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Deception Island, Antarctica, harbors a diverse assemblage of wood decay fungi

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ARTICLE INFO

Article history:
Received 4 October 2016
Received in revised form
21 November 2016
Accepted 22 November 2016
Available online 8 December 2016
Corresponding Editor:
John Dighton

Keywords:
Ascomycota
Basidiomycota
Biodeterioration
Fungal diversity
Historic preservation
Polar biology

ABSTRACT

Very little is known about fungal diversity in Antarctica as compared to other biomes and how these important organisms function in this unusual ecosystem. Perhaps one of the most unusual ecosystems is that of Deception Island; an active volcanic island part of the South Shetland Islands of the Antarctic Peninsula. Here we describe the fungal diversity associated with historic wood from structures on the island, which reveals a diverse fungal assemblage of known wood decay fungi as well as the discovery of undescribed species. The major group of wood decay fungi identified were species of *Cadophora* and as shown in previous studies in other geographic regions of Antarctica, they caused a soft-rot type of decay in the introduced woods. Additionally, unlike other areas of Antarctica that have been studied, filamentous basidiomycetes (*Hypochniciellum* spp. and *Pholiota* spp.) were also identified that have different modes of degradation including brown and white rot. Matches of fungal sequences to known species in temperate regions likely introduced on building materials indicates human influences and volcanic activity have greatly impacted fungal diversity. Lahars (mudslides from volcanic activity) have partially buried many of the structures and the buried environment as well as the moist, warm soils provided conditions conducive for fungal growth that are not found in other regions of Antarctica. The diverse assemblage of decay fungi and different forms of wood decomposition add to the difficulty of conserving wooden structures at these important polar heritage sites.

Introduction

Deception Island, part of the South Shetlands, is a small Antarctic island with unique ecological characteristics, unusual geological features and a rich historical past. The island is an active volcano that has a flooded caldera with narrow entrance to the interior (Fig 1). Early sealers and whalers utilized this geologic feature for protection from the open ocean when they visited the island as early as 1820. Historic wooden structures still exist on the island today and are listed as Historic Sites and Monuments. Hektor whaling station (Norwegian) on Whalers Bay was established in 1911 as a land based operation and numerous factory whaling ships used the harbour in subsequent years. Later, in 1944 following the crash of the whale oil market, the British used the site and added a wooden building called Base B. Following that, the British Antarctic Survey (BAS) used the site as a base for aerial surveys of the Peninsula, at which time a runway was made

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http://dx.doi.org/10.1016/j.funbio.2016.11.009

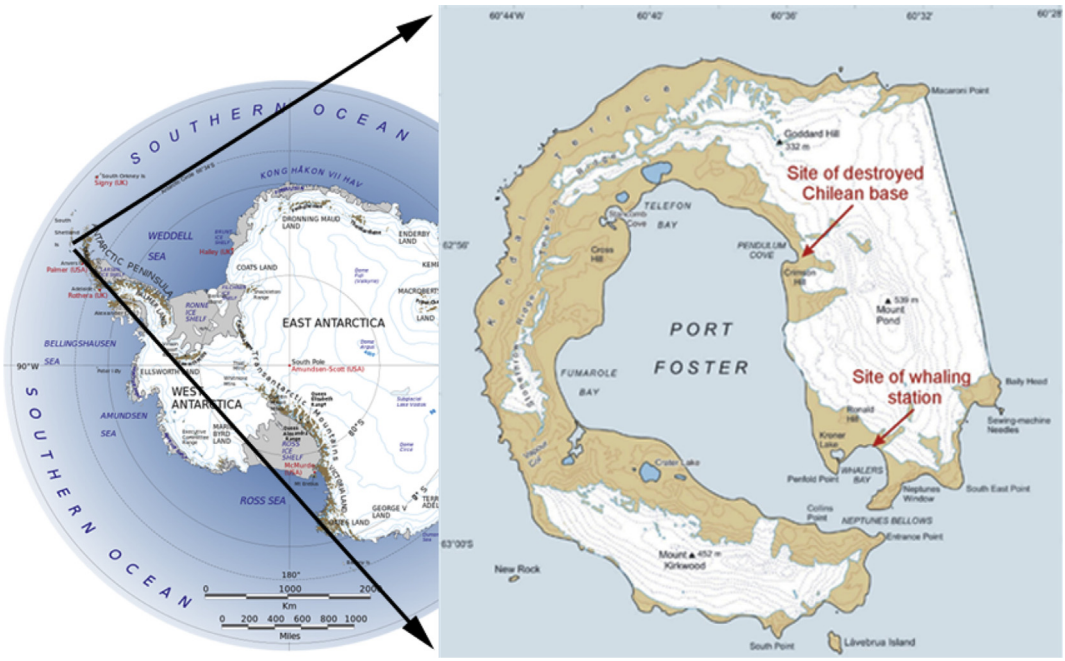

Fig 1 – Map of Antarctica (left) and Deception Island (right) showing the sites where samples were collected.

and airplane hangar built. Many buildings, structures, and remnants from the whaling station and later activities on the island are still present today in varying stages of deterioration and are protected as an Antarctic Historic Site or Monument (HSM-71), under the Antarctic Treaty.

Pendulum Cove, approximately 4 km north of Whalers Bay is the location of an additional historic site, the Chilean research base, Presidente Pedro Aguirre Cerda Station (Fig 1). This station was built in 1955 and used until 1967 when it was destroyed by volcanic activity. While very little of the station is remaining, the site and remaining structures are protected as an Antarctic Historic Site and Monument (HSM-76).

The geological history of the Island includes an eruption of the volcano approximately 10 000 years ago that created Port Foster and the interior bay (Olsacher 1956). Numerous other eruptions have occurred, including several during the past two centuries that have changed the topography of the island significantly. Subsequently, ash has covered glaciers, which occupy 57 % of the island. Many areas on the island have geothermal activity that produce fumaroles, heated soils, and steaming beaches. These unusual environmental conditions in the polar environment provide a unique opportunity for microbial activity to take place that is not seen in other parts of Antarctica. Investigations on the island also provide an opportunity for comparative analysis of microbial diversity with other areas of Antarctica where wood and other introduced nutrient sources have been deposited, such as the historic expedition huts of the Ross Sea and historic structures on the Antarctic Peninsula. Compared to temperate biomes, very little is known about fungal diversity and decomposition in polar environments. However, previous research on fungal diversity and degradation of wooden structures and artifacts in Antarctica has shown that fungi are important decomposers despite the extreme environment (Held *et al.* 2005; Arenz *et al.* 2006; Duncan *et al.* 2006; Held *et al.* 2006; Arenz & Blanchette 2009; Arenz *et al.* 2010; Blanchette *et al.* 2010). The only type of wood decay previously found occurring in Antarctica has been classified as a soft rot caused by Ascomycota and occurs primarily in wood that is in contact with soil on Ross Island (Blanchette *et al.* 2004; Arenz *et al.* 2006; Held *et al.* 2006; Blanchette *et al.* 2010) and on the Antarctica Peninsula (Arenz & Blanchette 2009). The common types of decay in temperate and tropical areas, brown and white rot caused by basidiomycetes, have not previously been found.

The study objectives were to identify fungi associated with and causing decay of historic wood on Deception Island and to further understand the microbial diversity and decomposition processes that exist in this unusual polar environment where soil temperatures range from freezing to 90 °C. This work also provides a unique opportunity to investigate alien fungi presumably introduced on building materials into a polar environment. In addition to advancing knowledge of fungal biology and ecology in Antarctica, the outcomes of this study will provide needed information on the fungi causing decay in historic wooden structures and will benefit conservation strategies to protect these valuable cultural resources.

Materials and methods

Samples were collected from wooden structures and artifacts at Whalers Bay and Pendulum Cove, Deception Island (62°57′S, 60°38′W) that appeared to be decayed and in various stages of decomposition. Small segments (approximately 1 mm × 0.5 mm) of wood were collected and placed in sterile plastic bags and kept cool while transporting them back to the laboratory. Under sterile conditions in the laboratory, the wood samples were cut and placed onto the following types of

growth media: malt extract agar (1.5 % Difco malt extract), malt extract agar (1.5 %) amended with 0.5 g of streptomycin sulphate and a semi-selective medium used to culture basidiomycetes (2.0 % Difco malt extract, 0.2 % yeast extract, 0.006 % benlate with 0.2 % lactic acid and 0.001 % streptomycin sulphate added after autoclaving) (Worrall 1991). Isolations were made from 188 samples from Whalers bay (Hektor whaling station, Base B, and BAS hangar) and 30 from the Chilean base. Isolates were cultured at 8 and 20 °C for several weeks after which transfers were made to another plate to obtain pure cultures. DNA was extracted from fungal cultures using an adapted chloroform procedure (Arenz & Blanchette 2011). The internal transcribed spacer (ITS) region of ribosomal DNA was targeted for PCR amplification with the primers ITS1 + ITS4 and LROR + LR5 for large subunit amplification (White *et al.* 1990). PCR amplifications were done using Amplitaq Gold PCR Master-mix (Applied Biosystems, Foster City, CA) and 1 μl of template DNA using the following parameters: 94 °C for 5 min, 35 cycles of 94 °C for 1 min, 50 °C for 1 min, 72 °C for 1 min, and a final extension step of 5 min at 72 °C. PCR amplicons were visualized on a 1 % agarose gel using SYBR green 1 (Life Technologies, Grand Island, NY) prestain and a Dark Reader DR45 transilluminator (Clare Chemical Research, Denver, CO). Primers used for PCR were used for sequencing reactions on a ABI Prism 377 automated DNA sequencer using a ABI PRISM Dye Terminator Cycle Sequencing Ready reaction kit (Applied Biosystems).

Consensus sequences were assembled using Geneious 9.0 (Kearse *et al.* 2012) and compared to those in GenBank using BLASTn for identification. Multiple sequence alignments were done using the MAFFT v7.222 (Katoh & Standley 2013) alignment plugin in Geneious R9. Phylogenetic trees were constructed using the MrBayes 3.2.6 plugin (Huelsenbeck & Ronquist 2001) in Geneious R9 where 1 100 000 MCMC generations were used with a sampling frequency every 200 generations and burn-in length of 100 000. The appropriate substitution model was selected using jModelTest 2.1.10 (Darriba *et al.* 2012) according to Corrected Akaike Information Criterion (AICc).

Decay studies using fungal cultures isolated from samples were carried out in microcosms over a 16 week period. Isolates were selected after sequencing and identification from BLAST searches. Glass filters (55 mm) were sterilized by autoclaving and placed in 100 mm petri plates containing media. A malt yeast agar (2 % malt extract agar, 0.2 % yeast extract) was used for the basidiomycete cultures and a minimal selective media for soft rot fungi (Worrall *et al.* 1991) was used for the Ascomycota cultures. Wafers measuring 1.5 × 1.5 × 0.3 cm were cut from sound birch (*Betula* sp.) and pine (*Pinus* sp.) wood blocks and dried at 105 °C for 24 h and weighed to determine dry weight. Wafers were then hydrated and sterilized by autoclaving before placing on glass filters in decay microcosms. Plugs (0.4 mm) were transferred from growing fungal cultures and placed on the medium surface adjacent to the filter. After a 16 week incubation period, 10 wafers from each treatment were removed and oven dried to determine biomass loss. Two wafers from each treatment were not oven dried and used for micromorphological study.

The methods for the decay study using Ascomycota were the same as the Basidiomycota study but a different medium was used. Instead of malt yeast agar, a minimal media consisting of 1.5 g NH_4NO_3, 2.5 g KH_2PO_4, 2 g K_2HPO_4, 1 g $MgSO_4{-}7H_2O$, 2.5 g glucose and 0.1 g thiamine per litre was used (Abrams 1948; Worrall *et al.* 1991). In addition, instead of using water to hydrate wafers, a solution of same ingredients as the medium exclusive of the agar was used. The incubation period was also 16 weeks.

Wood samples for fungal decay observations were prepared for scanning electron microscopy (SEM) by infiltrating with a 25 % TBS™ Tissue Freezing Medium™ (Triangle Biomedical Sciences, Durham, NC, U.S.A.) under vacuum followed by mounting on brass stubs, freezing at −20 °C and sectioning in a cryostat freezing microtome. Samples were cut transversely to prepare a clean surface for examination. Cut samples were thawed and rinsed several times in water, air dried before mounting on aluminium stubs with carbon tape and coated with gold using a sputter coater. Samples were viewed using a Hitachi S3500N scanning electron microscope to determine characteristics of decay and signatures of fungal colonization in the cell wall structure.

Results

Fungal isolation attempts from samples collected at Deception Island yielded 326 isolates from 218 samples. The majority (79 %) of the isolates belonged to the Ascomycota and were comprised of 53 taxa, followed by 11 taxa (24 %) in the Basidiomycota and four Zygomycota taxa (6 %). Some of the most relatively abundant Ascomycota were *Cadophora* (29 %), *Phialocephala* (10 %), *Lecythophora*—*Coniochaeta* (9 %), *Cosmospora* (8 %), and *Phoma* (8 %). Within the *Cadophora* group, several species were found including *Cadophora fastigiata/melinii* (55 %), *Cadophora malorum* (22 %), *Cadophora luteo-olivaceae* (9 %), and undescribed species *C.* sp. *NH1-2* (13 %) and *C.* sp. 5R24-1 (2 %). Among the most relatively abundant genera in the Basidiomycota were *Hypochniciellum* (55 %), *Pholiota* (18 %), *Cerinosterus* (11 %), and *Tulasnella* (8 %). In addition, there were 15 taxa (ten Ascomycota, four Basidiomycota, and one Zygomycota) that matched at or below 97 % sequence identity with described taxa. LSU sequences were used in addition to ITS sequences for *Hypochniciellum* isolates because the nearest percent sequence identity for ITS BLAST searches was a 85 % match to *Amyloathelia crassiuscula*. However, BLAST searches using LSU sequence data showed a 99 % sequence identity to *Hypochniciellum molle* for which ITS sequence is not in GenBank. Due to the fact that the LSU region does not resolve species effectively and that reference sequences of the ITS region for this or other *Hypochniciellum* species were unavailable, the species of the isolate we cultured remains uncertain. However, phylogenetic analysis of LSU sequences reveal the isolates most closely resemble *H. molle* in this gene region (Fig 2). Analysis of the ITS gene region from *Pholiota* spp. sequences form several clades that are different from other known species. One clade is comprised of isolates exclusively from the Chilean base that group with *Pholiota multicingulata*. The second clade has both an isolate from the Chilean

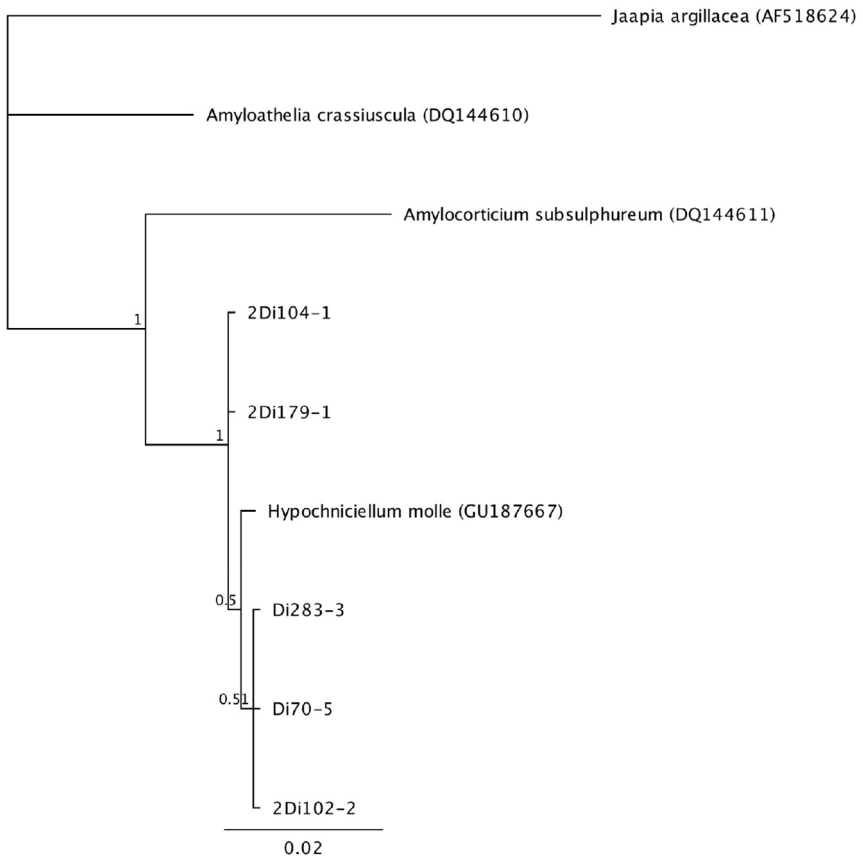

Fig 2 – Bayesian tree constructed using LSU Basidiomycota sequences showing *Hypochniciellum* spp. and related genera. GenBank accession numbers follow known isolates. Posterior probabilities are shown at branches. *Jaapia argillacea* was used as the outgroup. Scale bar = substitutions per site.

base (2Di94-5) in addition to Whalers Bay (isolated from Biscoe house, Di267-2). A second isolate from Biscoe house, Whalers Bay (2Di41-2) does not group with any other isolates from Deception Island or known isolates in GenBank (Fig 3).

Some of the most common genera among all Ascomycota and Basidiomycota isolated were *Cadophora* (20 %), *Hypochniciellum* (13 %), *Phialocephala* (7 %), *Cosmospora* (5 %), *Phoma* (5 %), *Pholiota* (4 %), *Lecythophora/Coniochaeta* (6 %), and *Cerinosterus* (3 %). Most of the taxa isolated from the Chilean base samples (separated by approx. 4 km) were also isolated from Whalers Bay, with the exception of *Arthrobotrys superba*, *Coprinellus micaceus*, *Helotiales* sp., *Sistotrema brinkmannii*, and Sordariomycetes sp. (Table 1). However, many that were isolated from Whalers Bay were not isolated from the Chilean base.

Analysis of historic wood at these sites indicated that decay fungi are active and extensive decay was present in many of the historic woods, which consisted of a combination of pine (*Pinus* sp.) and spruce (*Picea* sp.). Much of the wood that is near the soil or buried in the soil is severely degraded. However, significant decay is also occurring in many areas well above the ground (Fig 4). This occurred extensively on the north side of the Biscoe House and also in the wooden boats on Whalers Bay beach. Microscopic observations of decayed wood samples indicated that three major types of wood decay were found in samples taken at Whalers Bay and Pendulum Cove: white, brown, and soft rot. Soft and brown rots were observed at both locations, while white rot decay was identified in wood samples from only at the Chilean base site and in all cases it was found in wood just beneath the soil surface.

Laboratory decay studies showed substrate weight losses for *Pholiota* sp. 131-2, *Pholiota* sp. 80-3, *Jaapia argillacea*, *Coniophora puteana*, *Hypochniciellum* sp. Di283-3, *Hypochniciellum* sp. Di17-1 ranged from 14 to 32 % in pine and 34 to 64 % in birch, while *Cerinosterus luteoalbus* did not show weight loss (Fig 5). Scanning electron microscopy of decayed samples showed that *Pholiota* spp. caused a white rot, degrading all cell wall material (Fig 6). The decay caused by *J. argillacea* is unusual because it appears to cause a white rot type of decay in pine and more closely resembles a brown rot decay pattern in birch. *Hypochniciellum* spp. and *C. puteana* cause a brown rot type of decay with decay patterns similar to other brown rot fungi found in temperate areas that degrade cellulose and hemicellulose (Fig 6).

Laboratory decay studies showed mass losses for *Phialocephala dimorphospora*, *Lecythophora hoffmannii*, *Lecythophora* sp., *Mollisia minutella*, *Mollisia cinera*, *Phoma herbarum*, *Cosmospora vilior* on birch (*Betula* sp.) ranged from 1.8 to 21.2 % and on pine (*Pinus* sp.) from 1.8 to 2.6 % (Fig 7). Scanning electron microscopy analysis revealed unique decay processes in four of the species tested, excluding *C. vilior*, for which no

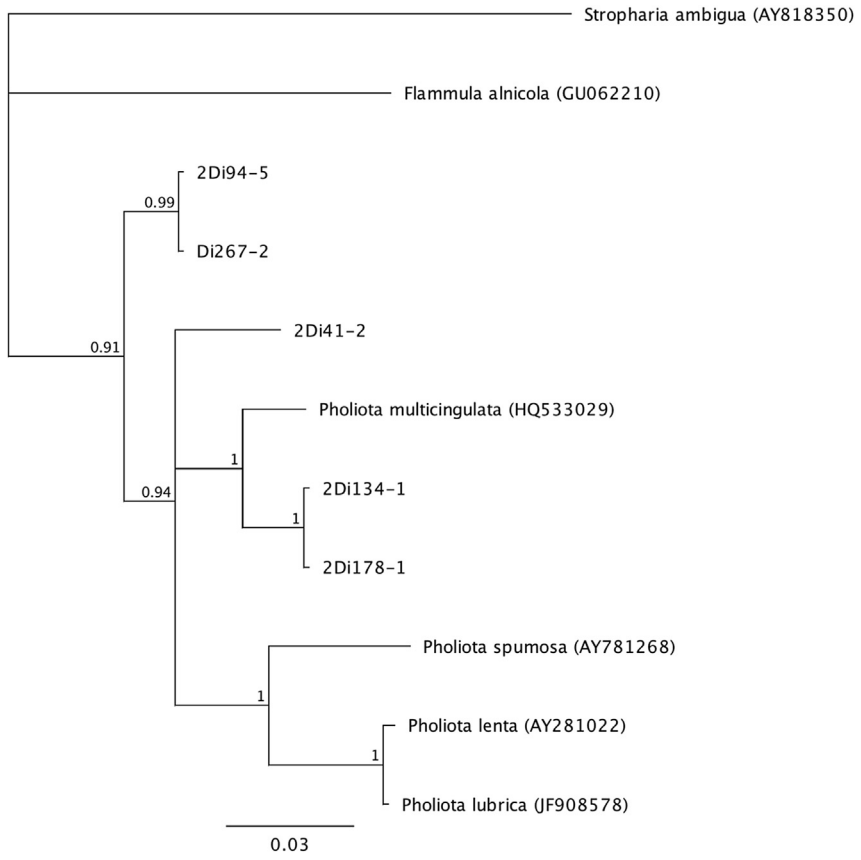

Fig 3 – Bayesian tree constructed using ITS sequences of *Pholiota* spp. GenBank accession numbers are in parentheses. Posterior probability values are shown at nodes. *Stropharia ambigua* was used as the outgroup. Scale bar = substitutions per site.

Table 1 – List of taxa isolated in this study including the best BLAST match with percent identity and overall nucleotide overlap of the ITS gene region.

Best BLASTn match	Percent identity	Overlap	# of samples		GenBank accession #
			Whalers Bay	Chilean station	
Ascomycota					
Acremonium atrogriseum (AB540569)	99	515/518	6	–	KC514842
Antarctomyces psychrotrophicus (AJ133431)	99	465/469	2	–	KC514843
Arthrobotrys superba (EF445988)	98	539/547	–	1	KC514844
Arthrinium sacchari (EF076712)	95	466/491	1	–	KC514845
Ascocoryne solitaria (HM152545)	100	520/520	1	–	KC514846
Ascomycete sp. HK-S209 (AM084476)	99	459/461	1	–	KC514847
Ascomycota sp. PV Wi 0b (EU740392)	99	447/451	5	–	KC514848
Cadophora fastigiata (AY781232)	99	495/496	18	3	KC514850
Cadophora luteo-olivaceae (GU212374)	100	522/522	6	–	KC514851
Cadophora malorum (GU212434)	100	512/512	12	2	KC514852
Cadophora melinii (JN689950)	99	461/465	14	–	KC589024
Cadophora sp. NH1-2 (AY371513)	100	468/468	6	2	KC514853
Cadophora sp. 5R24-1 (DQ317330)	100	468/468	1	–	KC514854
Cladophialophora minutissima (EF016384)	99	488/490	1	–	KC514855
Coniochaeta ligniaria (AY198390)	99	532/535	2	7	KC514856
Cosmospora vilior (GU726751)	97	506/524	15	2	KC514857
Exophiala xenobiotica (KC311483)	100	516/516	1	–	KC514859
Fungal endophyte sp. ECD-2008 (EU686037)	99	476/480	2	–	KC514860
Geomyces sp. JZ-174 (HQ637306)	99	520/523	6	1	KC514864
Helotiales sp. NK251 (FR846472)	96	413/432	–	3	KC514865

(*continued on next page*)

Table 1 – (*continued*)

Best BLASTn match	Percent identity	Overlap	# of samples		GenBank accession #
			Whalers Bay	Chilean station	
Helotiales sp. PIMO_102 (HQ845745)	99	466/469	1	–	KC514866
Helotiales sp. MMW-2013a (JX001640)	100	443/443	1	–	KC514870
Holwaya mucida (DQ257357)	95	496/517	2	–	KC514867
Hormonema dematioides (AY253451)	100	581/581	1	–	KC514868
Hyaloscypha aureliella (EU940229)	99	352/358	1	–	KC514869
Lecythophora hoffmannii (AY805566)	100	456/456	9	2	KC514871
Leptodontidium elatius (AY805569)	99	470/472	3	–	KC514872
Neostagonospora elegiae (KF251164)	98	549/563	1	–	KC514877
Mollisia cinerea (AY259135)	97	515/531	1	–	KC514849
Mollisia sp. aurim650 (DQ069036)	98	482/491	4	2	KC514873
Oidiodendron truncatum (AF062809)	99	513/522	2	–	KC514875
Phaeosphaeria sp. (HQ324780)	97	492/510	2	–	KC514876
Phialocephala dimorphospora (AF486121)	99	449/455	22	1	KC514878
Phialophora lagerbergii (AF083197)	99	474/478	2	–	KC514879
Phoma cladoniicola (JQ238623)	96	530/554	3	–	KC514883
Phoma herbarum (AY293800)	100	501/501	8	–	KC514880
Phoma sp. 2 (AF218789)	99	565/566	9	–	KC514881
Pochonia sp. LS-2013 (KC626045)	100	525/526	2	–	KC514858
Pseudeurotium sp. olrim976 (AY787729)	100	432/432	2	–	KC514882
Pyrenopeziza sp. KUS-F52417 (JN033413)	97	444/459	2	–	KC514874
Sordariomycetes sp. (JQ761957)	100	467/467	–	2	KC514861
Thelebolus microsporus (DQ028268)	99	451/452	2	–	KC514885
Ulocladium atrum (AF229486)	100	480/480	1	–	KC514886
Uncultured *Clathrosphaerina* clone (HQ212333)	97	506/519	1	1	KC514887
Uncultured *Helotiales* (FN565271)	98	523/536	1	2	KC514888
Uncultured *Lachnum* clone 6_h03 (HQ211775)	99	512/519	2	–	KC514889
Uncultured Phaeosphaeriaceae (JF449593)	100	523/523	1	–	KC514884
Uncultured Sordariomycetes clone (FJ475724)	98	499/512	1	–	KC514890
Uncultured Thelebolales clone (GU910625)	99	521/526	1	–	KC514892
Xenopolyscytalum pinea (HQ599581)	99	470/474	1	–	KC514893
Xylariales sp. (KP297401)	95	443/464	7	–	KC514891
Basidiomycota					
Hypochniciellum molle (GU187667)[a]	99	866/867	40	4	KC514894
Cerinosterus luteoalbus (AY618667)	100	446/446	7	2	KC514894
Coniophora puteana (AM946631)	100	1295/1295	1	–	KC514900
Coprinellus micaceus (HM240519)	96	619/647	–	1	KC514901
Hyphodontia radula (GQ411525)	99	561/564	1	–	KC514902
Hypochnicium sp. WY-DT1 (KP980549)	97	509/523	1	–	KC514903
Jaapia argillacea (GU187524)	98	560/566	1	–	KC514904
Pholiota multicingulata (HQ533029)	95	628/660	4	9	KC514905
Pholiota multicingulata (HQ533029)	97	860/863		1	KC514906
Postia pelliculosa (JX090101)	99	558/560	1	–	KC514907
Sistotrema brinkmannii (DQ899094)	99	568/569	–	1	KC514908
Tulasnella violea (DQ457643)	99	485/487	6	–	KC514909
Zygomycota					
Mortierella alpina (FJ161918)	100	595/595	10	7	KC514910
Mortierella parvispora (EU484279)	100	567/567	1	–	KC514911
Mortierella amoeboidea (GU559984)	99	531/532	2	3	KC514912
Mortierella sarnyensis (FJ161927)	97	460/477	1	–	KC514913

a Large subunit sequences were used for these isolates because ITS sequences were not in GenBank for this species.

decay was evident. *Lecythophora* sp., *M. minutella*, and *P. herbarum* caused a Type 2 soft rot decay, in which the secondary wall layers of the wood cells were eroded, leaving only the middle lamella remaining. *L. hoffmannii*, *P. dimorphospora*, and *M. cinera* form cavities in the S_2 region of the cell wall, indicative of a Type 1 soft rot decay. These cavities were located within the secondary wall and the middle lamella was not affected (Fig 8).

Discussion

Basidiomycota component

A diverse fungal assemblage was found associated with wood decomposing the historic structures and artifacts on Deception Island. This includes fungi in the Basidiomycota that

Fig 4 – The historic structures on Deception Island. Upper left; several structures showing buildings in various stages of decomposition. Upper right; the side of the Biscoe House, a building at Whalers Bay on Deception Island, showing extensive decay of wall boards and other timbers. Lower left; remnants of a structure that served as a dispensary/store that has been severely damaged by volcanic activity. Lower right; the remains of what was once the Chilean research base, Presidente Pedro Aguirre Cerda Station.

cause a white and brown rot type of wood decay. The occurrence of white and brown rot fungi in Antarctica is quite unique and has not been previously reported on continental or maritime Antarctica. However, other studies have reported decay attributed to saprotrophic Basidiomycota from sub-Antarctic Islands (Pegler 1980; Smith 1984). Fungi isolated from Deception Island sites were, 79 % Ascomycota, 15 % Basidiomycota, and 6 % Zygomycota as compared to 82 % Ascomycota, 15 % Basidiomycota, and 3 % Zygomycota found on the Antarctic Peninsula (Arenz & Blanchette 2009) and 75 % Ascomycota, 21 % Basidiomycota, and 1 % Zygomycota at Ross Island (Arenz *et al.* 2006). While the distribution of phyla represented are generally consistent among these polar locations, there are important differences. Most significantly, nearly all of the Basidiomycota isolated from the previous studies in Antarctica were comprised of yeasts whereas the Basidiomycota from Deception Island were filamentous wood decay fungi. In addition, Deception Island lies in an area that is considered maritime Antarctic, which is characterized as having a cold, moist climate and mean monthly air temperatures of >0 °C for 3–4 months of the year (Aleksandrova 1980; Smith 1984) and 560 mm of precipitation per year. While Ross Island has a colder, drier climate where there are no months with the average temperature >0 °C and only 190 mm of precipitation per year. Pegler *et al.* (1980) reported *Trametes versicolor* (which causes a white rot type of decay) on wood brought to South Georgia that was used in the whaling station there. Since the wood was introduced, it is likely that the fungus was brought in with the wood, and this fungus is not endemic. However, other decomposer basidiomycetes have been found that presumably exist naturally in bryophyte and grass ecosystems. Smith (1994) reported 37 Basidiomycota on South Georgia including species of *Collybia*, *Galerina*, *Omphalina*, and *Coprinus* associated with plant litter.

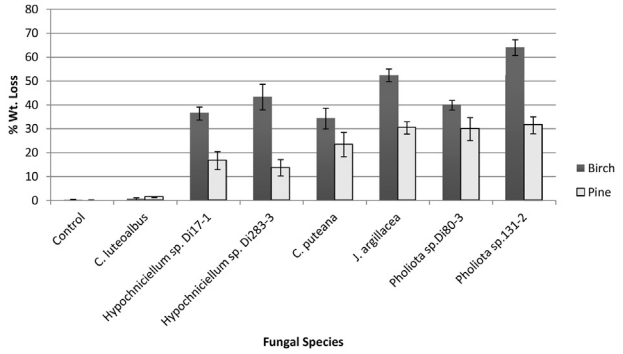

Fig 5 – Weight losses of birch and pine wood wafers after decay in the laboratory by species of Basidiomycota isolated from Deception Island, Antarctica.

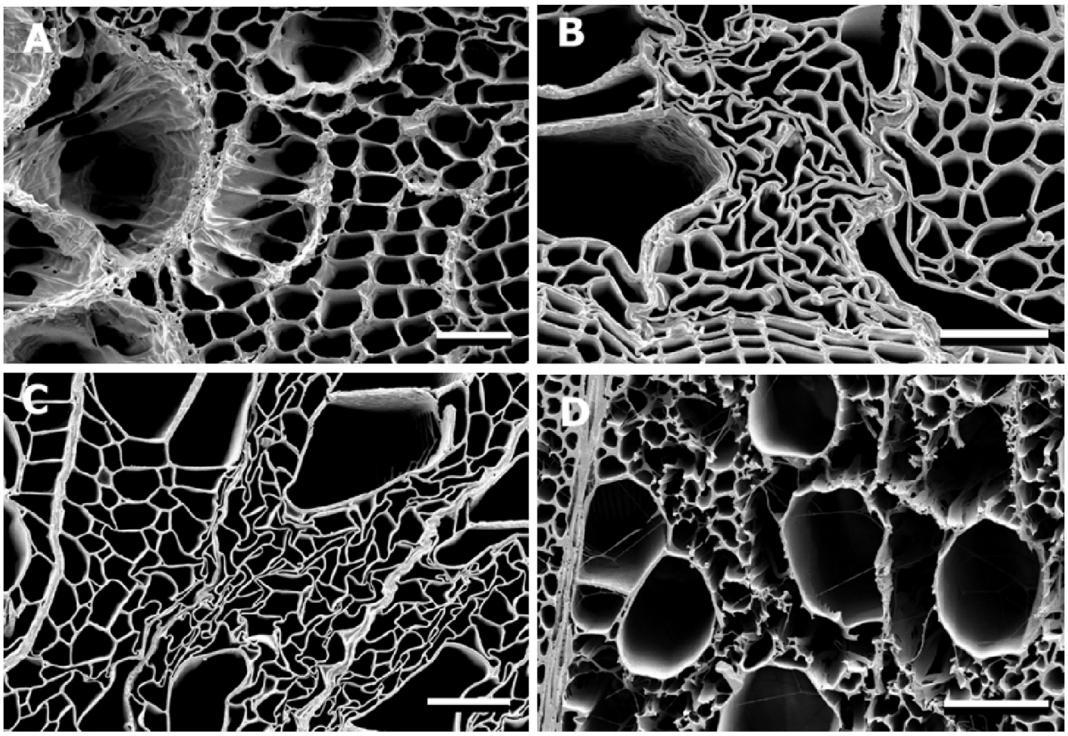

Fig 6 – Scanning electron micrographs of transverse sections of samples from the Basidiomycota decay study showing decay patterns produced by tested fungal strains. (A) Pine wood decayed by *Jaapia argillacea* showing complete disintegration of the cell walls characteristic of a white rot (bar = 125 μm). (B) Birch wood decayed by *Jaapia argillacea* showing alteration of the cell wall and loss of cell structure (bar = 50 μm). (C) *Hypochniciellum* sp. causing a brown rot on birch wafers showing fibre cell walls that have been weakened and collapsed from the loss of cellulose (bar = 100 μm). (D) Typical white rot decay occurring on birch caused by *Pholiota* sp. showing all cell wall layers attacked (bar = 50 μm).

Omphalina antarctica, found on Deception Island, was the first described Basidiomycota from maritime Antarctica and was associated with mosses (Singer 1957). In temperate and some tropical areas, filamentous decomposer Basidiomycota are the most common types of decay fungi found and in those biomes the Basidiomycota out compete and exclude soft rot fungi (Rayner & Boddy 1988). At Deception Island, conditions suitable for growth of Basidiomycota may be abated enough by the extreme environment to allow soft rot fungi to compete for the same resources.

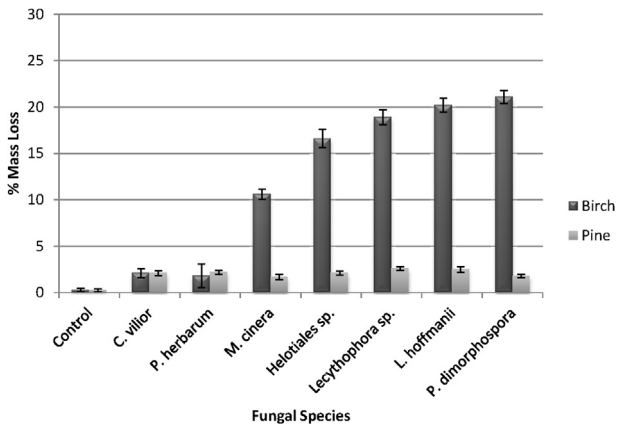

Fig 7 – Weight losses in birch and pine wood wafers following 16 weeks of decay in the laboratory using various DSE fungi isolated from Deception Island, Antarctica.

The dominant species of Basidiomycota isolated from samples in this study is a species of the brown rot fungus, *Hypochniciellum* sp. Arenz & Blanchette (2009) also isolated a similar fungus (referred to as fungal species BB1) from wood at Wordie House, another historic site on Winter Island on the Antarctic Peninsula. Fruiting bodies of this species were not observed in any areas where samples were taken. Mattsson *et al.* (2010) showed that *Hypochniciellum molle* was the dominant decay fungus identified in wood from structures on the Arctic archipelago Svalbard. It has also been reported as causing deterioration in buildings in Norway and Germany (Alfredsen *et al.* 2005; Schmidt & Huckfeldt 2011), on driftwood in Iceland (Hallgrimsson & Hauerslev 1995) and sporadically distributed in Italy (Bernicchia *et al.* 2008). It appears that this fungus is adapted to cold environments and may play an important role in nutrient cycling in many Polar Regions. An adaptive strategy of *H. molle* in cold climates may be the production of thick walled chlamydospores which likely aid in dispersal and survival. Its noted occurrence in Norway suggests the fungus was introduced from Norway to Deception Island since much of the lumber used to build the original Norwegian Hektor whaling station originated from Norway. Microcosm studies showed that this fungus causes a brown rot and extensive biomass can be degraded during relatively short laboratory incubation periods. With the abundance of

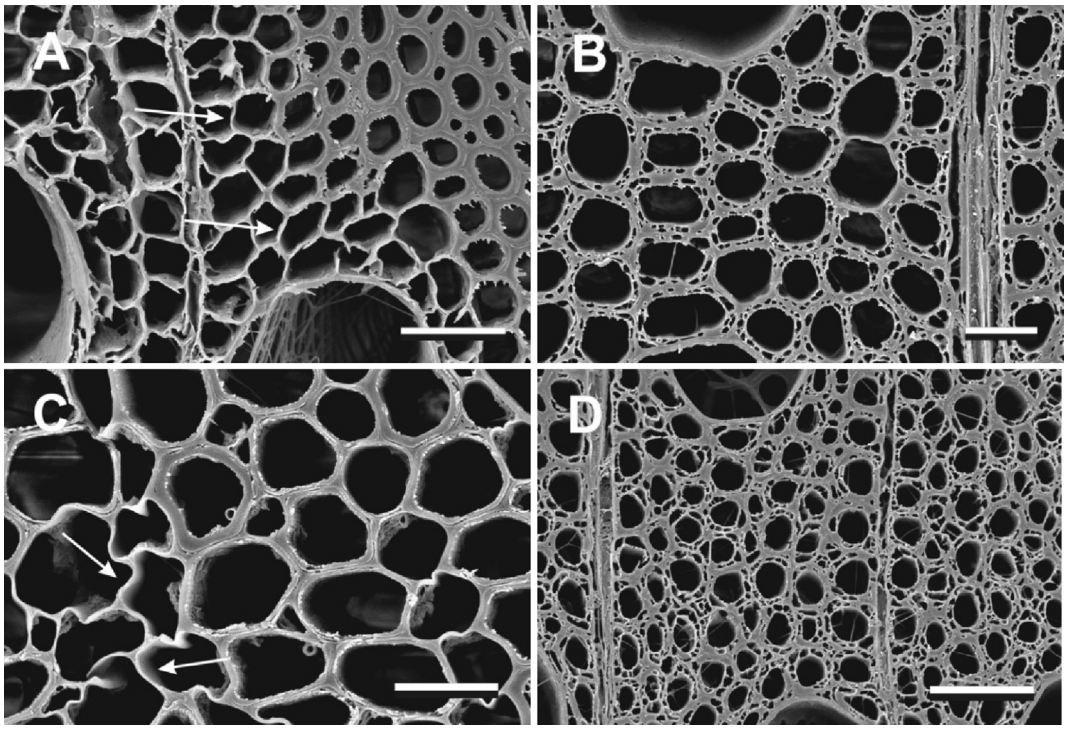

Fig 8 – Scanning electron micrographs of transverse sections from historic wood showing decay patters of various DSE related fungi after growing on wood wafers (birch) in a microcosm decay experiment. (A) An example of a Type 2 soft rot decay where cell walls are eroded leaving the middle lamella intact (arrows) caused by *Lecythophora* sp. (bar = 25 μm). (B) Type 1 soft rot cavities formed in the S2 layer of the secondary wall caused by *Lecythophora hoffmanii* (bar = 25 μm). (C) Type 2 soft rot caused by *Phoma herbarum* (bar = 25 μm). Arrows indicate areas where the secondary cell has been eroded to the middle lamella. (D) *Phialocephala dimorphospora* causing a Type 1 soft rot, showing numerous cavities in cell walls (bar = 50 μm).

brown rot found at Deception Island and from the frequency with which this fungus was isolated, our study suggests that this fungus is a major cause of the brown rot decay taking place on the Island.

Fruiting of several other Basidiomycota (*Pholiota* spp. and *Omphalina* spp.) have been previously reported on Deception Island (Singer 1967), which indicates that conditions can be conducive for some Basidiomycota to complete their life cycle. Singer (1967) described a *Pholiota* sp. fruiting body growing on one of the half buried wooden boats at the beach in Whalers Bay. This area is adjacent to thermally heated soil and water, which may have contributed to conditions favourable for fruiting. No fruiting bodies were observed during our field events to Deception Island for these studies. Based on past observations of fruiting bodies, it is interesting that *Pholiota* spp. was infrequent from samples in Whalers Bay, but was dominant at the Chilean base. Likely, this fungus was also introduced to Deception Island with building materials for the Chilean base. Its activity strictly below the soil surface indicates that the below ground conditions are conducive on the island for continued fungal growth. The phylogenetic analysis reported here suggests three different species of *Pholiota* are present which indicates this fungus may have been introduced several different times.

Other Basidiomycota decay fungi that were isolated matched fungi that are commonly found in temperate regions. *Hypochnicium* sp. and *Hyphodontia radula* are known to cause a white rot type of decay (Gilbertson *et al.* 1975; Larsson *et al.* 2006), *Coniophora puteana* and *Postia pelliculosa* are both brown rot fungi that belong to genera that cause significant problems in wooden structures and are important decomposer fungi in temperate regions. These species were each isolated from only one sample and do not appear to be prevalent on Deception Island. *Tulasnella violea* was also isolated infrequently and is a cosmopolitan genus found in many temperate areas that has saprotrophic and mycorrhizal characteristics (Preussing *et al.* 2010).

Once thought to be a species complex, a recent study demonstrated that the corticioid genus *Jaapia* is in fact comprised of two species; *Jaapia argillacea* and *Jaapia ochroleuca* (Telleria *et al.* 2015). *Jaapia argillacea*, the species isolated at Deception Island, has a wide distribution in Europe but is also considered a rare species (Nannfeldt & Eriksson 1953). As with the other Basidiomycota that have been isolated from the wood at Deception Island, they possibly were introduced with the wooden materials brought to the island. However, the rarity of *J. argillacea* in Europe suggests that its introduction from Europe may be unlikely and additional investigation on the distribution of *Jaapia* may resolve its origin. The wood decay produced by *J. argillacea* in laboratory decay studies reveals an unusual pattern. Observations from scanning electron microscopy, shows a decay pattern in pine that resembles the characteristics of a white rot and in the birch wood the decay appears different and resembles that of a brown rot. It is

uncharacteristic for a single fungal species to cause both a white and brown rot. However, a recent study involving genome analysis suggests that the white and brown rot dichotomy may not be as delineated as previously thought (Riley *et al.* 2014). In this study, *J. argillacea* was one of the fungi tested and it showed that it has CAZymes typical of a white rot but lacks class II peroxidases which is a characteristic found among brown rot fungi. Additional studies, including chemical analyses of degraded cell wall components, are needed to determine the different wood constituents being metabolized by this fungus.

Ascomycota component

Cadophora species were the most commonly isolated fungi from wood at Deception Island. The relative abundance of *Cadophora* spp. obtained in this study was similar to the amount found at other Antarctic Peninsula and Ross Island sites where other investigations studied fungi from historic wooden structures. The difference at Deception Island, however, is that the diversity of species of *Cadophora* is greater than other Antarctic locations and several possible new species were isolated. This supports previous research showing the predominance of *Cadophora* spp. functioning as important decomposer fungi in polar environments (Blanchette *et al.* 2004; Arenz *et al.* 2006; Held *et al.* 2006; Arenz & Blanchette 2009; Arenz *et al.* 2010; Blanchette *et al.* 2010; Farrell *et al.* 2011). While *Cadophora malorum*, *Cadophora fastigiata*, and *Cadophora luteo-olivaceae* have been identified in other biomes, their identification in this study points to the proclivity of this group to thrive in polar environments especially, when wood is present as a primary nutrient source. Most of the known *Cadophora* species identified (*C. fastigiata* (also referred to as *Cadophora melinii*), *C. luteo-olivaceae*, and *C. malorum*) in this study have been shown to cause a Type 1 soft rot decay in wood, in which fungal hyphae create cavities in the S_2 layer of the wood cell wall by enzymatic degradation. Based on preliminary observations, it appears that there are differences in size of cavities produced by the different species and sub groups within the Type 1 soft rot group. More precise measurements are needed to characterize the different forms of soft rot found and whether this may be attributed to aggressiveness of different species. Further research is needed with several strains of each species to confirm this. Some soft rot fungi also cause another form of degradation referred to as Type 2 in which the cell walls are eroded from the inside of the lumen toward the middle lamella.

A large component of fungi isolated from wood at Deception Island was similar to genera that have been classified by other investigators as dark septate endophytes (DSE) associated with plant roots. These include species of *Coniochaeta*, *Lecythophora*, *Leptodontium*, *Mollisia*, *Phialocephala*, and *Phoma*. DSE's are generally categorized as endophytic fungi having dematiaceous septate hyphae and are restricted to plant roots. They are primarily Ascomycota, have a wide host range, and have been identified in a many ecosystems ranging from polar to tropical regions (Jumpponen & Trappe 1998; Jumpponen 2001). The broad geographic and host range for these fungi suggests that they have low host specificity (Porras-Alfaro & Bayman 2011). Indeed, a mutualistic relationship has been identified between the much studied DSE *Phialocephala fortinii* in Pinaceae, Cyperaceae, Ericaceae, Salicaceae, and Rosaceae (Jumpponen 2001) and they have been identified in roots of nearly 600 plant species. Unlike true mycorrhizal fungi, DSE frequency in roots does not decrease with an increase in latitude (Upson *et al.* 2008). Instead, a high incidence of DSE have been found in roots of plants in numerous polar regions that have been studied (Christie & Nicolson 1983; Treu *et al.* 1996; Laursen *et al.* 1997; Ormsby *et al.* 2007; Upson *et al.* 2008) and appear to be the most widespread root-fungal association at these sites (Newsham *et al.* 2009). The abundance of DSE in high stress polar environments has led to the hypothesis that they confer tolerance to adverse conditions and lead some to hypothesize that they may be more important to healthy ecophysiology functioning in plants than previously realized (Rodriguez *et al.* 2009). The delineation of DSE species is not well defined, either ecologically or taxonomically, and their function has not been well studied. They are most commonly isolated from healthy plants but differ from mycorrhizal fungi in that they do not form arbuscules or coils in host roots to obtain nutrients (Newsham *et al.* 2009).

The study reported here reveals that many fungi classified as DSE can be found associated with decaying wood, but the more typical niche on Deception Island could be association with local flora (mosses and grasses). Plants found in this area consist of herb-lichen-moss formations with only two vascular plants found on the island: a pearlwort, *Colobanthus quitensis* and a grass *Deschampsia antarctica* (Smith 1984). DSE fungi have been found associated with these two plants in different areas (Upson *et al.* 2009). Flora diversity on Deception Island is exceptional for a polar location with 18 species of bryophytes and lichen that have not been found elsewhere in Antarctica as well as two species which appear to be endemic. In addition, the island has the largest known community of Antarctic pearlwort (Deception Island Management Group 2002). Studies have shown that several genera of DSE fungi (*Cadophora*, *Leptodontium*, *Lecythophora*, and *Phialocephala*) were capable of decomposing bryophyte material (Day & Currah 2011).

Decay studies reported here with DSE species that were isolated from Deception Island show they are efficient decomposers of wood, capable of functioning solely as saprotrophs. Although Menkis *et al.* (2004) reported species belonging to the DSE genus *Phialocephala* isolated from a wide range of ecological niches, including healthy root tips, decayed coarse roots, live healthy looking stems, decomposing stumps, and fine woody debris, the saprophytic nature of this group of fungi is often overlooked. The capability to live as a saprotroph as well as an endophyte suggests they have highly specialized functions and pronounced ecological plasticity. In polar environments where spore production, dispersal, and colonization of new substrates may be difficult, fungi with endophytic capabilities would be able to colonize the plant over a long period of time and then capture resources quickly once the plant tissue dies (Jumpponen *et al.* 1998; Porras-Alfaro & Bayman 2011). As saprotrophs, it appears that this group of fungi employ different decomposition mechanisms as seen in different patterns of decay (Fig 8). *Mollisia*, *Lecythophora*, *Phialocephala*, and *Phoma* spp. all cause a soft rot type of decay, but they vary between soft rot Type

1 and Type 2 in birch wood. Very little biomass loss occurred on pine, suggesting that these fungi have specific requirements for certain woods (preference for hardwood vs. conifer) for decay to occur.

Anthropogenic effects

For nearly two centuries, there have been many opportunities for alien fungi to be introduced to Deception Island. The strong anthropogenic effects over the past decades and those continuing today with tourists visiting the sites, has undoubtedly impacted the fungal diversity and ecology on the island. The likely avenue for many of the introductions of wood degrading fungi was the timber and wood used for buildings and for the wooden boats, barrels, and other items that came from Europe, South America, and other countries. The presence of both brown and white rot types of wood decay at this location and not at other Antarctic locations suggests the environment at Deception Island influences what alien organisms survive. The introduction of Basidiomycota decomposer fungi is also confirmed by the fact that these fungi are considered forest fungi and found decaying woody substrates, which did not exist on Deception Island before human activity. Additionally, previous research has shown that fungal abundance of Antarctic soils is most positively correlated with the percent of organic carbon compared to other soil characteristics (Arenz & Blanchette 2011). The high degree of fungal diversity associated with historic wood at Deception Island indicates that the large organic carbon input on the island from whaling and other activities is likely a driving factor for fungal abundance.

In addition to cellulosic nutrient sources brought to the island for buildings and other materials associated with the whaling activities, there are also many reports of live domestic animals that were housed on the island (Smith 1996). In the early 1900's pigs were kept at the whaling station (Hacquebord 1992) as well as an occasional sheep or cow for a food source (Scott Polar Research Institute Archives, unpublished data). The Chilean Base had anywhere from 30 to 60 sheep brought to the station every year in addition to hens and an occasional pig or cow (Smith 1996). Hay and corn was also brought to feed the animals (Smith 1996). Whale processing byproducts (Hacquebord 1992) and various animal populations provided a large input of nutrients that would greatly aid decomposition by fungi, in an otherwise nutrient lacking volcanic soil.

Conclusions

These findings show that all three known types of wood decay (white, brown, and soft rot) are active and causing extensive decay in the historic wooden structures and other wooden artifacts at Deception Island, Antarctica. This is in contrast to only soft rot fungi identified in wood at other locations in Antarctica. It also appears that brown and white rot Basidiomycota were brought in with the wood and building materials and have flourished. The dynamic nature of the ecosystem of Deception Island with soils that range in temperature from freezing to 90 °C and the large amount of wood present at the site providing a carbon source apparently allows many of the introduced fungi to survive. The input of wood also appears to have influenced the indigenous population of fungi such as the DSE types found in native plants to expand their saprophytic existence and colonize the introduced wood. The fungi colonizing the historic woods are causing extensive decay that will gradually result in the loss of the historic structures.

There are many fungal isolates from this study which remain unidentified or with poor matches to sequences in GenBank, which suggests that some of these isolates are new species and may be indigenous to Antarctica. *Cadophora* spp. were the dominant group isolated from Deception Island as well as other previously studied sites in Antarctica, which further suggests this group of fungi plays an important role in decomposition and nutrient cycling in cold ecosystems.

Additional studies focussing on fungal soil communities and plant-associated fungi would aid in understanding how alien fungi brought to Deception Island has affected fungal populations and ecosystem functioning.

Acknowledgements

The authors would like to thank Brett Arenz and Andy Graves for assistance in collecting samples, the staff and crew of the Lawrence M. Gould research vessel. This research is supported by National Science Foundation grant #0537143.

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