Minerals in soil select distinct bacterial communities in their microhabitats

Jennifer K. Carson1, Louise Campbell1, Deirdre Rooney2, Nicholas Clipson3 & Deirdre B. Gleeson1

1Soil Biology Group, School of Earth and Geographical Sciences M087, University of Western Australia, Crawley, WA, Australia; 2Department of Biology, University of York, York, UK; and 3Microbial Ecology Group, School of Biological and Environmental Sciences, University College Dublin, Belfield, Dublin, Ireland

Correspondence: Jennifer K. Carson, Soil Biology Group, School of Earth and Geographical Sciences M087, University of Western Australia, 35 Stirling Highway, Crawley 6009, WA, Australia. Tel.: +61 8 6488 3595; fax: +61 8 6488 1050; e-mail: jdavis@graduate.uwa.edu.au

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Abstract
We tested the hypothesis that different minerals in soil select distinct bacterial communities in their microhabitats. Mica (M), basalt (B) and rock phosphate (RP) were incubated separately in soil planted with Trifolium subterraneum, Lolium rigidum or left unplanted. After 70 days, the mineral and soil fractions were separated by sieving. Automated ribosomal intergenic spacer analysis was used to determine whether the bacterial community structure was affected by the mineral, fraction and plant treatments. Principal coordinate plots showed clustering of bacterial communities from different fraction and mineral treatments, but not from different plant treatments. Permutational multivariate ANOVA (PERMANOVA) showed that the microhabitats of M, B and RP selected bacterial communities different from each other in unplanted and L. rigidum, and in T. subterraneum, bacterial communities from M and B differed (P < 0.046). PERMANOVA also showed that each mineral fraction selected bacterial communities different from the surrounding soil fraction (P < 0.05). This study shows that the structure of bacterial communities in soil is influenced by the mineral substrates in their microhabitat and that minerals in soil play a greater role in bacterial ecology than simply providing an inert matrix for bacterial growth. This study suggests that mineral heterogeneity in soil contributes to the spatial variation in bacterial communities.

Introduction
The soil habitat exhibits extreme spatial variability and adjacent microhabitats can differ widely in their physico-chemical properties. Soil is composed of a spatially heterogeneous mixture of minerals that differ in elemental composition and a diverse array of organic compounds. Bacterial communities are influenced by a range of microhabitat properties, including pore size (Strong et al., 2004), particle size (Ranjard et al., 2000; Sessitsch et al., 2001) and the availability of water and carbon (Killham et al., 1993; Chenu et al., 2001). Although even adjacent microhabitats can differ in their mineral composition, no studies have investigated whether bacterial communities in soil are influenced by the minerals in their microhabitat.

Studies of other environments provide evidence that different minerals in soil may select distinct bacterial communities in their microhabitats (Roberts, 2004; Gleeson et al., 2005, 2006a; Boyd et al., 2007; Mauck & Roberts, 2007). On an exposed pegmatite, adjacent minerals were colonized by microbial communities with a unique structure (Gleeson et al., 2005, 2006a). Three minerals incubated in an aquifer selected for different subdivisions of Proteobacteria, and the authors concluded that the heterogeneous mixture of minerals in this environment influenced the structure and diversity of the microbial community (Boyd et al., 2007). Because soil is a mixture of minerals and most soil microorganisms live attached to surfaces (Holm et al., 1992), it seems likely that the structure of bacterial communities in soil is influenced by the minerals in their microhabitat.

In situ studies of soil microorganisms and minerals also provide evidence that minerals influence the bacterial communities living in their microhabitats (Certini et al., 2004; Carson et al., 2007). Certini et al. (2004) found that the
microbial community colonizing the surface of 2–10-mm rock fragments and adjacent soil had patterns of substrate use different from those in the surrounding soil particles (< 2 mm) and concluded that the rock fragments were not microbiologically inert. In a previous study, we demonstrated that changing the mineral composition of soil influenced the structure of bacterial and fungal communities. However, we did not show whether the microbial communities affected were in the microhabitats of added minerals or in the surrounding soil matrix.

Minerals in soil may have more influence on the bacterial community structure in their microhabitats when they contain elements that are absent or at low concentrations in soil. Gleeson et al. (2005, 2006a) found that the presence of specific bacterial ribotypes (or species) was related to particular chemical elements in the minerals. In nutrient-limiting aquifers, minerals containing nutrients exhibited denser microbial colonization and different community structures compared with minerals without nutrients (Roberts, 2004; Rogers & Bennett, 2004; Mauck & Roberts, 2007). Mauck & Roberts (2007) suggest that in nutrient-limiting environments, discrete mineral grains containing limiting nutrients may create ‘hot spots’ of microbial activity.

Here, we tested the hypothesis that the microhabitats of different mineral substrates in soil select bacterial communities with distinct structures. We incubated large grains (1–2 mm) of mica (M), basalt (B) or rock phosphate (RP) in soil that was largely composed of quartz. We used a molecular community profiling approach [automated ribosomal intergenic spacer analysis (ARISA)] to describe the structure of the bacterial communities in the microhabitats of mica, basalt and RP and the soil they had been incubated in.

**Materials and methods**

**Soil and minerals**

Soil (0–10 cm) was collected in March (summer) 2005 from a managed pasture site 130 km south of Perth, Western Australia (latitude 32° 60′, longitude 115° 50′). The soil is a Haplic Podzol (FAO, 1998) and the parent material is wind-blowen, siliceous marine sand (McArthur, 2004). The 0–10-cm layer (< 2 mm) had 99.8% sand, 3.5% organic carbon and a pH of 4.7 (1:5, soil: water). All the mineral particles in the soil are < 1 mm. The mineral component of the soil is composed of > 99% quartz (SiO₂, Table 1) and the soil therefore has a low capacity to retain cations (6.4 cmol kg⁻¹) and is naturally deficient in nutrients, including P (19 μg g⁻¹), K, Ca and Mg. The dominant pasture species were Italian ryegrass (*Lolium multiflorum*), with some annual ryegrass (*L. rigidum cv. Wimmera*) and lotus minor (*Lotus subtilisflorus*).

The minerals were obtained from a company that supplies ground minerals to organic farmers as fertilizers. The minerals were chosen because each provided elements that were absent from the soil or were present at very low concentrations (Table 1). The elemental content of the minerals was determined using X-ray fluorescence (Philips PW1404 XRF) after being fused with 12:22 lithium metaborate tetraborate flux at a ratio of 1:10 at 1050 °C (Norrish & Hutton, 1969). Although the surface properties of the minerals may also have differed, that was not the focus of this study and we did not measure surface properties. We were unable to extract bacterial DNA from the minerals, confirming that they were not a source of microorganisms for the microcosms.

**Microcosms**

Microcosms were prepared as described by Carson et al. (2007) and are briefly described here. The three mineral treatments were either M, B or RP added separately. Each microcosm contained 8 g of mineral grains that were 1–2 mm in size in 80 g soil. Because the mineral grains added were 1–2 mm in size and all the mineral particles in the original soil were < 1 mm, each microcosm consisted of two fractions based on size: the mineral fraction (> 1 mm) and the soil fraction (< 1 mm). The mineral fractions were incubated in the soil matrix for the duration of the experiment and separated at the end by sieving to 1 mm.

Plant treatments were annual ryegrass (*L. rigidum cv. Concord*), subterranean clover (*Trifolium subterraneum cv. Trikka*) and an unplanted treatment. Microcosms representing rhizosphere soil were used because microbial activity and mineral dissolution are higher in the rhizosphere compared with the nonrhizosphere soil (Hinsinger et al.,...
Pasture plants were chosen because their high root density increases the dissolution of minerals compared with other plants (Bolan et al., 1990; Harley & Gilkes, 2000). Because plants were grown in only 80 g soil and roots infiltrated the entire soil volume, all of the soil in the planted pots was influenced by roots and could be considered as rhizosphere soil. Microcosms were incubated for 70 days from April to July 2005. At harvest, a subsample from each pot was sieved to 1 mm to separate the mineral fraction (> 1 mm) and the soil fraction (< 1 mm), which were stored at - 20 °C for molecular analysis. We considered soil particles (quartz and organic matter) that strongly adhered to the mineral grains and did not pass through the 1-mm sieve to have been in the microhabitat of the mineral grains during the incubation, as in Certini et al. (2003).

**Bacterial community structure using ARISA**

Total DNA was extracted from both the soil and the mineral fractions using the MoBio PowerSoil™ DNA isolation kit (Carlsbad) with the following modifications: 0.5 g soil or mineral was used and samples were homogenized using a Mini-BeadBeeper-8 (Biospec Products, Bartlesville) at 3200 r.p.m. for 2 min (Carson et al., 2007).

Bacterial ARISA PCR was performed with the following modification to the method of Gleeson et al. (2006b): the DNA extract from the soil fraction was diluted 1:10 before the PCR and no hot start was performed. Briefly, the intergenic spacer (ITS) region between the 16S and the 23S rRNA genes was amplified using primer set S-D-Bact-1522-b-S-20 (eubacterial rRNA small subunit, 5’-TGCGGCTGGATCCCTCCTT-3’) and L-D-Bact-132-a-A-18 (eubacterial rRNA large subunit, 5’-CCGGGTTCGCCATTCCGG-3’) (Normand et al., 1996). Amplified sequences contained the ITS plus c. 130 bp of the 23S rRNA gene. The forward primer was labelled with Beckman Coulter fluorescent dye D4 (Proligo). After quantification of PCR products by gel electrophoresis, aliquots (1–2 μL) of the PCR products were mixed with 38.4 μL deionized formamide, 0.2 μL of Beckman Coulter size standard 600 (dye D1) and 0.4 μL of a custom-made marker labelled with Beckman Coulter dye D1 (Bioventures, Murfreesboro) as in Gleeson et al. (2006b).

Analysis of ITS profiles was performed using an automated sequencer and fragment analysis software (Beckman Coulter, CEQ™ 8000 and algorithm v 2.1.3) (Gleeson et al., 2006b). Only amplicons with a fluorescence > 1% of the total fluorescence were included in the analyses. ARISA amplicons were assigned to ribotypes using the program RIBOSORT (Scallan et al., 2008) and the statistical software R (R Core Development Team, 2007) (both available free from http://www.cran.r-project.org). ARISA amplicons that differed by < 0.5 bp in different profiles were considered identical (Dunbar et al., 2001). In order to make comparisons of microbial communities more reliable, a modification of an analytical procedure proposed by Dunbar et al. (2001) was used. Amplicon lengths that were present in two or more replicates were used to produce a representative ARISA profile of each bacterial community.

**Statistical analyses**

The experimental design consisted of three factors: mineral (three levels, fixed), fraction (two levels, fixed) and plant (three levels, fixed), with four replicates (36 microcosms in total). Multivariate statistical analyses were performed to test for significant effects of mineral, fraction and plant treatments on bacterial ARISA profiles using Primer 6 (Primer-E Ltd, UK). Multivariate analyses were performed on bacterial ARISA profiles that were standardized by total fluorescence and square root transformed. Square root transformation was chosen to balance the advantages of using untransformed data, which preserve relative abundance information, and binary data, which down-weigh abundant groups (Thorne et al., 1999). Bray–Curtis similarity was used as a measure of similarity because unlike some other measures of similarity, it is not affected by ribotypes that are jointly absent between samples, which is common in ARISA data (Clarke & Warwick, 2001).

To determine whether the structure of bacterial communities was affected by the mineral and fraction treatments, ordinations by principal co-ordinate analysis (PCO) were produced for each plant treatment separately. In PCO plots, the distance between points is proportional to the similarity of the bacterial community profiles of those samples (Clarke & Warwick, 2001). To determine the effect of plant treatments on the structure of bacterial communities, PCO plots were produced for each fraction and mineral separately, and with all replicates in a single plot. A permutational multivariate ANOVA (PERMANOVA) was performed to determine the statistical significance of the effects of mineral, fraction and plant treatments on the bacterial community structure observed in the PCO plots (Clarke & Warwick, 2001). PERMANOVA constructs an F-ratio from sums of squared distances within and between groups that is analogous to Fisher’s F-ratio (Anderson, 2001a). Pairwise comparisons were performed within each plant treatment to determine whether bacterial communities differed significantly (P < 0.05) between different mineral treatments within each fraction and whether bacterial communities differed significantly between the mineral and the soil fractions. In addition, pairwise comparisons were also performed within each fraction and mineral treatment to determine whether there were significant differences between bacterial communities in different plant treatments.
The relationships between bacterial communities and the elemental concentrations of M, B, RP and the soil were analysed using nonparametric multivariate regression (DISTLM) in PRIMER 6 (Anderson, 2001b). Backward selection was used to determine what percentage of the variance in bacterial communities was explained by individual elemental concentrations. In addition, elemental concentrations without covariance (P₂O₅, K₂O, MgO and Na₂O) were subjected to a backward selection procedure to develop a model to explain the variance in the bacterial communities. P-values for individual and backward selection tests were obtained using 9999 permutations.

Results

Mineral treatment

PERMANOVA showed that the mineral treatment significantly influenced the structure of the bacterial communities (P = 0.001). Within the mineral fraction in the PCO plots, the three mineral treatments form separate clusters (Fig. 1). The clustering of mineral treatments is clearer in the unplanted and the L. rigidum treatments. This indicates that in each plant treatment, the microhabitats of M, B and RP selected bacterial communities with structures different from each other. Within the mineral fraction, all pairwise comparisons of bacterial communities between different mineral treatments were significant in the unplanted and L. rigidum treatments (P < 0.041). In the T. subterraneum treatment, bacterial communities in microhabitats of M and B were different from each other (P = 0.046), but bacterial communities in the microhabitat of RP did not differ from either (P = 0.079 and 0.093).

In the soil fraction, the effect of mineral treatment on the structure of bacterial communities was smaller than in the mineral fraction. In contrast to the mineral fraction, within the soil fraction in the PCO plots, clustering of different mineral treatments was weak in the unplanted treatment and not evident in the T. subterraneum treatment. However, there was clear clustering of different mineral treatments in the L. rigidum treatment. Pairwise comparisons of bacterial communities confirmed the smaller effect of mineral treatment in the soil fraction, with fewer significant differences than in the mineral fraction. In the unplanted treatment, bacterial communities in soil in which RP was added differed from those in soil with M and B (P = 0.044 and 0.045), but the bacterial communities in soil with M and B were not different (P = 0.066). In the T. subterraneum treatment, bacterial communities in soil with mica and RP added were different (P = 0.011), but neither was different from bacterial communities in soil with basalt (P = 0.168 and 0.059). Within the L. rigidum treatment, bacterial communities from soils in which M, B and RP were added were all different from each other (P < 0.026).

Individual correlations found using DISTLM indicated that the bacterial communities in each plant treatment were significantly correlated to all of the elemental concentrations.
of the variance. In the planted treatments, P$_2$O$_5$, K$_2$O and MgO individually explained a significant percentage of the variance in bacterial communities and together explained 44% and 35% of the variance in bacterial communities. In the unplanted treatment, P$_2$O$_5$, MgO and Na$_2$O individually explained a significant percentage of the variance in bacterial communities. PCO plots of the bacterial communities from each plant treatment show that replicates from different plant treatments all differed significantly (Fig. 3). This indicates that the effect of the mineral and fraction treatments on the structure of bacterial communities was stronger than the effect of the plant treatment. However, pairwise comparisons within each fraction and mineral treatment showed that there were some significant differences in bacterial communities between plant treatments. In the mineral fraction, when mica was added, bacterial communities from different plant treatments did not differ from those in $T. subterraneum$ and $L. rigidum$.

<table>
<thead>
<tr>
<th>Element</th>
<th>Unplanted</th>
<th>$T. subterraneum$</th>
<th>$L. rigidum$</th>
</tr>
</thead>
<tbody>
<tr>
<td>P$_2$O$_5$</td>
<td>4.5</td>
<td>$&lt; 0.001$</td>
<td>3.4</td>
</tr>
<tr>
<td>K$_2$O</td>
<td>4.4</td>
<td>$&lt; 0.001$</td>
<td>2.3</td>
</tr>
<tr>
<td>CaO</td>
<td>4.7</td>
<td>$&lt; 0.001$</td>
<td>3.5</td>
</tr>
<tr>
<td>MgO</td>
<td>3.1</td>
<td>0.002</td>
<td>2.2</td>
</tr>
<tr>
<td>Al$_2$O$_3$</td>
<td>3.8</td>
<td>$&lt; 0.001$</td>
<td>2.3</td>
</tr>
<tr>
<td>SiO$_2$</td>
<td>5.3</td>
<td>0.001</td>
<td>3.8</td>
</tr>
<tr>
<td>Fe$_2$O$_3$</td>
<td>3.0</td>
<td>0.001</td>
<td>2.3</td>
</tr>
<tr>
<td>Na$_2$O</td>
<td>2.0</td>
<td>0.031</td>
<td>2.2</td>
</tr>
<tr>
<td>SO$_3$</td>
<td>4.9</td>
<td>$&lt; 0.001$</td>
<td>3.7</td>
</tr>
</tbody>
</table>

Each elemental concentration was analysed individually using backward selection. The table shows pseudo $F$ values ($F$), probability values ($P$) and the percentage of variance in bacterial communities explained by each element ($\%$).

Fraction treatment

The PCO plots and pairwise comparisons in PERMANOVA show that the fraction treatment affected the structure of bacterial communities. PCO plots of the bacterial communities from each plant treatment that replicate from the mineral and soil fractions form two clusters (Fig. 1). This indicates that within each plant treatment, bacterial communities from replicates of the mineral fraction were more similar to each other than to replicates from the soil fraction and vice versa. PERMANOVA confirmed that fraction significantly affected the bacterial communities ($P = 0.001$) and showed that there was a significant interaction between fraction, mineral and plant treatments ($P = 0.001$). Within each plant and mineral treatment, all pairwise comparisons of bacterial communities between soil and mineral fractions were significantly different ($P < 0.05$). The mean number of ribotypes (fragments) in bacterial communities was 60 in the mineral fraction and 85 in the soil fraction ($P = 0.001$, LSD = 15). The percentage of ribotypes that occurred in the microhabitat of only one mineral was 46% in the unplanted treatment, 59% in $T. subterraneum$ and 65% in $L. rigidum$ (expressed as a percentage of the total number of ribotypes detected in the mineral fractions of each plant treatment, Fig. 3).

Plant treatment

The effect of plant treatments on the structure of bacterial communities was weaker than the effect of the mineral or the fraction treatment. When bacterial communities from the mineral and soil fractions were plotted on two separate PCO plots, there was no clustering of replicates from different plant treatments (Fig. 2). Plotting PCO plots of all replicates and of each mineral treatment separately did not reveal clustering of different plant treatments (results not shown). This indicates that the effect of the mineral and fraction treatments on the structure of bacterial communities was stronger than the effect of the plant treatment. However, pairwise comparisons within each fraction and mineral treatment showed that there were some significant differences in bacterial communities between plant treatments. In the mineral fraction, when mica was added, bacterial communities from different plant treatments all differed significantly ($P < 0.047$). When basalt was added, the bacterial communities in unplanted and $T. subterraneum$ treatments differed ($P = 0.039$), and when RP was added the bacterial communities in unplanted and $L. rigidum$ treatments differed ($P = 0.031$). In the soil fraction when mica was added, the bacterial communities in unplanted treatments did not differ from those in $T. subterraneum$ ($P = 0.074$), but both differed from the bacterial communities in $L. rigidum$ ($P = 0.023$ and 0.019). When basalt was added, the bacterial communities in unplanted and $L. rigidum$ soils differed ($P = 0.019$), and when RP was added, the bacterial communities from all plant treatments differed ($P < 0.019$). All other pairwise comparisons between plant treatments were not significant ($P > 0.05$).
Discussion

This study showed that in soil, different minerals select bacterial communities with distinct structures in their microhabitats. Pairwise comparisons showed that the microhabitats surrounding M, B and RP were each colonized by bacterial communities with a different structure and, in the PCO plots, bacterial communities from replicates of different mineral treatments formed separate clusters (Fig. 1). This finding is supported by studies in other environments that have demonstrated that different minerals select different microbial communities colonizing their surfaces. In an aquifer, three minerals (haematite, saprolite and quartz) were shown to select for different subdivisions of Proteobacteria (Boyd et al., 2007). On an exposed pegmatite, the different minerals (quartz, plagioclase, K-feldspar and muscovite) were colonized by bacterial and fungal communities with a unique structure (Gleeson et al., 2005, 2006a).

In this study, we have shown that the selection of different bacterial communities by different minerals also occurs in a soil environment. This suggests that adjacent mineral particles in soil of different compositions may support different bacterial communities in their microhabitats. In this way, the heterogeneous distribution of minerals in soil may influence the spatial variation in bacterial communities in soil.

When added to soil, M, B and RP created microhabitats that differed not only from each other but also from the surrounding soil. In a previous study, we showed that mixing ground M, B and RP (< 250 µm) into soil altered the bacterial community structure (Carson et al., 2007). However, that study did not show whether the bacterial communities in the microhabitats of the minerals had structures different from those in the surrounding soil. In this study, PCO plots (Fig. 1) and pairwise comparisons in PERMANOVA showed that the bacterial communities in the microhabitats of M, B and RP differed significantly from those in the surrounding soil. Our finding is supported by Certini et al. (2004), who found that the microbial community in the 2–10-mm fraction containing fragments of partially weathered parent rock and strongly adhering soil differed from the microbial community in the < 2-mm fraction of the surrounding soil matrix in their patterns of substrate use. Certini and colleagues proposed the existence of a distinct microhabitat around the rock fragments consisting of the rock surface and the soil immediately adjacent.
to it, which they called the ‘stonesphere’, similar to the rhizosphere around roots. Like the rhizosphere, the microhabitats surrounding M, B and RP grains in soil may have selected bacterial communities with different structures because the mineral grains altered the physicochemical conditions in the adjacent soil.

M, B and RP may have selected bacterial communities with distinct structures in their microhabitats because of differences in their element and nutrient concentrations. Gleeson and colleagues correlated the presence of specific ribotypes on the surfaces of quartz, plagioclase, K-feldspar and muscovite to the presence of certain elements including Ca, K, Na, P, Fe, Al and Si (Gleeson et al., 2005, 2006a). In nutrient-limiting environments, the presence of limiting nutrients in minerals can cause them to be preferentially colonized by microbial communities with different structures. In aquifers limited in P and Fe, silicate minerals containing these nutrients were preferentially colonized by microorganisms and supported microbial communities with different structures compared with minerals without these elements (Roberts, 2004; Rogers & Bennett, 2004; Mauck & Roberts, 2007). The minerals used in this study each contained elements and nutrients that were absent or at low concentrations in other minerals and soil: mica K, Mg and Al; basalt Mg, Na, Al and Fe; and rock phosphate Ca and P (Table 1). DISTLM analysis showed that the concentrations of P, K, Ca, Mg, Al, Si, Fe, Na and S in the minerals and soil each showed a significant percentage of the variance in bacterial communities. In particular, the concentrations of P, K, Mg and Na in the minerals and soil showed between 33% and 44% of the variance in bacterial communities. M, B and RP may have selected distinct bacterial communities because they contained these elements and released them into their microhabitats as they dissolved.

This experiment showed that the effect of plant species on the structure of bacterial communities was smaller than the effect of mineral and fraction treatments. We expected plant species to influence the bacterial community structure in the rhizosphere (Kennedy et al., 2004; Lejon et al., 2005) by releasing root exudates of different compositions (Baudoin et al., 2003) and by causing different amounts of mineral dissolution (Hinsinger & Gilkes, 1997; Wang et al., 2000). Although pairwise comparisons showed that there were some differences in bacterial communities between plant treatments, there was no clustering of replicates from plant treatments in PCO plots of each fraction (Fig. 2) and mineral treatment separately, or all replicates in a single plot (data not shown). Because there was clear clustering of replicates from fraction and mineral treatments (Fig. 1), we concluded that the effect of plant treatment was weaker than the effect of fraction and mineral treatments. Similar results were found in another microcosm study using molecular fingerprinting techniques that showed that although plant species had some influence on the structure of bacterial communities, lime and nitrogen treatments had greater effects (Kennedy et al., 2004).

This study has shown that the structure of bacterial communities in soil depends on which minerals are in their microhabitat. Our findings provide evidence that the role of minerals in influencing bacterial communities in soil is not limited to providing an inert matrix for bacterial growth. Instead, we have shown that a microhabitat exists around different minerals in soil where distinct bacterial communities occur. Further work may identify individual bacterial ribotypes that were selected by the microhabitats of each mineral. In this study, the selection of different bacterial communities by the microhabitats of M, B and RP may have been driven by the presence of P, K, Mg and Na in the minerals and their release into the microhabitat of the mineral grains. The findings of this study suggest that the heterogeneous distribution of minerals in soil may increase the variation between soil microhabitats and contribute to the spatial variation in bacterial communities in this habitat.

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