RESEARCH ARTICLE

Microbial diversity of eolian dust sources from saline lake sediments and biological soil crusts in arid Southern Australia

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Abstract

While microbial communities of aerosols have been examined, little is known about their sources. Nutrient composition and microbial communities of potential dust sources, saline lake sediments (SLS) and adjacent biological soil crusts (BSC), from Southern Australia were determined and compared with a previously analyzed dust sample. Multivariate analyses of fingerprinting profiles indicated that the bacterial communities of SLS and BSC were different, and these differences were mainly explained by salinity. Nutrient concentrations varied among the sites but could not explain the differences in microbial diversity patterns. Comparison of microbial communities with dust samples showed that deflation selects against filamentous cyanobacteria, such as the *Nostocales* group. This could be attributed to the firm attachment of cyanobacterial filaments to soil particles and/or because deflation occurs mainly in disturbed BSC, where cyanobacterial diversity is often low. Other bacterial groups, such as *Actinobacteria* and the spore-forming *Firmicutes*, were found in both dust and its sources. While *Firmicutes*-related sequences were mostly detected in the SLS bacterial communities (10% of total sequences), the actinobacterial sequences were retrieved from both (11–13%). In conclusion, the potential dust sources examined here show highly diverse bacterial communities and contain nutrients that can be transported with aerosols. The obtained fingerprinting and sequencing data may enable back tracking of dust plumes and their microorganisms.

Introduction

Airborne dust can affect global climate, human health as well as ocean and terrestrial environments (Stoorvogel *et al.*, 1997; Griffin *et al.*, 2001; McTainsh *et al.*, 2005). Dust plumes from the Sahara in Northern Africa, known as the largest source of soil to Earth's atmosphere, are known to spread over long distances across the Atlantic Ocean and as far as the Caribbean, SE United States and the Amazon basin (Swap *et al.*, 1992; Prospero, 1999; Prospero *et al.*, 2005), whereas Chinese dust, in one occasion, was known to have traveled one full circuit around the globe in about 13 days (Uno *et al.*, 2009). Recently, it became evident that aerosols are rich in viable bacterial populations and can act as a carrier for a variety of microorganisms that may impact human health and the environment (Griffin *et al.*, 2001; Prospero *et al.*, 2005; Brodie *et al.*, 2007). In the Southern Hemisphere, Australia is the main source of dust, which exits the continent frequently and deposits into the Tasman Sea and can go as far as New Zealand as well into the eastern Indian Ocean (Bowler, 1976; Hesse, 1994; McGowan *et al.*, 2000; De Deckker *et al.*, 2010). Numerous dust storms have been documented in Australia (Liversidge, 1902; Raupach *et al.*, 1994), including the dust plume that engulfed Canberra in October 2002 (McTainsh *et al.*, 2005; De Deckker *et al.*, 2008) and more recently Sydney in September 2009. A detailed characterization of dust samples from the former event showed that the dust was generated from wind erosion of the regolith in arid and semi-arid regions and harbored a large diversity of soil-related microorganisms (De Deckker *et al.*, 2008). Using satellite

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imagery and geochemical fingerprinting, the primary source of this dust was identified to be from inland saline lake sediments (SLS) and adjacent biological soil crusts (BSC) of southeastern Australia. Although the microbial composition of dusts from Australia has been studied using cultivation and molecular tools (De Deckker *et al.*, 2008; Munday C & Allison G, unpublished), little is known about the bacterial community structure of their sources. It is essential to create a microbiological database of deflating areas, which erode as a consequence of sand and dust being removed from SLS and BSC by the wind, to gain a better understanding of the origin, bacterial composition and transport pathways of eolian dust.

Inland saline lakes are numerous in Australia, encompassing a wide range of salinities (up to 35%) and differ in their morphometry, geology and degree of permanence (Williams, 1981b; De Deckker, 1988; De Deckker & Williams, 1988). The Southern Australian lakes are characterized by their semi-arid to arid environments, with a maximum temperature of > 45 °C reached in some summers and an annual evaporation rate of well over 1000 mm (Williams, 1981b). These lakes have been studied for their geology, chemical limnology and biota (Williams, 1981a, b; De Deckker & Williams, 1988 and references therein); however, little is known about their microbial composition. Likewise, the BSC surrounding these lakes have not been investigated for the diversity of their microorganisms, although much is known about the Australian crusts' eukaryotic diversity (i.e. mosses and lichen) and their role in soil stability and fertilization (Eldridge, 2001 and references therein; Eldridge *et al.*, 2006; Read *et al.*, 2008). We will consider the possibility that the BSC community near a lake is influenced by the adjacent lake community because of the deposition of lake bottom sediment.

The aim of this study is threefold: (1) to create a database of DNA fingerprints and 16S rRNA sequences of microbial communities in SLS and their adjacent BSC, identified previously as potential sources of the Canberra 2002 dust plume, (2) to find out the effects of different environmental parameters on their structure, and (3) to compare bacterial communities of the dust sample with those potential sources.

Materials and methods

Sampling sites and nutrient analysis

A total of 34 samples from SLS and BSC were collected from 18 dry lake beds in Southern Australia and their surrounding sand dunes (Fig. 1, Table 1). The sampled lakes differed in their salinity, geological surroundings, soil type and vegetation, whereas the BSC were dry and had different surface color. From each locality, 3–8 replicates were collected and immediately stored in liquid nitrogen for further molecular analysis. The samples were shipped frozen to the Max-Planck Institute in Bremen where they were analyzed for nutrient concentrations and microbial community composition.

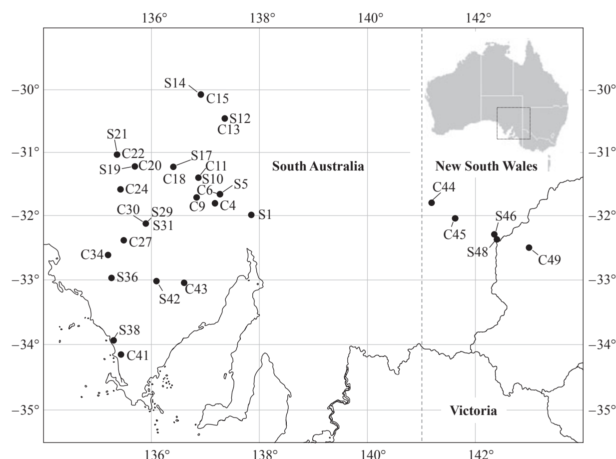

Fig. 1. A map of Southern Australia and New South Wales, separated by the dotted line, showing the sampling locations. Samples labeled with S and C refer to those collected from SLS and BSC, respectively.

For nutrient analysis (silicate, phosphate, ammonium, nitrite and nitrate), dry samples were placed in 15 mL falcon tubes and 10 mL of distilled water was added. The tubes were shaken at a speed of 150 rpm for 24 h in a cold room (T = 4 °C). The water phase was collected by centrifugation and was then filtered through 2-μm filter syringes. The nutrients were measured in the water samples using a nutrient analyzer (San Plus Analyzer; Skalar analytical GmbH, Erkelenz, Germany). For the iron (Fe) extraction, 10 mL of 0.5 M hydrochloric acid (HCl) was added to 0.2 g of sediment in a plastic tube. The tubes were shaken for 1 h and then centrifuged at 4000 rpm for 5 min at room temperature. The supernatant was collected in a separate tube and kept at 4 °C until analysis could be performed. A solution of Ferrozin [3-(2-pyridye)-5,6-diphenyl-1,2,4-triazine-4′, 4″-disulfonic acid monosodium salt/HEPES (N-2-hydroxyethylpiperazine-N-2-ethanesulfonic acid)] buffer was freshly prepared (12 g HEPES + 1 g Ferrozin in 1 L distilled water), and 200 mL of this solution was used to dissolve 2 g of Hydroxlaminchloride (Ferrozin buffer). Different volumes of the sediment extracts were mixed with 2 mL of the Ferrozin buffer, and the mixture was incubated for 15 min. The developed violet color was measured at 562 nm using a spectrophotometer (Shimadzu UV-160A Spectrophotometer, Duisburg, Germany).

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Table 1. Geographical location and nutrient composition of SLS and nearby BSC identified as potential dust sources

Lake name/ locality	Sample Number	Sample type	Salinity (%)	Latitude S	Longitude E	Nutrient concentration (μmol g^{-1})					
						Fe	Silicate	Phosphate	Ammonium	Nitrite	Nitrite and nitrate
Dutton	SI	SLS	4.2	31°59.090′	137°50.899′	NA	NA	NA	NA	NA	NA
	C4	BSC	0.5	31°47.909′	137°11.162′	39.1	0.77	0.01	0.27	0.01	0.09
Pernatty	S5	SLS	6.0	31°39.739′	137°16.424′	76.3	0.54	0.20	0.12	0.00	0.03
	C6	BSC	0.1	31°40.084′	137°16.629′	14.3	0.75	0.01	0.07	0.01	0.05
Finniss	C9	BSC	0.1	31°42.447′	136°49.657′	3.5	0.31	0.03	0.10	0.01	0.06
Island	S10	SLS	5.3	31°24.049′	136°52.016′	247.6	0.36	2.69	0.84	0.00	0.04
Lagoon	Cll	BSC	0.2	31°23.916′	136°52.214′	3.8	0.06	0.01	0.04	0.00	0.06
Torrens	S12	SLS	5.0	30°28.273′	137°21.399′	47.8	0.54	0.24	0.29	0.00	0.02
	C13	BSC	0.3	30°28.129′	137°21.485′	14.8	0.41	0.00	0.07	0.01	0.02
Pan	S14	SLS	0.2	30°07.420′	137°02.133′	20.8	0.82	0.01	0.03	0.01	0.10
	C15	BSC	0.1	30°07.460′	137°02.313′	5.3	0.71	0.00	0.18	0.01	0.02
Hart	S17	SLS	4.4	31°13.526′	136°24.246′	35.4	0.51	0.01	0.09	0.00	0.02
	C18	BSC	0.5	31°13.648′	136°24.435′	4.4	0.34	0.00	0.07	0.00	0.01
Gairdner	S19	SLS	5.0	31°13.249′	135°41.324′	92.0	1.28	0.01	0.16	0.00	0.01
	C20	BSC	0.2	31°13.101′	135°41.445′	18.9	0.62	0.00	0.02	0.00	0.00
Harris	S21	SLS	3.7	31°01.644′	135°21.877′	42.3	0.89	0.01	0.14	0.00	0.01
	C22	BSC	0.3	31°01.653′	135°21.989′	46.0	1.12	0.01	0.06	0.02	0.10
Edward	C24	BSC	0.6	31°35.773′	135°25.887′	78.2	1.19	0.01	0.09	0.02	0.03
	C26	BSC	0.4	32°18.738′	134°59.390′	2.6	0.23	0.00	0.02	0.00	0.00
Gairdner	C27	BSC	0.2	32°23.166′	135°29.386′	2.1	1.00	0.00	0.25	0.01	0.02
South	S29	SLS	6.6	32°07.469′	135°53.877′	25.1	0.12	0.00	0.04	0.00	0.01
	C30	BSC	0.5	32°07.399′	135°53.810′	5.4	0.94	0.01	0.20	0.05	0.16
	S31	SLS	2.2	32°07.399′	135°53.810′	17.5	0.14	0.00	0.10	0.00	0.00
Scrubby Peak	C34	BSC	0.1	32°36.657′	135°11.346′	14.3	0.91	0.02	0.07	0.03	0.05
Yaninee	C36	BSC	0.3	32°57.995′	135°16.236′	13.6	0.80	0.00	0.04	0.01	0.03
Round	S38	SLS	3.0	33°56.470′	135°16.498′	1.6	3.37	0.01	3.58	0.01	0.02
Greenly	C41	BSC	0.1	34°09.324′	135°26.833′	15.2	1.27	0.00	1.10	0.01	0.01
Gilles	S42	SLS	5.4	33°01.905′	136°06.165′	23.9	0.69	0.03	1.00	0.00	0.01
	C43	BSC	1.5	33°01.913′	136°36.127′	52.4	0.04	0.44	2.38	0.00	0.04
Mundi Mundi Plains	C44	BSC	1.5	31°47.346′	141°11.141′	112.1	0.03	0.36	1.25	0.00	0.07
Menindee	C45	BSC	1.5	32°03.058′	141°37.044′	203.5	0.03	1.09	3.17	0.00	0.04
	S46	SLS	3.2	32°17.750′	142°22.260′	17.9	0.05	1.34	1.58	0.00	0.04
	S48	SLS	3.5	32°21.284′	142°24.053′	74.0	0.04	1.73	3.23	0.00	0.00
	C49	BSC	1.2	32°30.401′	143°00.700′	46.2	0.03	0.99	0.70	0.00	0.09

NA, data not available.

Microbial community analysis by automated rRNA intergenic spacer analysis (ARISA)

The upper 1–2 mm of the samples (*ca.* 300–500 mg each) were subjected to DNA extraction using the UltraClean soil DNA isolation kit (MOBIO laboratories, Inc., Carlsbad, CA) according to the manufacturer's instructions. Polymerase chain reaction (PCR) amplification was performed in triplicate with the same amounts of DNA (as determined by Nanodrop, Thermo Scientific, Germany) using the universal primer ITSF and the FAM-labeled eubacterial ITSReub primer (Cardinale *et al.*, 2004) at an annealing temperature of 55 °C. The PCR products were purified using Sephadex G-50 Superfine (Sigma-Aldrich, Munich, Germany). 150 ng of DNA was then mixed with 0.5 μL of internal size standard MapMarker 1000 ROX (50–1000 bp; BioVentures Inc., Washington, DC), and the amplified fragments were discriminated by capillary electrophoresis on an ABI PRISM 3130*xl* Genetic Analyzer (Applied Biosystems, Carlsbad, CA). The ARISA profiles were analyzed using the GeneMapper software v 3.7 (Applied Biosystems). The total peak area per sample was normalized to one, and only fragments between 100 and 1000 bp were considered. A 'fixed window' binning

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strategy with a bin size of 2 bp was applied to the ARISA data (Ramette, 2009), and the binning frame that offered the highest pairwise similarities among samples was subjected to multivariate analyses. An operational taxonomic unit (OTU) was considered present in a given sample only if it was detected at least twice among the three replicated PCRs from the DNA extracts of that particular sample (Ramette, 2009).

Statistical analysis of ARISA fingerprints was carried out using the PAST program (Paleontological Statistics, ver. 1.47, http://folk.uio.no\ohammer\past). A multivariate analysis of all sites was performed using multidimensional scaling (MDS) based on Bray–Curtis similarities as described in (Ramette, 2007). Ordination of the Bray–Curtis similarities was performed using non-metric MDS, with 100 random restarts, and the results were plotted in two-dimensions. The consensus ARISA table containing samples by OTUs was used to calculate pairwise similarities among samples based on the Bray–Curtis similarity index. Analysis of similarities (ANOSIM) was carried out to test for significant differences between SLS and BSC microbial communities. ANOSIM produces a sample statistic (R), which represents the degree of separation between test groups (Clarke, 1993; Ramette, 2007).

Canonical redundancy analysis (RDA) was used to investigate the significance of salinity, sample type (SLS vs. BSC), geographical location, vegetation, soil type, and rainfall on the shape of microbial communities in SLS and BSC samples. ARISA profiles were first Hellinger transformed (Legendre & Gallagher, 2001; Ramette, 2007), and the effect of different parameters was investigated by canonical variation partitioning (Borcard *et al.*, 1992; Ramette & Tiedje, 2007), where the variation and covariation of these parameters were partitioned into pure and covarying fractions. For each response data model, the most significant variables were selected by RDA using stepwise selection and by minimizing the Akaike Information Criterion. Statistical significances were assessed by 1000 permutation of the reduced models. All statistical calculations were performed with the R statistical platform using the VEGAN and MASS packages.

Pyrosequencing and sequence analyses

Purified DNA extracts of 20 representative SLS and BSC samples (10 each) from different geological provinces were submitted to the Research and Testing Laboratory (RTL, Lubbock, TX) for tag pyrosequencing. Bacterial tag-encoded FLX amplicon pyrosequencing (bTEFAP) was performed as described before (Dowd *et al.*, 2008a, b) using the GS FLX titanium sequencing kit XLR70. One-step PCR was performed using a mixture of hot start and hot start high fidelity tag polymerases resulting in amplicons that extend 350–450 bp from the 27F region (*Escherichia coli* rRNA numbering). The bTEFAP sequencing was performed according to the RTL protocols (www.researchandtesting.com). Obtained sequences were trimmed; low quality ends and tags were removed and were checked for chimeras using custom software (Dowd *et al.*, 2008b) and the Black Box Chimera Check software B2C2 (freely available at http://www.researchandtesting.com/B2C2.html). Sequences < 300 bp were excluded from further analysis, and the rest were checked for high quality based on criteria utilized by RDP ver 9 (Cole *et al.*, 2009). These sequences were analyzed and taxonomically classified using a distributed BLASTN.NET algorithm (Dowd *et al.*, 2005) against a database of high quality 16S rRNA gene sequences obtained from NCBI. The outputs were compiled and validated using taxonomic distance methods (Dowd *et al.*, 2008a, b). Rarefaction curves, OTU number, and diversity estimates (Chao 1, ACE) were calculated using the software ESPRIT (Sun *et al.*, 2009) available freely at http://www.biotech.ufl.edu/people/sun/esprit.html. For large sequence datasets, the average diversity indices were calculated after performing 3–5 randomized selection of 4500 and 3000 sequences for SLS and BSC samples, using a custom script.

Results

Iron and nutrients composition

The analyzed suite of nutrients was selected because they have been shown to disperse with dust over large distances (McTainsh & Strong, 2007). Clear variations were observed in Fe and nutrient concentrations among the studied sites (Table 1). Fe concentration ranged from 1.6 to 248 μmol g^{-1} soil with the lowest values detected in Round Lake and Lake Gairdner South and highest in Island Lagoon and the Menindee region. Most samples collected from near Menindee had higher concentrations of Fe, phosphate, and ammonium than the other samples, whereas the concentrations of silicate were lower. Phosphate concentration was < 0.2 μmol g^{-1} in all samples except in the Menindee samples where it ranged between 0.36 and 1.73 μmol g^{-1}. The SLS had higher phosphate concentrations than the surrounding BSC. Nitrite and nitrate concentrations were < 0.16 μmol g^{-1} in all samples, while ammonium concentrations ranged from 0.02 to 3.58 μmol g^{-1}. Both SLS and BSC samples from the Menindee-Broken Hill area showed the highest total nitrogen concentrations of all samples. The N:P ratio showed clear variations between sites and ranged from 1 : 1 to 600 : 1, thus some sites were nitrogen-limited while others were phosphate-limited.

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Fingerprinting analysis

ARISA fingerprinting of bacterial communities from samples of SLS and their adjacent BSC showed significant variations in community composition as well as OTU richness. A total pool of 419 distinct OTUs (i.e. binned ARISA peaks) distributed among all samples were identified. The average number of OTUs for the SLS samples was 82 with the highest detected in Pan and Round Lake sediments (i.e. 136 and 138, respectively) and the lowest in Lake Harris and Lake Gairdner sediments (i.e. 20 and 28, respectively; Fig. 2 left panel). The highest OTU number of BSC was detected in Finniss Lake and Island Lagoon sites with 156 and 160 OTUs, respectively, and the lowest in Lakes Hart and Greenly with 53 and 77 OTUs, respectively. Multivariate analyses of ARISA profiles of SLS identified specific bacterial signatures when compared to the surrounding BSC, and the bacterial communities of the two groups clearly clustered separately, yet with a certain degree of overlap (Fig. 2 right panel, ANOSIM $R = 0.45$, $P < 0.0001$). Pairwise comparison of presence/absence of OTUs in the SLS and BSC of 10 selected sites showed only < 18% shared OTUs among all samples with the highest average shared OTUs detected in Lake Harris and lowest in Lake Gairdner (Fig. 2 left panel).

To obtain additional information on the environmental parameters that shaped the microbial communities in SLS and BSC, the relationships between ARISA fingerprints and salinity, sample type (SLS vs. BSC), geographical location, rainfall, vegetation, soil/regolith type, nutrients and Fe concentrations were statistically evaluated (Table 2). Among all parameters, salinity was the most

Table 2. Effects of contextual parameters on variation in bacterial community structure

Explanatory factors	*N*	R^2 (%)	*F*-ratio	*P* value
Chemistry				
Total effects	5	21.6	1.21	0.017*
Pure effects		0.8	1.03	*ns*
Salinity				
Total effects	1	10.7	3.1	0.001***
Pure effects		0.02	1.04	*ns*
Sample type				
Total effects	2	8.8	2.52	0.001***
Pure effects		0.1	1.01	*ns*
Vegetation				
Total effects	2	0.8	1.12	*ns*
Pure effects		0	0	*ns*
Precipitation (rain)				
Total effects	1	4.6	1.26	0.083-
Pure effects		0	0	*ns*
Soil type				
Total effects	2	13.4	0.89	*ns*
Pure effects		0	0	*ns*
Sample type controlling for space	2	5	2.48	0.001***
Space controlling for sample type	2	1	1.22	0.017*

Total and the pure effects (i.e. when controlling for all other factors of the analysis) of explanatory factors were calculated by using canonical RDA models on the subset of data associated with complete contextual parameters ($n = 28$ samples). The proportion of explained community variation is expressed as R^2 values and was adjusted for the given number of parameters considered (*N*) for calculating pure effects. Significances of the respective *F*-ratios were tested by performing 1000 Monte Carlo permutation tests and are indicated by – marginally significant ($P < 0.1$), *significant ($P < 0.05$), ***highly significant ($P < 0.001$), and ns when not significant ($P > 0.05$).

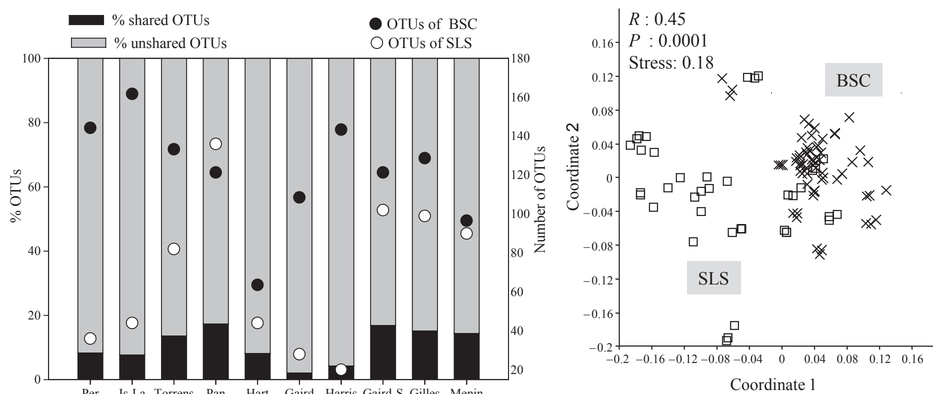

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination (based on a Bray–Curtis distance matrix) of ARISA fingerprints (left) from SLS and BSC samples, identified as potential sources of eolian dust. The right-hand figure shows the percentage of shared and not shared OTUs in 20 representative SLS and BSC from 10 sampling locations. Per, Pernatty; Is-La, Island Lagoon; Gaird, Gairdner; Gair-S, Gairdner South; Menin, Menindee. The white and black circles represent the number of OTUs obtained from ARISA profiles of SLS and BSC at each location, respectively.

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important structuring factor (10.7% of variance explained, $P = 0.001$) followed by the SLS or BSC sample type (Table 2). Some covariation among factors was detected, and pure effects (i.e. effects because of a single factor taking all other factors into account) were generally not significant. All other factors accounted for < 1% of the variations in ARISA patterns.

Pyrosequencing and sequence analysis

A total of 155 779 sequences of 16S rRNA gene were generated after discarding low quality reads and primer sequences (out of 209 507 sequences before trimming) from BSC (25 965) and SLS (129 814), respectively. The number of sequences ranged from 522 to 8607 sequences in BSC samples C14 and C48, and 3374 to 44 701 in the SLS sites S11 and S15, respectively (Table 3). The number of detected OTUs in BSC was relatively lower than in SLS, which could be as a result of variation in sequencing depth. Analysis of rarefaction curves revealed that the curves did not level off at the 97% cut-off level, even for the samples with the greatest number of sequences (Fig. 3). OTU richness, as determined by Chao1 index based on a 97% sequence similarity threshold to define OTU, ranged from 97 to 2532 in BSC samples and 1004 to 3944 in SLS samples (Table 3).

Sequences were affiliated to 21 phyla (Fig. 3), among which Cyanobacteria, *Proteobacteria*, and Gram-positive bacteria (*Actinobacteria* and *Firmicutes*) encompassed the majority of sequences (> 77%) in most samples (only in samples S19, S31, and S42 they encompassed < 58% of the total sequences). Cyanobacteria constituted the major fraction of BSC microbial communities with the highest abundance detected in Pan (sample C15; 89%). Surprisingly, cyanobacterial sequences constituted only 0.1% of the total sequences in the Menindee BSC (sample C49), which could be the result of the heavy disturbance by cattle. Most of detected cyanobacterial sequences in BSC belonged to the nitrogen-fixing *Nostocales* group (> 22%), while the rest were affiliated with sequences of uncultured cyanobacteria. In SLS, cyanobacterial sequences constituted between 2% and 42% of the total number, being the highest in the Menindee area (i.e. 42%) and lowest in Lake Torrens (i.e. 2%), and the sequences were mainly affiliated to uncultured cyanobacteria. Among the proteobacterial classes, *Alpha*-, *Beta*- and *Gammaproteobacteria* were most frequently encountered with few sequences from *Delta*- and *Epsilon-proteobacteria* ($\leq$ 3%). *Alphaproteobacteria* constituted between 5–56% and 4–35% of the total sequences in BSC and SLS, respectively. The highest occurrence of *Alphaproteobacteria* in BSC was detected in Island Lagoon

Table 3. Pyrosequencing and bacterial diversity estimators for 20 samples from SLS and BSC

	Number of sequences		At 97% cut-off			
Sample ID	Before cleaning	After cleaning	No. of OTUs	Chao 1 (lower/upper)	ACE	No. of ARISA OTUs
SLS samples						
S6	9111	6607	859*	1667 (1487/1899)*	1742*	141
S11	4484	3374	1106	1929 (1761/2140)	1951	160
S13	11 046	8349	994*	1987 (1780/2244)*	2077*	129
S15	57 984	44 701	1363*	3219 (2973/3740)*	3638*	116
S18	49 591	36 556	879*	1777 (1580/2029)*	1952*	53
S20	9074	6950	1719*	3944 (3620/4328)*	4116*	102
S22	7551	5835	640*	1004 (908/1136)*	1047*	140
S30	4567	3659	1046	2051 (1848/2305)	2114	116
S43	8027	6073	1078*	2172 (1956/2440)*	2375*	124
S49	10 233	7710	1422*	3085 (2801/3427)*	3391*	89
BSC samples						
C5	1766	1208	172	208 (189/249)	208	36
C10	952	548	64	97 (75/159)	90	44
C12	1149	687	584	2250 (1813/2843)	2381	82
C14	760	522	140	168 (152/200)	170	136
C17	7589	5367	325*	429 (388/496)*	428*	44
C19	3630	2186	226	283 (254/339)	274	28
C21	3379	1923	255	363 (315/450)	332	20
C31	4348	3293	387*	705 (604/855)*	752*	102
C42	3007	1624	195	261 (228/327)	245	99
C48	11 259	8607	1018*	2532 (2231/2908)*	2817*	90

The diversity indices marked with an asterisk represent the average values calculated after performing three randomized sampling of the sequences to enable comparison among different samples. The number of sequences after cleaning indicates the number after removing short (< 300 bp) and low quality sequences.

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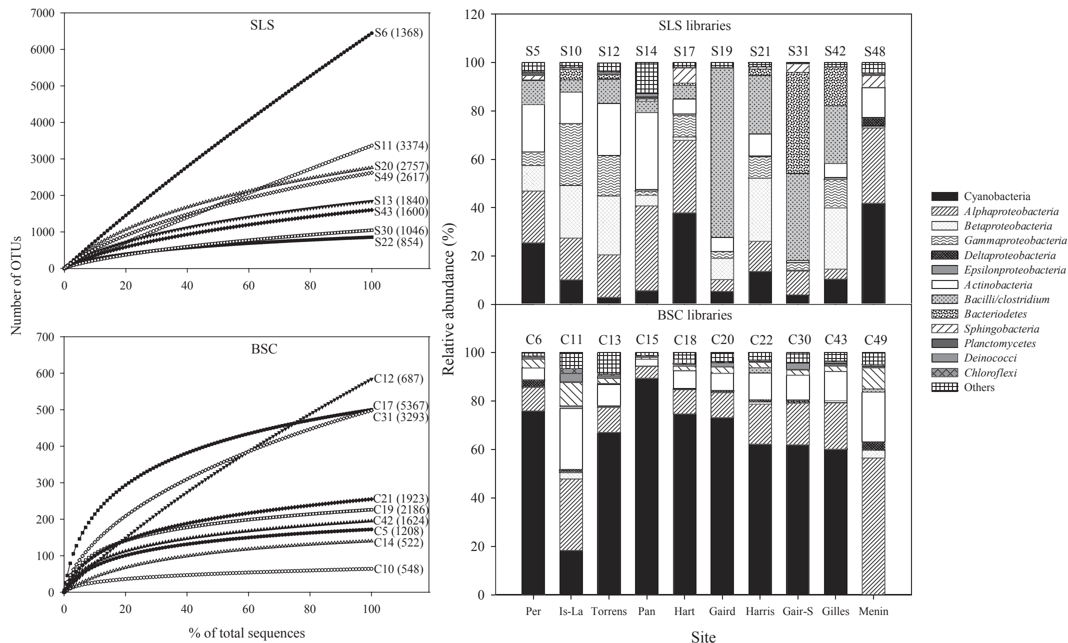

Fig. 3. Rarefaction curves of bacterial communities (left panel) and taxonomic affiliation and relative abundance (right panel) of the most common bacterial groups encountered by pyrosequencing of 20 samples of SLS and BSC. Per, Pernatty; Is-La, Island Lagoon; Gaird, Gairdner; Gair-S, Gairdner South; Menin, Menindee.

and the Menindee area (i.e. 29% and 56%, respectively) and most of these sequences were phylogenetically affiliated to *Microvirga flocculans*, *Skermanella parooensis*, *Microvirga subterranea*, and *Rubellimicrobium thermophilum*. In SLS, the sequences were related to the genera *Rhodovibrio*, *Azospirillum*, *Defluviicoccus*, *Roseomonas*, *Microvirga*, *Magnetospirillum*, and *Rubellimicrobium*. The *Beta*- and *Gammaproteobacteria* were more dominant in SLS samples than in BSC (3–47% vs. 0.2–3%) and contained sequences related to *Delftia acidovorans* and *Pseudomonas* spp., respectively. *Actinobacteria*-related sequences were detected in all studied SLS and BSC with an abundance of < 20% of total sequences in some samples (e.g. samples 5, 11, 12, 14, and 49). Sequences from this high GC group included the radiation-resistant species *Rubrobacter radiotolerans*, *Thermoleophilum album*, and *Patulibacter minatonensis*. The spore-forming *Firmicutes* group was much more abundant in SLS than in BSC, where they only formed $\leq$ 2% of the total sequences. This group accounted for 70% of the total sequences detected in Gairdner (sample 19) and contained sequences related to different species of *Bacillus*, *Clostridium*, and *Staphylococcus*. The remaining less dominant groups were distributed among *Bacteriodetes*, *Deinococcus*, *Sphingobacteria*, *Planctomycetes*, *Chloroflexi*, *Gemmatimonadetes*, *Thermomicrobia*, *Chlorobia*, *Spartobacteria*, *Caldilineae*, *Solibacteres*, and *Ktedonobacteria*.

Discussion

The combination of ARISA and pyrosequencing provided detailed information on the microbial communities occurring at the sites identified as potential sources of eolian dust in Australia. SLS and BSC represent tremendous sources of unconsolidated sediments available for deflation and eolian transport (Blank *et al.*, 1999; Reynolds *et al.*, 2006; Neff *et al.*, 2008). The investigated samples from SLS and the surrounding BSC harbored a wide variety of microorganisms, with a large proportion of novel types that had no close match in publicly available 16S rRNA gene databases. The microbiological data obtained in this study may eventually help back tracking of regional dust sources.

The differences in microbial communities between SLS and BSC, shown by ARISA fingerprinting, were further supported by pyrosequencing. Pyrosequencing provided greater resolution and a more complete picture of bacterial diversity than ARISA, as indicated by the higher number of OTUs and the rarefaction curves generated from pyrosequencing data. The differences of bacterial communities of SLS and BSC could not be explained by variation in nutrients, soil type, vegetation, precipitation, or geology of the region but were mainly attributed to significant differences in salinity and sample type. Salinity has been shown to control the diversity and functions of

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microbial communities (Casamayor *et al.*, 2002; Abed *et al.*, 2007; Lozupone & Knight, 2007). The higher water content, steep chemical gradients of SLS, and limited exchange between these adjacent biota can also account for these differences. Our nutrient analysis showed that SLS and BSC varied in their Fe, P, and N composition, with some soils limited in P while others were limited in N. However, it is remarkable that these ambient differences in these nutrients were not associated with observable differences in community structure. Bacterial diversity has been shown to follow a chaotic pattern when species compete for three or more resources (e.g. nutrients), which means that diversity of bacterial communities is not explained only by external factors but also potentially by other interactions, such as competition among species (Huisman & Weissing, 1999; Winter *et al.*, 2010). Even in a stable ecosystem with controlled environmental parameters, bacterial diversity has been shown to change dramatically (Fernandez *et al.*, 1999).

The microbial communities of dust sources studied here were compared with those of a previously determined Australian dust sample (De Deckker *et al.*, 2008) to find common bacterial groups. Although the samples were analyzed using two different techniques (i.e. pyrosequencing and Sanger sequencing), comparison was still possible because both techniques were previously shown to yield similar results in spite of their methodological biases (Tedersoo *et al.*, 2010). Both techniques are similarly based on PCR amplification but differ only in terms of sequencing depth. The comparison of dust and dust sources bacterial communities suggests that deflation of bacteria with dust is a selective process. Although cyanobacteria constituted a major fraction of the dust sources (16% and 56% of the total sequences of SLS and BSC, respectively), their contribution to the dust sample was only 2% (De Deckker *et al.*, 2008). Cyanobacterial fraction was also shown to be minor (only 2.7%) in the bacterial communities of African dust (Polymenakou *et al.*, 2008). This low representation of cyanobacteria in dust could be attributed to their filamentous structure and to the production of extrapolymeric substances that allow them to stick firmly to substrate, thus preventing their dispersal during deflation. It could also be owing to the fact that disturbed BSC, which normally contain low abundance of cyanobacterial filaments (Belnap & Eldridge, 2001), are more likely to deflate by wind and thus may be primary contributors to aerosols. The low detection of cyanobacteria in the disturbed BSC of Menindee, a known deflating area in Australia (McTainsh *et al.*, 2005), supports this assumption. Cyanobacteria constituted the major component (20–76%) of the prokaryotic community in the studied BSC, most of which belonged to the known heterocystous nitrogen-fixing *Nostocales*. This ecologically important group of cyanobacteria was found to be dominant in many BSC in arid and semi-arid environments worldwide, as their nitrogen fixation is essential for the surrounding vegetation (Dodds *et al.*, 1995; Potts, 2000; Yeager *et al.*, 2007; Abed *et al.*, 2010). Although *Nostocales* includes species that are desiccation-tolerant and highly adapted to life under strong UV radiation through the production of the UV sunscreen pigment scytonemin (Dillon & Castenholz, 2003; Fleming & Castenholz, 2007), which are advantageous features for the survival of these microorganisms at higher altitudes, their detection in dust samples was not common.

Other bacterial groups, on the other hand, identified in the studied SLS and BSC were similar to those found in the Canberra dust sample from 2002 (De Deckker *et al.*, 2008), implying that microorganisms from these ecosystems can be readily transported with dust. For example, *Proteobacteria*, *Actinobacteria*, and *Firmicutes* were among the most common groups in dusts and their sources. Gram-positive bacteria (i.e. *Actinobacteria* and *Firmicutes*) were detected in all the source sediments examined here. This widespread distribution and the ability of these bacteria to form spores and tolerate desiccation and high UV levels explain their prevalence in dust samples (Griffin *et al.*, 2001; De Deckker *et al.*, 2008). Gram-positive bacteria accounted for 23% of the total microbial communities in the Australian dust (De Deckker *et al.*, 2008). This group was also found dominant in African dusts (Polymenakou *et al.*, 2008). *Actinobacteria* inhabit extreme environments like hypersaline lakes, thermal springs, and arid soils and also include a large number of spore-forming plant and animal pathogens (Stackebrandt & Schumann, 2006). Our *Actinobacteria* sequences were related to thermal and UV-resistant species like *Rubrobacter radiotolerans*, *Thermoleophilum album*, but not to known pathogens. The presence of *Firmicutes* mainly in SLS but not in BSC indicates that saline lakes are the major source of this group in dust samples. This group of microorganisms constituted 23% of the total 16S rRNA sequences obtained from the Australian dust (De Deckker *et al.*, 2008) and related strains were readily cultured from the same sample (Chris Munday, person. commun.). While our *Firmicutes* sequences were related to 15 different *Bacillus* species and 2 *Clostridium* species, cultured species of this group were mainly affiliated to the genera *Arthrobacter*, *Bacillus*, *Planomicrobium*, *Paenibacillus*, *Curtobacterium*, *Macrococcus*, and *Staphylococcus* (Chris Munday, pers. commun.). The ability to cultivate spore-forming *Firmicutes*-related species from aerosols shows their resilience against the extreme atmospheric conditions of water scarcity and high levels of UV radiation, with dust probably the important distribution vector for these microorganisms. Many spores are few microme-

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ters in diameter and could survive within cracks of soil particles and clay platelets, which would protect them from UV radiation, or they may also attach to large particles or clumps (Griffin *et al.*, 2001; Prospero *et al.*, 2005). Indeed, it was shown that 50% of the UV radiation is attenuated within large dust plumes through back scatter (Herman *et al.*, 1999). In our study, no pathogenic microorganisms were found, although *Actinobacteria* and *Firmicutes* are known to include pathogens (Stackebrandt & Schumann, 2006; Pakarinen *et al.*, 2008). Interestingly, a correlation between the predominance of Gram-positive bacteria in Russian dusts and the occurrence of atopy (i.e. allergic reactions) was found (Pakarinen *et al.*, 2008). Conversely, fungi, which were not studied here, are a major constituent of BSC and can be a major cause of asthma and fever. Consequently, it is possible that aerosols can transfer microorganisums that may be of concern to human health (Griffin, 2007).

The highest concentrations of Fe, P, and N were detected in soils from Menindee, an area previously identified as a major dust source in Australia (McTainsh *et al.*, 2005; De Deckker *et al.*, 2008). It is likely that ecosystems downwind from these sites receive nutrients by dust emanating from SLS and BSC of the region as proposed previously (McTainsh & Strong, 2007). The direct transfer of N and P from source soils may affect soil formation and fertility (Cattle *et al.*, 2002; Hesse & McTainsh, 2003; McTainsh & Strong, 2007). For instance, dust was shown to deposit at an average of 31.4 t km^{-2} $year^{-1}$ onto the upper Namoi River Valley in New South Wales, which is known to be a very productive agricultural region (Cattle *et al.*, 2002). P is commonly a limiting nutrient in desert soils and can govern plant growth and productivity, as well as affect carbon and nitrogen mineralization rates in deserts (Reynolds *et al.*, 2006). In theory, the nitrogen-fixing cyanobacteria in BSC, once transported with dust, could lead to increased fertility of the sink soil. However, we found low numbers of these organisms in dust, and it is debatable whether these organisms, adapted to a specific environment, will proliferate in the sink. Dust may also act as an agent for the spread of soluble salts, because the studied saline lakes with salinities up to 22% have been shown to be highly erodible dust source areas in Australia (McTainsh *et al.*, 1999). Indeed, soluble salt content of Australian dusts was found to be between 2.7% and 9.3% (McTainsh *et al.*, 1999). Iron was also found in high concentrations in some of our dust source samples. Large-scale iron fertilization experiments significantly boosted primary productivity in oceans (Griffin & Kellogg, 2004 and reference therein). However, rarely a clear relation between the occurrence of phytoplankton blooms and dust storms has been reported and most dust deposition events did not result in blooms (McTainsh & Strong, 2007).

In conclusion, our study shows that dust sources are highly diverse in UV-resistant and spore-forming bacterial communities and also contains nutrients that can be transported with the aerosols, thus rendering dust not only as a medium for long-range transport of viable microorganisms, but also a periodic source of nutrients for nutrient-depleted terrestrial and marine environments. Our work, however, does not preclude the possibility that dust microorganisms could have been derived from sources other than those presented in this study, as microorganisms could be recruited from other ecosystems into dust plumes during their journey prior to being deposited. Nonetheless, our study provides a comprehensive molecular baseline that would help in back tracking microorganisms in dust samples.

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