1 **Deception Island, Antarctica Harbors a Diverse Assemblage of Wood Decay Fungi**

2
3 Benjamin W. Held¹ and Robert A. Blanchette

4
5
6
7 Department of Plant Pathology, University of Minnesota
8 495 Borlaug Hall, 1991 Upper Buford Circle
9 St. Paul, MN 55108, USA

10 ¹Corresponding author: email: bheld@umn.edu Phone: 612-625-6231

11
12
13
14
15 **Abstract**

16
17 Very little is known about fungal diversity in Antarctica as compared to other biomes and
18 how these important organisms function in this unusual ecosystem. Perhaps one of the
19 most unusual ecosystem is that of Deception Island; an active volcanic island part of the
20 South Shetland Islands of the Antarctic Peninsula. Here we describe the fungal diversity
21 associated with historic wood from structures on the island, which reveals a diverse
22 fungal assemblage of known wood decay fungi as well as the discovery of undescribed
23 species. The major group of wood decay fungi identified were species of *Cadophora* and
24 as shown in previous studies in other geographic regions of Antarctica, they caused a
25 soft-rot type of decay in the introduced woods. Additionally, unlike other areas of
26 Antarctica that have been studied, filamentous basidiomycetes (*Hypochniciellum* spp. and
27 *Pholiota* spp.) were also identified that have different modes of degradation including
28 brown and white rot. Matches of fungal sequences to known species in temperate regions
29 likely introduced on building materials indicates human influences and volcanic activity
30 have greatly impacted fungal diversity. Lahars (mudslides from volcanic activity) have
31 partially buried many of the structures and the buried environment as well as the moist,

32 warm soils provided conditions conducive for fungal growth that are not found in other
33 regions of Antarctica. The diverse assemblage of decay fungi and many different forms
34 of aggressive wood decomposition add to the difficulty of conserving wooden structures
35 at these important polar heritage sites.

36 Key words:
37 Ascomycota, Basidiomycota, biodeterioration, historic preservation, polar biology, fungal
38 diversity
39

40 **Introduction**

41 Deception Island, part of the South Shetlands, is a small Antarctic island with unique
42 ecological characteristics, unusual geological features and a rich historical past. The
43 island is an active volcano that has a flooded caldera with narrow entrance to the interior
44 (Fig. 1). Early sealers and whalers utilized this geologic feature for protection from the
45 open ocean when they visited the island as early as 1820. Historic wooden structures still
46 exist on the island today and are listed as Historic Sites and Monuments. Hektor whaling
47 station (Norwegian) on Whalers Bay was established in 1911 as a land based operation
48 and numerous factory whaling ships were used the harbor in subsequent years. Later, in
49 1944 following the crash of the whale oil market, the British used the site and added a
50 wooden building called Base B. Following that, the British Antarctic Survey (BAS) used
51 the site as a base for aerial surveys of the Peninsula, at which time a runway was made
52 and airplane hangar built. Many buildings, structures and remnants from the whaling
53 station and later activities on the island are still present today in varying stages of
54 deterioration and are protected as an Antarctic Historic Site or Monument (HSM-71),
55 under the Antarctic Treaty.

56 Pendulum Cove, approximately 4 kilometers north of Whalers Bay is the location

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

61 The geological history of the Island includes an eruption of the volcano
62 approximately 10,000 years ago that created Port Foster and the interior bay (Olsacher
63 1956). Numerous other eruptions have occurred, including several during the past two
64 centuries that have changed the topography of the island significantly. Subsequently, ash
65 has covered glaciers, which occupy 57% of the island. Many areas on the island have
66 geothermal activity that produce fumaroles, heated soils and steaming beaches. These
67 unusual environmental conditions in the polar environment provide a unique opportunity
68 for microbial activity to take place that is not seen in other parts of Antarctica.
69 Investigations on the island also provide an opportunity for comparative analysis of
70 microbial diversity with other areas of Antarctica where wood and other introduced
71 nutrient sources have been deposited, such as the historic expedition huts of the Ross Sea
72 and historic structures on the Antarctic Peninsula. Compared to temperate biomes, very
73 little is known about fungal diversity and decomposition in polar environments.
74 However, previous research on fungal diversity and degradation of wooden structures and
75 artifacts in Antarctica has shown that fungi are important decomposers despite the
76 extreme environment (Arenz et al. 2006; Arenz and Blanchette 2009; Arenz et al. 2010;
77 Blanchette et al. 2010; Duncan et al. 2006; Held et al. 2005; Held et al. 2006). The only
78 type of wood decay previously found occurring in Antarctica has been classified as a soft
79 rot caused by Ascomycota and occurs primarily in wood that is in contact with soil on

80 Ross Island (Arenz et al. 2006; Blanchette et al. 2004; Blanchette et al. 2010; Held et al.
81 2006) and on the Antarctica Peninsula (Arenz and Blanchette 2009). The common types
82 of decay in temperate and tropical areas, brown and white rot caused by basidiomycetes,
83 have not previously been found.

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

93

94 **Materials and methods**

95 Samples were collected from wooden structures and artifacts at Whalers Bay and
96 Pendulum Cove, Deception Island (62°57'S, 60°38'W) that appeared to be decayed and in
97 various stages of decomposition. Small segments (approximately 1 mm x 0.5 mm) of
98 wood were collected and placed in sterile plastic bags and kept cool while transporting
99 them back to the laboratory. Under sterile conditions in the laboratory, the wood samples
100 were cut and placed onto the following types of growth media: malt extract agar (1.5%
101 Difco malt extract), malt extract agar (1.5%) amended with 0.5g of streptomycin sulfate
102 and a semi-selective medium used to culture basidiomycetes (2.0% Difco malt extract,

103 0.2% yeast extract, 0.006% benlate with 0.2% lactic acid and 0.001% streptomycin
104 sulfate added after autoclaving) (Worrall 1991). Isolations were made from 188 samples
105 from Whalers bay (Hektor whaling station, Base B and BAS hangar) and 30 from the
106 Chilean base. Isolates were cultured at 8 and 20°C for several weeks after which transfers
107 were made to another plate to obtain pure cultures. DNA was extracted from fungal
108 cultures using an adapted chloroform procedure (Arenz and Blanchette 2011). The
109 internal transcribed spacer (ITS) region of ribosomal DNA was targeted for PCR
110 amplification with the primers ITS1 + ITS4 and LROR + LR5 for large subunit
111 amplification (White et al. 1990). PCR amplifications were done using Amplitaq Gold
112 PCR Master-mix (Applied Biosystems, Foster City, CA) and 1 µl of template DNA using
113 the following parameters: 94°C for 5 min, 35 cycles of 94°C for 1 min, 50°C for 1 min,
114 72°C for 1 min and a final extension step of 5 min at 72°C. PCR amplicons were
115 visualized on a 1% agarose gel using SYBR green 1 (Life Technologies, Grand Island,
116 NY) prestain and a Dark Reader DR45 transilluminator (Clare Chemical Research,
117 Denver, CO). Primers used for PCR were used for sequencing reactions on a ABI Prism
118 377 automated DNA sequencer using a ABI PRISM Dye Terminator Cycle Sequencing
119 Ready reaction kit (Applied Biosystems).

120 Consensus sequences were assembled using Geneious 9.0 (Kearse et al. 2012) and
121 compared to those in GenBank using BLASTn for identification. Multiple sequence
122 alignments were done using the MAFFT v7.222 (Katoh et al. 2002) alignment plugin in
123 Geneious R9. Phylogenetic trees were constructed using the MrBayes 3.2.6 plugin
124 (Huelsenbeck and Ronquist 2001) in Geneious R9 where 1,100,000 MCMC generations
125 were used with a sampling frequency every 200 generations and burn-in length of

126 100,000. The appropriate substitution model was selected using jModelTest 2.1.10
127 (Darriba et al. 2012) according to Corrected Akaike Information Criterion (AICc).

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

142 The methods for the decay study using Ascomycota were the same as the
143 Basidiomycota study but a different medium was used. Instead of malt yeast agar, a
144 minimal media consisting of 1.5 g NH₄NO₃, 2.5 g KH₂PO₄, 2 g K₂HPO₄, 1 g MgSO₄-
145 7H₂O, 2.5 g glucose and 0.1 g thiamine per liter was used (Abrams 1948; Worrall et al.
146 1991). In addition, instead of using water to hydrate wafers, a solution of same
147 ingredients as the medium exclusive of the agar was used. The incubation period was also
148 16 weeks.

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

158

159 **Results**

160 Fungal isolation attempts from samples collected at Deception Island yielded 326 isolates
161 from 218 samples. The majority (79%) of the isolates belonged to the Ascomycota and
162 were comprised of 53 taxa, followed by 11 taxa (24%) in the Basidiomycota and 4
163 Zygomycota taxa (6%). Some of the most relatively abundant Ascomycota were
164 *Cadophora* (29%), *Phialocephala* (10%), *Lecythophora-Coniochaeta* (9%), *Cosmospora*
165 (8%) and *Phoma* (8%). Within the *Cadophora* group, several species were found
166 including *C. fastigiata/melinii* (55%), *C. malorum* (22%), *C. luteo-olivaceae* (9%) and
167 undescribed species *C. sp. NH1-2* (13%) and *C. sp. 5R24-1* (2%). Among the most
168 relatively abundant genera in the Basidiomycota were *Hypochniciellum* (55%), *Pholiota*
169 (18%), *Cerinosterus* (11%) and *Tulasnella* (8%). In addition, there were 15 taxa (10
170 Ascomycota, 4 Basidiomycota and 1 Zygomycota) that matched at or below 97%
171 sequence identity with described taxa. LSU sequences were used in addition to ITS

172 sequences for *Hypochniciellum* isolates because the nearest percent sequence identity for
173 ITS BLAST searches was a 85% match to *Amyloathelia crassiuscula*. However, BLAST
174 searches using LSU sequence data showed a 99% sequence identity to *Hypochniciellum*
175 *molle* for which ITS sequence is not in GenBank. Due to the fact that the LSU region
176 does not resolve species effectively and that reference sequences of the ITS region for
177 this or other *Hypochniciellum* species were unavailable, the species of the isolate we
178 cultured remains uncertain. However, phylogenetic analysis of LSU sequences reveal the
179 isolates most closely resemble *H. molle* in this gene region (Fig. 2). Analysis of the ITS
180 gene region from *Pholiota* spp. sequences form several clades that are different from
181 other known species. One clade is comprised of isolates exclusively from the Chilean ase
182 that group with *P. multicingulata*. The second clade has both an isolate from the Chilean
183 base (2Di94-5) in addition to Whalers Bay (isolated from Biscoe house, Di267-2). A
184 second isolate from Biscoe house, Whalers Bay (2Di41-2) does not group with any other
185 isolates from Deception Island or known isolates in GenBank (Fig. 3).

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

194 Analysis of historic wood at these sites indicated that decay fungi are active and

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

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

215 Laboratory decay studies showed mass losses for *Phialocephala dimorphospora*,
216 *Lecythophora hoffmannii*, *Lecythophora sp.*, *Mollisia minutella*, *Mollisia cinera*, *Phoma*
217 *herbarum*, *Cosmospora vilior* on birch (*Betula sp.*) ranged from 1.8-21.2% and on pine

218 (*Pinus* sp.) from 1.8-2.6% (Fig.7). Scanning electron microscopy analysis revealed
219 unique decay processes in four of the species tested, excluding *C. vilior*, for which no
220 decay was evident. *Lecythophora* sp., *M. minutella* and *P. herbarum* caused a Type 2 soft
221 rot decay, in which the secondary wall layers of the wood cells were eroded, leaving only
222 the middle lamella remaining. *L. hoffmannii*, *P. dimorphospora* and *M. cinera* form
223 cavities in the S₂ region of the cell wall, indicative of a Type 1 soft rot decay. These
224 cavities were located within the secondary wall and the middle lamella was not affected
225 (Fig. 8).

226

227 **Discussion**

228 **Basidiomycota component**

229 A diverse fungal assemblage was found associated with wood decomposing the historic
230 structures and artifacts on Deception Island. This includes fungi in the Basidiomycota
231 that cause a white and brown rot type of wood decay. The occurrence of white and brown
232 rot fungi in Antarctica is quite unique and has not been previously reported on continental
233 or maritime Antarctica. However, other studies have reported decay attributed to
234 saprotrophic Basidiomycota from sub-Antarctic Islands (Pegler 1980; Smith 1984). Fungi
235 isolated from Deception Island sites were, 79% Ascomycota, 15% Basidiomycota and 6%
236 Zygomycota as compared to 82% Ascomycota, 15% Basidiomycota and 3% Zygomycota
237 found on the Antarctic Peninsula (Arenz and Blanchette 2009) and 75% Ascomycota,
238 21% Basidiomycota and 1% Zygomycota at Ross Island (Arenz et al. 2006). While the
239 distribution of phyla represented are generally consistent among these polar locations,
240 there are important differences. Most significantly, nearly all of the Basidiomycota

241 isolated from the previous studies in Antarctica were comprised of yeasts whereas the
242 Basidiomycota from Deception Island were filamentous wood decay fungi. In addition,
243 Deception Island lies in an area that is considered maritime Antarctic, which is
244 characterized as having a cold, moist climate and mean monthly air temperatures of $>0^{\circ}\text{C}$
245 for 3-4 months of the year (Aleksandrova 1980; Smith 1984) and 560mm of precipitation
246 per year. While Ross Island has a colder, drier climate where there are no months with
247 the average temperature $>0^{\circ}\text{C}$ and only 190mm of precipitation per year. Pegler et al.
248 (1980) reported *Trametes versicolor* (which causes a white rot type of decay) on wood
249 brought to South Georgia that was used in the whaling station there. Since the wood was
250 introduced, it is likely that the fungus was brought in with the wood, and this fungus is
251 not endemic. However, other decomposer basidiomycetes have been found that
252 presumably exist naturally in bryophyte and grass ecosystems. Smith (1994) reported 37
253 Basidiomycota on South Georgia including species of *Collybia*, *Galerina*, *Omphalina* and
254 *Coprinus* associated with plant litter. *Omphalina antarctica*, found on Deception Island,
255 was the first described Basidiomycota from maritime Antarctica and was associated with
256 mosses (Singer 1957). In temperate and some tropical areas, filamentous decomposer
257 Basidiomycota are the most common types of decay fungi found and in those biomes the
258 Basidiomycota out compete and exclude soft rot fungi (Rayner and Boddy 1988). At
259 Deception Island, conditions suitable for growth of Basidiomycota may be abated enough
260 by the extreme environment to allow soft rot fungi to compete for the same resources.

261 The dominant species of Basidiomycota isolated from samples in this study is a
262 species of the brown rot fungus, *Hypochniciellum* sp. Arenz and Blanchette (2009) also
263 isolated a similar fungus (referred to as fungal species BB1) from wood at Wordie House,

264 another historic site on Winter Island on the Antarctic Peninsula. Fruiting bodies of this
265 species were not observed in any areas where samples were taken. Mattsson et al. (2010)
266 showed that *H. molle* was the dominant decay fungus identified in wood from structures
267 on the Arctic archipelago Svalbard. It has also been reported as causing deterioration in
268 buildings in Norway and Germany (Alfredsen et al. 2005; Schmidt and Huckfeldt 2011),
269 on driftwood in Iceland (Hallgrímsson and Hauerslev 1995) and sporadically distributed
270 in Italy (Bernicchia et al. 2008). It appears that this fungus is adapted to cold
271 environments and may play an important role in nutrient cycling in many Polar Regions.
272 An adaptive strategy of *H. molle* in cold climates may be the production of thick walled
273 chlamydospores which likely aid in dispersal and survival. Its noted occurrence in
274 Norway suggests the fungus was introduced from Norway to Deception Island since
275 much of the lumber used to build the original Norwegian Hektor whaling station
276 originated from Norway. Microcosm studies showed that this fungus causes a brown rot
277 and extensive biomass can be degraded during relatively short laboratory incubation
278 periods. With the abundance of brown rot found at Deception Island and from the
279 frequency with which this fungus was isolated, our study suggests that this fungus is a
280 major cause of the brown rot decay taking place on the Island.

281 Fruiting of several other Basidiomycota (*Pholiota* spp. and *Omphalina* spp.) have
282 been previously reported on Deception Island (Singer 1967), which indicates that
283 conditions can be conducive for some Basidiomycota to complete their life cycle. Singer
284 (1967) described a *Pholiota* sp. fruiting body growing on one of the half buried wooden
285 boats at the beach in Whalers Bay. This area is adjacent to thermally heated soil and
286 water, which may have contributed to conditions favorable for fruiting. No fruiting

287 bodies were observed during our field events to Deception Island for these studies. Based
288 on past observations of fruiting bodies, it is interesting that *Pholiota* spp. was infrequent
289 from samples in Whalers Bay, but was dominant at the Chilean base. Likely, this fungus
290 was also introduced to Deception Island with building materials for the Chilean base. Its
291 activity strictly below the soil surface indicates that the below ground conditions are
292 conducive on the island for continued fungal growth. The phylogenetic analysis reported
293 here suggests three different species of *Pholiota* are present which indicates this fungus
294 may have been introduced several different times.

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

304 Once thought to be a species complex, a recent study demonstrated that the
305 corticioid genus *Jaapia* is in fact comprised of two species; *J. argillacea* and *J.*
306 *ochroleuca* (Telleria et al. 2015). *J. argillacea*, the species isolated at Deception Island,
307 has a wide distribution in Europe but is also considered a rare species (Nannfeldt and
308 Eriksson 1953). As with the other Basidiomycota that have been isolated from the wood at
309 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 (Arenz et al. 2006; Arenz and

333 Blanchette 2009; Arenz et al. 2010; Blanchette et al. 2004; Blanchette et al. 2010; Farrell
334 et al. 2011; Held et al. 2006). While *C. malorum*, *C. fastigiata* and *C. luteo-olivaceae*
335 have been identified in other biomes, their identification in this study points to the
336 proclivity of this group to thrive in polar environments especially, when wood is present
337 as a primary nutrient source. Most of the known *Cadophora* species identified (*C.*
338 *fastigiata* (also referred to as *C. melinii*), *C. luteo-olivaceae* and *C. malorum*) in this
339 study have been shown to cause a Type 1 soft rot decay in wood, in which fungal hyphae
340 create cavities in the S₂ layer of the wood cell wall by enzymatic degradation. Based on
341 preliminary observations, it appears that there are differences in size of cavities produced
342 by the different species and sub groups within the Type 1 soft rot group. More precise
343 measurements are needed to characterize the different forms of soft rot found and
344 whether this may be attributed to aggressiveness of different species. Further research is
345 needed with several strains of each species to confirm this. Some soft rot fungi also cause
346 another form of degradation referred to as Type 2 in which the cell walls are eroded from
347 the inside of the lumen toward the middle lamella.

348 A large component of fungi isolated from wood at Deception Island was similar to
349 genera that have been classified by other investigators as dark septate endophytes (DSE)
350 associated with plant roots. These include species of *Coniochaete*, *Lecythophora*,
351 *Leptodontium*, *Mollisia*, *Phialocephala*, and *Phoma*. DSE's are generally categorized as
352 endophytic fungi having dematiaceous septate hyphae and are restricted to plant roots.
353 They are primarily Ascomycota, have a wide host range, and have been identified in a
354 many ecosystems ranging from polar to tropical regions (Jumpponen and Trappe 1998;
355 Jumpponen 2001). The broad geographic and host range for these fungi suggests that they

356 have low host specificity (Porrás-Alfaro and Bayman 2011). Indeed, a mutualistic
357 relationship has been identified between the much studied DSE *P. fortinii* in Pinaceae,
358 Cyperaceae, Ericaceae, Salicaceae, and Rosaceae (Jumpponen 2001) and they have been
359 identified in roots of nearly 600 plant species. Unlike true mycorrhizal fungi, DSE
360 frequency in roots does not decrease with an increase in latitude (Upton et al. 2008).
361 Instead, a high incidence of DSE have been found in roots of plants in numerous polar
362 regions that have been studied (Christie and Nicolson 1983; Laursen et al. 1997; Ormsby
363 et al. 2007; Treu et al. 1996; Upton et al. 2008) and appear to be the most widespread
364 root-fungal association at these sites (Newsham et al. 2009). The abundance of DSE in
365 high stress polar environments has led to the hypothesis that they confer tolerance to
366 adverse conditions and lead some to hypothesize that they may be more important to
367 healthy ecophysiology functioning in plants than previously realized (Rodríguez et al.
368 2009). The delineation of DSE species is not well defined, either ecologically or
369 taxonomically, and their function has not been well studied. They are most commonly
370 isolated from healthy plants but differ from mycorrhizal fungi in that they do not form
371 arbuscules or coils in host roots to obtain nutrients (Newsham et al. 2009).

372 The study reported here reveals that many fungi classified as DSE can be found
373 associated with decaying wood, but the more typical niche on Deception Island could be
374 association with local flora (mosses and grasses). Plants found in this area consist of
375 herb-lichen-moss formations with only two vascular plants found on the island: a
376 pearlwort, *Colobanthus quitensis* and a grass *Deschampsia antarctica* (Smith 1984).
377 DSE fungi have been found associated with these two plants in different areas (Upton et
378 al. 2009). Flora diversity on Deception Island is exceptional for a polar location with 18

379 species of bryophytes and lichen that have not been found elsewhere in Antarctica as well
380 as two species which appear to be endemic. In addition, the island has the largest known
381 community of Antarctic pearlwort (Group 2002). Studies have shown that several genera
382 of DSE fungi (*Cadophora*, *Leptodontium*, *Lecythophora* and *Phialocephala*) were
383 capable of decomposing bryophyte material (Day and Currah 2011).

384 Decay studies reported here with DSE species that were isolated from Deception
385 Island show they are efficient decomposers of wood, capable of functioning solely as
386 saprotrophs. Although Menkis et al. (2004) reported species belonging to the DSE genus
387 *Phialocephala* isolated from a wide range of ecological niches, including healthy root
388 tips, decayed coarse roots, live healthy looking stems, decomposing stumps, and fine
389 woody debris, the saprophytic nature of this group of fungi is often overlooked. The
390 capability to live as a saprotroph as well as an endophyte suggests they have highly
391 specialized functions and pronounced ecological plasticity. In polar environments where
392 spore production, dispersal and colonization of new substrates may be difficult, fungi
393 with endophytic capabilities would be able to colonize the plant over a long period of
394 time and then capture resources quickly once the plant tissue dies (Porrás-Alfaro and
395 Bayman 2011; Jumpponen et al. 1998). As saprotrophs, it appears that this group of fungi
396 employ different decomposition mechanisms as seen in different patterns of decay (Fig.
397 8). *Mollisia*, *Lecythophora*, *Phialocephala* and *Phoma* spp. all cause a soft rot type of
398 decay, but they vary between soft rot Type 1 and Type 2 in birch wood. Very little
399 biomass loss occurred on pine, suggesting that these fungi have specific requirements for
400 certain woods (preference for hardwood vs. conifer) for decay to occur.

401 **Anthropogenic effects**

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

419 In addition to cellulosic nutrient sources brought to the island for buildings and
420 other materials associated with the whaling activities, there are also many reports of live
421 domestic animals that were housed on the island (Smith 1996). In the early 1900's pigs
422 were kept at the whaling station (Hacquebord 1992) as well as an occasional sheep or
423 cow for a food source (Scott Polar Research Institute Archives, unpublished data). The
424 Chilean Base had anywhere from 30-60 sheep brought to the station every year in

425 addition to hens and an occasional pig or cow (Smith 1996). Hay and corn was also
426 brought to feed the animals (Smith 1996). Whale processing byproducts (Hacquebord
427 1992) and various animal populations provided a large input of nutrients that would
428 greatly aid decomposition by fungi, in an otherwise nutrient lacking volcanic soil.

429 **Conclusions**

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

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

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

451 **Acknowledgements**

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

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					
<i>Acremonium atrogriseum</i> (AB540569.1)	99	515/518	6	-	KC514842
<i>Antarctomyces psychrotrophicus</i> (AJ133431)	99	465/469	2	-	KC514843
<i>Arthrobotrys superba</i> (EF445988)	98	539/547	-	1	KC514844
<i>Arthrinium sacchari</i> (EF076712.1)	95	466/491	1	-	KC514845
<i>Ascocoryne solitaria</i> (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
<i>Cadophora fastigiata</i> (AY781232)	99	495/496	18	3	KC514850
<i>Cadophora luteo-olivacea</i> (GU212374)	100	522/522	6	-	KC514851
<i>Cadophora malorum</i> (GU212434)	100	512/512	12	2	KC514852
<i>Cadophora melinii</i> (JN689950)	99	461/465	14	-	KC589024
<i>Cadophora</i> sp. NH1-2 (AY371513)	100	468/468	6	2	KC514853
<i>Cadophora</i> sp. 5R24-1 (DQ317330)	100	468/468	1	-	KC514854
<i>Cladophialophora minutissima</i> (EF016384.1)	99	488/490	1	-	KC514855
<i>Coniochaeta ligniaria</i> (AY198390)	99	532/535	2	7	KC514856
<i>Cosmospora vilior</i> (GU726751.1)	97	506/524	15	2	KC514857
<i>Exophiala xenobiotica</i> (KC311483)	100	516/516	1	-	KC514859
Fungal endophyte sp. ECD-2008 (EU686037)	99	476/480	2	-	KC514860
<i>Geomyces</i> sp. JZ-174 (HQ637306.1)	99	520/523	6	1	KC514864
Helotiales sp. NK251 (FR846472.1)	96	413/432	-	3	KC514865
Helotiales sp. PIMO_102 (HQ845745)	99	466/469	1	-	KC514866
<i>Helotiales</i> sp. MMW-2013a (JX001640)	100	443/443	1	-	KC514870
<i>Holwaya mucida</i> (DQ257357.1)	95	496/517	2	-	KC514867

Best BLASTn Match	Percent Identity	Overlap	Whalers Bay	Chile Station	Genbank Accession #
<i>Hormonema dematioides</i> (AY253451)	100	581/581	1	-	KC514868
<i>Hyaloscypha aureliella</i> (EU940229.1)	99	352/358	1	-	KC514869
<i>Lecythophora hoffmannii</i> (AY805566.1)	100	456/456	9	2	KC514871
<i>Leptodontidium elatius</i> (AY805569.1)	99	470/472	3	-	KC514872
<i>Neostagonospora elegiae</i> (KF251164)	98	549/563	1	-	KC514877
<i>Mollisia cinerea</i> (AY259135.1)	97	515/531	1	-	KC514849
<i>Mollisia</i> sp. aurim650 (DQ069036.1)	98	482/491	4	2	KC514873
<i>Oidiodendron truncatum</i> (AF062809)	99	513/522	2	-	KC514875
<i>Phaeosphaeria</i> sp. (HQ324780.1)	97	492/510	2	-	KC514876
<i>Phialocephala dimorphospora</i> (AF486121.1)	99	449/455	22	1	KC514878
<i>Phialophora lagerbergii</i> (AF083197.1)	99	474/478	2	-	KC514879
<i>Phoma cladoniicola</i> (JQ238623.1)	96	530/554	3	-	KC514883
<i>Phoma herbarum</i> (AY293800.1)	100	501/501	8	-	KC514880
<i>Phoma</i> sp. 2 (AF218789.1)	99	565/566	9	-	KC514881
<i>Pochonia</i> sp. LS-2013 (KC626045)	100	525/526	2	-	KC514858
<i>Pseudeurotium</i> sp. olrim976 (AY787729.2)	100	432/432	2	-	KC514882
<i>Pyrenopeziza</i> sp. KUS-F52417 (JN033413.1)	97	444/459	2	-	KC514874
<i>Sordariomycetes</i> sp. (JQ761957.1)	100	467/467	-	2	KC514861
<i>Thelebolus microsporus</i> (DQ028268)	99	451/452	2	-	KC514885
<i>Ulocladium atrum</i> (AF229486)	100	480/480	1	-	KC514886
Uncultured <i>Clathrosphaerina</i> clone (HQ212333.1)	97	506/519	1	1	KC514887
Uncultured Helotiales (FN565271)	98	523/536	1	2	KC514888
Uncultured <i>Lachnum</i> clone 6_h03 (HQ211775.1)	99	512/519	2	-	KC514889
Uncultured Phaeosphaeriaceae (JF449593)	100	523/523	1	-	KC514884
Uncultured Sordariomycetes clone (FJ475724.1)	98	499/512	1	-	KC514890
Uncultured Thelebolales clone (GU910625.1)	99	521/526	1	-	KC514892
<i>Xenopolyscytalum pinea</i> (HQ599581.1)	99	470/474	1	-	KC514893

Best BLASTn Match	Percent Identity	Overlap	Whalers Bay	Chile Station	Genbank Accession #
<i>Xylariales</i> sp. (KP297401)	95	443/464	7	-	KC514891
Basidiomycota					
<i>Hypochniciellum molle</i> (GU187667.1)*	99	866/867	40	4	KC514894
<i>Cerinosterus luteoalbus</i> (AY618667.1)	100	446/446	7	2	KC514894
<i>Coniophora puteana</i> (AM946631.1)	100	1295/1295	1	-	KC514900
<i>Coprinellus micaceus</i> (HM240519.1)	96	619/647	-	1	KC514901
<i>Hyphodontia radula</i> (GQ411525.1)	99	561/564	1	-	KC514902
<i>Hypochnicium</i> sp. WY-DT1 (KP80549)	97	509/523	1	-	KC514903
<i>Jaapia argillacea</i> (GU187524.1)	98	560/566	1	-	KC514904
<i>Pholiota multicingulata</i> (HQ533029.1)	95	628/660	4	9	KC514905
<i>Pholiota multicingulata</i> (HQ533029.1)	97	860/863		1	KC514906
<i>Postia pelliculosa</i> (JX090101)	99	558/560	1	-	KC514907
<i>Sistotrema brinkmannii</i> (DQ899094.1)	99	568/569	-	1	KC514908
<i>Tulasnella violea</i> (DQ457643.1)	99	485/487	6	-	KC514909
Zygomycota					
<i>Mortierella alpina</i> (FJ161918.1)	100	595/595	10	7	KC514910
<i>Mortierella parvispora</i> (EU484279.1)	100	567/567	1	-	KC514911
<i>Mortierella amoeboides</i> (GU559984.1)	99	531/532	2	3	KC514912
<i>Mortierella sarneyensis</i> (FJ161927.1)	97	460/477	1	-	KC514913

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

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

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.

Fig. 3 Bayesian tree constructed using 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.

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.

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=125µm). (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 fiber 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).

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.

Fig. 8 Scanning electron micrographs of transverse sections from historic wood showing decay patterns 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).

References

- Abrams E (1948) Microbiological deterioration of organic materials. Its prevention and methods of test., vol 188. National Bureau of Standards, Washington, DC
- Aleksandrova VD (1980) The Arctic and Antarctic: Their Division into Geobotanical Areas. Cambridge Univeristy Press, Cambridge, UK
- Alfredsen G, Solheim H, Jenssen KM Evaluation of decay fungi in Norwegian buildings. In, 2005. International Research Group on Wood Protection IRG/WP, p 12
- Arenz BE, Blanchette RA (2009) Investigations of fungal diversity in wooden structures and soils at historic sites on the Antarctic Peninsula. *Canadian Journal of Microbiology* 55:46-56
- Arenz BE, Blanchette RA (2011) Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula. *Soil Biology and Biochemistry* 43 (2):308-315
- Arenz BE, Held BW, Jurgens JA, Blanchette RA (2010) Fungal colonization of exotic substrates in Antarctica. *Fungal Diversity* 49 (1):13-22
- Arenz BE, Held BW, Jurgens JA, Farrell RL, Blanchette RA (2006) Fungal diversity in soils and historic wood from the Ross Sea Region of Antarctica. *Soil Biology and Biochemistry* 38 (10):3057-3064
- Bernicchia A, Benni A, Venturella G, Gargano ML, Saitta A, Gorjon SP (2008) Aphyllophoraceous wood-inhabiting fungi on *Quercus* spp. in Italy. *Mycotaxon* 104:445-448
- Blanchette RA, Held BW, Arenz BE, Jurgens JA, Baltes NJ, Duncan SM, Farrell RL (2010) An Antarctic hot spot for fungi at Shackleton's historic hut on Cape Royds. *Microbial Ecology* 60:29-38
- Blanchette RA, Held BW, Jurgens JA, McNew DL, Harrington TC, Duncan SM, Farrell RL (2004) Wood destroying soft rot fungi in the historic expedition huts of Antarctica. *Applied and Environmental Microbiology* 70:1328-1335
- Christie P, Nicolson TH (1983) Are mycorrhizas absent from the Antarctic? *Transactions of the British Mycological Society* 80:557-560
- Darriba, D, Taboada, GL, Doallo, R, Posada, D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* 9:772
- Day MJ, Currah RS (2011) Role of selected dark septate endophyte species and other hyphomycetes as sapropes on moss gametophytes. *Botany* 89:349-359
- Duncan SM, Farrell RL, Thwaites JM, Held BW, Arenz BE, Jurgens JA, Blanchette RA (2006) Endoglucanase-producing fungi isolated from Cape Evans historic expedition hut on Ross Island, Antarctica. *Environmental Microbiology* 8:1212-1219
- Farrell RL, Arenz BE, Duncan SM, Held BW, Jurgens JA, Blanchette RA (2011) Introduced and indigenous fungi of the Ross Island historic huts and pristine areas of Antarctica. *Polar Biology* 34:1669-1677
- Gilbertson RL, Burdsall HH, Larsen MJ (1975) Notes on wood-rotting hymenomyces in New Mexico. *The Southwestern Naturalist* 19:347-360
- Group DIM (2002) Deception Island Management Package.
- Hacquebord L (1992) Hector Station on Deception Island (South Shetland Islands, Antarctica) an environmental assesement study of a whaling station. *Circumpolar Journal* 1-2:72-97
- Hallgrimsson H, Hauerslev K (1995) Lignicolous jelly fungi and aphyllophorales in Iceland. *Acta Botanica Islandica* 12:35-52
- Held BW, Jurgens JA, Arenz BE, Duncan SM, Farrell RL, Blanchette RA (2005) Environmental factors influencing microbial growth inside the historic huts of Ross Island, Antarctica. *International Biodeterioration and Biodegradation* 55:45-53
- Held BW, Jurgens JA, Duncan SM, Farrell RL, Blanchette RA (2006) Assessment of fungal diversity and deterioration in a wooden structure at New Harbor, Antarctica. *Polar Biology* 29:526-531
- Jumpponen A (2001) Dark septate endophytes - are they mycorrhizal? *Mycorrhiza* 11:207-211

- Jumpponen A, Mattson KG, Trappe JM (1998) Mycorrhizal functioning of *Phialocephala fortinii* with *Pinus contorta* on glacier forefront soil: interactions with soil nitrogen and organic matter. *Mycorrhiza* 7:261-265
- Jumpponen A, Trappe JM (1998) Dark septate endophytes : a review of facultative biotrophic root-colonizing fungi. *New Phytologist* 140:295-310
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772-780
- Kearse, M, Moir, R, Wilson, A, Stones-Havas, S, Cheung, M, Sturrock, S, Buxton, S, Cooper, A, Markowitz, S, Duran, C, Thierer, T, Ashton, B, Mentijies, P, Drummond, A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647-1649
- Larsson KH, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA (2006) Hymenochaetales a molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98:926-936
- Laursen GA, treu R, Seppelt RD, Stephenson SL (1997) Mycorrhizal. Arctic, Antarctic, and Alpine Research 29:483-491
- Mattsson J, Flyen AC, Nunez M (2010) Wood-decaying fungi in protected buildings and structures on Svalbard. *Agarica* 29:5-14
- Menkis A, Allmer J, Vasiliauskas R, Lygis V, Stenlid J, Finlay R (2004) Ecology and molecular characterization of dark septate fungi from roots, living stems, coarse and fine woody debris. *Mycological Research* 108:965-973
- Nannfeldt JA, Eriksson J (1953) On the Hymenomycetous genus *Jaapia* Bres. and its taxonomical position. *Sven Bot Tidskr* 47:177-189.
- Newsham KK, Upson R, Read DJ (2009) Mycorrhizas and dark septate root endophytes in polar regions. *Fungal Ecology* 2:10-20
- Olsacher J (1956) Contribución a la geología de la Antártida Occidental: I. Contribución al conocimiento geológico de la Isla Decepción. *Contr Rev Inst Ant Arg* 2:1-76
- Ormsby A, Hodson E, Li Y, Basinger A, Kaminsky S (2007) Quantitation of endorhizal fungi in High Arctic tundra ecosystems through space and time: the value of herbarium archives. *Canadian Journal of Botany* 85:599-606
- Pegler DN, Spooner BN, Lewis Smith RI (1980) Higher fungi of Antarctica, the subantarctic zone and Falkland Islands. *Kew Bulletin* 35 (3):499-562
- Porras-Alfaro A, Bayman P (2011) Hidden fungi, emergent properties: endophytes and microbiomes. *Annual Review of Phytopathology* 49:291-315
- Preussing M, Nebel M, Oberwinkler F, Weiss M (2010) Diverging diversity patterns in the *Tulasnella* (Basidiomycota, Tulasnellales) mycobionts of *Aneura pinguis* (Marchantiophyta, Metzgeriales) from Europe and Ecuador. *Mycorrhiza* 20:147-159
- Rayner ADM, Boddy L (1988) *Fungal Decomposition of Wood: Its Biology and Ecology*. Wiley, New York
- Riley R, Salamov AA, Brown DW, Nagy LG, Floudas F, Held BW, Levasseur A, Lombard V, Morin E, OtillarR, Lindquist EA, Sun H, LaButti KM, Schmutz J, Jabbour D, Luo H, Baker SE, Pisabarro AG, Walton JD, Blanchette RA, Henrissat B, Martin F, Cullen D, Hibbett DS, Grigoriev IV. (2014) Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proceedings of the National Academy of Sciences* 111:9923-9928.
- Rodriguez RJ, White JF, Jr., Arnold AE, Redman RS (2009) Fungal endophytes: diversity and functional roles. *New Phytologist* 182:314-330
- Schmidt O, Huckfeldt T (2011) Characterization and identification of indoor wood-decaying basidiomycetes. In: Adan OCG, Samson RA (eds) *Fundamentals of mold growth in indoor environments and strategies for healthy living*. Wageningen, Wageningen, pp 117-168

- Singer R (1957). *Sydowia* 1:16-23
- Singer R (1967) Fungi Distribution. In: Bushnell VC (ed) *Terrestrial Life of Antarctica*, vol 5. American Geographical Society, New York,
- Smith RIL (1984) Terrestrial plant biology of the sub-Antarctic and Antarctic. In: Laws RM (ed) *Antarctic Ecology*. Academic Press, London, pp 61-162
- Smith RIL (1994) Species-diversity and resource relationships of South Georgian fungi. *Antarctic Science* 6:45-52
- Smith RIL (1996) Introduced plants in Antarctica: potential impacts and conservation issues. *Biological Conservation* 76:135-146
- Telleria MT, Dueñas M, Melo I, Salcedo I, Martín, M (2015) Spelling out *Jaapia* species. *Mycological Progress* 14:57.
- Treu R, Laursen GA, Stephenson SL, Landolt JC, Densmore R (1996) Mycorrhizae from Denali National Park and Preserve, Alaska. *Mycorrhiza* 6:21-29
- Upton, R, Newsham, K.K., Bridge, P.D., Pearce, D.A., Read, D.J. (2009) Taxonomic affinities of dark septate root endophytes of *Colobanthus quitensis* and *Deschampsia antarctica*, the two native Antarctic vascular plant species. *Fungal Ecology* 2: 184-196.
- Upton R, Newsham KK, Read DJ (2008) Root-fungal associations of *Colobanthus quitensis* and *Deschampsia antarctica* in the maritime and Subantarctic. *Arctic, Antarctic, and Alpine Research* 40:592-599
- White TJ, Bruns T, Taylor J (1990) Amplification and direct sequencing of fungal genes for phylogenetics. In: Innis MA, Gelfand GH, Sninsky JJ, White TJ (eds) *PCR Protocols: A Guide To Methods and Applications*. Academic Press, New York, pp 315-322
- Worrall JJ (1991) Media for selective isolation of hymenomycetes. *Mycologia* 83:296-302
- Worrall JJ, Anagnost SE, Wang CJK (1991) Conditions for soft rot of wood. *Canadian Journal of Microbiology* 37:869-874

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.