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ORIGINAL PAPER

The short-term effects of surface soil disturbance on soil bacterial community structure at an experimental site near Scott Base, Antarctica

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Abstract Humans are visiting Antarctica in increasing numbers, and the ecological effect of rapid soil habitat alteration due to human-induced physical disturbance is not well understood. An experimental soil disturbance trial was set up near Scott Base on Ross Island, to investigate the immediate and short-term changes to bacterial community structure, following surface soil disturbance. Three blocks, each comprising an undisturbed control, and an area disturbed by removing the top 2 cm of soil, were sampled over a time series (0, 7, 14, 21, and 35 days), to investigate changes to bacterial community structure using DNA profiling by terminal restriction fragment length polymorphism. The simulated disturbance did not cause any major shifts in the structure of the bacterial communities over the 35-day sampling period. Ordination showed that the bacterial community composition correlated strongly with soil EC ($R^2 = 0.55$) and soil pH ($R^2 = 0.67$), rather than the removal of the top 2 cm of surface material. Although the replicate blocks were visually indistinguishable from one another, high local spatial variability of soil chemical properties was found at the study site and different populations of bacterial communities occurred within 2 m of one another, within the same landscape unit. Given the current knowledge of the drivers of bacterial community structure, that is, soil EC, soil pH, and soil moisture content, a follow-up investigation incorporating DNA and RNA-based analyses over a time frame of 2–3 years would lead to a greater understanding of the effects of soil disturbance on bacterial communities.

Keywords Antarctica · TRFLP · Bacteria · Human disturbance · Soil physiochemical properties

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Introduction

Approximately 23,000 km^2, or half of Antarctica's ice-free, and soil forming, areas are found in the Ross Sea region of Antarctica (Fox and Cooper 1994; British Antarctic Survey 2005). Ross Sea region ice-free areas are found discontinuously distributed around the coastal margins and in the McMurdo Dry Valleys, the largest continuous expanse of ice-free ground. Soil ecosystems in the Ross Sea region terrestrial environment are characterised by low and fluctuating temperatures, high aridity, low precipitation, low moisture availability, desiccating winds, high exposure to UV radiation, and low levels of organic matter (Campbell and Claridge 1987; Wynn-Williams 1990). Despite the hostile environment, Antarctic mineral soils can harbour bacterial numbers of up to 10^9 cells/g dry soil (Bölter 1995; Aislabie et al. 2006, 2008; Xiao et al. 2007; Cannone et al. 2008; Ganzert et al. 2011).

Ross Sea region soils comprise a surface desert pavement and seasonally thawed active layer overlying permafrost. Mature, undisturbed Ross Sea region desert pavements are typically characterised by a closely packed layer of gravel, cobble, and boulder-sized rock material, which depending on its age, can be ventifacted, and coated with desert varnish (Campbell and Claridge 1987;

Bockheim 2010). Desert pavement clasts are embedded into a finer matrix, and their undersides are often coated in salts. The soils beneath are alkaline, generally lack structural development and coherence, and are coarsely textured with very low organic matter contents (Campbell and Claridge 1987; Balks et al. 2002; Aislabie et al. 2004). Soils of the coastal regions, such as Scott Base, contain ice-cemented permafrost (Balks et al. 2002; Bockheim and McLeod 2006), and predominantly NaCl and $NaSO_4$ salts consistent with direct marine input (Campbell and Claridge 1987; Campbell et al. 1998). Mean annual soil temperatures in the Ross Sea region range from −15 °C to −40 °C; however, during the continuous daylight of the summer months, surface soils are subject to large daily temperature fluctuations and near-surface soil temperatures can reach 20 °C (Balks et al. 2002). The lack of plant roots and limited available water means that carbon and nutrients are not translocated easily down the soil profile, and as a result, the dominant food web, including bacteria, is limited to the near-surface environment (Wall and Virginia 1999).

In polar climates, a high spatial variability in soil abiotic factors can exist, and the structure of bacterial communities has been observed to be controlled predominantly by soil pH (Yergeau et al. 2007; Aislabie et al. 2008, 2011; Chong et al. 2012), soil salinity (Aislabie et al. 2006), soil moisture (Aislabie et al. 2006; Barrett et al. 2006; Cary et al. 2010; Ganzert et al. 2011) and nutrient availability (Barrett et al. 2006; Hopkins et al. 2006; Sparrow et al. 2011). Soil pH is thought to influence nutrient availability, soil carbon, and soil cation solubility (Lauber et al. 2009), as well as to influence bacteria competitiveness, and their ability to grow and survive outside optimum soil pH (Lauber et al. 2009). Microbes are sensitive to the concentration of soluble salts in soils, and past studies have shown that high salinity in soil moisture reduces microbial biomass (Wichern et al. 2006), amino acid uptake, and protein synthesis (Norbek and Blomberg 1998) and reduces soil respiration (Gennari et al. 2007). Ross Sea region soils contain high levels of soluble salts, and small pulses of water from a snowfall event (Ball et al. 2011, 2012), or an influx resulting from human disturbance to underlying permafrost (such as the removal of the permafrost-insulating soil active layer and consequent thawing of the salt-rich ice contained in the upper part of the permafrost), can create unfavourable habitats for soil biota, releasing salts into the soil profile, or accumulating salts at the ground surface as salt efflorescences (Campbell et al. 1993, 1998; Balks et al. 1995). Microbes have semi-permeable membranes capable of rapidly equilibrating with surrounding water. Increased available moisture over short periods may have had a positive impact on microbial communities as previous studies have shown increases in soil CO_2 efflux (Treonis et al. 1999; Moorhead et al. 2003; Ayres et al. 2010). Conversely, frequent wetting and drying events and fluctuations in soil temperature can also be stressful to microbes, as they must expend energy to regulate osmotic pressure to their microenvironment (Nkem et al. 2006; Ball and Virginia 2012) and bacterial metabolism may be affected. As the soil dries out again, the matric potential of the soil decreases, salts concentrate, and water films around aggregates become thinner and disconnected. Water is held more tightly to the aggregate surfaces and restricts nutrient diffusion (Chowdhury et al. 2011), bacterial activity, and growth. To achieve osmotic regulation, bacteria synthesise amino acids and other organic compounds, as solutes (Csonka 1989). Accumulating and disposing of solutes can be energetically expensive for organisms, and it is those organisms that have adapted to survive episodic stresses that are likely to dominate soil environments (Schimel et al. 2007).

Under Annex I and II of the Protocol on Environmental Protection to the Antarctic Treaty, all activities undertaken in Antarctica must be planned and coordinated to limit adverse impacts on the environment and associated ecosystems [Annex II, Article I (d) and I (h)]. Over recent decades, there has been a rapid increase in the number of people visiting Antarctica, with annual visitor numbers for the 2010/2011 season exceeding 34,000 people (IAATO 2011). The majority of visits concentrate around the limited ice-free areas where the national programme stations, historic huts, and wildlife hotspots are located. With increasing human presence comes increased human-induced disturbance of the ice-free areas and potentially the organisms and communities residing within the soil. Desert pavement disturbance can arise from a number of sources, and at different intensities, ranging from human trampling, to vehicles that cause overturning of large stones. In the Ross Sea region, overturned stones are visible as undersides are often less weathered, lighter coloured, and coated in salts. Other disturbances range from indentation and compression of sub-surface soils, bulldozer blade scrapes, and removal of tens of centimetres of material for road fill, to base construction and complete re-contouring of the immediate landscape. The physical effects of human disturbance on soil properties were first studied in the Ross Sea region by Campbell et al. (1993, 1994, 1998), who reported increased soil compaction with increasing trampling intensity, as well as increases in soil albedo (due to the exposure of lighter subsurface material following surface disturbance). An experimental trial undertaken by Balks et al. (1995) replicated moderate-to-high intensity physical disturbance by physically removing the soil active layer at two sites in the Ross Sea region (Scott Base and Marble Point). Balks et al. (1995) observed the precipitation of salt efflorescence's on the surface of the recently disturbed sites as the exposed underlying material

equilibrated with the environment. Changes to soil surface albedo, soil moisture, and the soil surface (slumping) were also noted as a consequence of removal of the soil active layer (Balks et al. 1995).

Previous human disturbance research in Antarctica has focussed little attention on the impacts caused to biotic communities and biogeochemical cycling. Biota-focussed studies have been limited to two trampling studies investigating the long-term impacts to soil fauna. The first investigated changes to nematode populations in walking tracks within the US McMurdo Dry Valleys Long-Term Ecological Research project site (Ayres et al. 2008); and the second focussed on changes to soil collembola populations at different trampling intensities on Livingston Island in the South Shetland Islands, Antarctic Peninsula (Tejedo et al. 2009). Ayres et al. (2008) compared nematode populations (abundance, ratio of living to dead individuals, and dominant species) in tracks used continuously for 10 years during summer months to those used for 2 years. Ayres et al. (2008) showed increased nematode mortality, lower abundances, and a greater level of physical disturbance to the surface of tracks which were used at higher intensities and at longer durations, compared with newer tracks and control areas. Tejedo et al. (2009) showed the dominant species of collembola in Livingston Island soils decreased with increasing trampling intensity and increasing soil compaction. Overall, little is known about the response of Antarctic soil microbial communities to human disturbance or what timescale responses can be detected.

The objective of this study was to investigate the immediate and short-term changes to bacterial community structure in response to simulated soil surface disturbance. We hypothesised that soil environmental factors, such as soil salinity, pH, and soil moisture, would be altered by the simulated disturbance and would result in a shift and detectable difference in the bacterial community structure at disturbed and undisturbed sites. We also attempted to determine which environmental variables had the greatest influence on the bacterial community structure at the site.

Materials and methods

Site description and sample collection

The trial was undertaken near Scott Base, on Ross Island, in the Ross Sea region of Antarctica (Fig. 1; Table 1). The trial site was on a hillside approximately 200 m NW of Scott Base in an area where the desert pavement was largely undisturbed, though some surface trampling from people walking across the area had inevitably occurred since establishment of Scott Base in 1957. Scott Base experiences moderate snowfall (mean snowfall 90 days a year) (Claridge et al. 1999), with each snowfall generally amounting to a few millimetres, but occasional falls of a few centimetres can occur during a 24-h period (Bromley 1994). When the experiment was established in December 2009, the study site was free from snow but during subsequent samplings in January 2010, the site was intermittently covered by several centimetres of snow which was cleared before sampling on Days 14 and 21. It can therefore be assumed that the area is occasionally flushed by melting snow or downslope water flow. Soils of the study site were Typic Haplorthels (Soil Survey Staff 2010).

Soil sampling and experimental design

Three replicate blocks (Block 1, 2, and 3) were marked out using metal pegs (Fig. 2). Each block was 150 cm × 75 cm and randomly assigned a control and a disturbed quadrant (75 cm × 75 cm). Using a sterilised trowel, the top 2 cm of one half of each block was removed (to form the disturbed quadrant). Replicate blocks were approximately 2 m apart and occurred on the same landscape unit on a flat shoulder area (0–2 degrees slope) within the overall hillslope.

Soil samples were collected aseptically at four depth intervals. Depth A = desert pavement (DP) to 2 cm, Depth B = immediately below, 2–5 cm depth, and Depth C = 2–5 cm, new surface, and Depth D = 5–8 cm immediately below the new surface (Fig. 3), on Day 0, 7, 14, 21, and 35. The disturbed sites were sampled twice on

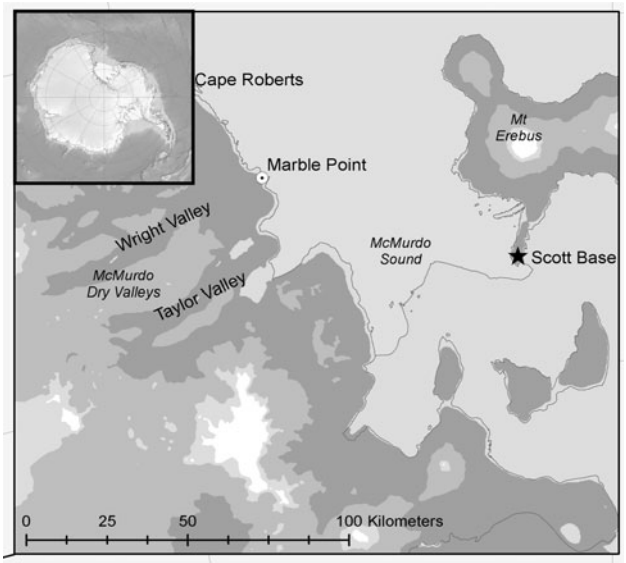

Fig. 1 *Map* showing the location of the Scott Base study site (denoted by a *star*) located on Hut Point Peninsula, Ross Island, in the Ross Sea region of Antarctica

Table 1 Description, geographical, geological, and pedological characteristics of the study site

Site description and landform	Flat shoulder area of a hillslope comprising small terracettes. Slope of 0–2°, aspect 135° and elevation of 41 m.a.s.l. The site is approximately 300 m NW of Scott Base, and 50 m NW of the Scott Base climate station[a]
GPS coordinates	77°50′53.3″S, 166°45′37.5″'E
Parent material	Weakly weathered scoriaceous basalt boulders through gravel, with some granite and sandstone gravel and sand-sized clasts
Soil classification[b]	Typic Haplorthel
Brief soil description	2 cm of desert pavement scoriaceous gravels and cobbles, over loose stony gravelly sands
	Ice-cemented permafrost ~ 32 cm[c]. Depth to ice-cement at time of sampling, 30 cm
	Weathering stage 1[d]. Salt stage 1[e]
Soil climatic zone[f]	Oceanic subserous
Ross Sea Region climatic zone[g]	Moist coastal mountain; mean annual temperature −19 °C, annual precipitation 188 mm

[a] Scott Base climate station, installed Jan. 1999, provides continuous climate and soil climate records: http://soils.usda.gov/survey/scan/antarctica/ScottBase/

[b] Soil Classification after Soil Survey Staff (2010)

[c] Depth to permafrost from Adlam et al. (2010), calculated over eight successive summers from 1999/2000 to 2006/2007

[d] Soil weathering stage after Campbell and Claridge (1975)

[e] Soil salt stage after Bockheim (1997)

[f] Soil climatic zones after Campbell and Claridge (1969)

[g] Ross Sea Region climatic zones after Campbell and Claridge (1987)

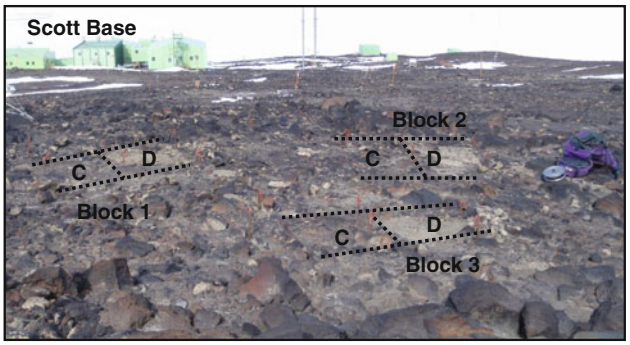

Fig. 2 Scott Base study site, showing *blocks 1–3*. Control quadrants are denoted by the *letter* "*C*" and disturbed quadrants by the *letter* "*D*" (photo taken on Day 0 after disturbance and sampling)

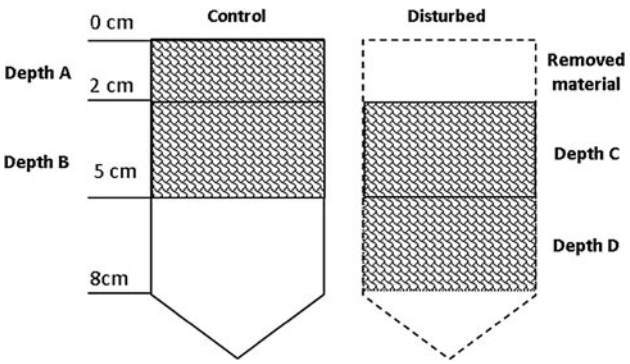

Fig. 3 Schematic diagram of sampling depths in control and disturbed quadrants of each block

Day 0, immediately before disturbance (Day 0_{pre}), and again, immediately after disturbance (Day 0_{post}).

In this experiment, we considered Depth B of the control was equivalent material (in stratigraphic succession) to Depth C of the disturbed quadrant. Depth C had been exposed at the surface by the removal of the top 2 cm of material.

A composite sample of approximately 200 g was collected with a sterile spatula, from the disturbed and control quadrants of Blocks 1, 2, and 3, at each depth interval. Homogenised samples were sieved to 2 mm and double bagged into a Whirlpak® bag (Fisher Scientific Ltd., Ontario, Canada), frozen at −20 °C, and transported back to New Zealand for processing.

Soil bacterial community structure analysis

DNA was extracted in duplicate from 1 g of soil (wet weight) through mechanical cell disruption using zirconium beads, phosphate buffer (100 mM NaH_2PO_4, pH 8.0), SDS (sodium dodecyl sulphate) lysis buffer (100 mM NaCl, 10 % SDS, 500 mM Tris, pH 8.0), and chloroform after Foght et al. (2004).

Polymerase chain reaction (PCR) was undertaken following Singh et al. (2006). Samples were amplified by PCR using an Eppendorf Master Cycler Gradient using bacteria primers 63f VIC and 1087r (Applied Biosystems). Samples were run on the MTRFLP PCR step-cycle

programme as follows: initial activation step of 95 °C for 15 min, followed by 30 cycles of a 30-s denaturation step at 95 °C; 45-s annealing at 55 °C; and a 90-s elongation step at 72 °C; with a final extension step for 30 min at 72 °C (QIAGEN Multiplex PCR Handbook, 02/2008). PCR amplification products were visualised on a 1.5 % w/v agarose/0.5× TBE gel (Bio-Rad MB certified). PCR products were purified using the QIAquick PCR Purification Kit (Qiagen), following the manufacturer's instructions. The DNA concentrations of the purified PCR products were quantified using a Nanovue spectrometer (GE Life Sciences). The PCR products were digested with *MspI* and *HhaI* in a 30 µL reaction mixture containing 400 ng of PCR products, NEBuffer 4, acetylated BSA, and water. Samples were incubated at 37 °C for 3 h followed by an inactivation step at 95 °C for 15 min (QIAGEN Multiplex PCR Handbook, 02/2008). The digests were purified using a MinElute reaction cleanup kit (Qiagen), following the manufacturer's instructions, and 1 µL aliquots of each sample containing the fluorescent labelled terminal restriction fragments were separated using an ABI PRISM 3100 Genetic Analyser (Applied Biosystems).

TRFLP profiles were produced using Gene-Mapper (version 4.0) software (Applied Biosystems), and terminal restriction fragments (TRFs) were quantified using the advanced mode and second-order algorithm. TRF analysis was performed between 50 and 500 base pair (bp) as previously described by MacDonald et al. (2008, 2009), which was within the linear range of the internal size standard. For microbial community analysis, two TRF peaks separated from one another by >1 bp were considered as distinct TRFs. The relative abundance was calculated as a proportion of the total peak height of all the TRFs in the profile. All peaks with heights that were less than 0.5 % of the total peak height were removed from the data before statistical analysis. To condense the two subsamples for each replicate to a single value, the maximum peak height between the two samples was used for each TRF.

Ordination of microbial communities

Data input into the ordination was relative amount of each individual TRF found in the soil samples over time, depth, and disturbance, with the Bray and Curtis (1957) metric as the measure of community distance. PC-Ord software (McCune and Mefford 2011) was used to determine directionality and correlation of gradients in the measured soil parameters. Multi-response permutation analysis (MRPP), a nonparametric multivariate analysis procedure, was used to test the bacterial community response to disturbance (Mielke 1984).

Soil chemical analyses

The sampled soils (air-dried and sieved to <2 mm size) were analysed for gravimetric soil moisture, soil pH, soil electrical conductivity (EC), and total phosphorus using standard methods (Blakemore et al. 1987). Total carbon and nitrogen were measured using a LECO FP 2000 analyser at 1,050 °C (LECO, St Joseph's, Michigan). All soil chemical properties were rated (as high, medium, low etc.) following Blakemore et al. (1987) and were the mean of two sub-samples per depth.

Soil pH, soil EC, moisture, total P, N, and C were $\log(n + 1)$ transformed prior to analysis to meet assumptions of normality and homogeneity of variance. A restricted maximum likelihood (REML) linear mixed model (LMM) was used to assess both time and treatment effects. Time, treatment, and time*treatment were the fixed effects and block*time*treatment, the random effect. The REML approach was used over a univariate repeated measures ANOVA because preliminary statistics indicated that treatment variance differentially varied over time (as demonstrated by epsilon values <0.6). Day, depth, and day*depth interactions were considered significant at $p < 0.05$. We considered p values <0.10 marginally significant. Comparison between depths A and C (the surface

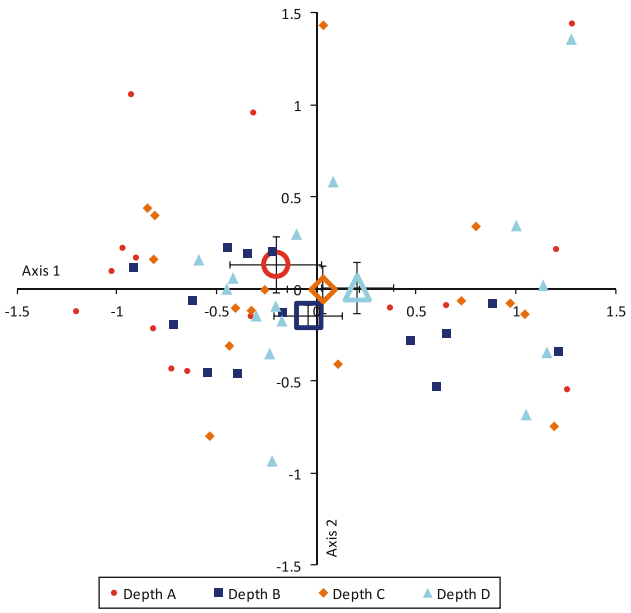

Fig. 4 PC-Ord ordination showing the effects of treatment (disturbance) on the bacterial community composition at the Scott Base disturbance trial. The overall treatment means of each depth over time are shown, and centroids show the average position of the individual treatments in the ordination space. *Circles* Depth A, control 0–2 cm; *Squares* Depth B, control 2–5 cm; *Diamonds* Depth C, disturbed 2–5 cm (post-disturbance exposure surface); *Triangles* Depth D, disturbed 5–8 cm. Depths B and C are equivalent depths. *Standard errors* are shown

layers after disturbance) (Fig. 3) and between B and C (the pre-disturbance equivalent layers) was of interest, and compared by contrast, all other comparisons were made by least significant difference only if the ANOVA was significant (i.e. Fishers protected LSD) at $\alpha = 0.05$.

Results

Treatment effects on bacterial community structure

Ordination was used to illustrate bacterial community composition as indicated by TRFLP profiles (Fig. 4). Only, the first two axes of ordination are presented as these accounted for most of the variance in bacterial community composition (Axis 1 = 60 %, Axis 2 = 20 %). There was no significant grouping of plots in the ordination space by treatment. Permutation analysis (MRPP) also did not indicate significant differences between the post-disturbance surface layers (Depths A vs. C) or the equivalent pre-disturbance sub-surface layers (Depth B vs. C) (Fig. 4), as the standard errors of the centroids overlap, but did indicate significant difference between the A and D (a consequence of differences in depth, p value <0.03). Overall, the removal of the top 2 cm of soil did not appear to cause any major shifts in the structure of the bacterial communities over the 35-day sampling period.

There was, however, a significant grouping of TRFs in the ordination space by block (Fig. 5). We will explore the similarities and differences in soil chemical characteristics in each block and the effect on TRF clustering in the next section.

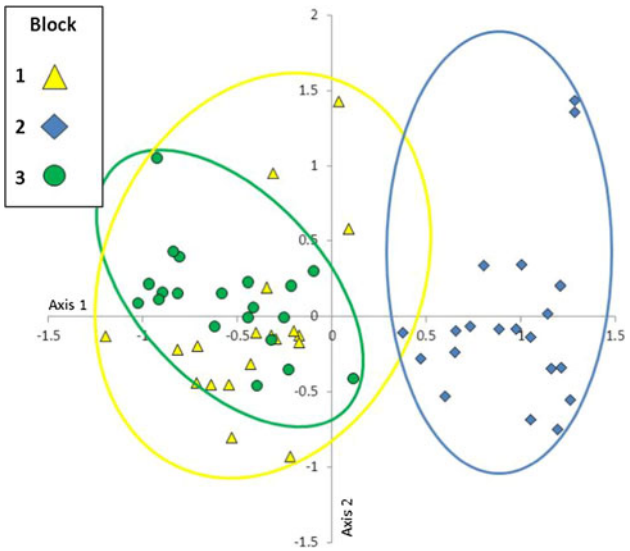

Fig. 5 PC-Ord ordination of the Scott Base disturbance trial soil samples based on TRF profiles of bacterial community composition. A significant "block effect" of the ordination space are depicted. *Triangles* Block 1, *Diamonds* Block 2, and *Circles* Block 3

Soil chemical characteristics

Soil means of measured soil parameters over all time periods for treatments and depths are presented in Table 2. Soil pH and soil electrical conductivity data are presented for each individual block (Tables 3 and 4).

Water content was low in all blocks and increased with depth, from 1–2 % in surface samples to 2–3 % in subsurface samples, of the treated (disturbed) and untreated quadrants. There was a moistening effect from snowfall that occurred between Day 14 and Day 21, which penetrated to at least Depth D (8 cm below the surface). During this time, soil moisture increased from about 1 % to 9 % between Day 14 and Day 21 and then dried out back to background at the surface within 2 weeks (by Day 35), but remained elevated at subsurface depths during the sampling period. There was a significant time interaction for water (Table 5).

All samples were strongly alkaline (pH 8.8–10.1), and soil pH showed some slight increases with depth but was not consistent across all blocks (Tables 2 and 3). Blocks 1 and 3 were slightly more alkaline than Block 2 (Table 3). Depth C (disturbed) had a similar pH to the Depth B as they were effectively an equivalent depth (Fig. 3; Table 3). Blocks showed some small variability in soil pH with time (Table 5), which could be due to sample variability with respect to salt, rather than treatment.

Electrical conductivity (EC) was highly variable between blocks and with depth and ranged between 0.04 and 1.23 mS/cm (Table 4). EC was highest in the Depth A (0–2 cm) samples in each block (ranging from 0.10 to 1.23 mS/cm) and decreased with depth in all blocks (ranging from 0.04 to 0.91 mS/cm) and with treatment (Tables 2 and 5). This is because removal of the top 2 cm of surface material in the disturbed quadrants of each block effectively removed the thickness of soil which had the highest salt concentration. Prior to initial disturbance on Day 0, the top 2 cm of the "to be" disturbed quadrant of Block 3 had the highest EC of all blocks at 2.42 mS/cm. After disturbance, the top of the exposed "new surface" Depth C had an EC of 0.91 mS/cm; disturbance effectively removed 62 % of the original salt content (and residing microbes in the upper 2 cm of soil). Block 2 had the lowest EC (and lowest pH) at both surface and subsurface depths compared with Blocks 1 and 3. There was a decrease in EC across all blocks, depths, and treatments, which coincided with snowfall between Day 14 and Day 21 (Tables 4 and 5) and increased soil moisture.

The organic C content was low (0.1–0.28 %), and Total N was very low (0.01–0.04 %) in all blocks and did not show much variation with depth, treatment, or time. C/N ratios were low and ranged between 6 and 10 and did not change significantly with time or treatment. Total P ranged from 1,600 mg/kg to 1,000 mg/kg and decreased in all

Table 2 Soil means over all time periods for treatment and depths

Variable	Control		Disturbed	
	Depth A	Depth B	Depth C	Depth D
Water (%)	3.5 (0.70)[a]	3.9 (0.45)[b]	3.5 (0.66)[a]	4.1 (0.46)[b]
pH	9.5 (0.07)[a]	9.6 (0.07)[a]	9.6 (0.12)[a]	9.5 (0.12)[a]
EC (mS/cm)	0.49 (0.09)[a]	0.36 (0.07)[ab]	0.31 (0.07)[bc]	0.21 (0.04)[c]
Organic C (%)	0.14 (0.02)[a]	0.13 (0.01)[a]	0.15 (0.01)[a]	0.12 (0.01)[a]
Total N	0.02 (0.003)[a]	0.02 (0.001)[a]	0.02 (0.002)[a]	0.02 (0.002)[a]
C/N	7 (0.34)[a]	7 (0.31)[a]	7 (0.24)[a]	7 (0.21)[a]
Total P (mg/kg)	1,333 (30.30)[a]	1,354 (37.43)[a]	1,308 (38.18)[a]	1,305 (34.81)[a]

Depth A = Control desert pavement to 2 cm, Depth B = immediately below, 2 to 5 cm, Depth C = disturbed 2 to 5 cm (new surface), and Depth D = 5–8 cm immediately below the new surface. Data shown are mean ± standard error, and $n = 3$. Values with the same superscript letters within a row are not significantly different

Table 3 pH of soil samples analysed for bacterial community composition studies (mean of two sub-samples at each depth and treatment)

Soil ph	Day 0	Day 7	Day 14	Day 21	Day 35
Block 1					
Depth A control	9.7	9.3	9.8	9.6	9.6
Depth B control	9.7	9.5	9.9	9.8	10.1
Depth C disturbed	9.7	9.7	9.9	9.8	9.8
Depth D disturbed	9.6	9.6	9.9	9.5	9.8
Block 2					
Depth A control	9.3	9.2	9.3	9.3	9.2
Depth B control	9.3	9.4	9.2	9.2	9.2
Depth C disturbed	9.0	8.8	9.0	9.1	8.9
Depth D disturbed	8.8	9.0	9.1	8.9	8.9
Block 3					
Depth A control	9.7	9.6	9.7	10.1	9.8
Depth B control	9.6	9.7	9.9	10.0	9.8
Depth C disturbed	9.9	9.7	10.1	10.0	10.0
Depth D disturbed	10.0	9.8	10.0	9.9	10.1

Table 4 Electrical conductivity (mS/cm) of soil samples analysed for bacterial community composition studies (mean of two sub-samples at each depth and treatment)

Soil EC	Day 0	Day 7	Day 14	Day 21	Day 35
Block 1					
Depth A control	0.35	0.35	0.45	0.18	0.57
Depth B control	0.20	0.41	0.40	0.17	0.37
Depth C disturbed	0.33	0.25	0.19	0.25	0.19
Depth D disturbed	0.12	0.15	0.21	0.19	0.13
Block 2					
Depth A control	0.22	0.26	0.13	0.14	0.10
Depth B control	0.11	0.09	0.13	0.11	0.08
Depth C disturbed	0.08	0.06	0.07	0.08	0.04
Depth D disturbed	0.07	0.05	0.06	0.07	0.04
Block 3					
Depth A control	1.23	1.01	1.07	0.68	0.61
Depth B control	0.57	0.62	0.91	0.77	0.28
Depth C disturbed	0.91	0.78	0.60	0.35	0.55
Depth D disturbed	0.47	0.52	0.34	0.44	0.27

blocks, and depths, over time (Table 5, $p < 0.001$), but did not change significantly with disturbance.

Soil chemical characteristic effects on bacterial community structure

Correlation of the soil characteristics to the ordination axis showed that axis 1 scores were strongly correlated with the gradients of soil pH ($R^2 = 0.67$) and EC ($R^2 = 0.55$) and also correlated with organic C ($R^2 = 0.30$) and Total N ($R^2 = 0.47$), indicating that differences in soil pH, soil EC, and C and N are likely to be the drivers of bacterial community composition (Fig. 6). Axis 2 scores correlated less strongly with water ($R^2 = 0.20$) and also sampling date ($R^2 = 0.24$) which was most likely driven by changes in water content. From the bioplots (Figs. 5 and 6), it is evident that there is an overriding "block effect" (i.e. Block 2 differs from Block 1 and Block 3. Block 2 $R^2 = 0.83$) where heterogeneity in significant soil parameters between blocks is clustering TRFs (Fig. 5). From these results, it can be inferred that the bacterial community structures of Blocks 1 and 3 were influenced by higher soil pH and higher soil salinity (EC). The structure of the bacterial community of Block 2 was primarily related to lower salinity, lower pH, and slightly higher organic C (Tables 3 and 4).

Discussion

In this study, we used TRFLP analysis to investigate the immediate and short-term changes to bacterial community

Table 5 *F* values from overall analysis of variance of soil parameters over all time periods

Variable	Water	pH	EC	Organic C	Total N	C/N	Total P
Block[a]	0.12	28.36***	140.07***	6.19**	14.22***	10.82***	1.54
Treatment	6.41**	0.22	17.18***	1.27	1.47	0.74	0.79
Time	209.87***	3.08^	2.32	3.64*	0.79	1.79	59.76***
Treatment × time	9.87***	1.04	1.51	1.63	1.71	1.18	1.20

[a] Block statistics from repeated measures ANOVA

Preliminary statistical analysis indicated a significant "block effect" $p < 0.001$ for EC, pH, Total C, Total N, and C/N, and not significant for water or Total P, $p > 0.5$

Significance: ^ $p < 0.1$,* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

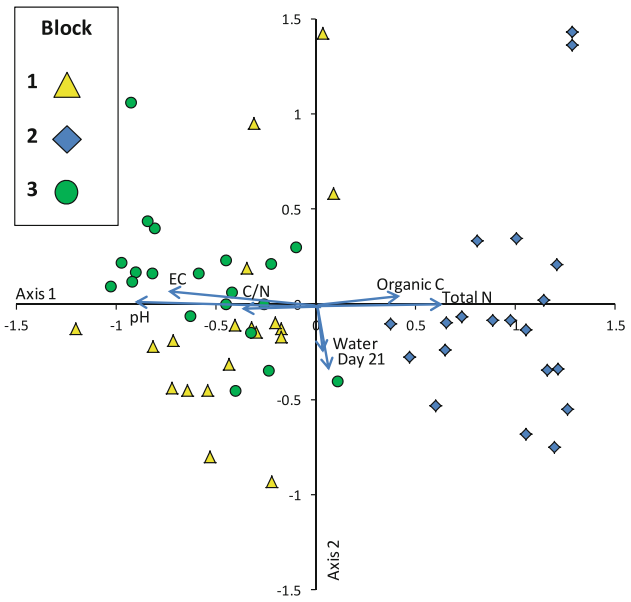

Fig. 6 Bioplot showing the PC-Ord ordination of the Scott Base disturbance trial soil samples based on TRF profiles of bacterial community composition. The gradients of environmental variables with a statically significant fit, $R^2 > 0.2$, to the ordination space are depicted. *Note* TRFs clustering into blocks. *Triangles* Block 1, *Diamonds* Block 2, and *Circles* Block 3

structure in response to soil surface disturbance. We hypothesised that there would be a measurable difference in bacterial community composition between disturbed and undisturbed sites, following removal of the surface material. However, in the time frame of the experiment, we did not see clear changes to the structure of the bacterial communities at the study site.

Given that the drivers of bacterial community structure are predominantly soil EC, soil pH, and soil moisture (Barrett et al. 2006; Yergeau et al. 2007; Aislabie et al. 2008, 2011; Ganzert et al. 2011; Chong et al. 2012), we would expect that a disturbance of sufficient intensity to affect those properties mentioned (e.g. changes to soil EC and soil moisture resulting from soil active layer disturbance, Balks et al. 1995) and cause a shift in bacterial community structure. Furthermore, any soil disturbance that would affect ecosystem functioning at a higher level, for example, Ayres et al. (2008) reported declines in nematode abundance with increased surface compaction from human trampling, could also have an indirect effect on bacterial community structure (or in this case, declines in nematode abundance could be due to shifts in bacterial diversity and abundance). A possible reason why we did not see a shift could relate to the time frame of the experiment (Ayres et al. 2010; Sparrow et al. 2011) and the life cycle of the bacterial communities (Schimel et al. 2007). Schimel et al. (2007) states that damage from environmental stresses is usually greater when microbes are active and growing, so at certain times in an organism's life cycle, they will be more vulnerable to environmental change. The use of RNA-based analyses could better reflect changes in metabolically active community structure (Griffiths et al. 2003; Yergeau and Kowalchuk 2008). Some CO_2 efflux studies have suggested that metabolic processes, such as respiration, are detectable and responsive to changes in environmental variables (Cary et al. 2010; Sparrow et al. 2011) and may be more sensitive indicators of early alterations in bacterial community structure, following soil disturbance. However, Shanhun et al. (2012) have suggested that much of the CO_2 evolution from Antarctic soil that correlates with changes in temperature and moisture is derived from abiotic changes in CO_2 in soil solution, and thus microbial respiration may have often been overestimated.

Abiotic soil factors contributing to bacterial community structure

Ordination showed that the bacterial community composition at the study site correlated strongly with soil EC and soil pH (Fig. 6). Although the replicate blocks were visually indistinguishable from one another, high local spatial variability of soil chemical properties existed at the study site and distinct bacterial communities were present within 2 m of one another and within the same landscape unit (i.e. the "block effect", $R^2 = 0.83$). TRF profiles showed that

Block 2 supported a bacterial community distinct from that of Blocks 1 and 3 (Fig. 5), and complementary soil chemical analyses revealed that the biota of Block 2 were residing in soil which had an order of magnitude lower EC and lower pH than Blocks 1 and 3 (Tables 3 and 4). High local spatial variability in soil distribution is a common feature in Ross Sea region soils (McLeod 2012). As a consequence, high local spatial variability in environmental parameters, such as soil organic matter, salinity, and local moisture, at 10–500 m scales have been shown to influence microbial community abundance and diversity (Barrett et al. 2004; Brinkmann et al. 2007; Chown and Convey 2007; Engelen et al. 2008; Chong et al. 2009; Ball and Virginia 2012). Studies by Aislabie et al. (2008, 2012) supported this observation and found that the composition of bacterial communities in Ross Sea region soils tended to be more similar from the same site and differ by geographic location (Aislabie et al. 2012), as soil clone libraries revealed that community composition could be discriminated on the basis of soil properties (Aislabie et al. 2008).

The local variation in salt content within the study site and the ability for local bacterial communities to tolerate osmotic stress is likely to account for some of the distinct community structure differences observed across the blocks. Bacteria can be sensitive to the concentration of soluble salts in soils which can also be influenced by repeated and rapid wetting and drying cycles associated with snowfall events (Table 4). Studies by Ayres et al. (2010) have shown that topsoil salinity can fluctuate with snow accumulation and melt, which along with associated changes to soil moisture was reflected in changes in dominant species of soil nematodes. Ball and Virginia (2012) observed a similar trend of highly variable soil characteristics coinciding with proximity to sometimes small scale, discontinuous seep patches (a product of melt water pulses from permafrost, glaciers, and snow patches). Studies by Ball et al. (2011) and Ball and Virginia (2012) suggest that the nearby McMurdo Dry Valleys have recently experienced several discrete warm events. Warmer temperatures result in increased availability of liquid water, which in turn can redistribute salts and affect biological communities and biogeochemical cycling. Ball and Virginia (2012) found that EC and pH in particular were significantly influenced by position along the seep patch transects, and EC was significantly higher towards the middle of the patch and at the soil surface. The decline in surface and subsurface soil EC between Day 14 and Day 21 was observed across all blocks, was most pronounced in the surface of the more saline Blocks 1 and 3, and was less pronounced in Block 2, likely due to lower background salt concentrations. As soils dry back down after a wetting event, microbes can encounter additional stress as water potentials decline, salts can concentrate, and cells must accumulate solutes to reduce their internal water potential to avoid dehydrating and dying (Harris 1981). The spatial variability in salt concentration evident across the blocks is potentially the result of a number of microtopographic variations including effects of uneven distribution of surface rocks on shading, hence evaporation and salt accumulation, moisture movements, and trapping of windblown snow. Any of these factors could account for the differences seen in soil EC and pH, thereby may influence habitat suitability over short distances.

Heterogeneity

Local scale heterogeneity in measured soil parameters made it difficult to determine the communities' response to the simulated disturbance. Limitations in the design of this experiment included the number of replicate blocks and the length of the sampling period. Both limitations were governed by the opportunistic nature of this experiment and limited time at Scott Base.

There is a question whether or not the one-off, low level, disturbance simulated in this experiment was of sufficient intensity to cause a shift in bacterial community structure at the study site. Inherently, the larger the perturbation outside natural environmental variations, the larger the stress on the biotic system, which may or may not have the ability to quickly adapt to the new conditions and avoid local decimation. Previous studies by Campbell et al. (1994) at Marble Point and in the vicinity of Scott Base (Balks et al. 1995) have shown moderate disturbance from earthworks and construction activities disturbed underlying permafrost and resulted in lowering of the surrounding ground surface (by up to 10 cm in 1 year, Balks et al. 1995), slumping, and release of salts that were contained within the permafrost. At Marble Point, Campbell et al. (1994) observed salt efflorescences on surfaces disturbed during earthworks carried out in the 1958/59 summer, which were still visible some 40 years after the initial disturbance (and on sampling had a soil EC of 1.6 mS/cm in the top 2 cm of the soil surface, 40 years on). We would propose that any moderate intensity disturbance, capable of modifying soil moisture and releasing soluble salts into biological communities' resident in the near-surface environment, is likely to have a negative and measurable impact on the local community.

A long-term experiment would eliminate those soil parameters which showed temporal fluctuations over the 35-day sampling period, such as water content, which were influenced by snowfall events. At present, any small changes we observed over the short sampling period may simply reflect variation in response to another factor, rather than the response to the simulated surface disturbance. Soil

sampling over a longer period of time may eliminate this uncertainty and also ensure that the complete life cycle of the community was represented. An investigation by Sparrow et al. (2011) showed that the response of the soil microbial community to addition of C and N substrates, although detectable, was slow and only apparent after 2 years. A further example by Ayres et al. (2010) undertaking long-term snow accumulation experiments in the McMurdo Dry Valleys saw a clear shift in the dominant nematode species over and above the local temporal variations in soil moisture associated with snow fall and snow melt.

Conclusions

The simulated disturbance (removal of the top 2 cm of soil) at the Scott Base experimental site did not cause any major shifts in the structure of the bacterial communities over the 35-day summer sampling period. TRFLP analysis revealed that the soil replicate blocks investigated supported distinct bacterial communities, and the composition of communities reflected the different spatial variability in soil physiochemical properties of the blocks. Soil EC and pH strongly correlated with TRFLP patterns and can be inferred as the most important factors controlling bacterial composition at the study site. Our data highlight the importance of local scale heterogeneity in structuring soil bacterial communities and that distinct communities are possible within 2 m of one another and within the same landscape unit. Given the current knowledge of the drivers of bacterial community structure, that is, soil EC, soil pH, and soil moisture content, we expect that a disturbance of sufficient intensity to affect those properties mentioned will cause a shift in bacterial community structure, over and above the time frame measured in this experiment. A more rigorous follow-up investigation incorporating DNA-RNA-based analyses and CO_2 efflux studies over a time frame of 2–3 years would lead to a greater understanding of the effects of soil disturbance on bacterial communities.

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