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Microbial biomass and community structure changes along a soil development chronosequence near Lake Wellman, southern Victoria Land

JACKIE AISLABIE[1], JAMES BOCKHEIM[2], MALCOLM MCLEOD[1], DAVID HUNTER[1], BRYAN STEVENSON[1] and GARY M. BARKER[2]

[1]*Landcare Research, Private Bag 3127, Hamilton, New Zealand*
[2]*Department of Soil Sciences, University of Wisconsin, Madison, WI 53706-1299, USA*
aislabiej@landcareresearch.co.nz

Abstract: Four pedons on each of four drift sheets in the Lake Wellman area of the Darwin Mountains were sampled for chemical and microbial analyses. The four drifts, Hatherton, Britannia, Danum, and Isca, ranged from early Holocene (10 ka) to mid-Quaternary (*c.* 900 ka). The soil properties of weathering stage, salt stage, and depths of staining, visible salts, ghosts, and coherence increase with drift age. The landforms contain primarily high-centred polygons with windblown snow in the troughs. The soils are dominantly complexes of Typic Haplorthels and Typic Haploturbels. The soils were dry and alkaline with low levels of organic carbon, nitrogen and phosphorus. Electrical conductivity was high accompanied by high levels of water soluble anions and cations (especially calcium and sulphate in older soils). Soil microbial biomass, measured as phospholipid fatty acids, and numbers of culturable heterotrophic microbes, were low, with highest levels detected in less developed soils from the Hatherton drift. The microbial community structure of the Hatherton soil also differed from that of the Britannia, Danum and Isca soils. Ordination revealed the soil microbial community structure was influenced by soil development and organic carbon.

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Key words: Darwin Mountains, high latitude soils, microbial phospholipid fatty acids

Introduction

At 3780 km^2, the Darwin-Hatherton glacier region is the second largest ice-free region in the Transantarctic Mountains. Little is known about the glacial history, geomorphology, soils, and microbiology of the Darwin region, as compared with the larger McMurdo Dry Valleys (6700 km^2). The Darwin-Hatherton region can be subdivided into the Britannia Range (1560 km^2), the Cook Mountains-Brown Hills (1300 km^2), and the Darwin Mountains (920 km^2).

The Darwin Mountains are largely cut into the Ferrar Dolerite and the Beacon Sandstone. At least seven glaciations have been identified in the study area primarily from damming of the Hatherton Glacier by ice shelf grounding in the south-western Ross embayment (Bockheim *et al.* 1989). These glaciations include four gravel drift sheets of late Quaternary age beside Hatherton Glacier, from youngest to oldest, Hatherton, Britannia I, Britannia II, and Danum. From local ^{14}C dates, an early Holocene age was assigned to the Hatherton drift, a late Wisconsin age (*c.* 12–24 ka) to the Britannia drifts, and an age of marine isotope stage 6 to Danum drift. Based on dating of Taylor II and Taylor III drifts in Arena Valley (Brook *et al.* 1993) and central Taylor Valley (Higgins *et al.* 2000), the Danum drift may be *c.* 200 k.y. old. Bockheim *et al.* (1989) also identified two stages of Isca drift (IV and V) and undifferentiated or pre-Isca drifts throughout the Darwin Mountains. The Isca IV drift represents early damming of the Hatherton Glacier in the Ross embayment, and the Isca V results from expansion of alpine glaciers in mountain cirques above 2000 m a.s.l. Isca drifts are probably of mid-Quaternary age and pre-Isca drifts of early Quaternary age (Bockheim *et al.* 1989). Recent cosmogenic dating of moraines in the Lake Wellman area suggested that the Hatherton, Britannia, Danum, and Isca drifts were 8 k.y., 40 k.y., 310 k.y., and 1.1 m.y. old, respectively (Storey *et al.* 2010).

Bockheim *et al.* (1989) distinguished the glaciations primarily on the basis of moraine morphology, surface boulder composition and weathering, and soil development. They concluded that the variability of soil morphological characteristics on individual drift sheets was far less than the variability among drift sheets, suggesting soil morphologic and surface boulder weathering characteristics form a powerful basis for deciphering local drift sequences and for correlating drift sequences of similar parent lithology in the Transantarctic Mountains. Bockheim *et al.* (1989) also provided detailed information about soils of the Darwin Mountains, including chemistry of soil:water extracts, particle-size distribution, and clay mineralogy. Calcium and sulphate were the dominant ions in soil:water extracts and total water soluble salts increased with soil age. The fine earth (< 2 mm) soil fraction contained predominantly

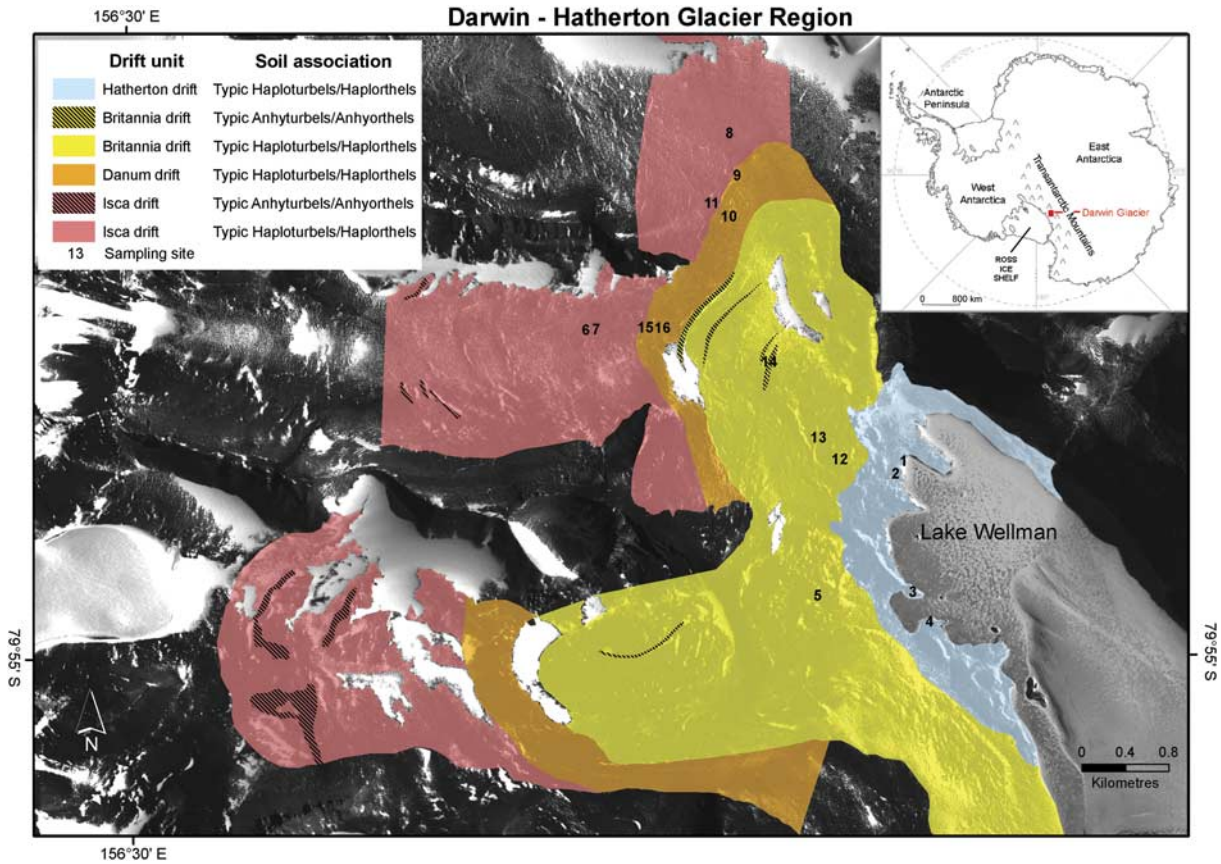

Fig. 1. Map showing distribution of soils on drifts in the Lake Wellman area of the Darwin Mountains with numbered sampling sites.

sands with < 4% silt and < 5% clay. Quartz and hydrous mica were the dominant minerals in the clay size fraction (< 2 μm) (Bockheim *et al*. 1989).

Knowledge of the microbial community composition of high latitude soils such as those of the Darwin Mountains is sparse but increasing. Early investigations of soil from the vicinity of Scott Glacier (86°S) reported the presence of bacteria, fungi and algae with highest numbers of bacteria detected in wet soils or those associated with lichen (Claridge *et al*. 1971). Subsequently, bacteria were isolated from soils of La Gorce Mountains (86°30'S) and Mount Howe (87°12'S) (Cameron *et al*. 1971, Cameron 1972). Bacteria, fungi and algae have also been cultured from soil of the Pensacola Mountains (82°S) (Parker *et al*. 1982). Broady & Weinstein (1998) described algae, cyanobacteria and a few fungi from La Gorce Mountains; some of their cultures also yielded heterotrophic bacteria (Aislabie *et al*. 2006a). Following a recent expedition to Dufek Massif in the Pensacola Mountains, cyanobacteria were reported to be the dominant life form in soils, old lake beds, lakes and ponds and green algae and bacteria were also present (Hodgson *et al*. 2010).

The primary objective of the present study was to test the hypothesis that microbial biomass and structure of microbial communities relates to soil development. As the environmental factors that influence soil development in Antarctica (temperature, moisture and salinity) are major influences on soil microbial community structure, we hypothesized that the patterns of microbial community structure in soils from the Darwin Glacier region can be explained in terms of soil development. Accordingly, we sampled a chronosequence of soils on moraines ranging from early Holocene (10 ka) to mid-Quaternary (*c.* 900 ka) in age.

Materials and methods

Study area, soil description, sampling and mapping

Studies were conducted within a 6 km radius of Lake Wellman (79°55'16.2"S, 156°55'30.7"E) in the south-eastern Darwin Mountains (Fig. 1). The area has an approximate mean annual temperature of -35° to -40°C and a mean annual water equivalent precipitation of 100–150 mm (Bockheim *et al*. 1989). Measured air temperatures at Lake Wellman ranged from 0 to -14°C from 3–21 December 2007 (www.lgp.aq/article/6341.html#8809, accessed May 2011). The taxonomic richness and abundance of lichens, mosses and invertebrates was noticeably lower relative to other areas in the Transantarctic Mountains (e.g. Caruso *et al*. 2009, Demetras *et al*. 2010).

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The experimental design included sampling at three depths and three faces (1 m^2) of four soil pits (1–7 m^3) on each of four drifts for a total of 144 samples. Sampling depths were dictated by local soil conditions but included the desert pavement (DP), which varied from 0.5–2 cm in thickness, the horizon underlying the desert pavement, which varied from 4–18 cm in thickness, and the upper 5 cm of soil above the ice-cemented layer. Where the ice-cemented layer did not exist in the upper 70 cm, sampling was done at the 65–70 cm depth. Soils were sampled on Hatherton, Britannia, Danum, and Isca drifts. When soils are referred on a given drift sheet, the drift sheet name was used to identify the soil.

Full methods used in this study are provided in Bockheim (2002) and are only highlighted here. Soil pits were excavated to a depth of at least 70 cm, unless ice cement prevented digging to that depth. Detailed soil descriptions were made using standard techniques (Schoeneberger *et al.* 2002).

Several soil morphological features, which have proved useful for distinguishing among drift sheets in the McMurdo Dry Valleys (Bockheim & McLeod 2006), were measured in the field. The depth of staining refers to the thickness of the layers showing the strongest hues and chromas from oxidation of iron-bearing minerals and corresponds to the bottom of the Bw horizon. The depth of coherence refers to the thickness of consolidated soil from accumulation of weathering products such as salts and iron oxide; soil readily caves into the pit below the depth of coherence. The depth of "ghosts" (pseudomorphs) refers to the depth to which highly weathered clasts can be observed *in situ*. This parameter varies with rock type as well as soil age.

The depth of visible salts refers to the maximum depth at which salts can be observed in a soil pit. A six stage salt sequence, developed by Bockheim (1990) that includes encrustations, flecks, and salt cementation, was employed. The depth to buried or ground ice or ice-cemented layer when less than 70 cm was determined. The weathering stage, an overall representation of the landscape/material based on the degree of surface boulder weathering, soil morphology, and patterned ground, was determined using criteria derived from Campbell & Claridge (1975).

Soils were classified into the Gelisol order to the family level (Soil Survey Staff 2010). Mineral soils showing cryoturbation are classified as Turbels, mineral soils without obvious cryoturbation are Orthels. Both suborders are divided into great groups on the basis of soil climate and other soil properties. Soils with comparatively high soil moisture contents are classified as Haploturbels and Haplorthels. In areas of low soil moisture, the soils are anhydrous, i.e. the mean annual precipitation is < 50 mm water equivalent, an ice-cemented layer is not present in the upper 70 cm, the moisture content averaged over the 10–70 cm layer is $\leq 3\%$ by weight, and the dry consistence of the 10–70 cm layer is loose to slightly hard except where a salt-cemented horizon is present, and are classified into the Anhyturbel or Anhyorthel great groups.

Soils were mapped using a geo-rectified remote sensed image of the Lake Wellman area as a base map. The map area was about 70 km^2 and included 27 soil mapping points, 16 from this study and 11 from Bockheim *et al.* (1989).

Soil chemical analyses

Soil samples were analysed for water content, pH, electrical conductivity (EC), nitrate-N, total phosphorus, water soluble cations (Ca, Mg, K, Na) and anions (Cl, NO_3, SO_4-) using standard methods (Blakemore *et al.* 1987). Total organic carbon and nitrogen were determined in a Leco FP-2000 analyser at 1050°C. All soil chemical properties were rated from very low to very high, based on criteria for New Zealand soils (Blakemore *et al.* 1987).

Microbial analyses

Analysis of phospholipid fatty acids (PLFA) was used to assess soil microbial community biomass and composition. Soils analysed were those sampled from the DP and layer below the DP. Soil sampled from the lower layer was excluded from analysis as preliminary investigations indicated that at this depth few, if any, PLFAs were detectable. The PLFA analysis method used was that of White *et al.* (1979), except that PLFA was extracted from 3 g of soil from each of three replicate samples collected per pit and the extracts were then combined before lipid fractionation, methylation and gas chromatographic (GC) analysis. The fatty acid methyl esters were identified and quantified by chromatographic retention time and mass spectral comparison using a bacterial acid methyl ester standard (Supeloc Bacterial Acid Methyl Esters mix 47080-U). For each soil the abundance of each of the individual fatty acids extracted was expressed as relative nmoles per gram of dry soil using standard nomenclature. The PLFAs i-15:0, a-15:0, i-16:0, i-17:0, 16:1ω7c, cy-17:0 and cy-19:0 were chosen to represent bacteria and the PLFA 18:2ω6 to represent fungi. In addition to the above PLFAs 14:0, 15:0, 16:0, 17:0, 18:0, and 18:1ω9c were used for the calculation of total PLFA and ordination analyses. To convert the PLFA data to total counts the conversion of 20 cells per fmol PLFA was used (Connon *et al.* 2007).

Numbers of culturable heterotrophic microbes were determined by plating soil (*c.* 0.1 g) or soil dilutions (10^{-1}–10^{-4}), in phosphate buffered saline, on R2A (Difco) agar plates with incubation at 15°C for up to three months.

Discrimination analysis

Discrimination of microbial communities was examined by semi-strong-hybrid (SSH) multidimensional scaling ordination (Belbin 1991), with the Bray & Curtis (1957) metric as the measure of community distance. Data input

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Table I. Weathering stage and soil properties on drifts in the Lake Wellman area. THo = Typic Haplorthel, TAo = Typic Anhyorthel, and TAt = Typic Anhyturbel. The profile number refers to the sampling sites depicted in Fig. 1.

Drift	Profile number	Weathering stage	Salt stage	Depth to ice cement (cm)	Depth of staining (cm)	Depth of ghosts (cm)	Depth of visible salts (cm)	Depth of coherence (cm)	Classification	GPS altitude (m)	Age
Hatherton	LW01	1	1	46	0	0	1	46+	THo	866	Early
	LW02	1	1	51	0	0	1	51+	THo	876	Holocene
	LW03	1	1	50	0	0	1	50+	THo	860	
	LW04	1	1	35	0	0	1	35	THo	854	
	AVG	1	1	45.5	0	0	1	>45.5		864	
Britannia	LW05	2	1	63	0	20	1	63+	THo	980	Late
	LW12	2	1	>76	8	5	9	76+	TAo	971	Wisconsin
	LW13	2	1	49	9	26	1	49+	THo	970	
	LW14	2	1	>70+	0	18	1	28	TAt	1038	
	AVG	2	1	>64.5	4.3	17.3	3	>54		992	
Danum	LW09	2.5	2	>75	19	19	19	75+	TAo	1204	Marine
	LW10	2.5	2	76	16	24	75+	76+	TAo	1200	isotope
	LW15	2.5	2	33	9	13	13	33+	THo	1154	stage
	LW16	3	2	35	35+	19	17	35+	THo	1123	6
	AVG	2.6	2	>54.7	>19.7	18.7	31	>54.7		1170	
Isca	LW06	3	2	63	33	30	33	63+	THo	1191	Older
	LW07	3	2	68	30	37	30	68+	THo	1187	than
	LW08	3	2	70	39	23	25	70+	THo	1216	Danum
	LW11	2.8	2	40	12	18	12	40+	THo	1224	
	AVG	2.9	2	60.2	28.5	27	25	>60.2		1204	

into the ordination was amounts for each individual PLFA detected in the soil samples. For the ordination trace levels of PLFA were recorded as 0.05 nmoles g^{-1} soil, which was 50% of the quantification limit of 0.10 nmole g^{-1} of soil. Trace levels refer to PLFA detected at levels too low to be quantified. The ordination was implemented in the PATN software package (Belbin 1995). Principal component correlation (PCC) analysis (Belbin 1991) was then performed in PATN to examine directionality and correlation, in the ordination space, of gradients in the measured soil parameters.

Table II. Properties of soils from a chronosequence near Lake Wellman in the Darwin Mountains. Soils were sampled from three layers, the desert pavement (DP), below the desert pavement, and the layer either 5 cm above the ice-cemented layer (IC) or 65–70 cm depth (see Table I). Data shown are means ± standard error, and $n = 4$ soil pits per soil type. Values with the same superscript letter within a column are not significantly different where the first letter refers to differences between horizons in each soil type and the second letter refers to a comparison of the same horizon across all soil types.

Soil	Layer	Water content (% dry weight)	pH (water)	Electrical conductivity (mS cm^{-1})	Organic C (%)	Total N (%)	Total P (mg kg^{-1})	C:N
Hatherton	DP	1.40 (0.25)^{a,e}	8.30 (0.09)^{a,g}	1.42 (0.53)^{a,e}	0.24 (0.06)^{b,f}	0.04 (0.02)^{ab,e}	255 (14)^{a,e}	7.92 (1.97)^{a,f}
	Below the DP	1.54 (0.28)^{a,e}	8.11 (0.08)^{a,f}	1.58 (0.39)^{a,e}	0.26 (0.06)^{b,f}	0.04 (0.00)^{b,e}	252 (6)^{a,e}	6.46 (1.21)^{a,g}
	Above the IC	2.09 (0.34)^{a,e}	8.62 (0.08)^{b,f}	1.04 (0.16)^{a,ef}	0.1 (0.04)^{a,e}	0.10 (0.04)^{a,e}	261 (3)^{a,f}	5.57 (0.80)^{a,f}
Britannia	DP	1.21 (0.24)^{a,e}	7.87 (0.14)^{a,f}	2.29 (0.30)^{a,f}	0.09 (0.05)^{a,e}	0.08 (0.02)^{a,f}	263 (16)^{b,e}	1.30 (0.67)^{ab,e}
	Below the DP	1.64 (0.26)^{a,e}	7.85 (0.08)^{a,ef}	3.49 (0.87)^{a,f}	0.08 (0.02)^{a,e}	0.12 (0.04)^{a,ef}	250 (16)^{ab,e}	1.05 (0.35)^{a,f}
	Above the ICP	1.86 (0.38)^{a,e}	7.95 (0.08)^{a,e}	2.34 (0.69)^{a,f}	0.09 (0.03)^{a,e}	0.06 (0.02)^{a,f}	231 (20)^{a,ef}	1.65 (0.06)^{b,f}
Danum	DP	0.81 (0.04)^{a,e}	7.34 (0.17)^{a,e}	1.38 (0.2)^{a,ef}	0.02 (0.00)^{a,e}	0.06 (0.02)^{b,ef}	237 (5)^{a,e}	0.53 (0.18)^{a,e}
	Below the DP	2.10 (0.41)^{b,e}	7.52 (0.28)^{a,e}	4.07 (1.0)^{b,f}	0.05 (0.01)^{b,e}	0.16 (0.06)^{c,f}	239 (7)^{a,e}	0.68 (0.32)^{a,ef}
	Above the IC	1.84 (0.27)^{b,e}	8.07 (0.25)^{b,e}	1.13 (0.3)^{a,e}	0.04 (0.01)^{ab,e}	0.03 (0.01)^{a,ef}	224 (8)^{a,f}	1.60 (0.47)^{b,f}
Isca	DP	0.87 (0.10)^{a,e}	7.12 (0.04)^{a,e}	1.86 (0.40)^{b,ef}	0.02 (0.00)^{a,e}	0.08 (0.01)^{b,f}	272 (25)^{c,e}	0.28 (0.04)^{a,e}
	Below the DP	2.30 (0.19)^{b,e}	7.46 (0.05)^{b,e}	4.81 (0.33)^{c,f}	0.06 (0.02)^{a,e}	0.17 (0.02)^{c,f}	221 (3)^{b,e}	0.28 (0.06)^{a,e}
	Above the IC	1.65 (0.39)^{ab,e}	8.13 (0.04)^{c,e}	1.03 (0.32)^{a,e}	0.04 (0.01)^{a,e}	0.03 (0.01)^{a,ef}	197 (5)^{a,f}	1.64 (0.47)^{b,f}
Main effects								
Soil		NS	**	NS	***	NS	NS	***
Horizon		***	***	***	*	***	***	***
Soil*horizon		NS	***	**	NS	NS	*	*

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Table III. Water soluble cations and anions in soils from a chronosequence near Lake Wellman in the Darwin Mountains. Soils were sampled from three layers, the desert pavement (DP), below the desert pavement, and the layer either 5 cm above the ice-cemented layer (IC) or 65–70 cm depth (see Table I). Data shown are means ± standard error, and $n = 4$ soil pits per soil type. Values with the same superscript letter within a column are not significantly different where the first letter refers to differences between horizons in each soil type and the second letter refers to a comparison of the same horizon across all soil types.

Soil	Depth	Water soluble cations (mg kg^{-1})				Water soluble anions (mg kg^{-1})		
		Ca^{+2}	Mg^{+2}	K^{+1}	Na^{+1}	Cl^{-1}	NO_3^{-1}	SO_4^{-2}
Hatherton	DP	786 (312)^{ab,e}	300 (252)^{a,e}	18.9 (3.5)^{a,e}	555 (165)^{a,e}	865 (596)^{a,e}	189 (152)^{a,e}	2016 (450)^{a,f}
	Below the DP	862 (266)^{b,e}	128 (29)^{a,e}	18.0 (2.7)^{a,e}	583 (133)^{a,e}	1363 (478)^{b,e}	249 (86)^{b,e}	1616 (434)^{a,e}
	Above the IC	356 (43)^{a,e}	66 (11)^{a,e}	14.6 (5.5)^{a,e}	612 (109)^{a,e}	453 (131)^{a,e}	94 (29)^{a,e}	1523 (262)^{a,e}
Britannia	DP	826 (110)^{a,e}	203 (40)^{a,e}	16.1 (2.2)^{a,e}	1181 (316)^{a,e}	1807 (308)^{ab,f}	772 (209)^{a,f}	739 (167)^{a,ef}
	Below the DP	1758 (413)^{b,ef}	406 (96)^{a,f}	26.8 (5.0)^{b,ef}	1365 (430)^{a,e}	2445 (600)^{b,f}	1216 (411)^{a,f}	1759 (495)^{b,ef}
	Above the IC	1300 (466)^{ab,f}	276 (97)^{a,f}	16.5 (3.5)^{a,e}	890 (278)^{a,e}	1383 (358)^{a,f}	530 (219)^{a,f}	2279 (754)^{b,e}
Danum	DP	571 (116)^{a,e}	232 (42)^{a,e}	14.1 (2.3)^{a,e}	430 (45)^{a,e}	493 (43)^{a,e}	629 (142)^{ab,f}	453 (114)^{a,e}
	Below the DP	2658 (766)^{b,f}	717 (237)^{b,f}	36.5 (8.1)^{b,fg}	1120 (213)^{b,e}	1116 (237)^{a,e}	1684 (681)^{b,f}	4561 (1305)^{b,fg}
	Above the IC	599 (269)^{a,ef}	151 (52)^{a,ef}	14.4 (0.9)^{a,e}	388 (51)^{a,e}	331 (25)^{b,e}	342 (101)^{a,f}	1331 (670)^{a,e}
Isca	DP	974 (373)^{b,e}	248 (14)^{a,e}	14.4 (1.6)^{a,e}	666 (173)^{a,e}	548 (102)^{a,e}	732 (115)^{a,f}	2279 (754)^{a,f}
	Below the DP	3405 (249)^{c,f}	756 (69)^{b,f}	45.1 (3.6)^{b,g}	1261 (206)^{b,e}	1196 (100)^{b,e}	1879 (274)^{b,f}	7388 (942)^{b,g}
	Above the IC	323 (134)^{a,e}	129 (42)^{a,ef}	12.6 (1.9)^{a,e}	542 (178)^{a,e}	514 (191)^{a,e}	330 (89)^{a,f}	859 (373)^{a,e}
Main effects								
Soil		NS	*	NS	NS	**	***	NS
Horizon		***	***	**	***	***	***	***
Soil*horizon		***	NS	***	*	NS	NS	***

Statistical analysis

For statistical analysis, the faces within each pit were considered as subsamples and averaged to obtain a value for each depth within each pit. Comparison of mean soil values was made by a two-way ANOVA of log transformed data with soil and depth (nested within site) as major effects. When the overall ANOVA was significant Fisher's protected LSD ($P < 0.05$) was used to compare horizons within each soil type and the equivalent horizon in different soil types. Values were not depth weighted by horizon so that differences between soils represent the average values for those specific horizons and not the depth weighted average over the entire soil profile.

Table IV. Microbial indicators in soil from a chronosequence near Lake Wellman in the Darwin Mountains. Soils were sampled from three layers, the desert pavement (DP), below the desert pavement, and the layer either 5 cm above the ice-cemented layer (IC) or 65–70 cm depth (see Table I). Data are the mean of four replicates (± standard error). TR = trace levels detected, and BQL = below quantifiable levels. Total cells were determined from phospholipid fatty acids (PLFA) data where possible and NC = no count. Values with the same superscript letter within a column are not significantly different where the first letter refers to differences between horizons in each soil type and the second letter refers to a comparison of the same horizon across all soil types.

Soil	Layer	Total PLFA (nmol g^{-1} soil)	Bacterial PLFA (nmol g^{-1} soil)	Fungal PLFA (nmol g^{-1} soil)	Total cells (g^{-1} soil)	Culturable heterotrophs (g^{-1} soil)	Total: viable
Hatherton	DP	4.128 (1.556)	3.086 (1.08)	BQL	8.3×10^7	7.05×10^5 (3.29)^{a,f}	19
	Below the DP	3.538 (1.447)	2.756 (1.193)	BQL	7.1×10^7	2.19×10^6 (1.29)^{a,f}	32
	Above the ICP					6.45×10^3 (2.30)^{b,f}	
Britannia	DP	0.053 (0.053)	0.053 (0.053)	BQL	1.1×10^6	334 (118)^{a,e}	3.3×10^3
	Below the DP	0.091 (0.091)	TR	BQL	1.8×10^6	143 (51)^{a,e}	1.3×10^4
	Above the ICP					11.9 (1.0)^{b,e}	
Danum	DP	0.062 (0.062)	TR	TR	1.2×10^6	193 (79)^{b,e}	6.6×10^3
	Below the DP	0.526 (0.471)	0.180 (0.180)	0.094 (0.094)	1.1×10^7	136 (84)^{a,e}	8.1×10^4
	Above the ICP					362 (231)^{a,e}	
Isca	DP	TR	TR	BQL	NC	146 (99)^{b,e}	
	Below the DP	TR	TR	TR	NC	22 (12)^{ab,e}	
	Above the ICP					252 (249)$^{(1)a,e}$	

(1) For the Isca soil above the IC layer, there was one value for culturable heterotrophs that was several orders of magnitude greater than the other values; on transformation, the mean was significantly lower than the DP horizon for this soil.

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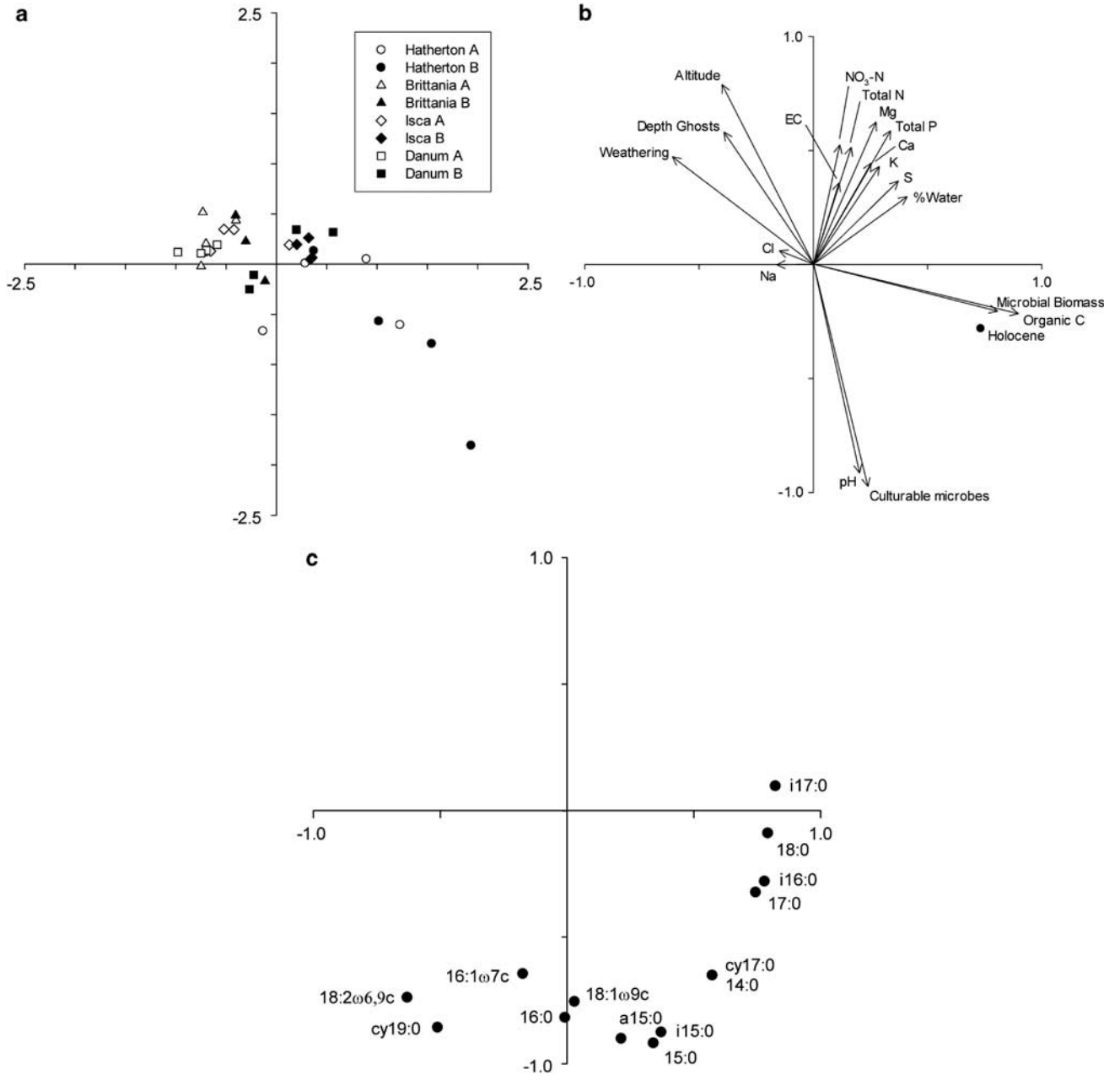

Fig. 2. Semi-strong-hybrid (SSH) ordination and principal component correlation (PCC) of the microbial community composition using phospholipid fatty acids (PLFA) data. **a.** Site ordination, where open symbols refer to DP and closed symbols to the depth below the DP. **b.** Gradients of soil development features and environmental variables fitted to the ordination. **c.** Phospholipid fatty acids ordination.

Results

Soils

The selected soils provided an excellent chronosequence for testing hypotheses regarding the relation between microbial community biomass structure and soil development (Fig. 1). The weathering stage increased from 1 on Hatherton and Britannia surfaces to 2 on Danum, and 3 on Isca (Table I). The salt stage varied from 1 in Hatherton and Britannia soils to 2 on Danum and Isca soils. The ice-cemented layer occurred from 33 cm to >70 cm and in general was shallowest in Hatherton drift, which features abundant thermokarst from melting and sublimation of interstitial ice. The depth of staining was 0, 4, >20, and 28 cm in Hatherton, Britannia, Danum, and Isca soils, respectively. The depth of ghosts, visible salts, and coherence varied similarly with age (Table I).

A soil map is provided in Fig. 1. The dominant soil map unit was Typic Haplorthels-Typic Haploturbels (78% of the area), followed by Typic Anhyorthels-Typic Anhyturbels ($<1\%$). Bare rock and snow patches constituted 22% of the area.

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Most (75%) of the soils map units were complexes of Typic Haplorthels-Typic Haploturbels, due to apparent recharge from windblown snow in high-centred polygon fissures. Typic Anhyorthels or Typic Anhyturbels with dry-frozen permafrost in the upper 70 cm occurred on Britannia and Danum surfaces.

Soil chemical and physical analyses

Chemical analyses, presented in Tables II & III, are the averages of twelve samples for three depths taken from four pits of each drift type, with three subsamples collected from each depth per pit. The water content of all samples was low (< 3%). Soil pH ranged from slightly alkaline (7.1–7.5) to strongly alkaline (8.4–9.0) and tended to increase with soil depth. Levels of organic carbon were very low (< 2%), total N were low to very low (< 0.3%), and total P was low (< 400 mg kg^{-1}). Levels of organic carbon in the desert pavement and layer below the desert pavement were significantly higher in the Hatherton soil compared with other soils collected along the chronosequence. In contrast, total N was significantly higher in the layer below the desert pavement for Danum and Isca soils. Electrical conductivity ranged from high (0.8–2) to very high (> 2). Electrical conductivity was highest in the layer below the desert pavement and was accompanied by significantly higher levels of water soluble anions and cations, notably calcium and sulphate in Danum and Isca soils (Table III). Whereas chloride was the dominant anion in Hatherton and Britannia soils, the older Danum and Isca soils contained primarily sulphate. Age related trends in soil chemical properties included a reduction in pH and organic carbon, and a decline in C:N with an increase in soil development. Concentrations of N and P were unrelated to soil age.

Microbial analyses

Microbial data is presented in Table IV. The levels of total PLFA in the soils were low (< 5 nmol g^{-1}) compared with temperate soils. Highest levels of total PLFA were detected in the Hatherton (up to 4.128 nmol g^{-1}), with levels in Britannia, Danum and Isca soils < 0.2 nmol g^{-1} except for the Danum sample from below the desert pavement which was 0.526 nmol g^{-1}. However, as indicated by the standard errors the PLFA data for the soil samples were variable (Table IV). Of note is that one of the four Hatherton pits analysed, pit 3, had consistently lower levels of PLFA than the other three pits. Also detected were higher levels of PLFA in soil from the depth below the desert pavement in one of the four Danum soil pits (pit 15) analysed. It is possible that this soil sample contained preserved microbial material such as a cyanobacteria mat or fungal hyphae with associated bacteria; certainly this was the only sample where we detected the fungal PLFA indicator 18:2ω6.

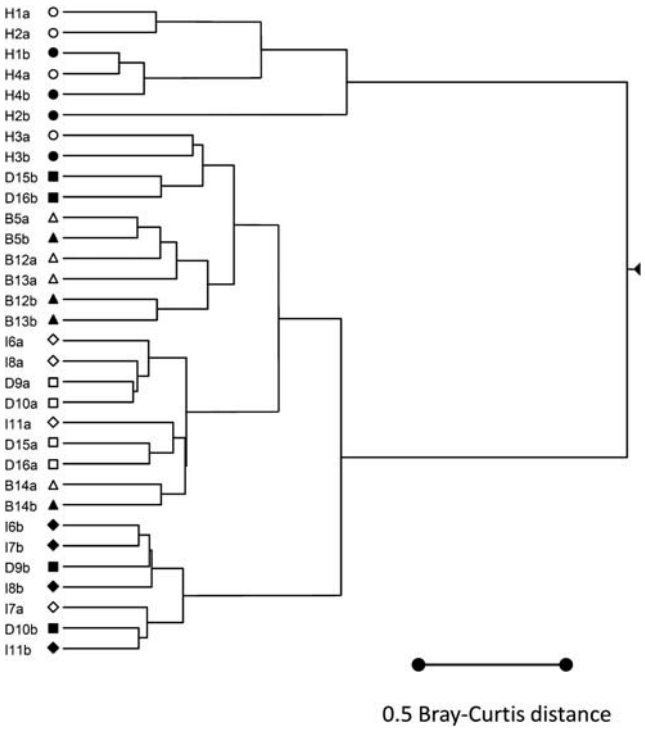

Fig. 3. Classification of sites based on Bray & Curtis dissimilarities of microbial community structures as indicated by ordination of the phospholipid fatty acids (PLFA) data. Where H = Hatherton, B = Britannia, D = Danum and I = Isca, open symbols refer to DP and closed symbols to the depth below the DP, and 1 through to 14 refer to the sampling sites and profile numbers (see Table I).

Bacteria were prevalent in the soils as all samples from the top two layers contained detectable levels of PLFAs indicative of bacteria (Table IV). Bacterial PLFAs indicators commonly detected in the soil included 16:1ω7c, i-15:0, a-15:0 and i-16:0 in decreasing prevalence with 16:1ω7c commonly used to indicate gram-negative bacteria and the others gram-positive bacteria.

Total counts estimates ranged from 8.3×10^{7}–1.1×10^{6} g^{-1} soil dry weight (DW) in the Hatherton and Britannia soils, respectively (Table IV). Due to the lack of quantifiable PLFAs, total counts were not estimated in some soils. Counts of culturable heterotrophs were 2×10^{1}–1×10^{4} -fold higher in Hatherton soils than those from Britannia, Danum and Isca soils. Numbers of culturable heterotrophs reached on average 2.2×10^{6} g^{-1} soil DW in the layer from below the DP in the Hatherton soil compared with < 3.7×10^{2} g^{-1} soil DW in Britannia, Danum and Isca soils (Table IV). Among the Hatherton soils, numbers of culturable microbes from pit 3 were consistently lower than other soils from the same drift, but were similar to those from Britannia, Danum and Isca drifts. In the Hatherton soils, numbers of culturable heterotrophs were significantly lower in the soil from above the ice cement, with numbers 100-fold lower than that of the DP or layer from below the DP. On average,

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lowest numbers of culturable heterotrophs were counted in Isca soils from below the DP. Six of the 12 samples analysed from this sample had fewer than ten colonies per plate with three containing no culturable microbes. The microbial colonies that grew on the soil plates were commonly pigmented: with red and yellow colonies prevalent in Hatherton soils and red, pink or orange colonies a feature of Britannia, Danum, and Isca soil samples with > 300 culturable heterotrophs per gram of soil DW.

Relation between soil development and soil properties and microbial distribution

Ordination was used to investigate microbial community patterns and their relationship to soil development and environmental gradients. Ordination runs using PLFA abundance data and PLFA presence/absence yielded similar results and Fig. 2a, b & c show the results for PLFA abundance. Only the first two axes of ordination are presented as these accounted for 65.2% of the variance in microbial community composition (stress values: axis 1 = 0.0737, axes 1 & 2 = 0.0715, axes 1–3 = 0.0576). The SSH ordination, depicting dispersion of sites shown in Fig. 2a, shows Hatherton soils grading into Britannia, Danum and Isca soil. However, as shown in the dendogram (Fig. 3), there is clear separation of the Hatherton soils, except those from pit 3, from the Britannia, Danum and Isca soils, which cluster together. Fig. 2b illustrates the gradients in the measured soil parameters within the ordination space (only those parameters with statistically significant fit to the ordination space are depicted). From the biplots (Fig. 2a & b), it is evident that sites primarily align along a gradient of soil development as defined by the parameters weathering, depth of ghosts and altitude, and associated with a gradient of microbial biomass and soil organic carbon. Salt, depth of staining and depth of salts as measures of soil development, while correlated with weathering ($r = 0.86$, 0.84, 0.57 respectively) and aligned strongly with the weathering gradient, exhibited poor correlation with the ordination space. The alignment of soil microbial biomass and soil carbon with axis 1 is consistent with observed higher values of these parameters in the Hatherton soils (Tables II & IV) and concordant with higher concentration/prevalence of PLFAs in these soils. Other influences on the microbial community structure are pH and water (Fig. 2b). The dispersion of the individual PLFAs in the ordination space (Fig. 2c) indicates a gradient more or less aligned with the inferred gradient of soil development. The bacterial PLFAs (e.g. i-15:0, a-15:0, and i-16:0) are more closely aligned to the Hatherton soils.

Discussion

A sharp decline in microbial biomass was detected along the soil chronosequence investigated in this study. Microbial biomass measured as PLFA and numbers of culturable heterotrophs were significantly higher in Hatherton soils compared with Britannia, Danum and Isca soils (Table IV). This observation is at odds with current understanding of the relation between soil development and microbial biomass in temperate regions as several studies have reported an increase in microbial biomass with increased soil development (Tscherko *et al*. 2004). Along with a decline in soil microbial biomass, the soil microbial community structure of the Hatherton soil differed from that of the Britannia, Danum and Isca soils. Influences on the soil microbial community structure include soil weathering, depth of ghosts and organic carbon (Fig. 2a & b). That the structure of Antarctic soil microbial communities varies with site has been reported previously (Aislabie *et al*. 2008, Yergeau *et al*. 2009, Cowan *et al*. 2010). However, the relationship between soil microbial community structure and abundance and soil development has been rarely considered in Antarctica (Bölter 2011).

Soil microbial community abundance and composition

The soil microbial community appears to be dominated by bacteria, the fungal PLFA marker 18:2ω6 was quantifiable in only one sample. At 3.185 nmole g^{-1} soil DW (or 0.943 μg g^{-1} soil DW), the levels of bacterial PLFA detected in the Hatherton soils were less than that reported for fell field soils of Signy Island (*c.* 10 μg g^{-1} soil DW). However, they were slightly higher than those found at Fossil Bluff (0.128 μg g^{-1} soil DW) and Coal Nunatak (0.195 μg g^{-1} soil DW) (Yergeau *et al*. 2007). In contrast, bacterial PLFAs in Britannia, Danum and Isca were lower (< 0.060 μg g^{-1} soil DW) than those reported for Fossil Bluff and Coal Nunatak (Yergeau *et al.* 2007).

Estimates of total cells in the soil were comparable to those of barren soils from King George Island in Maritime Antarctica (Bölter *et al*. 1997) and Victoria Land (Aislabie *et al*. 2006b). Numbers of culturable heterotrophs enumerated in the Hatherton soils were similar to those in soils from Scott Base and Marble Point (Aislabie *et al*. 2008), whereas those in Britannia, Danum and Isca soils are lower than we have previously detected, except for soils from Mount Fleming (Aislabie *et al*. 2006b). Similar to the Danum and Isca soils, those from Mount Fleming were highly developed with high EC, very low levels of organic carbon and nitrogen and alkaline pH (Aislabie *et al*. 2006b). Estimates of total counts and numbers of culturable heterotrophs in cold desert soils of the Darwin Mountains region are comparable with those reported for Atacama hot desert soil (Connon *et al*. 2007, Lester *et al*. 2007).

The ratio of total counts to culturable counts ranged from 32–8.1 x 10^4. It appears that a higher percentage of the microbial population in the Hatherton soils was viable compared with that of the Britannia and Danum soils. This may be because many of the viable cells present in the Britannia and Danum soil do not grow on R2A agar plates. Alternatively, estimates of total counts calculated from PLFA

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may be too high, due to preservation of PLFA in the arid soils. Although PLFA is commonly used to estimate viable biomass in soils and it is assumed that enzymes rapidly hydrolyse the phosphate groups upon cell death, this assumption may not apply to desert soils (Connon *et al*. 2007).

As for other Antarctic soils (Aislabie *et al*. 2006b, Yergeau *et al*. 2009), soil microbes that dominate soils of the Lake Wellman region are probably heterotrophs that derive carbon and energy from the oxidation of fixed carbon. Heterotrophic bacteria can be introduced into these soils with windblown microbial mats from nearby lakes or ponds, or with wind from even further afield (Vincent 2000). Historically, microbes could also have been introduced from subglacial environments. There is an increasing body of evidence that diverse bacterial communities are resident in subglacial environments where they participate in chemical weathering processes such as the dissolution of silicate minerals and cycling of sulphur (Wadham *et al*. 2010). As the glaciers retreated the exposed drift material with associated microbial communities could provide inocula for developing soils.

Gram-negative heterotrophic bacteria isolated from high latitude soils have been assigned to the phyla Bacteroidetes and Proteobacteria (Aislabie *et al*. 2006a). Bacteroidetes are frequently reported to produce pink or red pigmented colonies, including members of the genera *Hymenobacter* which produce extra-cellular enzymes such as lipases, proteases and phosphatases (Aislabie *et al*. 2006a) and Proteobacteria, including the yellow-pigmented heterotroph *Brevundimonas* (Aislabie *et al*. 2006a), a close relative of which was recently reported to be radiation resistant (Dartnell *et al*. 2010).

Among the gram-positive heterotrophic bacteria commonly isolated from high latitude soils is *Arthrobacter* from La Gorce mountains (1800 m altitude and 86°30'S) and Mount Howe (2800 m altitude and 87°12'S) (Cameron *et al*. 1971, Cameron 1972, Aislabie *et al*. 2006a). Characteristics of *Arthrobacter* that would support their survival in Antarctic soils include the ability to metabolise a wide range of substrates including sugars and amino acids, growth at low temperature, and tolerance of freeze-thaw, high pH and salt. Furthermore, colonies of *Arthrobacter* are often highly pigmented, with both yellow and red pigmented isolates reported from Antarctic sources (Aislabie *et al*. 2006a).

Many of the bacteria that grew on the soil isolation plates were pigmented. In heterotrophic bacteria, pigmentation is often due to the production of carotenoids or xanthophylls. These pigments may play various roles in the survival of bacteria in Antarctic soils, such as maintenance of membrane integrity and stability or absorption of UV radiation to provide protection from oxidative stress (Klassen 2010).

Influence of soil on microbial communities

Ordination revealed that key influences on the microbial composition of soils of the Lake Wellman region are soil development, and soil water content, organic carbon and pH (Fig. 2a & b).

A progressive increase over time in the development of soils at Lake Wellman is reflected by a steady breakdown in surface boulders from chemical and physical weathering (i.e. weathering stage, Table I), an increase in staining from release of iron from iron-bearing minerals such as pyroxenes, hornblende, and biotite (Table II), and an increase in salt stage, visible salts (Table II) and water soluble salts (Table III). Dominant ions in soil:water extracts were Ca and SO_4, which, along with NO_3, increased markedly with age. Although the soil increased in development from Hatherton to Isca drifts, in 15 of 16 instances they were classified as Typic Haplorthels. Soils with salt-enriched or salt-cemented horizons were absent in the Lake Wellman area, but are common in the McMurdo Dry Valleys on landforms that are of mid-Quaternary and older age (Bockheim & McLeod 2006).

Water availability in the soils was probably low due to low rates of precipitation and freezing temperatures. While precipitation may cover the landscape with snow up to several centimetres, most of it sublimates within hours or days in summer with little penetration into the soil, contributing to the accumulation of salts in the soil layer below the desert pavement (Table III), which is especially prevalent in older Danum and Isca soils. However, some of the snow that fell may be redistributed in the landscape by wind, as evidenced by the build-up of snow patches on the leeward side of terminal moraines or in troughs of high-centred polygons. Melting of the snow patches could provide a significant source of soil moisture for nearby soil microbial communities and impact on soil properties (Ayres *et al*. 2010). There is evidence for considerable recharge of the ice-cemented layer from snowmelt and for thermokarst on Hatherton and Britannia drifts.

However, overall the soil water content was low, and osmotic and matric forces limited the availability of water and consequently microbial growth and activity. The high EC values, particularly in the layer below the desert pavement of the older soils, indicated that salts will contribute to osmotic stress.

Availability of liquid water and organic carbon are considered the main influences on heterotrophic bacterial growth and activity in Antarctic soils (Barrett *et al*. 2006). Liquid water is essential for the hydration of biomolecules and as a solvent for biochemical processes. As for the Dry Valleys, potential sources of carbon would include *in situ* autotrophic activity by mosses, lichens, cyanobacteria and microalgae, spatial subsidies from microbial mats from modern lakes or ponds or coastal regions carried to the soils by aeolian dispersal and legacy carbon derived from ancient glacial tills and lakes (Hopkins *et al*. 2009). Contribution to soil carbon from cyanobacterial mats was probably greater in Hatherton soils near Lake Wellman, where meltwater on the margins may sometimes be available for autotrophic activity (Webster-Brown *et al*. 2010). Bockheim *et al*. (1989)

retrieved microbial cyanobacterial mat material within Hatherton soil profiles near Lake Wellman that, when carbon dated, was aged at 9320 yr BP. However, we and others did not observe microbial mats on the edge of Lake Wellman, or indeed lithic communities, lichens or mosses in the surrounding area (Webster-Brown *et al*. 2010). It is possible that organic carbon could be added to the soils in windblown material from nearby or closer to the coast. Cyanobacterial mats were reported in ponds of Grant Valley in the Darwin Mountains and Diamond Hill/Brown Hills (Webster-Brown *et al*. 2010).

The provenance of organic carbon in soils of the Lake Wellman region was not investigated. Much of the existing carbon is possibly derived from soil microbes as was reported for soils of the Garwood Valley (Feng *et al*. 2010). Once the microbes die they may be turned over when environmental conditions permit (Hopkins *et al*. 2009). Estimates of the residence time of soil carbon in Dry Valley soils range from 52–123 years (Hopkins *et al*. 2009). Soil carbon declined both with age and soil depth and we speculate that carbon inputs to the soils of the Lake Wellman region may be low, leading to a decline in microbial biomass and diversity over time.

For long-term survival and functioning in the soils of Lake Wellman, microbes need to be efficient in uptake of low concentrations of carbon and be tolerant of desiccation. Other factors that influence soil microbes in these soils include prolonged exposure to both low and fluctuating temperatures, radiation and low levels of nutrients (N and P). As in this study, pH was often shown to influence the structure of soil microbial communities of both temperate and polar regions (Aislabie *et al*. 2008, Lauber *et al*. 2009). Lauber *et al*. (2009) suggested that the influence of pH on the structure of the soil microbial community could be attributed to: 1) the direct or indirect modification on soil properties by pH such as nutrient availability, solubility of cations, and characteristics of soil carbon, and/or 2) pH imposing physiological constraints on bacteria which alters their competitiveness and hence ability to grow and survive outside a certain pH range.

Conclusions

A sharp decline in microbial biomass was detected along the soil chronosequence investigated in this study. Microbial biomass measured as PLFA and numbers of culturable heterotrophs were significantly higher in Hatherton soils compared with Britannia, Danum and Isca soils. This observation is at odds with current understanding of the relation between soil development and microbial biomass in temperate regions. On the basis of this study we propose that in the absence of, or low levels of, organic carbon input into soil, extant microbial communities, both microbial biomass and diversity, in exposed soils declines over time, leading to selection of microbes best able to survive long periods of exposure to Antarctic conditions.

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