully removed. The DNA pellet remaining was washed with 500 μl of 70% ETOH (stored at −20 °C) followed by centrifuging for 3 min at 21,130 rcf after which the ETOH was removed and tubes were left in a sterilized bio-safety cabinet to air dry. DNA was rehydrated with 100 μl of sterile water. The internal transcribed spacer (ITS) region of rDNA was amplified using the primer combination ITS1F/4 (Gardes and Bruns, 1993) via PCR. One μl of DNA template was used in each

Table 1
Collection sites for Arctic driftwood used in this study.

Country	Region	Latitude	Longitude	No. of samples
Greenland	Scoresbysund	70° 30′ N	25° 00′ W	17
	Kulusuk	65° 57′ N	37° 18′ W	8
Iceland	Westfjords	65° 38′ N	21° 38′ W	37
	Grimsey Island	66° 55′ N	18° 00′ W	6
Russia	Lena Delta	72° 31′ N	127° 03′ E	12