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# Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula, Ross Sea Region and McMurdo Dry Valleys

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Fungal abundance and diversity were studied from 245 soil samples collected in 18 distinct ice-free locations in Antarctica including areas in the McMurdo Dry Valleys, Ross Sea Region, and the Antarctic Peninsula. Cultivable fungal abundance in soil was found to be most positively correlated with percent carbon and nitrogen based on a Spearman's rank correlation test of six soil parameters. Soil moisture and C/N ratio were also positively correlated with fungal abundance while pH and conductivity were negatively correlated. These results suggest that nutrient limitations in these highly oligotrophic environments are a primary factor in determining the distribution and abundance of indigenous fungi. Other effects of the extreme Antarctic environment likely affect fungi indirectly by limiting the distribution and abundance of plant-derived sources of carbon.

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## 1. Introduction

More than 99% of the continent of Antarctica is covered by ice year-round (Fox et al., 1994). Areas free of ice and snow during the Austral summer include the McMurdo Dry Valleys and scattered locations around the coastal margin of the continent. The few exposed soil ecosystems are generally characterized by low microbial abundance and diversity relative to temperate locations. These two characteristics are commonly attributed to the environmental extremes present including low temperature, minimal soil moisture and organic matter, and high salinity and UV radiation.

Antarctic megafauna (seals, penguins, skuas, etc.) occupy terrestrial habitats for defined periods of time and are not considered year-round inhabitants of continental Antarctic (with the possible exception of breeding Emperor Penguins). Permanent terrestrial heterotrophs are limited to microscopic animals (nematodes, rotifers, tardigrades), springtails, mites, and bacteria, protists and fungi. Abundance and diversity of Antarctic terrestrial biota has been found to be primarily determined by abiotic factors (Hogg et al., 2006) with few well documented effects from species–species interactions such as competition or predation.

Fungi appear to play a variety of ecological roles in Antarctica. They are mycobiont partners of lichen symbiosis which in many areas of Antarctica are the only visible evidence of primary production, although they do not support populations of large herbivores as they do in the Arctic (Lindsay, 1978). Mycorrhizal associations appear to decrease with increasing latitude but have been found as far south as Livingstone Island (62′38S) in the Maritime Antarctic existing as arbuscular mycorrhizae on the roots of the Antarctic grass, *Deschampsia antarctica* (Upson et al., 2008). Mycorrhiza-like associations have also been reported on liverworts as far south as Granite Harbor (77′00S) (Williams et al., 1994). In addition, potential plant pathogens such as *Pythium* spp. have been identified on *D. antarctica* in the Maritime Antarctic (Bridge et al., 2009) and pathogens of non-vascular plants including moss, liverworts, and lichenicolous fungi have also been isolated in Antarctica (Pegler et al., 1980; Olech and Alstrup, 1996). Nematode trapping fungi have been reported from Antarctic soils (Gray and Lewis Smith, 1984) as well as a fungal predator of rotifers and tardigrades (McInnes, 2003). Lastly, and potentially most important, is the role of decomposer fungi in Antarctic ecosystems which most indigenous species of fungi isolated from the region are assumed to be (Adams et al., 2006). A functional gene microarray survey of the Antarctic Peninsula reported a high rate of detection of fungal decomposition genes and suggested that fungi were the

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dominant decomposers in the Antarctic (Yergeau et al., 2007). Despite the relative importance of this role to carbon and nitrogen cycling in the ecosystem, little is known about fungal decomposition processes in Antarctica except that filamentous basidiomycetes appear to have little presence or involvement in contrast to their relatively important role in decomposition in other parts of the world (Ludley and Robinson, 2008).

Antarctic ice-free locations differ significantly in the source and amount of potential resources for utilization by fungi. Exposed soil ecosystems at coastal areas on the Antarctic Peninsula and Ross Island are heavily affected by maritime influences. Although Antarctic terrestrial systems are characterized by low abundance and activity of primary producers, the cold Southern Ocean has relatively high levels of productivity. A small percentage of this fixed carbon is deposited along the coastal zones with the highest concentrations in the ornithogenic soils at penguin rookeries (Tatur, 2002).

The Dry Valley soil ecosystems located inland from the ocean are largely exempt from exogenous inputs of nutrients. Notable exceptions include the discovery of mummified seal carcasses up to 40 km from the sea (Barwick and Balham, 1967) and the subsequent creation of microhabitats in otherwise oligotrophic soils (Cary et al., 2010). This area is considered a relatively "closed" ecosystem with limited outside influences and primary production in most open soil areas is largely restricted to cryptoendoliths (De La Torre et al., 2003) and hypoliths. Ancient lacustrine sources of fixed carbon originally formed when Dry Valley lake levels were higher also appear to play a role in increasing the soil organic matter pool (Barrett et al., 2006; Burkins et al., 2000; Virginia and Wall, 1999) in addition to allochthonous wind redistribution from contemporary lacustrine sources (Hopkins et al., 2006).

Primary production in coastal areas including Ross Island and the Antarctic Peninsula is largely from the activity of lichens, free-living algae and non-vascular plants such as mosses and liverworts. Only two species of vascular plants are native to the Antarctic and they occur on the Antarctic Peninsula: *D. antarctica* and *Colobanthus quitensis* which are found as far south as 68° (Lewis-Smith and Poncet, 1985). Analysis of two Peninsula sites using a range of methods (DGGE, ergosterol, real time PCR, and CFU counts) found "fungal abundance was generally higher in vegetated plots" (Yergeau et al., 2007) although the different methods of detection utilized were not entirely in agreement.

The objective of the present study was to compare soil fungal distribution, abundance and species richness between three major ice-free regions in Antarctica: coastal areas and islands in the Antarctic Peninsula, Ross Island in the Ross Sea Region, and the McMurdo Dry Valleys. Soil characteristics including moisture, salinity, pH, percent carbon, percent nitrogen, and carbon/nitrogen ratio were also analyzed for correlations with fungal abundance.

## 2. Materials and methods

A total of 245 soil samples were obtained from 18 separate locations in Antarctica (Table 1). These locations included one from the McMurdo Dry Valleys (McKelvey Valley), five from the Ross Sea area (Cape Evans, Hut Point, Cape Royds from Ross Island and Cape Hallett and the ridge on the Adare Peninsula), and 12 locations on the Antarctic Peninsula (Detaille Island, Deception Island, Stonington Island, Humble Island, Hope Bay, Horseshoe Bay, Goudier Island, Snow Hill Island, Duse Bay, Winter Island, and areas around the current U.S. Palmer Station and the old Palmer Station site) (Fig. 1). Peninsula samples were collected in March 2007 while traveling with the British Antarctic Survey (BAS) on the HMS Endurance. Dry Valley samples were collected in January 2008 and Ross Island samples in January 2006 and 2008.

At each location, soil samples were chosen that represented a diversity of geomorphic features. Samples of soil at a 0–5 cm depth were collected using sterile scoops, placed in Whirl-Pak (Nasco, Ft. Atkinson, WI) bags, and kept at 4 °C until transported to the lab at the University of Minnesota where they were kept at −20 °C while awaiting analysis.

Soil was passed through a sterile 3 mm sieve for homogenization and to remove large particles before analysis. Analyses of soil properties were conducted using established methodology (Rhoades, 1996; Thomas, 1996). Briefly, soil moisture was determined by weighing subsamples before and after 2 h of oven drying at 120 °C. Soil pH was determined by preparing a 1:1 soil/distilled $H_2O$ solution and measurement with an Accumet Research AR15 pH meter (Fisher Scientific, Pittsburgh, PA). Relative soil salinity was determined by measuring soil conductivity based on a 1:5 soil/distilled $H_2O$ solution analyzed with an Orion model 122 conductivity meter (Orion Research Inc., Cambridge, MA). Percent carbon

**Table 1**
Locations where samples were collected for this study. Number of samples used as well as average soil characteristics and fungal colony-forming units (CFUs) per gram of soil are noted.

| Location | Sample Count | Moisture% | pH | EC (μS) | %C | %N | C/N ratio | CFU/gm | Latitude | Longitude |
|---|---|---|---|---|---|---|---|---|---|---|
| **Dry Valleys (McKelvey)** | 37 | 2.7 | 8.4 | 2806 | 0.07 | 0.05 | 1.4 | 553 | 77° 26′ S | 161° 33′ E |
| **Ross Island** | 82 | 6.8 | 8.0 | 1275 | 0.30 | 0.03 | 11.2 | 14743 | | |
| Hut Point | 12 | 4.3 | 8.3 | 1670 | 0.09 | 0.01 | 8.2 | 26149 | 77° 50′S | 166° 38′E |
| Cape Evans | 39 | 7.0 | 7.7 | 1702 | 0.37 | 0.03 | 10.8 | 2060 | 77° 38′S | 166° 24′E |
| Cape Royds | 32 | 7.4 | 8.3 | 607 | 0.29 | 0.02 | 12.4 | 25925 | 77° 33′S | 166° 10′E |
| **Victoria Land** | 5 | 3.7 | 7.6 | 2091 | 4.34 | 1.09 | 4.0 | 464 | | |
| Cape Hallett | 3 | 2.0 | 7.1 | 3398 | 7.18 | 1.80 | 4.0 | 484 | 72° 19′S | 170° 16′E |
| Adare Peninsula | 2 | 6.2 | 8.3 | 132 | 0.08 | 0.03 | 3.0 | 671 | 71° 40′S | 170° 25′E |
| **Peninsula** | 120 | 20.5 | 6.2 | 532 | 6.79 | 0.59 | 11.6 | 234900 | | |
| Detaille Island | 5 | 53.0 | 6.9 | 629 | 32.72 | 2.67 | 12.3 | 775504 | 66° 52′S | 66° 48′W |
| Deception Island | 26 | 13.8 | 6.5 | 577 | 0.45 | 0.02 | 18.7 | 27711 | 62° 59′S | 60° 34′W |
| Stonington Island | 10 | 9.9 | 6.1 | 1276 | 5.52 | 0.13 | 41.5 | 135554 | 68° 11′S | 67° 00′W |
| Humble Island | 3 | 76.7 | 4.1 | 1996 | 29.37 | 3.09 | 9.5 | 367400 | 64° 46′S | 64° 06′W |
| Hope Bay | 11 | 19.9 | 5.5 | 125 | 12.77 | 1.09 | 11.7 | 161961 | 63° 24′S | 56° 59′W |
| Horseshoe Bay | 19 | 15.8 | 6.1 | 186 | 4.90 | 0.31 | 16.0 | 467118 | 67° 49′S | 67° 18′W |
| Old Palmer Site | 4 | 18.9 | 4.6 | 80 | 0.34 | 0.06 | 6.0 | 4056 | 64° 46′S | 64° 05′W |
| Palmer Station | 10 | 30.7 | 4.8 | 62 | 7.12 | 0.59 | 12.0 | 2647 | 64° 47′S | 64° 04′W |
| GoudierIsland | 7 | 45.1 | 6.1 | 1202 | 18.82 | 2.29 | 8.2 | 1265577 | 64° 49′S | 63° 30′W |
| Snow Hill Island | 11 | 16.9 | 8.1 | 799 | 3.02 | 0.45 | 6.7 | 16115 | 64° 27′S | 57° 12′W |
| Duse Bay | 7 | 3.2 | 7.1 | 31 | 0.51 | 0.07 | 7.2 | 181057 | 63° 32′S | 57° 23′W |
| Winter Island | 6 | 12.3 | 7.1 | 608 | 3.60 | 0.08 | 46.1 | 16539 | 65° 15′S | 64° 16′W |

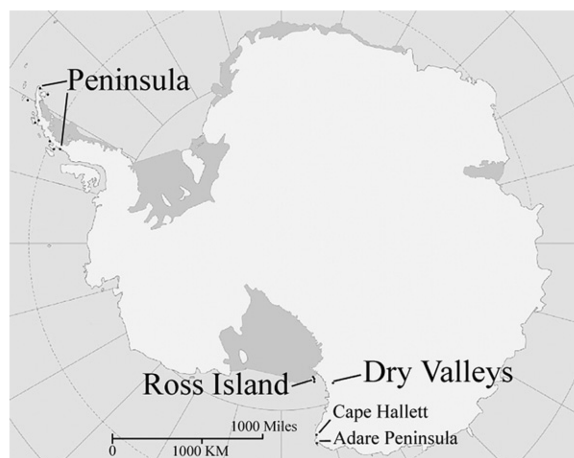


**Fig. 1.** Map of Antarctica showing locations of three sampling regions; Antarctic Peninsula, Ross Island, and the McMurdo Dry Valleys. The Ross Sea sampling area also included Cape Hallett and the ridge of the Adare Peninsula in Victoria Land.

and nitrogen content were measured with a Costech ECS 4010 CHNSO analyzer (Costech Analytical, Valencia, California).

Fungal colony-forming units (CFUs) were determined by making serial dilutions of soil and sterile distilled $H_2O$. One milliliter aliquots from a range of dilution series (1/10 to 1/100,000) were plated on both 1% Malt Extract Agar and a basidiomycete select agar (BSA) (1.5% malt extract, 1.5% agar, 0.2% yeast extract, 0.006% benlate, and with 0.2% lactic acid and 0.001% streptomycin added after autoclaving) (Worrall, 1999). Plates were incubated at either 20 °C or 4 °C for one week after which CFUs were counted and subcultures made of all morphologically distinct colonies from each sample. Plates that had no visible CFUs after one week were kept for at least two months to ensure slow growing isolates were not excluded.

Subcultures were incubated for another week and DNA extraction of individual isolations followed, based on an adapted chloroform extraction procedure. A small amount of fungal material (0.5 g) was combined with 500 μl of lysis buffer (10% Tris pH 8, 10% 0.5 M EDTA, 1% SDS) and vortexed with glass beads in a microcentrifuge tube. After removing the resulting solution to a clean tube, 275 μl 7 M ammonium acetate were added and the tube was incubated at 65 °C for 5 min followed by 5 min on ice. Five hundred microliters of chloroform were added and the solution was vortexed for 1 min followed by 5 min centrifuge at 20.2 g. The aqueous fraction was removed to a new tube and 1 ml isopropanol added, followed by 5 min incubation at room temp. The DNA was pelleted by 7 min centrifugation, after which the isopropanol was removed and the pellet washed twice with 70% ethanol. After the ethanol was removed, the pellet was allowed to dry for 30 min and resuspended with 100 μl 1× TAE. Nuclear rDNA of the Internal Transcribed Spacer (ITS) regions 1 and 2 along with the 5.8S region was amplified via PCR using the primers ITS1 and ITS4 (White et al., 1990). PCR products were sequenced at the University of Minnesota BioMedical Genomic Center (BMGC). Contigs of both forward and reverse sequence were constructed and sequences were compared to the NCBI GenBank database using a BLASTn search.

Spearman's rank correlation tests, ANOVA, and principal component analysis were performed with the program R, version 2.9.2 (R Development Core Team, 2009).

## 3. Results

From the 245 soil samples included in this study, 76 were found to yield no fungal CFUs on the media used. Although these samples were likely not sterile, they will be considered as such for the purposes of these results. The highest frequency of samples with no CFUs were obtained from the Dry Valley and Ross Island locations (78% and 42%, respectively) compared to few (9%) samples from the Antarctic Peninsula locations. From the remaining 169 soil samples, 455 fungal isolations were made. From these, 306 yielded high quality sequence results and were analyzed for probable taxonomic identity (Table 2). Ninety-two unique operational taxonomic units (OTUs) were identified based on rDNA BLASTn results.

Species richness was highest in Peninsula samples (80 OTUs) followed by the Ross Sea region (23 OTUs) and Dry Valley samples (3 OTUs). There was a limited amount of overlap between the locations (Table 2) with only 1 OTU being isolated from all three major areas. Although there was substantial variation within and among Peninsula fungal counts in general, they tended to be higher than those at the Dry Valleys or Ross Sea Region (Table 1).

Spearman's correlation analysis indicated that fungal abundance represented by fungal CFU was most highly positively correlated with carbon content in the soil (correlation coefficient: 0.55) (Table 3). This was followed by nitrogen content (0.46), percent moisture (0.36), and the C:N ratio (0.29). Conversely, fungal abundance was negatively correlated with pH (−0.48) and electrical conductivity (−0.26) (representing soil salinity). These correlations were all significant at $P < 0.05$. In addition, soils with no fungi had significantly lower soil moisture, percent carbon and nitrogen, C:N ratio and significantly higher conductivity and pH then soils with fungi based on ANOVA ($P < 0.01$) (Table 4).

The ten most frequently isolated groups of fungi as determined by BLASTn similarities were selected for principal components analysis. Average soil characteristics of samples from which each group was isolated as weighted by CFUs was determined and plotted as points while overall soil characteristics were plotted as vectors (Fig. 2).

### 3.1. Taxa found

All three major location areas were predominately represented by ascomycetes in both CFU abundance (94.5% Peninsula (P), 69% Ross Sea Region (RSR), 53% Dry Valley (DV)), and frequency of isolation (65.4% P, 53% RSR, 80% DV). The Peninsula had the highest zygomycete CFU abundance component (2.8% P, 0.03% RSR, 0% DV) and isolation component (12.6% P, 1.4% RSR, 0% DV). The Ross Sea Region and Dry Valleys had the most significant basidiomycete CFU abundance component (2.6% P, 30.8% RSR, 46.8% DV) and isolation frequency component (22% P, 45.7% RSR, 20% DV). OTUs were placed into genera based on a 95% identity BLASTn match criteria. The fungal genus isolated with the highest total CFU abundance was *Geomyces* from the Ross Sea Region and Peninsula locations (61% and 54% respectively) (Table 2). *Cadophora* spp. represented 22% of total CFU abundance from the Antarctic Peninsula and 1.9% from Ross Sea Region. The basidiomycetous yeast genera *Rhodotorula* and *Cryptococcus* made up 21% and 9.8% of Ross Sea Region total CFU abundance and 1.7% and 0.9% from the Peninsula, respectively. The single oomycete isolate found (best BLASTn match: Uncultured Pythium R021) was from a sampling site on the Antarctic Peninsula (Humble Island).

## 4. Discussion

The predominance of filamentous ascomycetes in studies of Antarctic soils is typical and the most abundant ascomycete genera found in this study, *Geomyces* and *Cadophora*, are widely reported from the Antarctic (Bridge et al., 2009) and an indigenous status for these fungi seems likely. These genera also seem to be particularly well-suited to exploit exotic substrates introduced by humans as

**Table 2**
Fungi isolated with best BLASTn comparisons with NCBI Genbank database based on the ITS 1, 2 and 5.8S regions amplified with ITS 1 and 2 primers. Total number of isolations are noted along with percent of total identified fungal CFU composition per location (RS: Ross Sea Region, DV: Dry Valley, P: Peninsula).

| Best Blast | Percent | Overlap | # Isolations | Locations | | | Accession |
|---|---|---|---|---|---|---|---|
| | | | | RS | DV | P | |
| **Ascomycete** | | | | | | | |
| *Alternaria* sp. IA317 (EF505090) | 100 | 462/462 | 1 | | | <0.01 | HM589216 |
| *Antarctomyces psychrotrophicus* (AM489755) | 100 | 502/502 | 1 | | | 0.06 | HM589217 |
| Ascomycete sp. BC15 (DQ317348) | 100 | 491/491 | 8 | 0.05 | | <0.01 | HM589218 |
| Ascomycete sp. nasa65 (DQ683978) | 88.9 | 433/487 | 1 | | | 0.11 | HM589219 |
| *Aspergillus sydowii* (EF652451) | 100 | 516/516 | 1 | | | <0.01 | HM589220 |
| *Aspergillus unguis* isolate NRRL 5041 (EF652497) | 99.6 | 523/525 | 1 | | | <0.01 | HM589221 |
| *Cadophora fastigiata* (DQ317326) | 100 | 546/546 | 1 | | | <0.01 | HM589222 |
| *Cadophora luteo-olivacea* isolate PhiK3II (FJ486274) | 99.6 | 571/573 | 1 | | | 0.23 | HM589223 |
| *Cadophora luteo-olivacea* isolate PhiK3II (FJ486274) | 99.8 | 580/581 | 1 | | | <0.01 | HM589224 |
| *Cadophora luteo-olivacea* strain 7R38-4 (GU212374) | 100 | 556/556 | 1 | | | 0.26 | HM589225 |
| *Cadophora malorum* strain 7R73 (GU212434) | 100 | 529/529 | 10 | 1.46 | | 0.11 | HM589226 |
| *Cadophora* sp. BDC-22-66e (FJ666350) | 98 | 551/562 | 4 | 0.4 | | 0.03 | HM589227 |
| *Candida glaebosa* (FM178351) | 90 | 566/572 | 1 | | | <0.01 | HM589228 |
| *Candida mesenterica* (FM178362) | 100 | 319/319 | 1 | | | <0.01 | HM589229 |
| *Candida* sp. K2 (AJ549823) | 99.2 | 381/384 | 1 | | | <0.01 | HM589230 |
| *Chaunopycnis* sp. ANT 03-065 (DQ402530) | 99.8 | 516/517 | 4 | 2.69 | 50 | | HM589231 |
| *Debaryomyces hansenii* strain CBS 940 (DQ249204) | 98 | 559/570 | 1 | | | 0.02 | HM589232 |
| *Debaryomyces hansenii* strain MA09-AK (GQ458025) | 100 | 587/587 | 2 | | | 0.05 | HM589233 |
| *Debaryomyces hansenii* voucher MCCC2E00222 (EF194843) | 100 | 616/616 | 1 | 0.76 | | | HM589234 |
| *Debaryomyces* sp. CBS 5572 (AM992909) | 100 | 583/583 | 4 | | | 0.20 | HM589235 |
| Environmental fungal clones (AM113721) | 98.8 | 499/505 | 1 | | | 0.11 | HM589236 |
| *Exophiala* sp. BC36 (DQ317336) | 99.6 | 555/557 | 1 | 1.52 | | | HM589237 |
| Fungal endophyte sp. ECD-2008 (EU686037) | 99 | 505/510 | 2 | | | 0.83 | HM589238 |
| Fungal sp. AB3 (FJ235936) | 100 | 511/511 | 1 | | | <0.01 | HM589239 |
| Fungal sp. AB32 (FJ235965) | 99.8 | 474/475 | 7 | | | 2.99 | HM589240 |
| Fungal sp. AB34 (FJ235967) | 100 | 502/502 | 13 | | | 4.59 | HM589241 |
| Fungal sp. AB47 (FJ235980) | 100 | 535/535 | 3 | | | 20.94 | HM589242 |
| Fungal sp. AB48 (FJ235981) | 98.8 | 499/505 | 2 | | | 0.23 | HM589243 |
| Fungal sp. AB48 (FJ235981) | 99.8 | 507/508 | 2 | | | 0.37 | HM589244 |
| Fungal sp. AB56 (FJ235989) | 99.8 | 545/546 | 5 | | | 2.91 | HM589245 |
| *Geomyces pannorum* strain ASIGP1 (DQ779788) | 93.3 | 472/506 | 4 | | | 23.21 | HM589246 |
| *Geomyces pannorum strain* ASIGP1 (DQ779788) | 92.9 | 443/477 | 1 | | | 0.40 | HM589247 |
| *Geomyces* sp. BC7 (DQ317337) | 100 | 503/503 | 35 | 35.14 | | 16.98 | HM589248 |
| *Geomyces* sp. BC7 (DQ317337) | 99.8 | 516/517 | 5 | | | 0.24 | HM589249 |
| *Geomyces* sp. BC9 (DQ317339) | 100 | 552/552 | 2 | 0.21 | | 6.9 | HM589250 |
| *Geomyces* sp. FFI 30 (AJ608960) | 99.6 | 523/525 | 11 | | | 1.09 | HM589251 |
| *Geomyces* sp. FMCC-3 (DQ499473) | 100 | 514/514 | 1 | | | <0.01 | HM589252 |
| *Geomyces* sp. T489/9b (AY345348) | 99.8 | 499/500 | 9 | 0.45 | | 0.92 | HM589253 |
| *Helotiales* sp. MK9 (EU700254) | 97 | 449/463 | 1 | | | <0.01 | HM589254 |
| *Holwaya mucida* (DQ257357) | 96.6 | 488/505 | 5 | | | 3.56 | HM589255 |
| *Hypocrea lixii* strain DIS 303A (FJ442646) | 100 | 553/553 | 1 | | | <0.01 | HM589256 |
| Onygenales sp. 7R11-3 (GU212399) | 100 | 507/507 | 9 | 25.08 | | 4.59 | HM589257 |
| Onygenales sp. 7R19-1 (GU212423) | 99.6 | 511/513 | 2 | | | 0.03 | HM589258 |
| *Phoma herbarum* (DQ132841) | 99.6 | 475/477 | 3 | 0.59 | | | HM589259 |
| *Pochonia chlamydosporia* strain Pt1 (GQ369959) | 89.5 | 479/535 | 1 | | | 0.34 | HM589260 |
| *Pseudeurotium bakeri* clone NS202B (DQ068995) | 99.4 | 517/520 | 1 | | | 0.20 | HM589261 |
| *Pseudeurotium desertorum* CBS 986.72 (AY129288) | 95.9 | 487/508 | 1 | | | <0.01 | HM589262 |
| *Stictis radiata* isolate MW6493 (AY527309) | 82.9 | 435/525 | 4 | | | 0.12 | HM589263 |
| *Teberdinia hygrophila* CBS 326.81 (AY129293) | 99.6 | 470/472 | 1 | | | 1.26 | HM589264 |
| Thelebolaceae sp. BC17 (DQ317350) | 100 | 524/524 | 1 | | | <0.01 | HM589265 |
| Thelebolaceae sp. BC18 (DQ317351) | 99.8 | 526/527 | 7 | 0.45 | 3.16 | 0.23 | HM589266 |
| *Thelebolus microsporus* (DQ402525) | 100 | 530/530 | 1 | 0.38 | | | HM589268 |
| Uncultured ascomycete isolate dfmo0690_022 (AY969478) | 99 | 481/486 | 1 | | | <0.01 | HM589269 |
| Uncultured ectomycorrhiza (Leotiomycetes) clone LTSP_EUKA_P6K14 (FJ554384) | 97.6 | 492/504 | 1 | | | 0.06 | HM589270 |
| Uncultured fungus clone G49 (EU620157) | 99 | 520/525 | 1 | | | 0.34 | HM589271 |
| Uncultured Tetracladium clone NG_P_E09 (GU055641) | 99.4 | 503/506 | 1 | | | 0.03 | HM589268 |
| **Basidiomycete** | | | | | | | |
| *Cryptococcus diffluens* (AM117836) | 100 | 571/571 | 1 | 0.07 | | | HM589272 |
| *Cryptococcus gastricus* (AB032677) | 100 | 590/590 | 1 | | | 0.09 | HM589273 |
| *Cryptococcus gastricus* (AB032677) | 99.8 | 578/579 | 6 | | | 0.07 | HM589274 |
| *Cryptococcus liquefaciens* strain SN1 (FJ515174) | 100 | 573/573 | 1 | 0.03 | | | HM589275 |
| *Cryptococcus* sp. NRRL Y-17490 (AF444449) | 100 | 612/612 | 5 | 1.95 | | | HM589276 |
| *Cryptococcus* sp. YSAR10 (AM922286) | 98.6 | 577/585 | 1 | | | <0.01 | HM589277 |
| *Cryptococcus* sp. YSAR10 (AM922286) | 99 | 606/612 | 8 | | | <0.02 | HM589278 |
| *Cryptococcus victoriae* strain CBS 8884 (AF444645) | 100 | 514/514 | 12 | 0.03 | | 0.70 | HM589279 |
| *Fibulobasidium murrhardtense* strain CBS9109 (GU327540) | 89.3 | 407/456 | 1 | | | <0.01 | HM589280 |
| Fungal sp. BB12 (FJ236003) | 99.5 | 440/442 | 5 | 5.33 | | | HM589281 |
| Fungal sp. BB14 (FJ236005) | 100 | 529/529 | 9 | | | 0.13 | HM589282 |

(*continued on next page*)

**Table 2** (*continued*)

| Best Blast | Percent | Overlap | # Isolations | Locations | | | Accession |
|---|---|---|---|---|---|---|---|
| | | | | RS | DV | P | |
| Fungal sp. BB17 (FJ236008) | 100 | 570/570 | 2 | | | <0.01 | HM589283 |
| Fungal sp. BB5 (FJ235996) | 98.5 | 449/456 | 10 | 7.7 | | | HM589284 |
| Fungal sp. BB8 (FJ235999) | 100 | 591/591 | 1 | | | <0.01 | HM589285 |
| *Leucosporidiella yakutica* VKM Y-2837T (AY212989) | 100 | 554/554 | 1 | | 46.84 | | HM589286 |
| *Rhodotorula laryngis* strain CBS2221 (AF190014) | 100 | 551/551 | 3 | 0.06 | | 0.01 | HM589287 |
| *Rhodotorula slooffiae* strain PYCC 4887 (AF444589) | 100 | 443/443 | 2 | 0.03 | | | HM589288 |
| *Rhodotorula* sp. BC22 (DQ317357) | 99.8 | 533/534 | 12 | 4.39 | | 0.24 | HM589289 |
| *Sporobolomyces lactosus* isolate C4 (EU551181) | 100 | 464/464 | 1 | | | <0.01 | HM589290 |
| *Tremella indecorata* HBZ194 (AF042432) | 98.8 | 496/502 | 1 | | | <0.01 | HM589291 |
| **Zygomycete** | | | | | | | |
| Fungal sp. ZB2 (FJ236010) | 100 | 592/592 | 1 | | | <0.01 | HM589292 |
| Fungal sp. ZB2 (FJ236010) | 99.8 | 601/602 | 2 | | | <0.01 | HM589293 |
| Fungal sp. ZB5 (FJ236013) | 100 | 604/604 | 1 | | | 0.03 | HM589294 |
| Fungal sp. ZB5 (FJ236013) | 99.5 | 604/607 | 4 | | | 0.07 | HM589295 |
| *Mortierella alpina* (AB476415) | 100 | 607/607 | 2 | | | 0.29 | HM589296 |
| *Mortierella* sp. 04M 158 (AY842393) | 100 | 606/606 | 1 | | | <0.01 | HM589297 |
| *Mortierella* sp. WD35C (EU240119) | 99.8 | 625/626 | 5 | | | 1.41 | HM589298 |
| Mortierellaceae sp. BC21 (DQ317354) | 99.8 | 606/607 | 1 | | | 0.06 | HM589299 |
| Mortierellaceae sp. BC21 (DQ317354) | 99.8 | 615/616 | 2 | 0.03 | | 0.06 | HM589300 |
| Mortierellaceae sp. BC21 (DQ317354) | 100 | 605/605 | 5 | | | 0.19 | HM589301 |
| Mortierellales sp. WD8I (EF126342) | 99.5 | 614/617 | 1 | | | <0.01 | HM589302 |
| *Mucor hiemalis* (AJ876489) | 99.7 | 592/594 | 1 | | | <0.01 | HM589303 |
| Uncultured fungus (FN397313) | 99.5 | 622/625 | 1 | | | <0.01 | HM589304 |
| Uncultured *Mortierella* clone LTSP_EUKA_P4O11 (FJ553914) | 99.5 | 579/582 | 1 | | | 0.03 | HM589305 |
| Uncultured soil fungus clone TC_fungal-F7-ITSFL (GU083113) | 99 | 585/590 | 1 | | | 0.63 | HM589306 |
| **Oomycete** | | | | | | | |
| Uncultured *Pythium* Ro21 (AY129553) | 99.5 | 875/879 | 1 | | | <0.01 | HM589307 |

their presence is widely noted in studies of fungal diversity of historic sites (Arenz and Blanchette, 2009; Arenz et al., 2006; Blanchette et al., 2010, 2004; Held et al., 2005). Based on their association with a wide variety of organic materials in the Antarctic including lichen and moss (Möller and Dreyfuss, 1996; Tosi et al., 2005) wood, leather and paper (Arenz et al., 2006), feathers (Marshall, 1998; Del Frate and Caretta, 1990), and a mummified seal carcass (Greenfield, 1981), these genera likely play important roles as generalist decomposers in the Antarctic soil environment.

The exclusive use of culture based fungal detection techniques limits the conclusions that can be drawn from this study. These techniques undoubtedly biased fungal abundance measurements towards species of fungi which readily grow on either of the culture media used here as well as species that had greater rates of sporulation. It is also possible that some very slow growing psychrophilic fungi were missed. Furthermore, many species of "unculturable" fungi have been detected only by use of molecular techniques (Jeewon and Hyde, 2007) and would not be represented in this study. However, previous research on soils from the Ross Sea area using similar media types as well as the molecular detection technique of denaturing gradient gel electrophoresis (DGGE) found that approximately 2/3 of total taxa could be detected using culturing-based investigations (Arenz et al., 2006).

Many of the sampling locations in this study are also sites that have had significant past or present human activity. The reason for this bias is that soil sampling for this study was done in conjunction with related studies on fungal diversity and deterioration effects at historic locations in the Antarctic (Arenz et al., 2006; Arenz and Blanchette, 2009). The two sites with the most significant current human impacts were Hut Point (within 200 m of McMurdo Station) on Ross Island and the Palmer site (within 100 m of Palmer Station) on the Antarctic Peninsula. All other sampling sites (except McKelvey) were relatively close to historic Antarctic sites and likely affected by past human inputs in the form of fungal introductions and influence on local soil organic matter content. The one exception to this was the sampling site at McKelvey Valley in the McMurdo Dry Valleys, which can be considered a relatively pristine site with little human influence.

### 4.1. Carbon and nitrogen

Carbon and nitrogen concentrations in soil, which are strongly positively correlated (Spearman's coefficient: 0.84), are reflective of abundance of primary producers present in the immediate environment or allocthonous inputs from other locations. In the

**Table 3**
Spearman's correlation matrix of measured soil properties. All values significant at $P < 0.05$ except those indicated by*.

| | Fungal CFU | Moisture | pH | EC | C | N | C/N |
|---|---|---|---|---|---|---|---|
| Fungal CFU | 1 | 0.36 | −0.48 | −0.26 | 0.55 | 0.46 | 0.29 |
| Moisture | 0.36 | 1 | −0.46 | 0 | 0.53 | 0.46 | 0.26 |
| pH | −0.48 | −0.46 | 1 | 0.24 | −0.46 | −0.53 | 0.09* |
| EC | −0.26 | 0 | 0.24 | 1 | −0.07* | 0.04* | −0.13 |
| C | 0.55 | 0.53 | −0.46 | −0.07* | 1 | 0.84 | 0.46 |
| N | 0.46 | 0.46 | −0.53 | 0.04* | 0.84 | 1 | 0.012* |
| C/N | 0.29 | 0.26 | 0.09* | −0.13 | 0.46 | 0.012* | 1 |

**Table 4**
Comparison of mean soil characteristics between samples which produced fungal CFUs and samples which produced no CFUs. Mean values and 95% confidence intervals are displayed. All 6 variables were significantly different between the 2 groups based on *F*-tests ($P < 0.01$).

| Variable | Fungi observed (169) | No Fungal CFU (76) |
|---|---|---|
| pH | 6.81 ± 0.22 | 8.11 ± 0.21 |
| Moisture (%) | 14.71 ± 2.69 | 6.86 ± 1.88 |
| EC (μS) | 545 ± 137 | 2522 ± 1631 |
| Carbon (%) | 5.01 ± 1.76 | 0.23 ± 0.12 |
| Nitrogen (%) | 0.45 ± 0.164 | 0.06 ± 0.04 |
| C/N | 14.3 ± 2.74 | 7.9 ± 1.68 |

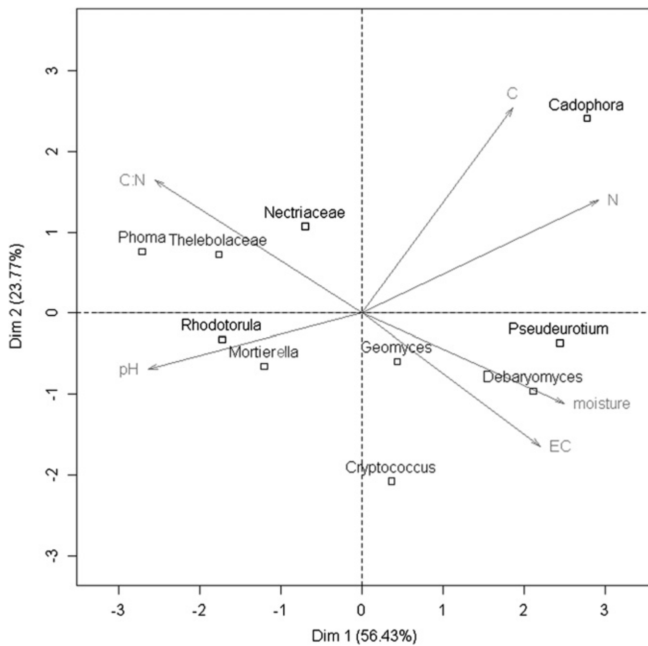


**Fig. 2.** Principal component analysis of soil properties and 10 most frequently isolated groups of fungi based on ITS rDNA analysis.

Antarctic, this is typically from penguin rookeries on the coastland. However, at many of the sites in this study the allocthonous input was by past and present activities of humans and the transport of wood, food stuffs, textiles, fuels, and other materials relatively high in carbon and/or nitrogen content (Arenz and Blanchette, 2009). Whatever the source of these materials, a consistent positive correlation between high carbon and nitrogen content and fungal abundance was found in this study. A positive carbon/fungal abundance relationship was also noted in Dry Valley soils by Connell et al. (2006). Malosso et al. (2004) found significant increases in both soil respiration and fungal biomass, as measured by ergosterol, when shredded *D. antarctica* leaves were added to soil collected from the Antarctic Peninsula. Addition of glucose, glycine, and $NH_4Cl$ in a Dry Valley soil experiment increased soil respiration rates indicating both C and N limitations on the activity of microbial heterotrophs (Hopkins et al., 2006).

### 4.2. C:N ratio

C:N ratios varied significantly among sites (Table 1) with very low values (1–2) occurring in McKelvey Valley to high levels averaging in the mid 40's at two sites on the Peninsula. These high values were reflective of the influence of woody substrates brought to these historic sites. Interestingly, the sites with the highest percent carbon (above 10%) had only intermediate C/N ratios (from 8 to 13). Nitrogen limitations have been linked to limiting decomposition of plant-based materials (Jingguo and Bakken, 1997) and Antarctic soil ecosystems may respond in a similar way. Significant nitrate content in very old Dry Valley soils (low C:N ratios) from long periods of atmospheric deposition may be preventing nitrogen from being a limiting factor in these areas (Barrett et al., 2006).

### 4.3. Moisture

Water availability has been described as the primary biological limiting factor in Antarctic soils (Kennedy, 1993) and has been correlated with fungal abundance in Dry Valley sites (Connell et al., 2006) but the correlation noted in the present study was not particularly strong (0.36). A possible explanation for this discrepancy is that of all the variables included in this study (moisture, salinity, pH, C, N), moisture is the soil characteristic that would vary the most on a temporal scale. The same location could have relatively high moisture for part of the year due to periodic meltwater availability but be dry at other times. Fungal activity will likely fluctuate rapidly during these times but overall abundance may not change drastically as fungi could survive the dry periods in a dormant state or as spores. Moisture was not found to be significantly correlated with bacterial abundance in areas around Wilkes Land, Antarctica with the same possible explanation being discussed (Heatholfe et al., 1989).

A related factor that could be masking a possible moisture effect is that moisture and C and N levels are highly correlated (0.53 and 0.46 respectively). Higher moisture levels and more frequent precipitation are likely supporting a greater abundance of primary producers, which would in turn provide C and N to soil fungi, and so moisture may be influencing fungi more indirectly than directly. Moisture has been found to be significantly positively correlated with microalgal colonization in Antarctic soil (Wynn-Williams et al., 1997). Another explanation for this relationship could be the that more highly vegetated sites have a much higher water holding capacity than the mineral soils at Ross Island and in the Dry Valleys. Humble Island, Detaille Island, Palmer Station, and Hope Bay contained a lot of vegetation with species of moss as well as the two Antarctic vascular plants, *D. antarctica* and *C. quitensis*. This vegetation level is reflected in the high soil C and N concentrations at these sites (Table 1) and the very high percentages of soil moisture that were observed there. The predominantly mineral soils at the Dry Valleys and Ross Island and other Peninsula sampling locations simply cannot reach these high levels of moisture even at saturation levels. In addition to capacity for much higher maximum moisture levels at these vegetated sites, the soils have a greater ability to retain moisture for longer periods of time providing a more stable resource for fungi and other microbes.

### 4.4. Salinity

Conductivity, which is a good indicator of soil salinity, was found to be significantly negatively correlated with fungal presence as well as abundance based on simple regression of all samples (Table 3). However, no significant correlation was found with multiple linear regression on abundance among the sample set that included only the samples that produced fungal CFUs. Connell et al. (2006) also found salinity to have no significant correlation with fungal abundance in their Dry Valley sample sites. However, salinity has been found to be negatively correlated with nematode presence and abundance in other studies at the Dry Valleys (Poage et al., 2008). It is possible that an indirect influence (similar to that from moisture discussed previously) is affecting fungi through effect of salinity on primary producer presence. Salinity is reported to have negative effects on *D. antarctica* (Ruhland and Krna, 2010) and is likely influencing the distribution of this grass as well as that of mosses and lichens (Broady, 1989).

### 4.5. pH

When all locations were evaluated together, pH was found to be significantly negatively correlated with fungal abundance. This finding conflicts with a previous study from the Dry Valleys which found filamentous fungal abundance to be positively correlated with pH ($R^2 = 0.39$) (Connell et al., 2006) and a decomposition study from moss communities of Signy Island which implicated low pH values in contributing to very low decomposition rates (Davis,

1986). In the present study there were an insufficient number of samples from the Dry Valleys that yielded fungal colonies to provide support or to refute these previous results. Roser et al. (1993) found an increase in fungal dominance of the microbial community with declining pH in ornithogenic soils as well as increases in algal abundance. pH may be associated with distribution of flora in non-ornithogenic soils but it is unclear if it is actively affecting primary producer presence or is merely reflective of overall precipitation at a site. High pH values are typically found in soils with very low precipitation and a negligible leaching effect of alkaline ions. In the study reported here, there was a negative correlation found between pH and soil moisture (−0.46). More research is needed on possible pH–fungal interactions as pH has been recently shown to be a powerful predictor of soil bacterial community structure on a wide ranging study of ecosystems in North and South America (Lauber et al., 2009). Varying pH in different areas of soil may provide a competitive advantage for certain fungal species but it is unclear if there is an overall direct effect on fungal abundance.

## 5. Conclusions

Constructing a putative model for Antarctic fungal distribution and abundance based on these results would involve direct effects from carbon and nitrogen concentrations and relatively indirect effects from moisture, salinity and pH. This model would support the generally accepted assumption that the majority of non-lichenized Antarctic fungi are operating as decomposers in their respective ecosystems. *Cadophora* and *Geomyces* spp. seem to be particularly successful generalist decomposers with a relatively wide distribution and diversity. Primary producers provide the main source of bio-available carbon in areas outside of ornithogenic soils and their distribution may be influenced more directly from moisture, salinity, as well as nitrogen. The results from this study support the theory that plant-derived nutrient limitations are a primary factor in determining distribution and abundance of fungi in Antarctic mineral soils, which is similar to the effect found for fungi in other arid regions (Zak, 2005).

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