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NOTE

Bacterial Diversity in Ornithogenic Soils Compared to Mineral Soils on King George Island, Antarctica§

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In the Narębski Point area of King George Island of Antarctica, ornithogenic soils form on land under Chinstrap and Gentoo Penguin rookeries. The purpose of this study was to compare the bacterial community compositions in the gradient of contamination by penguin feces; mineral soil with no contamination, and soils with medium or high contamination. The discrimination between mineral soils and ornithogenic soils by characterization of physicochemical properties and bacterial communities was notable. Physicochemical analyses of soil properties showed enrichment of carbon and nitrogen in ornithogenic soils. *Firmicutes* were present abundantly in active ornithogenic soils, *Bacteroidetes* and *Proteobacteria* in a formerly active one, and several diverse phyla such as *Proteobacteria*, *Actinobacteria*, and *Acidobacteria* in mineral soils. Some predominant species belonging to the *Firmicutes* and *Gammaproteobacteria* may play an important role for the mineralization of nutrients in ornithogenic soils. Results of this study indicate that dominant species may play an important role in mineralization of nutrients in these ecosystems.

Keywords: 16S rRNA, pyrosequencing, penguin rookeries, Narębski Point, Barton Peninsula

Soils existing on ice-free areas of continental Antarctica are generally arid of organic matter. On the other hand, the ornithogenic soils of the Antarctic coastal areas are enriched with a source of nutrients for terrestrial ecosystems surrounding penguin rookeries (Ugolini, 1970). Relatively warmer temperature and higher water availability in this habitat may enhance an intense cryoturbation, with mixing of bird detritus within the soil. In addition, the mineralization of this higher amount of organic matter can be biologically accelerated by bacterial growth.

These nutrient-rich soils include enormous microbial populations with 2×10^{10} cells/g by direct microscopic counts (Bowman *et al*., 1996) and their activity is notably increased during the summer breeding season (Barrett *et al*., 2006). Many scientists have contributed to the cultivation of bacteria, including novel species such as *Psychrobacter uratiorans*, *Psychrobacter frigidicola* from Vestfold Hills (Bowman *et al*., 1996), *Arthrobacter gangotriensis* and *Arthrobacter kerguelensis* from Kerguelen island (Gupta *et al*., 2004), *Agrobacterium radiobacter*, *Pasteurella* sp., *Pseudomonas fluorescens*, and *Sphingobacterium multivorum* from the Point Thomas rookery, Admiralty Bay (Zdanowski *et al*., 2005).

After the development of molecular approaches, some studies on the bacterial diversity in terrestrial ecosystems on Antarctica have been reported. Mineral soils from McMurdo Dry Valleys accommodated *Acidobacteria*, *Actinobacteria* and *Bacteroidetes* (Cary *et al*., 2010) and those from the Admiralty Mountains in northern Victoria Land contained members of the *Deinococcus-Thermus* group and *Xanthomonas* of the *Gammaproteobacteria* (Niederberger *et al*., 2008). On the other hand, actively penguin-colonized ornithogenic soils contained *Firmicutes* and the *Gammaproteobacteria*/*Psychrobacter* at Cape Hallett and Cape Bird, while at formerly penguin-colonized sites at Cape Hallett, around the Ross Sea region of Antarctica, contained *Actinobacteria* and *Xanthomonas* of the *Gammaproteobacteria* (Aislabie *et al*., 2009).

The Narębski Point area (62°13′S, 58°46′W), Antarctic Specially Protected Area (ASPA), on the southern coast of the Barton peninsula of King George Island of the maritime Antarctic region has a large concentration of gentoo (*Pygoscelis papua*, 1,800 pairs) and chinstrap (*Pygoscelis antarctica*, 3,000 pairs) penguins. In order to understand bacterial diversity in ornithogenic and mineral soils around this area, we conducted pyrosequencing based on 16S rRNA genes from mineral and ornithogenic soils around the Narębski Point.

Soil samples were taken during the austral summer of 2010/11 from the Narębski Point area of King George Island (62°14′S, 058°46′W) (Table 1). The sampling location con-

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sisted of three points, mineral soil and formerly- and actively penguin-colonized ornithogenic soil. These points were located within 40 m of each other. Mineral soils near skua nests were collected at two depths (surface to 5 cm depth as the upper layer denoted as MS-U and from 5 cm to 10 cm depth as the lower layer, MS-L). One formerly penguin-colonized ornithogenic soil (OS-F) with relatively high moisture content and two highly contaminated ornithogenic soils that are actively colonized by penguins (OS-A1 and OS-A2) were collected. The samples were homogenized and stored at -20°C for later analysis.

Soil samples for grain size analysis were reacted with H_2O_2 to remove the organic matter. The grain size distribution of grains larger than 63 mm (sand and gravel) was determined by dry sieving, and the finer grains (silt and clay) were determined by using Micrometrics Sedigraph 5100. For geochemical analyses of C and N, the powdered samples were dried in an oven at 105°C to remove H_2O and then cooled at room temperature in a desiccator. The total carbon (TC) and nitrogen (TN) contents were analyzed using a FlashEA 1112 elemental analyzer by measuring CO_2 and NO_2 generated by combustion at 950°C. The total inorganic carbon (TIC) content was analyzed using a UIC CO_2 coulometer by measuring the CO_2 gas generated by the reaction of approximately 50 mg powdered bulk samples with 42.5% phosphoric acid at 80°C for 10 min. The total organic carbon (TOC) content was determined by the difference between the TC and the TIC content.

All ornithogenic soils showed significantly higher TN, TC, and TOC contents than mineral soils (Table 1). Actively penguin-colonized ornithogenic soils had relatively higher levels of TIC than the other three sites. Carbon to nitrogen (C/N) ratio ranged from 1.06 to 11.66, with significantly larger C/N ratio in the formerly penguin colonized ornithogenic soil (OS-F). All soils were composed mainly of sand-size fraction (>50%). The soil type in mineral soils was gravelly muddy sand, whereas the sample of ornithogenic soils was sandy gravel or gravelly sand. Although our findings may have a limitation because of no replicate soil samples, previous studies also found a high concentration

Table 1. Physicochemical characteristics of soil samples. MS-U, mineral soil – upper layer; MS-L, mineral soil – lower layer; OS-F, formerly penguin-colonized ornithogenic soil; OS-A, actively penguin-colonized ornithogenic soil

Sample	Latitude	Longitude	Chemical components						Composition (%)				Textural parameters				Soil Type
			TN (%)	TC (%)	TIC (%)	TOC (%)	$CaCO_3$ (%)	C/N ratio	Gravel	Sand	Silt	Clay	Mean	Sorting	Skewness	Kurtosis	
MS-U	62° 14′ 08.5″ S	058° 46′ 15.7″ W	0.060	0.313	0.133	0.180	1.108	3.02	12.49	52.93	17.20	17.37	3.00	4.14	0.51	0.75	gmS[a]
MS-L	62° 14′ 08.5″ S	058° 46′ 15.7″ W	0.070	0.194	0.120	0.074	1.000	1.06	20.20	51.29	15.16	13.36	2.25	4.18	0.42	0.89	gmS
OS-F	62° 14′ 09.6″ S	058° 46′ 32.7″ W	2.526	29.603	0.135	29.467	1.125	11.66	42.01	55.00	1.71	1.28	-0.33	1.97	0.19	0.88	sG[b]
OS-A1	62° 14′ 10.0″ S	058° 46′ 33.7″ W	4.290	13.164	0.350	12.813	2.918	2.99	33.86	59.90	3.56	2.67	0.15	2.22	0.34	1.21	sG
OS-A2	62° 14′ 10.0″ S	058° 46′ 33.7″ W	6.954	20.771	0.376	20.396	3.129	2.93	25.23	67.44	4.19	3.14	0.41	2.36	0.34	1.44	gS[c]
Min			0.060	0.194	0.120	0.074	1.000	1.06	12.49	51.29	1.71	1.28	-0.33	1.97	0.19	0.75	
Max			6.954	29.603	0.376	29.467	3.129	11.66	42.01	67.44	17.20	17.37	3.00	4.18	0.51	1.44	
Average			2.780	12.809	0.223	12.586	1.856	4.33	26.76	57.31	8.36	7.56	1.09	2.97	0.36	1.03	
STD			2.937	12.853	0.128	12.811	1.070	4.18	11.53	6.52	7.23	7.29	1.44	1.09	0.12	0.28	

gmS[a], gravelly muddy sand; sG[b], sandy gravel; gS[c], gravelly sand.

Table 2. Summary of pyrosequencing results and diversity indices

Samples	Original pyrosequencing libraries						After subsampling								
	Total reads	Bacteria	Eukaryota	Chimera	Unmatched[a]	OTUs	Coverage	OTUs	Chao1	ACE	Shannon	NpShanon	Simpson	ShannonEven	Simpsoneven	Coverage
MS-U	9285	8706	516	28	35	1220	0.94	741	1296	1654	5.81	6.01	0.006	0.88	0.210	0.87
MS-L	3042	2882	153	6	1	596	0.90	589	934	1278	5.10	5.32	0.027	0.80	0.063	0.90
OS-F	14719	14603	8	39	69	1094	0.97	521	889	1201	4.97	5.16	0.019	0.80	0.102	0.91
OS-A1	5326	5324	0	55	2	233	0.98	180	285	364	3.51	3.60	0.064	0.68	0.087	0.97
OS-A2	10811	10709	0	100	2	255	0.99	160	246	273	3.30	3.39	0.100	0.65	0.064	0.98
All samples	43183	42169	677	228	109	2632	0.98									
AVG	8637	8446	135	46	22	680	0.96	438	730	954	4.54	4.70	0.043	0.76	0.105	0.93
MIN	3042	2886	0	6	1	233	0.90	160	246	273	3.3	3.39	0.006	0.65	0.063	0.87
MAX	14719	14603	516	100	69	1220	0.99	741	1296	1654	5.81	6.01	0.100	0.88	0.210	0.98

Unmatched[a]: There are no significant found in EzTaxon-e and GenBank.

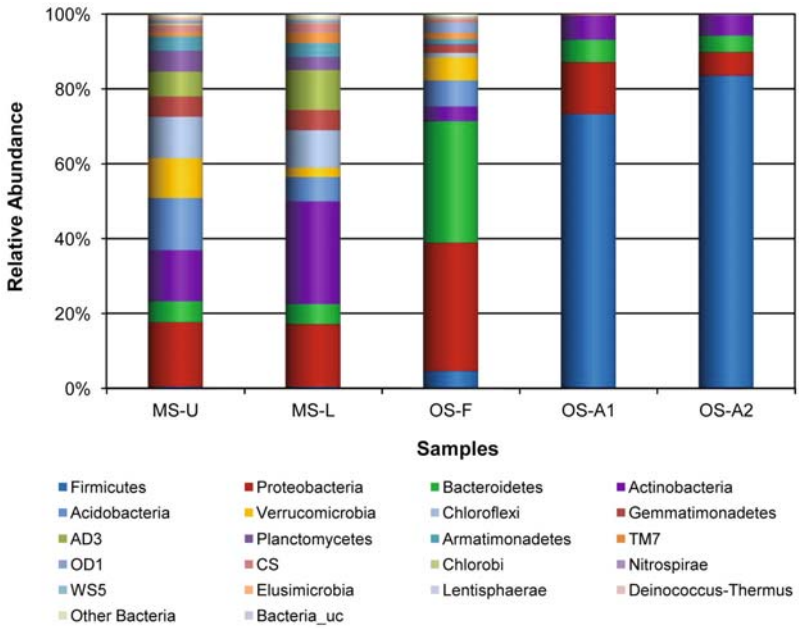

Fig. 1. Relative abundance of bacterial communities at the phylum level. Other Bacteria contain phyla detected at less than 1%, including *Lentisphaera*, GN02, *Deinococcus-Thermus*, SR1, NKB19, TM6, *Fibrobacteres*, OP11, SM2F11, *Fusobacteria*, *Synergistetes*, WS6, *Chlamydiae*, *Spirochaetes* and *Tenericutes*. Bacteria_uc means unclassified bacteria.

of organic carbon in ornithogenic soils (Simas *et al*., 2007; Zhu *et al*., 2009; Smith *et al*., 2010).

Genomic DNA from 0.3 g soil was extracted using an MPBio DNA kit (MPBio) according to the manufacturer's guidelines, followed by PCR amplification using barcoded primers (Na *et al*., 2011). The DNA sequencing was performed by DNALink Inc. (Korea) using the 454 GS FLX Titanium Sequencing System (Roche).

Pre-treatment of individual pyrosequence reads was performed using PyroTrimmer (http://pyrotrimmer.kobic.re.kr) (Oh *et al*., 2012). All reads from different soil samples were separated by unique barcodes. The barcode, linker, and PCR primers were removed from both ends of the reads. Then the reads over 250 bp were subjected to quality controls. The maximum primer mismatch allowed 3 nucleotides, 5 of window size and 20 of average quality value cutoff in 3′ end

OUT	MS-U	MS-L	OS-F	OS-A1	OS-A2	Phylum	Class	Order	Family	Genus	Species	Acc No	Similarity
OTU_0001	0.0	0.0	0.0	18.6	28.5	Firmicutes	Clostridia	Clostridiales	Thermohalobacter_f	*Thermohalobacter_f_uc*		FR749894	0.91
OTU_0002	0.6	0.5	7.7	0.0	0.0	Bacteroidetes	Sphingobacteria	Sphingobacteriales	Chitinophagaceae	*Ferruginibacter*	AY218615_s	AY218615	0.98
OTU_0003	0.0	0.0	0.0	5.8	6.9	Firmicutes	Bacilli	Bacillales	Bacillaceae	GQ068997_g	GQ068997_g_uc	GQ068997	0.96
OTU_0004	0.0	0.0	6.8	0.0	0.0	Bacteroidetes	Bacteroidia	Bacteroidales	FJ437992_f	FJ437992_g	FJ437992_s	FJ437992	0.98
OTU_0005	0.0	0.0	0.0	6.7	4.8	Firmicutes	Clostridia	Clostridiales	Tissierella_f	*Tissierella_f_uc*		X80227	0.92
OTU_0006	0.0	0.0	0.0	6.1	4.6	Firmicutes	Clostridia	Clostridiales	Tissierella_f	Tissierella_f_uc		X80833	0.90
OTU_0007	0.0	0.0	0.5	6.7	2.8	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Moraxellaceae	*Psychrobacter*	*Psychrobacter faecalis*	AJ421528	0.99
OTU_0008	0.0	0.0	0.3	4.4	3.2	Bacteroidetes	Bacteroidia	Bacteroidales	Porphyromonadaceae	EF559089_g	EF559089_g_uc	EF559089	0.96
OTU_0009	0.0	0.0	0.0	1.6	4.8	Firmicutes	Bacilli	Lactobacillales	Carnobacteriaceae	Carnobacteriaceae_uc		AF445248	0.91
OTU_0010	0.0	0.0	0.0	4.2	3.3	Firmicutes	Clostridia	Clostridiales	Thermohalobacter_f	Thermohalobacter_f_uc		FR749894	0.92
OTU_0011	2.1	13.4	0.0	0.0	0.0	Actinobacteria	Actinobacteria_c	Micrococcales	Intrasporangiaceae	*Oryzihumus*	GQ397075_s	GQ397075	0.97
OTU_0012	0.0	0.0	0.0	4.2	3.3	Actinobacteria	Actinobacteria_c	Propionibacteriales	Propionibacteriaceae	*Tessaracoccus*	DQ521508_s	DQ521508	0.98
OTU_0013	0.0	0.0	3.7	0.0	0.0	Proteobacteria	Betaproteobacteria	Sterolibacteriun_o	Sterolibacterium_f	*Sulfuritalea*	*Sulfuritalea_uc*	4P000070	0.96
OTU_0014	0.2	0.2	3.3	0.0	0.0	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	*Polaromonas*	*Polaromonas jejuensis*	EU030285	0.98
OTU_0015	3.8	4.2	0.0	0.0	0.0	AD3	AD3_c	AD3_o	AD3_f	EU335368_g	EU335368_g_uc	AY913277	0.94
OTU_0016	0.0	0.0	0.0	4.5	2.0	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	*Pseudomonas*	*Pseudomonas caeni*	EU620679	0.98
OTU_0017	0.0	0.0	0.0	2.8	2.8	Firmicutes	Clostridia	Clostridiales	Thermohalobacter_f	*Thermohalobacter_f_uc*		FR749894	0.91
OTU_0018	0.0	0.0	0.0	2.7	2.7	Firmicutes	Clostridia	Clostridiales	Peptococcaceae	*Desulfonispora*	*Desulfonispora_uc*	Y18214	0.94
OTU_0019	0.0	0.0	2.6	0.0	0.0	Proteobacteria	Gammaproteobacteria	Xanthomonadaes	Xanthomonadaceae	*Rhodanobacter*	*Rhodanobacter fulvus*	AB100608	0.99
OTU_0020	0.0	0.1	2.6	0.0	0.0	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	*Curvibacter*	FJ660572_s	FJ660572	0.97
OTU_0021	0.0	0.0	2.5	0.0	0.0	Bacteroidetes	Bacteroidia	Bacteroidales	Prolixibacter_f	AB240270_g	AY188321_s	AY188321	0.97
OTU_0022	0.2	0.3	2.2	0.0	0.0	Bacteroidetes	Sphingobacteria	Sphingobacteriales	Chitinophagaceae	*Ferruginibacter*	*Ferruginibacter_uc*	EU861917	0.96
OTU_0023	0.5	0.7	1.9	0.0	0.0	Acidobacteria	Acidobacteria_c	Acidobacteriales	Acidobacteriaceae	*Edaphobacter*	EU861948_s	EU861948	0.98
OTU_0024	2.0	0.0	0.0	0.0	0.0	AD3	AD3_c	AD3_o	EF018548_f	EF019899_g	EF019899_s	EF019899	0.99
OTU_0025	0.0	0.0	0.0	2.3	1.9	Firmicutes	Clostridia	Clostridiales	Thermohalobacter_f	*Thermohalobacter_f_uc*		FR749894	0.92
OTU_0026	0.0	0.2	2.1	0.0	0.0	Acidobacteria	Acidobacteria_c	Acidobacteriales	Acidobacteriaceae	*Edaphobacter*	*Edaphobacter_uc*	FJ466432	0.97
OTU_0027	0.0	0.0	0.0	1.6	2.0	Firmicutes	Clostridia	Clostridiales	Clostridiales_uc			GQ014615	0.89
OTU_0028	0.0	0.0	0.0	2.1	1.5	Firmicutes	Clostridia	Clostridiales	Clostridiales_uc			EU250961	0.85
OTU_0029	0.0	0.0	0.0	2.1	1.4	Firmicutes	Clostridia	Clostridiales	Clostridiales_uc			X96956	0.89
OTU_0030	0.0	0.0	1.7	0.0	0.0	Proteobacteria	Betaproteobacteria	Nitrosomonadales	Gallionellaceae	*Gallionella*	DQ228376_s	DQ228376	0.99

0 0.5 1.0 5.0 10.0 15.0

Fig. 2. Heat map representing the most abundant thirty operational taxonomic units (OTUs) through all samples. Percentages, with the color code grading from blue to white in the map, indicate the relative abundances of the highest to the lowest.

trimming and 25 of average quality value cutoff for full length sequence in quality filtering. The qualified sequence reads were clustered using the program TBC (Lee *et al.*, 2012) 97% cutoff values as an OTU. Chimera check was performed using UCHIME (Edgar *et al.*, 2011) with the *h* value set at 1.0 for the minimum score threshold. Representative OTUs were assigned taxonomically using EzTaxon-e database (http://eztaxon-e.ezbiocloud.net) (Kim *et al.*, 2012). Diversity analysis using Mothur (Schloss *et al.*, 2009) was carried out, after random subsampling of 2,882 reads fitting into the lowest number of sequence reads in order to reduce the bias of variable pyrosequencing library sizes (Gihring *et al.*, 2012). A total of 42,169 bacterial sequence reads, 8,706 (MS-U) and 2,882 (MS-L) from mineral soils and 14,603 (OS-F), 5,324 (OS-A1) and 10,709 (OS-A2) from ornithogenic soils, were recovered with high quality by pyrosequencing 16S rRNA genes (Table 2). These were clustered into 2,632 OTUs, with the highest number in MS-U (1,220) and the lowest number in OS-A1 (233). Comparing the bacterial diversity after subsampling, several diversity indices indicated the highest diversity in MS-U and the lowest diversity in OS-A2.

As a result of the bacterial community comparison, phylotypes representing 42 phyla were recovered from soil samples, and a significant differentiation in phylum levels with the gradient of contamination by penguin droplets was shown (Fig. 1). At the phylum level, *Firmicutes* accounted for the vast majority of reads with 32.2% of total reads. This phylum was prevalent in the actively penguin-colonized ornithogenic soils (73.3% in OS-A1 and 83.5% in OS-A2). A similar finding, that *Firmicutes* was the most dominant phylum in the actively penguin-colonized soils was reported for samples taken at Cape Hallett and Cape Bird in Victoria Land (Aislabie *et al.*, 2009). Additionally, this phylum is widely predominated in the feces or the intestines of birds (Scupham, 2007; Lu *et al.*, 2008). The second most dominant phylum was *Proteobacteria*, which was found in all samples with 34.3% in OS-F, 17.2% in MS-U, 16.7% in MS-L, 13.8% in OS-A1 and 6.3% in OS-A2. Interestingly, *Bacteroidetes* was abundant in the OS-F sample, making up 32.5% of the total reads. Aislabie and collegues (2009) also observed ribotypes assigned to the *Bacteroidetes*, but with small proportions.

Minor numbers of diverse phyla were observed throughout all samples, including *Actinobacteria* (8.3%), *Acidobacteria* (5.7%), *Verrucomicrobia* (4.5%), *Chloroflexi* (3.4%), *Gemmatimonadetes* (2.2%), *Planctomycetes* (1.5%), *Armatinomadetes* (1.5%), *Chlorobi* (0.2%), *Nitrosospirae* (0.2%), *Elusimicrobia* (0.1%), *Lentisphaera* (0.1%) and *Deinococcus-Thurmus* (0.1%), and phyla with less than 0.1% including *Spirochaetes, Fibrobacteres*, *Fusobacteria*, *Tenericutes, Chlamydiae*, and *Synergistetes*, as well-known phyla. In addtion, many sequences were assigned as candidate phyla to AD3 (2.1%), TM7 (1.0%), OD1 (1.0%), CS (0.8%), WS5 (0.1%), DQ404828_p, JX172748_p, BRC1, SR1, TM6, GN02, OP11, MATCR, OP8, WS6, 4P001694_p, DQ499300_p, FJ516972_p, GN04, 4P001887_p and EF688356_p.

Analyzing with a fine-scale resolution at the OTU level (Fig. 2 and Supplementary data Fig. S1), certain discrimination between mineral soils and ornithogenic soils was found. The bacterial communities prevailing in ornithogenic soils

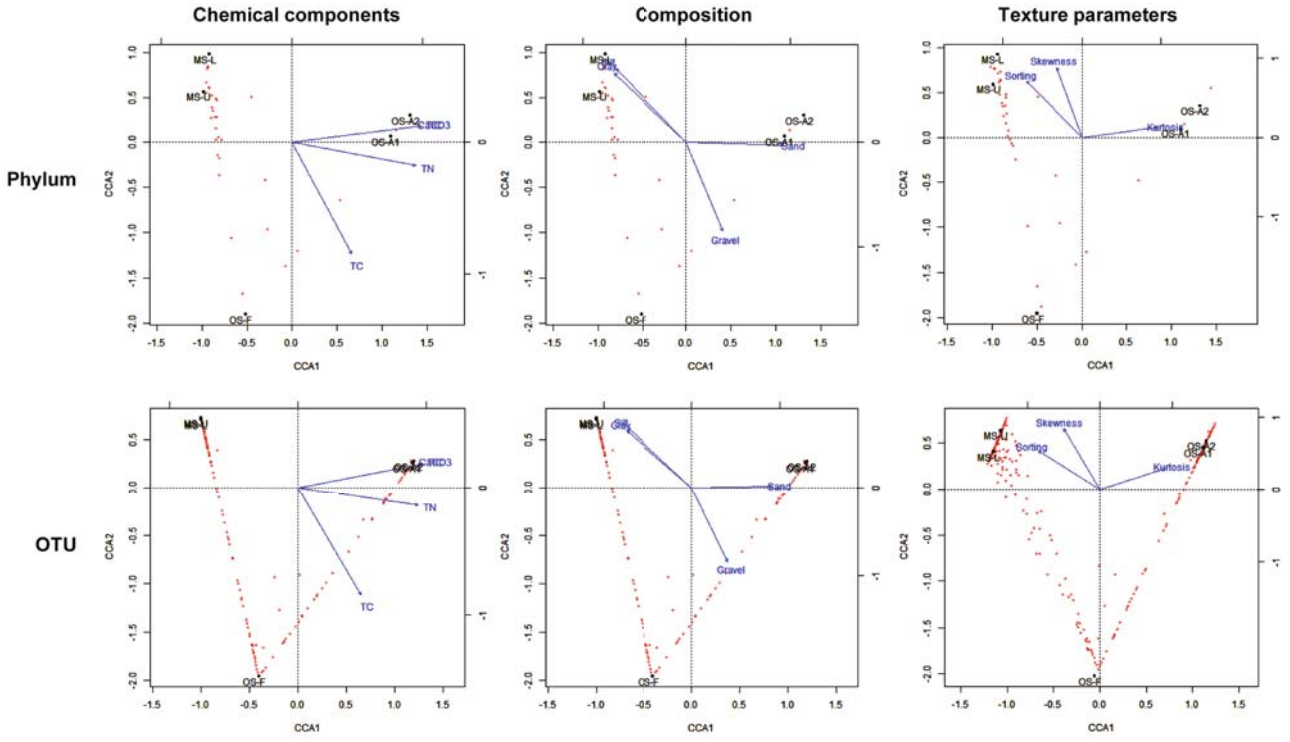

Fig. 3. **Canonical correlation analysis (CCA) using the bacterial frequencies at the phylum (upper) and OTU (lower) level and the environmental factors classified by chemical components (left), composition (middle) and texture parameters (right).**

depended on the influence of nutrients from the penguin excrement. In this study, the genera *Thermohalobacter*, *Tissierella*, *Carnobacteriaceae*, *Desulfonispora* of *Firmicutes* and the genera *Psychrobacter* and *Pseudomonas* of *Gammaproteobacteria* were dominant in actively penguin-colonized soils, whereas the genus *Ferruginibacter* of *Bacteroidetes*, the genera *Sulfuritalea* and *Polaromonas* of *Betaproteobacteria* and the genus *Rhodanobacter* of *Gammaproteobacteria* dominated soil of formerly colonized sites. This suggests that these bacterial groups are adapted to environments with a high concentration of nutrients. Several studies have demonstrated that *Psychrobacter* were dominant in uric acid degradation, as revealed with isolates (Bowman *et al*., 1996; Zdanowski *et al*., 2005) and clone libraries (Aislabie *et al*., 2009) in ornithogenic soils. It has also been reported that a dominant ribotype similar to some species of *Firmicutes*, which can utilize uric acid and purines, was observed to be abundant at cape Hallett (Aislabie *et al*., 2009).

The effect of abiotic soil properties on the bacterial community was appraised by canonical correlation analysis (CCA) using the software R (www.R-project.org) (González *et al*., 2008). We found strong correlations between the bacterial community and soil physicochemical properties, in good agreement with previous studies (Fig. 3) (Aislabie *et al*., 2009; Smith *et al*., 2010). Bacterial frequencies at the phylum and OTU level correlated with the environmental factors with chemical components, composition and texture parameters. TN, TIC, $CaCO_3$, sand and kurtosis were linked to the actively penguin-colonized ornithogenic soils. In contrast, silt, clay and skewness were correlated with mineral soils. The contribution of OTUs to the separation was not evident; rather, a combination of several peaks better explained the difference of the samples.

Taken all together, bacterial communities and physicochemical properties were significantly discriminated between ornithogenic soils and mineral soils; however, the bacterial function in this habitat is still not clear, even though we have information on bacterial communities and physicochemical properties. Some studies have demonstrated the notable effects of global warming potential by greenhouse gas emission in this area (Sun *et al*., 2002; Zhu *et al*., 2009). These findings give a basis for future studies on microbial functions in this ecosystem, linking with fine-scale fraction of organic matters and gas flux.

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