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Effects of vegetation on the structure and diversity of soil bacterial communities in the Arctic tundra

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Abstract The relatively simple vegetation of the Arctic tundra provides an ideal site in which to study the relationships between plants, bacterial communities and soil chemistry. Here, results of 16S rRNA gene sequencing of secondary Arctic brown soils collected from underneath colonies of *Dryasoctopetala*, *Luzulaconfusa* and *Bistortavivipara* in the Arctic tundra near Ny-Ålesund, Svalbard, Norway, reveal significant differences in bacterial communities related to soil environmental properties. Redundancy analysis shows that all measured geochemical factors were significant in structuring microbiomes, with strong correlations related to soil pH and organic matter contents. Vegetation is likely to affect the physical and chemical properties of the soil, which in turn affects the bacterial community and composition of the soil.

Keywords **Arctic tundra, Arctic soil, vegetation, bacterial community, chemical property**

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1 Introduction

The Arctic tundra encircles the North Pole and extends south to the coniferous forests of the taiga. Although the Arctic is cold, it is rich in biodiversity (Stow et al., 2008). The plants, which are usually short-rooted, dwarf specimens that reproduce asexually, inhabit the layer of soil above the permafrost (Sullivan et al., 2014).

Arctic bacteria have received increasing attention because of their ability to survive and thrive under extreme environmental conditions such as low temperatures and moisture (Jones et al., 2003). Moreover, diverse bacterial communities may be found among the various types of soils and under different temperatures (Derry et al., 1999) and vegetation (Kowalchuket al., 2002). However, the underlying reasons behind observed differences in bacterial communities and soil chemical properties and the associations of these with various forms of vegetation have

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been actively debated (Kielak et al., 2008; Teixeira et al., 2010). For example, many studies have shown that microbial diversity in the soil rhizosphere is affected by soil pH (Tam et al., 2001; Wang et al., 2016). Additionally, previous studies of Arctic tundra soils have indicated that bacterial communities are closely associated with type of overlying vegetation (Wallenstein et al., 2007; Eskelinen et al., 2009).

Bacterial communities in the Arctic region have been previously described using methods including traditional isolation and identification (e.g., Gosink, 1993; Junge et al., 2002; Groudieva et al., 2004; Miteva et al., 2005), Terminal Restriction Fragment Length Polymorphism (hereafter T-RFLP), Polymerase Chain Reaction-Denaturing Gradient Gel Electrophoresis (hereafter PCR-DGGE), cloning and sequencing, and real-time PCR and microarrays (e.g., Brown et al., 2001; Bano et al., 2002; Brinkmeyer et al., 2003; Li et al., 2005; Bhatia et al., 2006; Männistö et al., 2007). Recently, some bacterial communities in the Arctic region have also been examined by 454 Roche pyrosequencing (Ravenschlag et al., 1999; Campbell et al., 2010; Chu et al., 2010, 2011).

Vegetation in the Arctic is very simple and patchy, and each vegetation patch is covered by a single plant species (Jiang et al., 2011). Therefore, Ny-Ålesund, located in Svalbard, Norway, is an appropriate place for studying the relationships between plants, bacterial communities and soil chemical properties. To understand the correlations between bacterial communities and soil chemical properties under different forms of vegetation, as well as the impact of vegetation on the structure and diversity of soil bacterial communities, we examined bacterial communities collected from soils underneath *Dryasoctopetala*, *Luzulaconfusa* and *Bistortavivipara* colonies inhabiting the secondary Arctic brown soils at Ny-Ålesund using a 454 Roche pyrosequencing platform.

2 Methods

2.1 Soil collection and DNA extraction

Triplicate soil samples were collected at Ny-Ålesund (78.5°N, 11.5°E) in northwest Svalbard, Norway in July, 2013, during a Chinese National Arctic Research Expedition. In total, three vegetation patches, dominated by *D. octopetala* (sample Docto, 78°56′52”N, 11°47′30”E), *L. confusa* (sample Lconf, 78°56′48”N, 11°48′48”E) and *B. vivipara* (sample Bvivi, 78°56′40”N, 11°49′44”E), respectively, and one non-vegetation site as background (sample BG, 78°56′47”N, 11°49′08”E) were sampled (Figure 1). Triplicate samples are separated by about one meter in horizontal distance. Plant roots were removed from the soil surfaces with sterile forceps. Soils were then sealed in plastic bags and immediately stored at −80℃ in the survey vessel and then transferred and stored at −80℃ in the laboratory (Qingdao, China).

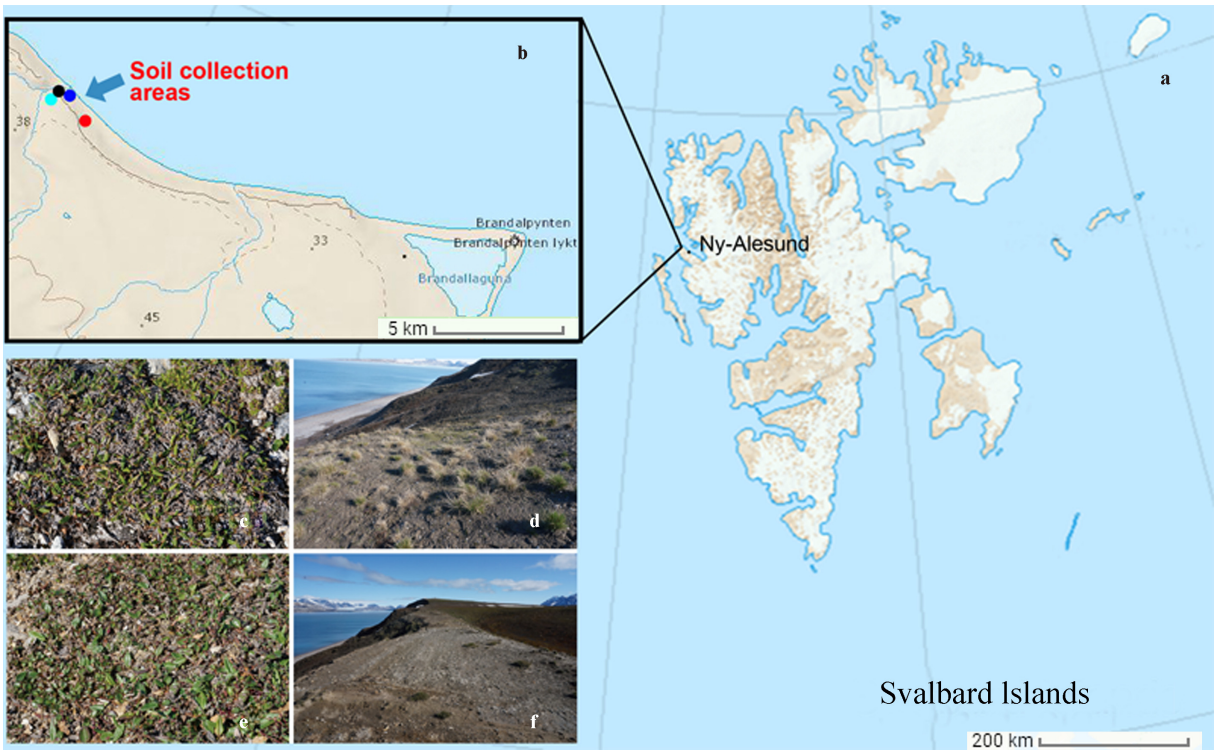

Figure 1 Sample collection area, local landscape and vegetation of four Arctic tundra soils. **a**, Map of the Svalbard Islands; **b**, Soil collection area (red dot: *D. octopetala*; blue dot: *L. confuse*; green dot: *B. vivipara*; black dot: background [bare] soil); **c**, *D. octopetala* colony; **d**, *L. confusa colony*; **e**, *B. vivipara colony*; **f**, Background soil.

2.2 Soil chemical property analysis

Two grams of wet soil were mixed with 10 mL of distilled water and allowed to settle for one hour. Soil pH was determined using a PHS-3C pH meter (Shanghai REX Instrument Company, China). Samples were dried at 105℃ to constant weight to calculate water content, which was determined as the proportion of water loss from the wet soil. The organic carbon (OC) and organic nitrogen (ON) contents of air-dried soil were determined using an elemental analyzer (EA3000, Euro VectorSpA, Italy). A nutrient auto-analyzer (QuAAtro, SEAL, Germany) was used to determine five other nutrients (NH_4^+-N, SiO_4^{2-}-Si, NO_3^--N, NO_2^--N and PO_4^{3-}-P).

2.3 DNA extraction and sequence processing

DNA was extracted from 0.25 g of wet soil using a PowerSoil DNA Isolation Kit (MOBIO Laboratories, Inc.) following the manufacturer's instructions. The PCR primers amplifying the hyper variable V3 region of bacterial 16S rRNA genes were 16S-533R (5'-CCATCTCATCCCTGC GTGTCTCCGACTCAG-NNNNNNNN-TTACCGCGGCT GCTGGCAC-3') (NNNNNNNN indicates the sample barcode) and 16S-8F (5'-CCTATCCCCTGTGTGCCTTGG CAGTCTCAGAGAGTTTGATCCTGGCTCAG-3'). All PCR reactions were carried out in 30 μL reactions, including 15 μL of Phusion High-Fidelity PCR Master Mix (New England Biolabs, Ipswich, MA, United States), 0.2 μM of forward and reverse primers and 10 ng of template DNA. The PCR was thermocycled at 95℃ for 2 min, followed by 25 cycles of denaturing at 95℃ for 30 s, annealing at 56.4℃ for 1 min and extending at 72℃ for 30 s and an extra extension at 72℃ for 5 min. The PCR products were purified using an AxyPrep DNA Gel Extraction Kit (Axygen Scientific, Inc., USA) and sequenced on a 454 GS FLX Titanium Platform (Roche Applied Science, USA).

Raw sequence reads were processed with Mothur v.1.33.3 software (Schloss et al., 2011). After trimming the barcode and primer, chimera and low quality sequences (quality score < 25) were discarded. Sequences longer than 200 bp were assigned taxonomy by referring to the SILVA reference database version 115 (Quast et al., 2013).

2.4 Statistical analysis

OTU rarefaction and coverage, Chao, Shannon's index, and taxonomic heat maps were calculated using Mothur v.1.33.3 software (Schloss et al., 2011). The dissimilarity among soils was determined using the OTU abundance-based Jaccard similarity coefficient. The correlations between communities and soil chemical properties were analyzed by Bray-Curtis distance-based redundancy analysis (db-RDA) using PC-ORD v.6 software (Oksanen, 2011). A network of the 50 most abundant OTUs was visualized using Cytoscape v2.8 software (Smoot et al., 2011). Differences among soils and among bacterial communities were determined by one-way analysis of variance (ANOVA) using Statistical Product and Service Solutions v. 17.0. We directly quantify the difference between a pair of soil or bacterial communities by a *t*-test. Correlation between soil bacterial community and physical and chemical characteristics are calculated as bivariate correlations using SPSS 17.0 software. A linear discriminant analysis effect size (LEfSe) method was used to identify the statistical significance of observed difference in bacterial taxa between sampling sites.

3 Results

3.1 Soil geochemical properties

The four soil samples collected from under different vegetation and non-vegetation conditions (hereafter soils) exhibited distinct chemical properties. While there were no significant differences in the contents of OC and ON, NH_4^+-N, SiO_4^{2-}-Si and NO_2^--N between *D. octopetala* and *L. confusa* colonized soils, the *B. vivipara* colonized soil was acidic (pH 6.5) while the others were alkaline, and its organic C and organic N were significantly different from the other soils (p<0.05). Additionally, the SiO_4^{2-}-Si content of the Lcon sample was obviously higher than in other soils (Table 1 and Appendix file 1).

Table 1 Chemical properties of collected soil samples

Chemical property	Docto	Lconf	Bvivi	BG
Water content/%	10.31 cont[a]	16.15 cont	59.96 conte[a,b]	13.44 cont[b]
Acidity/pH	8.31ityon[a]	8.26ityon[b]	6.50ityon[a,b,c]	7.98ctyon[c]
Organic C/%	0.345ic C/%[a,b]	0.241ic C/%[c,d]	5.825ic C/%[a,c,e]	1.349ic C/%[b,d,e]
Organic N/%	0.014ic N/%[a,b]	0.013ic N/%[c,d]	0.952ic N/%[a,c,e]	0.095ic N/%[b,d,e]
NH_4^+-N/(μg·g^{-1})	10.696c N/%n[a,b]	9.1386c N/[c,d]	22.477c N/%n[a,c]	17.601c N/%n[b,d]
SiO_4^{2-}-Si/(μg·g^{-1})	3.9121c N/%[a,b]	6.4861c N/%[a,c,d]	2.9701c N/%[c]	2.7671c N/%[b,d]
NO_2^--N/(μg·g^{-1})	0.3601c N/%[a]	0.3001c N/%[b]	0.1931c N/%[c]	0.9581c N/%[a,b,c]
PO_4^{3-}-P/(μg·g^{-1})	0.0371c N/%	ND	3.373±2.223	0.487±2.223
NO_3^--N/(μg·g^{-1})	0.426±2.223	0.398±2.223	0.456±2.223	0.530±2.223

Notes: Docto, *D. octopetala* soil; Lconf, *L. confusa* soil; Bvivi, *B. vivipara* soil; BG, background soil; ND, not detected. Means are calculated across sample replicates. Lowercase superscripts (a, b, c, d, e) indicate that sample replicates exhibit significantly different soil properties (*t*-testing, p<0.05). For example, the water contents of replicate a of Docto and Bvivi and replicate b of Docto and BG are significantly different from other samples obtained from these sites.

3.2 Sequencing results

In total, 367613 sequences of the V3 region of bacterial 16S rRNA gene were retrieved from the four soil sites. The number of retrieved sequences varied between 75493 and 109204 among the four soils with an average of 91903. These sequences were assigned to 51717 operational taxonomic units (OTUs) based on ≥97% of similarity and to different classification levels (Figure 2). Rarefaction curves indicate the rationality of the number of sequencing samples with flat curves leading to a smaller number of OTUs.

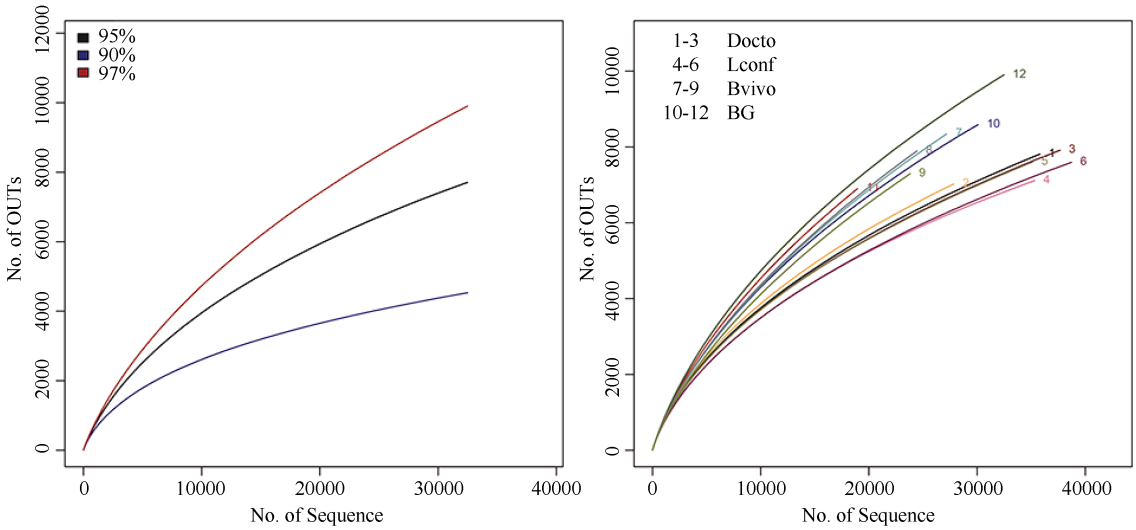

Figure 2 Operational taxonomic unit (OTU) similarity and rarefaction curves.

Calculated Chao, Shannon's and Simpson's indexes are shown in Table 2. Significant differences in these diversity indicators were found among soils. For example, the Shannon's index for Lconf was different from those of other soils; and the Simpson's index for Lconf was higher than that of BG. Additionally, obvious differences in Chao indexes were found among the different soils (Table 2). Similarity between samples can be determined using cluster analysis. From the data shown in Figure 3, it can be shown that the three soil samples collected from beneath each vegetation type were similar to each other, exhibiting only small differences between replicates.

Table 2 Percentage of observed operational taxonomic units (OTU) versus the expected total (coverage) and sample diversity (Chao and Shannon's and Simpson's indexes) calculated from the abundance of observed OTUs

	Docto	Lconf	Bvivi	BG
No. of reads	33787f rea	36401f rea[a]	25164f rea[a]	27185f rea
No. of OTUs	7584of O	7436of O	7845of O	8464of OT
Coverage/%	87.8rage[a,b]	89.2rage[a,c,d]	80.3dage[b,c]	80.9dage[d]
Chao	14452.8eTUsso[a,b]	14163.7eTUsso[c,d]	18456.2e883.9[a,c]	17948.3e883.9f[b,d]
Shannon's index	7.83dexe8[a]	7.67dexe8[a,b,c]	7.90cexe8[b]	8.09cexe8[c]
Simpson index	0.0014n index	0.0020n index[a]	0.0016n index	0.0011n index[a]

Notes: Docto, *D. octopetala* soil; Lconf, *L. confusa* soil; Bvivi, *B. vivipara* soil; BG, background soil; Means are compared in pairs. Lowercase superscripts (a, b, c, d, e) indicate that replicate samples exhibit significant differences (*t*-testing, $p<0.05$).

3.3 Rhizosphere soil and non-root soil community composition

Among the four soils investigated, more than 7000 OTUs were recovered for each sample, with similar numbers of sequences retrieved from each soil. Most of the bacterial sequences belong to common phyla, including *Proteobacteria*, *Actinobacteria*, *Acidobacteria* and *Bacteroidetes*. The phylum *Thermotogae*was not abundant and was only present in BG soil. The phylum *Deinococcus- Thermus* was unique to vegetated soils of all three vegetation types while the phylum *Deferribacteres* was specific to soils developed under Docto and Bvivo (Appendix file 2). The class *Thermotogae* was unique to BG while *Erysipelotrichi*, *Deinococci* and *Deferribacteres* were specific to vegetated soils with *Erysipelotrichi* being comparatively enriched in Lconf. The order *Thermotogales* was unique to BG and *Methylococcales* was unique to Lconf while *Hydrogenophilales* and

Erysipelotrichales were comparatively enriched in Lconf (Appendix file 3). Four families were unique to BG and 30 families were unique to vegetated soil samples. *Hydrogenophilaceae* and *Erysipelotrichaceae* were more abundant in Lconf than in Docto and Bvivo. Twenty-three and 114 genera were found to be specific to BG and vegetated soils, respectively. The most abundant genera in BG was *Rubrobacter*, while *Thiobacillus*, *Hydrogenophaga*, *Asteroleplasma*, *Lacibacter* and *Caenimonas* were the most abundant in vegetated soils. At the species level, beta proteobacteria BP-5 and DC2b-18 and *Flavobacteriumpectinovorum* were relatively high in abundance in Lconf.

Bacteria communities at the OTU level also show a similar pattern of distinct differences between soils. Among the top 50 most abundant OTUs, OTU5 and OTU15 exist only in Docto and Lconf (Figure 4d). Cluster analyses of the 12 soil samples based on the abundance of the 50 most

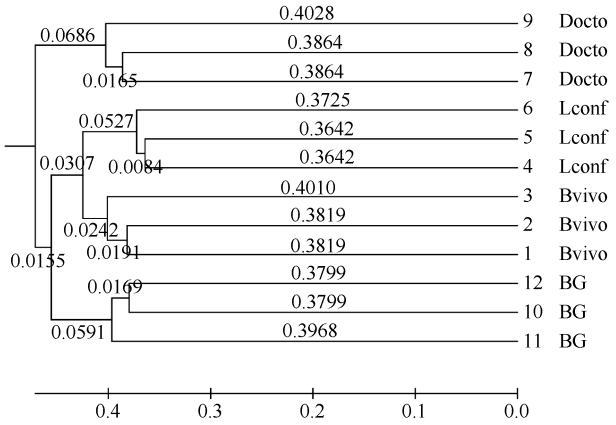

Figure 3 Dendrogram of bacterial communities in soil samples clustered by operational taxonomic unit (OTU) abundance-based Jaccard similarity.

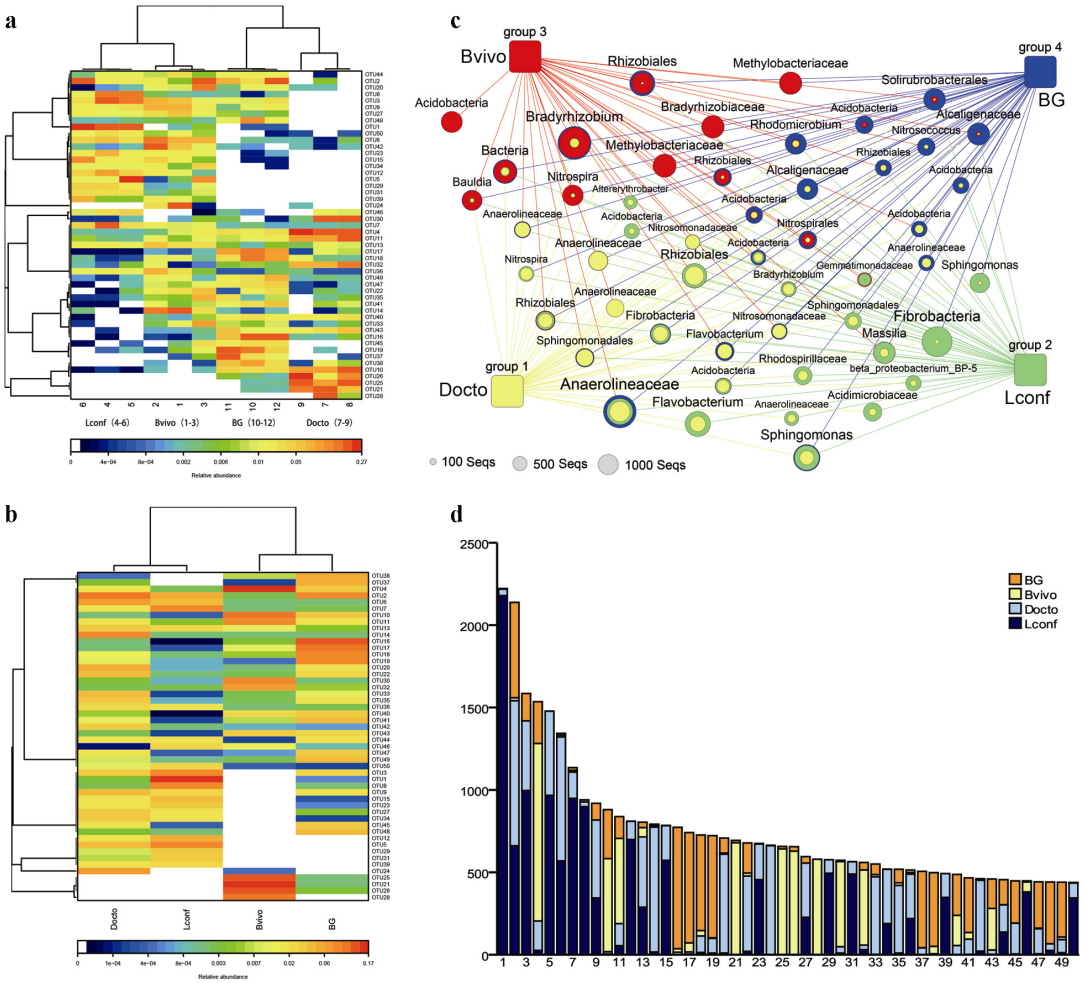

Figure 4 Detailed comparison of the 50 most abundant OTUs among soils collected from beneath the four vegetation types. **a**, A heatmap showing the abundance of the 50 most abundant OTUs and similarity among the 12 soil samples (columns 1–3, Docto; columns 4–6, Lconf; columns 7–9, Bvivo; columns 10–12, BG); **b**, A heatmap showing the abundance of these OTUs among the four soils; **c**, A network diagram showing distribution of the dominant 50 OTUs among the four soil samples; **d**, Abundances of the 50 most abundant OTUs for soils collected from under each of vegetation types.

abundant OTUs indicate that replicate samples cluster closely together while soils developed under each of the four vegetation types were clearly distinguished (Figures 4a, 4b). Soils from beneath each of the four vegetation types were also apparently different in the abundance of sequences representing different taxa (Figure 4c). All these observations indicated that each of the four soils hosts different bacterial communities. Besides the overall difference in community composition, we also focused on bacteria with large differences in bacterial abundance. Based on the LEfSe results, 23 taxa exhibited Linear Discriminant Analysis (LDA) scores greater than 4 (the cutoff for significance) among the 12 samples (Figure 5), such as *Rhizobiales*, *RB41*, *Sphingomonadales*, *Burkholderiales*, *Sphingomonadaceae*. Bivio had the most taxa, 14 out of 23 (61%) which were more abundant than at other sites.

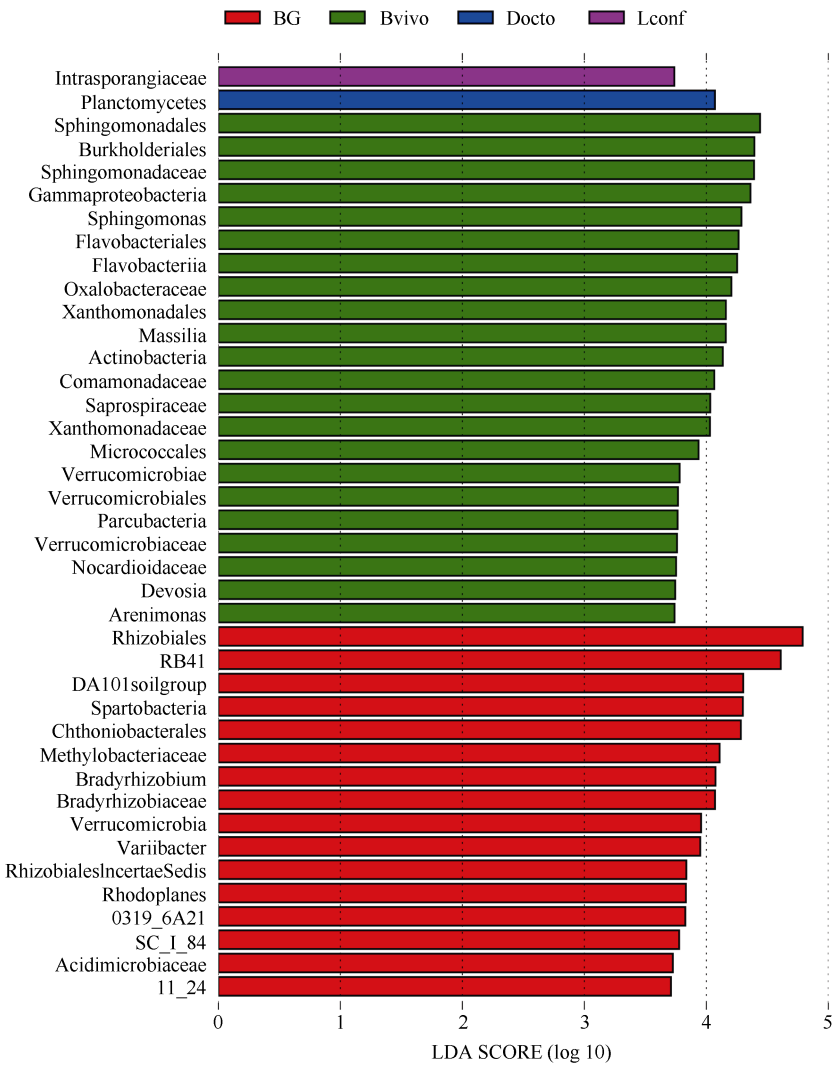

Figure 5 The Linear Discriminant Analysis (LDA) score distribution histogram used to search for bacteria showing a statistically significant difference between soil samples.

3.4 High correlations between bacterial communities and soil chemical properties

A Bray-Curtis distance-based redundancy analysis (db-RDA) of the collected Arctic tundra soils revealed strong correlations between soil chemical properties and bacterial communities using (Figure 6). First, we performed db-RDA analysis and found that the 12 soil samples were well separated from each other. Bvivo, Docto and BG had a similar distribution along the second principal component RDA2. The presence of *Bistortavivipara* was positively correlated with water content, OC and N, NH_4^+-N and PO_4^{3-}-P, but negatively correlated with acidity (pH). The presence of *Dryasoctopetala* or non-vegetation (BG) tended to be positively correlated with NO_2^--N and NO_3-N, while SiO_4^{2-}-Si was highly correlated with the presence of *Luzulaconfusa*. Based on the correlation with db-RDA (Table 3), pH (r^2=0.82, p<0.05) was the most significantly correlated variable with the bacterial community

composition in the study sites, followed by organic C (r^2=0.62, p<0.05) and water content (r^2=0.77, p<0.01). Of the 21 phyla identified in this study, two (*Bacteroidetes* and *Nitrospirae*) were found to be significantly correlated with soil acidity, seven with SiO_4^{2-}-Si, and six with NH_4^+-N (Appendix file 4). We also found that some bacterial communities in the soil were related to geochemical factors. Specifically, genera and families of order *Methylophilales* were significantly correlated with NH_4^+-N content (Table 4).

4 Discussion

In this study, we assessed the composition and diversity of soil bacterial communities under three vegetation types and bare soil. The high values of Shannon's diversity indices (H' =7.67–8.09) and the identification of 7436–8464 OTUs suggest a complex diversity of soil bacterial communities inhabited these samples. Previous studies comparing Arctic soil samples collected from London Island in 2016, which

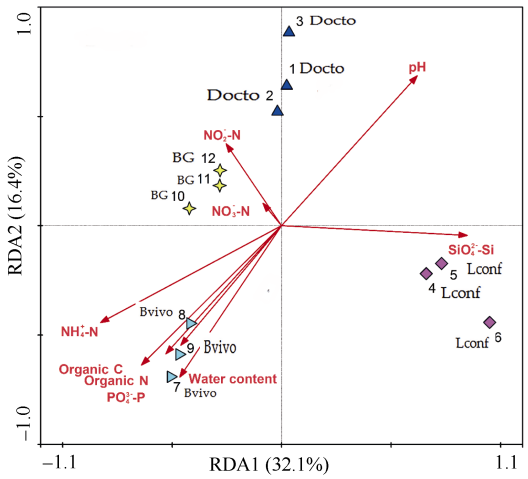

Figure 6 Bray-Curtis distance-based redundancy analysis showing correlations between the bacterial communities and environmental factors associated with the 12 samples collected from the four sampling sites.

Table 3 RDA and Monte Carlo permutation of the relationship between environmental factors and bacterial community composition

	RDA1	RDA2	r^2	Pr (>r)
Water content	−0.746805	0.665043	0.7689	0.006**
pH	0.676717	−0.736243	0.8177	0.003**
NH_4^+-N	−0.284354	0.958719	0.6842	0.012*
SiO_4^{2-}-Si	−0.055498	−0.998459	0.2086	0.338
NO_3^--N	0.442207	0.896913	0.1021	0.667
NO_2^--N	0.969767	0.244033	0.4462	0.06
PO_4^{3-}-P	−0.721772	0.692131	0.537	0.035*
Organic C	−0.577692	0.816255	0.6263	0.003**
Organic N	−0.774478	0.6326	0.6203	0.023*

Notes: R, correlation index; Pr, Pearson's p-value. Symbol of right column show significance (*: Pr < 0.05, **: Pr < 0.01, Without the labels of * or **: Pr<0.1)

Table 4 Correlation coefficients between the most common taxa and soil physicochemical characteristics

Rank	Name		Water content	Acidity /pH	Organic C	Organic N	NH_4^+-N	SiO_4^{2-}-Si	NO_2^--N	PO_4^{3-}-P	NO_3^--N
Class	Acidobacteria	R	0.305	−0.439	0.371	0.306	0.790**	−0.621*	0.464	0.186	0.269
		p	0.336	0.153	0.236	0.333	0.002	0.031	0.129	0.632	0.398
Order	Methylophilales	R	−0.401	0.563	−0.422	−0.474	−0.771**	0.839**	−0.340	−0.409	−0.054
		p	0.196	0.057	0.172	0.120	0.003	0.001	0.280	0.275	0.869
Family	Methylobacteriaceae	R	0.877**	−0.947**	0.525	0.880**	0.728**	−0.466	−0.432	0.696*	−0.079
		p	0.000	0.000	0.079	0.000	0.007	0.127	0.161	0.037	0.807
	Methylophilaceae	R	−0.401	0.563	−0.422	−0.474	−0.771**	0.839**	−0.340	−0.409	−0.054
		p	0.196	0.057	0.172	0.120	0.003	0.001	0.280	0.275	0.869
Genus	*Pedobacter*	R	−0.259	0.370	−0.303	−0.339	−0.640*	0.696*	−0.217	−0.560	−0.113
		p	0.416	0.236	0.338	0.281	0.025	0.012	0.498	0.117	0.726
	Methylotenera	R	−0.402	0.561	−0.422	−0.473	−0.771**	0.830**	−0.337	−0.405	−0.052
		p	0.195	0.057	0.172	0.120	0.003	0.001	0.284	0.279	0.873
	Janthinobacterium	R	−0.082	0.268	−0.102	−0.191	−0.397	0.856**	−0.268	0.605	−0.120
		p	0.801	0.400	0.753	0.553	0.201	0.000	0.399	0.084	0.710

Notes: R, correlation index; p, Pearson's p-value; (*: p<0.05, **: p<0.01)

resulted in calculated Shannon's diversity indices of 7.04–8.24 and identified 3462–3738 OTUs have shown that soil microorganisms under vegetation have higher community diversity (Wang et al., 2016). We found that most of the bacterial sequences belonged to common phyla, including *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Bacteroidetes*, *Verrucomicrobia* and *Planctomycetes*. Of these, *Proteobacteri*a, which is most common phylum in soil, has the highest abundance. Previous studies have indicated that higher abundances of organic carbon and nitrogen are correlated with higher levels of *Proteobacteria* (Parsons et al., 2004; Goldfarb et al., 2011).

Based on analyses of the microbial communities presented in this study, significant differences were observed between soils collected from beneath different plant species. Previous studies have proposed that plant species are related to the rhizosphere microbial community (e.g., Darrah, 1991; Pii et al., 2015). It has furthermore been proposed that plant roots exude organic nutrients and alter the physical and chemical properties of the soil, thereby shaping and altering bacterial diversity, and leading to an increase in the diversity and abundance of rhizobacteria (Marilley et al., 1998). At bacterial genus level, *Erysipelotrichi*, *Deinococci* and *Deferribacteres* were found in all of the vegetated soils, but not in the non-rhizosphere BG. Conversely, *Thermotogae* was unique to BG soil, and no *Thermotogae* were found in the vegetated soils (Appendix file 3). From the data presented in Figure 4, we found that there is a significant difference in OTUs between soil samples, and that the dominant OTUs in each soil type are also different. Lconf impacted soil was dominated by OTU5 (*Flavobacterium*) and OTU3 (*Sphingomonas*), whereas BG was dominated by OTU17 (*Solirubrobacter*) and OTU16 (*Alcaligenaceae*). These taxonomic differences between vegetated soil and bare soil imply that vegetation affects the composition of soil bacterial communities. The more plant root exudates, the more vigorous microbial growth, and the type of root exudates determines the type of rhizosphere microbes, which then leads to differential development of the plant rhizosphere (Agnès et al., 1987).

In the Arctic region, geochemical properties play an important role in determining the diversity of soil bacterial communities. There are significant differences between the chemical properties of the four investigated soils. Soil pH is commonly recognized to influence the soil bacterial community. Similarly, our RDA results indicate that differences in pH are associated with significant differences in the soil bacterial community. In this study, two phyla, *Bacteroidetes* and *Nitrospirae*, out of 21 total, were found to correlate significantly with pH. These phyla have degradation carbohydrate and nitrogen cycle metabolism functions (Bauer et al., 2010), respectively, and nitrospiraeare affected by soil pH (Vinther and Eiland, 1996). These phyla covered a very large portion of sequences retrieved in this study. Furthermore, the genera and families of order *Methylophilales* were significantly associated with NH_4^+-N concentrations. It has been previous demonstrated that *Methylophilales* can use ammonium salts as a nitrogen source (Garrity et al., 2005). These findings indicate that geochemical factors such as pH and NH_4^+-N are also associated with differences in the soil bacterial community. Organic carbon affects the life activities of heterotrophic bacteria in the soil. The phylum *Proteobacteria* contains many heterotrophic bacteria, which provides a possible explanation for the high level of correlation between the abundance of *Proteobacteria* and organic carbon and nitrogen concentrations (Parsons et al., 2004; Goldfarb et al., 2011).

Water content is an additionally important factor that affects the structure and diversity of soil bacterial communities. Soil moisture is also the main driver of soil C and N cycles, because it affects microbial activity and survival as a decrease in water content results in a decrease in the connectivity between the substrates and microorganisms (Chenu et al., 2014).

5 Conclusions

This study investigated the composition of soil bacterial communities collected from under *Dryasoctopetala, Luzulaconfusa* and *Bistortavivipara* colonies inhabiting the secondary Arctic brown soils around Ny-Ålesund. The composition of soil bacterial communities was determined by bacterial 16S rRNA genes on a 454 Roche pyrosequencing platform. A high correlation was found between soil pH and bacterial communities. This study successfully showed that there were significant differences in bacterial communities developed under different species of vegetation. These distinct differences may be caused by soil chemical properties (pH, organic carbon and water content) induced by plant species. Thus, this study demonstrates that different types of vegetation affect the diversity and composition of bacterial communities in soils. Since this experiment did not measure the macrogenome, it remains unclear how specific types of vegetation or plant-root secretion affected the soil bacterial community. However, in future studies, plant secretions, bacterial diversity, metagenomics, and macrotranscripts can be measured to conduct more detailed analyzes of the effects of vegetation types on microbial communities.

Abbreviations

ANOVA, analysis of variance; BG, background soil; Bvivi, *B. vivipara* soil; Docto, *D. octopetala* soil; Lconf, *L. confusa* soil; OTU, operational taxonomic unit; PCR-DGGE, polymerase chain reaction-denaturing gradient gel electrophoresis; RAD, redundancy analysis; SRA, sequencing read archive; T-RFLP, terminal restriction fragment length polymorphism.

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Supporting information

The data set supporting the results of this article is available in the NCBI as a sequencing read archive (SRA) under accession no.SRR1660463 (http://www.ncbi.nlm.nih.gov/Traces/sra/?view=run_browser&run=SRR1660463).

Additional supporting information may be found in the online version of this article (http://www.aps-polar.org/paper/2019/30/02/A190619000002):

Appendix file 1. Data on *T*-test statistics indicating significant differences in physical and chemical factors

Appendix file 2. Phyla found in three plant colony soils and one background soils (three collections each) and their abundances

Appendix file 3. The phylogenetic assignment of OTUs to the taxa at different taxonomical ranks. The size of the circles and the covering of fan on each circle represent the percentages of sequences representing each taxon found in each group of soil samples.

Appendix file 4. Calculated correlation coefficients between 21 phyla and physicochemical factors