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LETTER

The diversity and biogeography of the communities of Actinobacteria in the forelands of glaciers at a continental scale

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Abstract

Glacier forelands, where the initially exposed area is unvegetated with minimal human influence, are an ideal place for research on the distributions and biogeography of microbial communities. Actinobacteria produce many bioactive substances and have important roles in soil development and biogeochemical cycling. However, little is known about the distribution and biogeography of Actinobacteria in glacier forelands. Therefore, we investigated the patterns of diversity and the biogeography of actinobacterial communities of the inhabited forefields of 5 glaciers in China. Of the bacteria, the mean relative abundance of Actinobacteria was 13.1%, and 6 classes were identified in the phylum Actinobacteria. The dominant class was Actinobacteria (57%), which was followed in abundance by Acidimicrobiia (19%) and Thermoleophilia (19%). When combined, the relative abundance of the other three classes, the MB-A2-108, Nitriliruptoria and Rubrobacteria, was only 2.4%. A biogeographic pattern in the forelands of the 5 glaciers in China was not detected for actinobacterial communities. Compared with 7 other actinobacterial communities found in the forelands of glaciers globally, those in the Southern Hemisphere were significantly different from those in the Northern Hemisphere. Moreover, the communities were significantly different on the separate continents of the Northern Hemisphere. The dissimilarity of the actinobacterial communities increased with geographic distance ($r = 0.428$, $p = 0.0003$). Because of environmental factors, the effect of geography was clear when the distance exceeded a certain continent-level threshold. With the analysis of indicator species, we found that each genus had a geographic characteristic, which could explain why the communities with greater diversity were more strongly affected by biogeography.

1. Introduction

The phylum Actinobacteria is a primary phylogenetic clade in eubacteria, which contains a wide range of Gram-positive bacteria with high contents of G + C DNA (Sun *et al* 2010). Because Actinobacteria produce many types of bioactive, complex secondary metabolites, the metabolites are used in medicine and agriculture as antibacterial, antifungal and antitumor drugs (Hill *et al* 2011, Bérdy 2012). To identify new sources of bioactive substances, many researchers focus on the new strains in this phylum. The ocean was the focus of past research; therefore, the search to locate new species is becoming more difficult. In some of this research, unique species were identified in extreme environments (Jiang *et al* 2010, Jiang *et al* 2012, Stres *et al* 2013). In the extreme environment of the forelands of glaciers, the requirements for life are rigorous and the influence of humans is minimal. The soils are shallow, dry out rapidly, are

exposed to low air temperatures and high UV radiation, and have extremely low levels of soil nutrients (Schutte *et al* 2010, Blaalid *et al* 2012). In previous research, we found *Fodinibacter* and *Kineococcus*, among others, as well as a unique genus in the glacier forelands (Wu *et al* 2012, Jangid *et al* 2013). The glacier forelands are a largely unexplored source for the isolation of new microorganisms with the potential to produce biologically active secondary metabolites.

Typically the dominant inhabitants of soils, Actinobacteria have important roles in biogeochemical cycling (Goodfellow and Williams 1983, Holmalahti *et al* 1994, Hill *et al* 2011). Actinobacteria degrade and use complex organic compounds (El-Tarabily and Sivasithamparam 2006, Eisenlord and Zak 2010, Miao and Davies 2010) and are one of the few groups of saprotrophic microorganisms that oxidatively depolymerise lignin (Eisenlord and Zak 2010). They are also used for the bioremediation of contaminated sites and for a wide range of biotransformations (Larkin *et al* 2005, Kitagawa and Tamura 2008, Martinkova *et al* 2009). Moreover, Actinobacteria survive in harsh environments, and some species of Actinobacteria form mycelia to explore the bulk soil in search of water and nutrients (McCarthy and Williams 1990, Dion and Nautiyal 2008). Additionally, some species of Actinobacteria form spores to survive against extreme environments. Indeed, a previous study found that a dominant phylum in the soils of cold environments was Actinobacteria. The relative abundance of Actinobacteria was high in permafrost, ice cores, cryoconite and the forelands of glaciers (Wu *et al* 2012, Edwards *et al* 2013, Stibal *et al* 2015). Although the ecological roles of Actinobacteria are important, these roles are little understood (Miao and Davies 2010). The soil near the terminus of a glacier forms a new habitat for microbial colonisation as the glacier retreats. Therefore, to better understand the ecology of Actinobacteria in the early stages of soil development, it is important to learn the community pattern of Actinobacteria in the environment of the forelands of glaciers (Hill *et al* 2011).

In a previous study, we found some effects of geographic isolation on the actinobacterial community, and this effect of geographic isolation was larger than that of the developing soil chronosequence (Zhang *et al* 2016). In some recent studies, the microbial communities had a characteristic biogeography (Whitaker *et al* 2003, Schmidt *et al* 2011, Hazard *et al* 2013, Rysanek *et al* 2015). However, Dolan (2006) found that different groups of microbes may show very different biogeographies. Moreover, the distribution of Actinobacteria is apparently different from the distribution of the total bacterial community (Hill *et al* 2011). However, the research on the biogeography of Actinobacteria is limited and revealed only that the group had a pattern of geographical isolation (Davelos *et al* 2004, Newton *et al* 2007, Wawrik *et al* 2007). These results were intriguing, and we decided that the forelands of glaciers were the ideal environments to determine the patterns of biogeography in Actinobacteria. Different glacier forelands have similar environments, with little human influence and no vegetation. This environment may reduce the relative effect of soil nutrient heterogeneity and highlight the influence of spatial heterogeneity on the actinobacterial community.

To test this hypothesis, we collected soil samples from the forelands of 5 glaciers in China and used 454 pyrosequencing analyses. Additionally, in previous research, we collected 7 samples from the forelands of glaciers on other continents and also used the 454 pyrosequencing method. To reduce the effects of soil nutrient heterogeneity, we sampled and chose sites that were uninhabited and that were near the glacier terminus.

2. Materials and methods

2.1. Study sites and sampling

We sampled the soils from the forefields of five glaciers in China (table 1 and figure S1). The Urumqi Glacier No. 1 is located in the Tianshan Mountains, 120 km southwest of Urumqi. The annual average temperature is −4.12 °C, and the annual rainfall is 454 mm. The Qiyi Glacier and the Laohugou No. 12 Glacier are located in the Qilian Mountains. The annual average temperature is −6.37 °C and −5.90 °C, and the mean annual precipitation is 335.4 mm and 358.6 mm, respectively. The Dongkemadi Glacier is located in the Tanggula Mountains. The mean annual temperature and precipitation are −5.41 °C and 626 mm, respectively. The Baishui No. 1 Glacier is located in the Yulong Snow Mountains at low latitude, with a mean annual temperature and precipitation of 1.62 °C and 927 mm, respectively. The mean annual temperature and precipitation data were collected at each glacier terminus and were provided by the nearest Glaciological Station of the Chinese Academy of Sciences.

The soils of the Urumqi Glacier No. 1 and the Dongkemadi Glacier were sampled in August and May 2010, respectively. The soils of the Qiyi Glacier, the Laohugou No. 12 Glacier and the Baishui No. 1 Glacier were collected in August 2011. The soils were sampled in the forelands of the glaciers near the glacier termini (detailed information was in table 1). We collected three independent replicate samples at each site, and each replicate was sampled with a randomly placed core that was 5 cm deep within an area of 2 m × 2 m. The larger gravel was removed from the samples. The samples were transported on ice within 8 h and then were stored at −20 °C until the analyses.

2.2. Measurement of soil characteristics

The pH values were analysed in 1:5 soil: water mixtures with a pH metre (PT-10, Sartorius, Göttingen, Germany). The total organic carbon (TOC) and total nitrogen (TN) contents were quantified with an

Table 1. The information for the research sites and data sources.

Glacier	Abbr.	Longitude	Latitude	Elevation (m)	Distance (m)[a]	Years[+]	Vegetation[#]	Data source
Wuyuan No. 1 Glacier	WY	86°48′E	43°06′N	3900	23	6	Non	This work
Qiyi Glacier	QY	97°30′E	39°30′N	4200	10	<5	Non	This work
Laohugou No.12 Glacier	LHG	96°31′E	39°30′N	4721	10	<5	Non	This work
Dongkemadi Glacier	DK	92°04′E	33°04′N	5393	10	<5	Non	This work
Baishui No. 1 Glacier	YL	100°12′E	27°07′N	4400	10	<5	Non	This work
Himalaya	HM	88°07′E	27°48′N	6000	—	<25	Non	Stres *et al* 2013
Midre Love´n Glacier	ML	10°21′E	74°49′N	60	—	5	Few	Schutte *et al* 2010
Mendenhall Glacier	MD	134°32′W	58°21′N	20	—	6	Non	Knelman *et al* 2012
Lyman Glacier	LM	120°54′W	48°10′N	1900	0	Current year	Non	Brown and Jumpponen 2013
Damma Glacier	DM	8°28′E	46°38′N	2100	—	10	Non	Rime *et al* 2015
Franz Josef Glacier	FJ	170°11′E	43°28′S	240	—	60	Few	Jangid *et al* 2013
McMurdo Dry Valley	MM	163°00′E	77°30′S	932	—	—	Non	Van Horn *et al* 2013

[a] Distance from the glacier termini; + years since glacier retreat; # the vegetation of each sample point.

automatic element analyser (Elementar Vario-EL, Germany) (Liebner *et al* 2009).

2.3. DNA extraction and 454 pyrosequencing

The total DNA was isolated from the mixed soil samples of the three replicates using the PowerSoil DNA Isolation Kit (MoBio Mo Bio Laboratories, Inc., Carlsbad, CA), following the manufacturer's instructions. We used the bacterial universal primers 27F and 515R to amplify the V1–V3 region of the bacterial 16S rRNA genes. The amplification of the 16S rRNA genes used an initial denaturation step at 95 °C for 3 min, which was followed by 25 cycles of denaturation at 95 °C for 30 s, annealing at 50 °C for 30 s and an extension at 72 °C for 30 s, and a final extension step of 10 min at 72 °C. The amplicons were sequenced with a GS FLX Titanium System (454 Life Sciences, Roche Applied Science).

2.4. Sequence analyses

The raw pyrosequencing reads were sorted with barcodes and were quality trimmed using QIIME 1.8.0 (Caporaso *et al* 2010) in Bio-Liunx 8.0.5 (Field *et al* 2006). The parameters were as follows: at least 200 bp in length, a perfect match to the sequence tag (barcode) and the 16S rRNA gene primer, as well as no undetermined bases, including chimeric sequences. The sequences that remained were clustered into operational taxonomic units (OTUs) at 97% identity with QIIME and were taxonomically assigned according to the best matches in the Greengenes ribosomal database (version 13-8) (DeSantis *et al* 2006). The sequences of the phylum Actinobacteria were screened with QIIME from each library.

Seven other glaciers were previously studied, and we also selected the sequences from the forelands of these glaciers (table 1 and figure S1). The Mendenhall Glacier (Knelman *et al* 2012) and the Lyman Glacier (Brown and Jumpponen 2013) are in North America. The Midre Love´n Glacier (Schutte *et al* 2010) and the Damma Glacier (Rime *et al* 2015) are in Europe. One sample was from the Himalayas (Stres *et al* 2013), which are located in Asia, and the remaining two samples were from the Southern Hemisphere. The McMurdo Dry Valley (Van Horn *et al* 2013) is in Antarctica, and the Franz Josef Glacier (Jangid *et al* 2013), which is near Antarctica, is located on the western South Island. We chose sites in this letter which were unvegetated and the closest glacier terminus as far as possible (detailed information is in table 1). These data sets contained the sequences from the different variable 16S regions, which limited the possible direct sequence comparisons. The comparisons of the species distributions were performed after the taxonomic classification.

2.5. Statistical analyses

Statistical analyses were performed using the SPSS statistical software package 16.0 (SPSS Inc., IL) and were based on the genus abundance matrices. The relationships among the environmental variables and the compositions of the actinobacterial community were examined with redundancy analysis using the rda function implemented in the vegan package in R 3.1.3. The dissimilarity of the actinobacterial communities was calculated with beta_diversity.py in QIIME using the method of Bray–Curtis. The ordination analysis of the composition of the actinobacterial community was visualised using nonmetric multidimensional scaling (NMDS) based on the Bray–Curtis distance using the R language vegan package. The ANOSIM analysis was performed to access the isolation effects of the different continents or geological areas on microbial community. The number of permutations was set at 999; all other arguments used the default values setting. The indicator species analysis was performed using the multipatt function implemented in the indicspecies package in R; the analysis was with 99 999 permutations, and combinations were allowed among habitats to identify the genus, which led to the changes in the multivariate patterns (De Caceres *et al* 2010).

3. Results

3.1. Community composition of Actinobacteria

We obtained 4674 actinobacterial 16S rRNA sequences from this work (the bacterial community structures are shown in figure S2). The classification success of the actinobacterial sequences decreased at the lower taxonomic levels (figure 1). Six classes in the phylum Actinobacteria were identified. The class of Actinobacteria was dominant, with a relative abundance (57%) that was much higher than that of the other classes. Following the class of Actinobacteria, the relative abundance of the classes Acidimicrobiia and Thermoleophilia was 19% for each. The remaining three classes combined had a relative abundance of 2.4% (figure 1).

The differences in the structure of the actinobacterial communities were more apparent at the lower levels of classification. At the taxonomic level of class, Actinobacteria was the dominant class at all the sites except the QY Glacier. Thermoleophilia was the dominant class at the QY Glacier. The relative abundance of Actinobacteria was more than half of all the communities except those at the YL and the QY glaciers. At the taxonomic level of order, the actinobacterial communities of the 5 glacier forelands were significantly dissimilar (figure 2). Based on the cluster analysis of the actinobacterial communities at the taxonomic level of genus, the community structure of the LHG Glacier was different compared with the others. The structure was similar between the QY and YL glaciers and also the WY and DK glaciers. Although

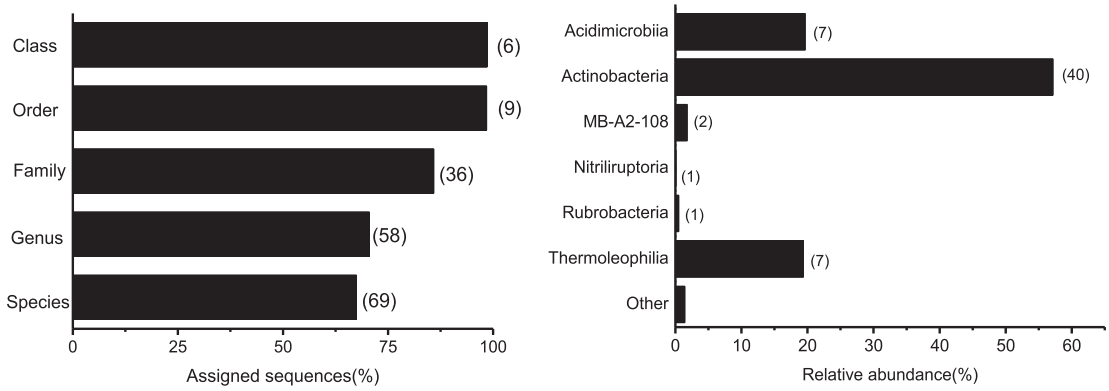

Figure 1. Overview of the actinobacterial community composition in the forelands of 5 glaciers in China. The left panel shows the percentage of sequences assigned (bars) and the number of classified taxa (in parentheses) for each taxonomic level. The right panel shows the relative abundance of the 7 classes and the number of classified genera (in parentheses) in each class.

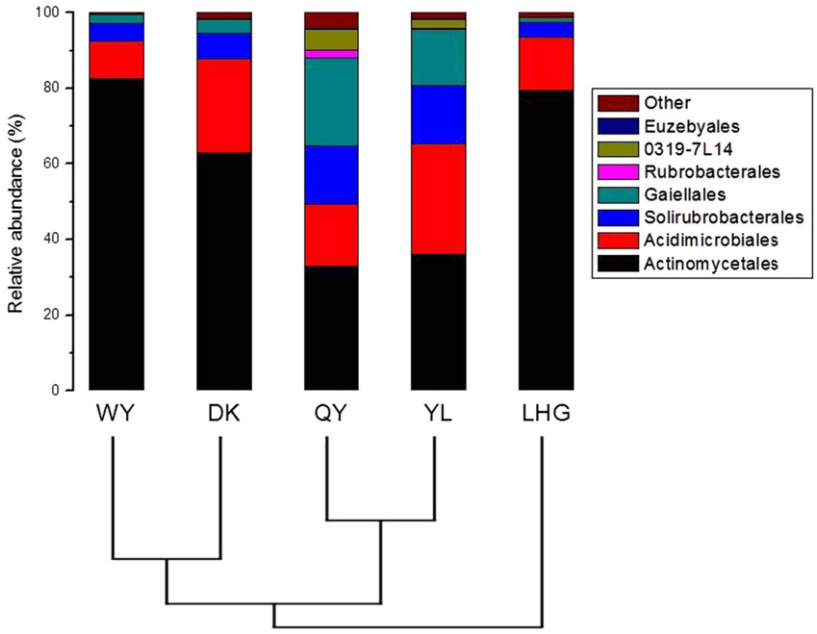

Figure 2. The top histograms show the composition of Actinobacteria at the taxonomic level of order in the forelands of 5 glaciers in China. The bottom graph shows the cluster results of the actinobacterial community at the level of genus by the Bray–Curtis method for the 5 glaciers.

the distance between the QY and LHG glaciers was only 83 km, the dissimilarity of the actinobacterial communities was the largest. Moreover, the greatest difference in the climate of the five glaciers was between the QY and YL glaciers, but the structures of the actinobacterial communities were the most similar. However, the actinobacterial communities in the forelands of glaciers in China did not show a biogeographical pattern.

3.2. Effect of environmental factors

Eight environmental factors (i.e., latitude, longitude, elevation, precipitation, temperature, TOC, TN, and pH) were correlated with the communities of Actinobacteria by redundancy analysis (figure 3). Axis 1 explained 51.0% of the variance, and axis 2 explained 25.2% of the variance. The partial RDA showed that longitude was the largest factor of the 3 spatial factors (i.e., latitude, longitude, and elevation). The soil pH was the largest factor of the 3 soil factors (i.e., TOC, TN, and pH), and it significantly influenced the community of Actinobacteria ($r^2 = 0.9722$, Pr = 0.025, Monte Carlo test). The climate factors (temperature and precipitation) were not correlated with the community of Actinobacteria. For the three types of environmental factors, the variance was explained in the order of spatial > soil > climate.

3.3. Effect of geographical isolation

To determine whether the actinobacterial community had a biogeographic pattern, we analysed the data for identical environments from 7 previous sites (table 1).

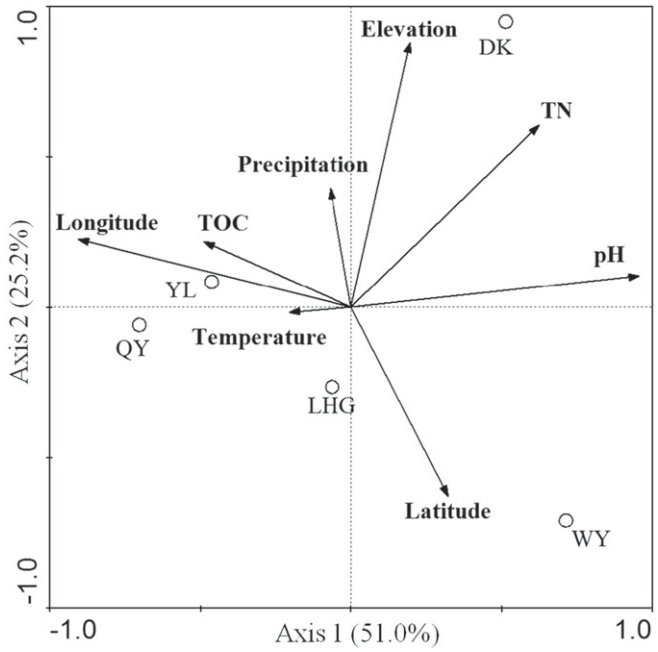

Figure 3. Bi-plot from the redundancy analysis (RDA) that shows the relationships between the actinobacterial community composition at the genus level and the environmental variables for the 5 glaciers (TOC = total organic carbon (%); TN = total nitrogen (%); Precipitation = the mean annual precipitation at the glacier terminus; and Temperature = the mean annual temperature at the glacier terminus).

Table 2. The alpha diversity and the relative abundance of Actinobacteria in the forelands of 12 glaciers.

Glacier	Chao1[a]	Shannon[a]	Relative abundance	Glacier	Chao1[a]	Shannon[a]	Relative abundance
ML	249.1	4.33	11.2	LHG	182.9	3.48	3.8
MD	1762.2	5.37	10.9	DK	265.4	4.43	11.4
LM	106.0	3.59	16.8	HM	224.6	4.22	8.0
DM	237.2	3.98	5.6	YL	437.6	4.81	11.8
WY	163.0	3.87	12.5	FJ	282.3	4.61	30.0
QY	502.5	4.92	26.1	MM	257.1	3.55	9.9

[a] These were calculated with the lowest number of sequences from the forelands of 12 glaciers (234, LHG).

We obtained a total of 16 689 sequences from the forelands of 12 glaciers. The alpha diversity indices did not change with the relative abundance of Actinobacteria (table 2). The FJ glacier, with Actinobacteria at 30% of the total, was ranked No. 4 based on the Chao1 and the Shannon diversity indices. Moreover, the MD glacier had the highest alpha diversity, but the relative abundance of Actinobacteria was less compared with the mean for all sites. The diversity and relative abundance of Actinobacteria in bacteria didn't show correlation with geographic features in the glacier foreland.

When the actinobacterial community in China was compared with the other locations, we found significant differences among the sites. The class OPB41 was not observed in the samples from China, and only 9 genera were found in China (1 in the class Acidimicrobiia, 6 in the class Actinobacteria, 1 in the class MB-A2-108, and 1 in Rubrobacteria). Moreover, the abundance of these genera was low, and *Rubrobacter* was the most abundant. Thirty-three genera were not found in China (2 in the class Acidimicrobiia, 27 in the class Actinobacteria, 1 in the class OPB41 and 2 in the Thermoleophilia). *Gardnerella*, *Propionibacterium* and *Corynebacterium* were the most abundant genera.

The dissimilarities in the composition of the actinobacterial communities among the 12 glaciers were identified with a nonmetric multidimensional scaling (NMDS) biplot (figure 4). Notably, the samples collected from one continent were aggregated. The LHG Glacier was isolated from the other 5; however, this separation might be because the relative abundance of Actinobacteria was the lowest for this glacier, and we obtained only 234 sequences, which might not represent the actual community structure. The MM Dry Valley and the FJ Glacier were in the Southern Hemisphere, and the actinobacterial communities at these sites were significantly different from those of the

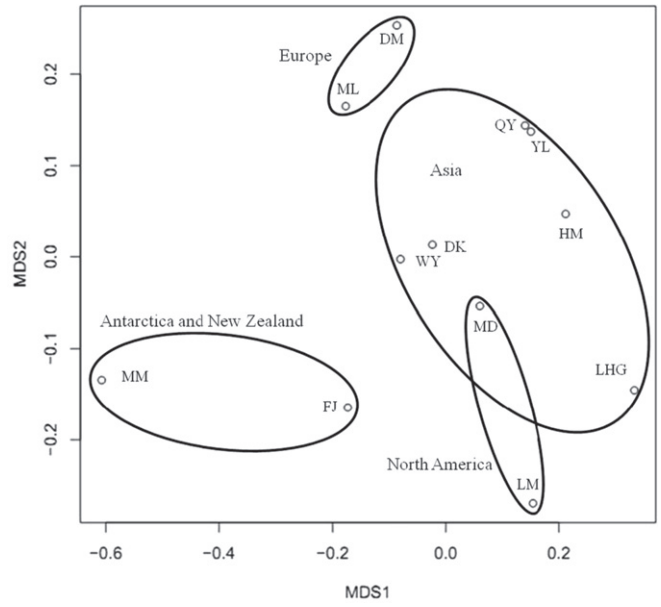

Figure 4. Non-metric multidimensional scaling (NMDS) biplot of a Bray–Curtis dissimilarity matrix that shows the actinobacterial community structure of 12 glaciers. An oval contains the sample points from one continent.

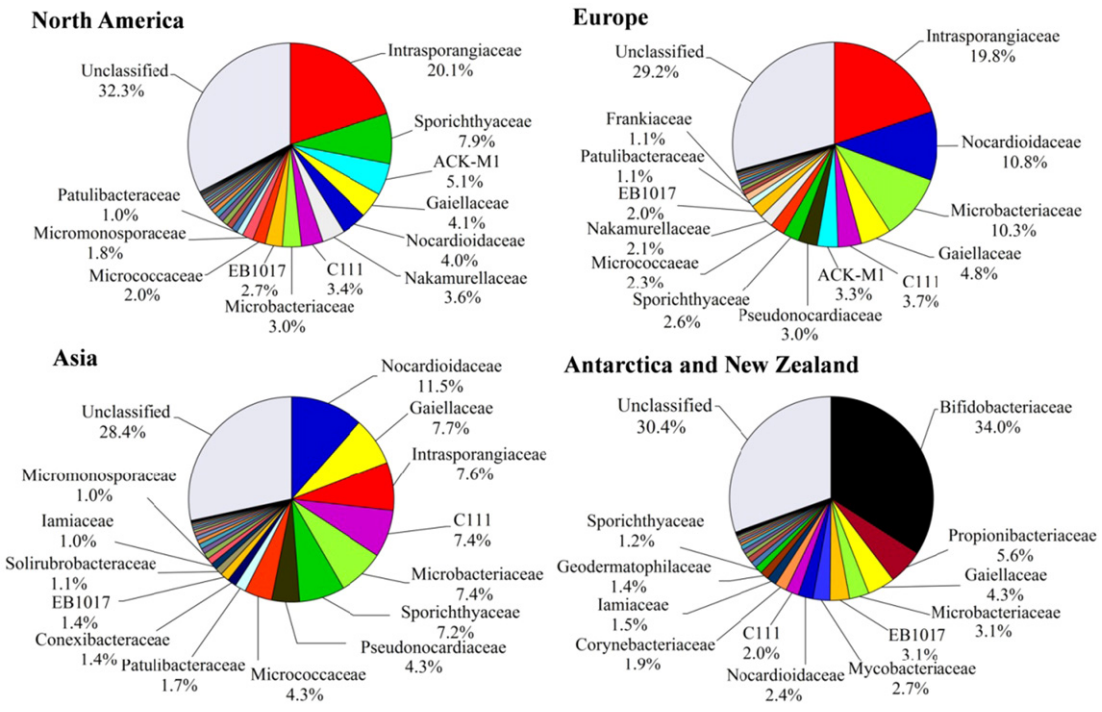

Figure 5. Family level taxonomic distribution of Actinobacteria in the forefronts of glaciers in North America, Europe, Asia and Antarctica. Only the genera with at least a 1% relative abundance are presented.

Northern Hemisphere. The communities of Europe, Asia and North America were relatively similar but with obvious differences. The differences in the actinobacterial communities among the 4 continents are shown in figure 5. At the family level, the actinobacterial communities of Antarctica and New Zealand were clearly different from those of the other continents. The classes of Bifidobacteriaceae and Propionibacteriaceae were the dominant groups. In Europe, Asia and North America, Intrasporangiaceae was one of the dominant class. For the orders in this class with a relative abundance of more than 1%, they appeared frequently on these 3 continents, but the type and the abundance were different.

Based on the correlation analyses between the community dissimilarities (Bray–Curtis distance) and the geographic distances, the structure of the actinobacterial community did not have a biogeographical

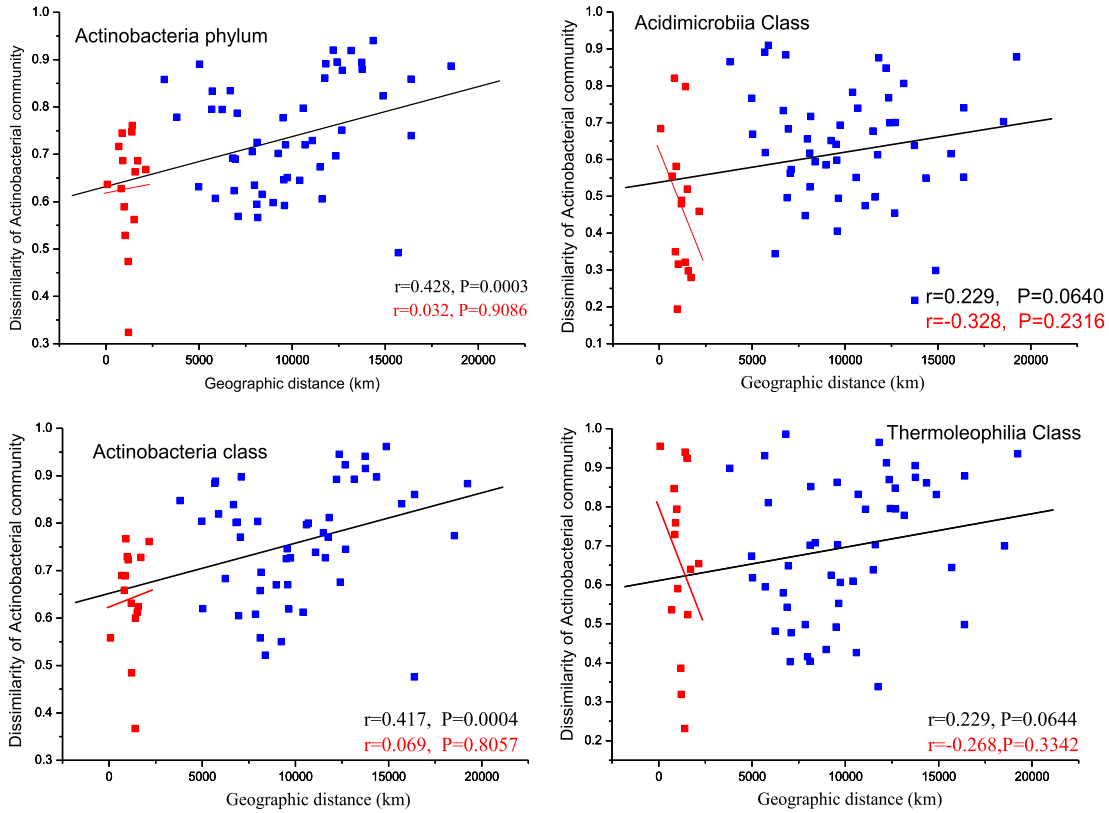

Figure 6. Correlations between community dissimilarities (Bray–Curtis distance) and geographic distances. The red points and lines represent the correlations between the samples in Asia. The dark line is the correlation based on all the samples.

pattern in Asia (figure 6). The community structures of the Actinobacteria phylum, the Acidimicrobiia class, the Actinobacteria class and the Thermoleophilia class were not correlated with the distances of the samples in Asia. However, the community structure of the phylum Actinobacteria showed a significant pattern among all the sites ($r = 0.428$, $p = 0.0003$; figure 6). At the lower level of taxa, the communities of the Acidimicrobiia and Thermoleophilia classes showed weak relationships between each pair of sites. Depending on the level of taxa examined, the biogeographical patterns were different in the different communities of Actinobacteria. Moreover, the structure in the smaller size communities was less affected by biogeography.

The value of indicator species is to assess the strength and the statistical significance of the relationships between the species occurrence/abundance and the site. The indicator species are also used as ecological indicators of community types, habitat conditions, and environmental changes. We used this analysis to determine whether the genera of Actinobacteria had a strong geographic pattern. Based on the analysis, 34 genera of 51 total showed a strong identification with one place (figure 7), and all of the genera had site-specific characteristics. Thus, with the genus-level analysis of the actinobacterial community, biogeographic patterns formed and these patterns were more clear when the community had more members.

4. Discussion

The distribution patterns of the actinobacterial community in the forelands of glaciers were examined at a continental scale. Significantly, Actinobacteria was a dominant phylum in the forelands of glaciers (table 2 and figure S2), and they were highly variable among the different locations. The mean relative abundance of Actinobacteria was 13.2% of the bacteria. The highest abundance was in the foreland of the FJ Glacier, which was almost 8-fold higher than the lowest abundance in the foreland of the LHG Glacier. The two glaciers, the QY and the LHG, were the closest at only 83 km, but the difference in the relative abundance was large (almost 7-fold). As shown in figure 4, the 12 glaciers were classified into 4 groups, none of which contained the 3 glaciers with highest relative abundance or the 2 glaciers with the lowest relative abundance. The alpha diversity of the actinobacterial community showed an identical separation. The alpha diversity indices were not affected by the relative abundance of Actinobacteria. Based on the Pearson correlation analyses, the relative abundance and the alpha diversity were not correlated with the latitude, the longitude, or the elevation. Thus, the diversity and the proportion of Actinobacteria in the bacteria did not have regional identifications. A possible reason for the lack of regional correlations could be the effect of the degree of development of the

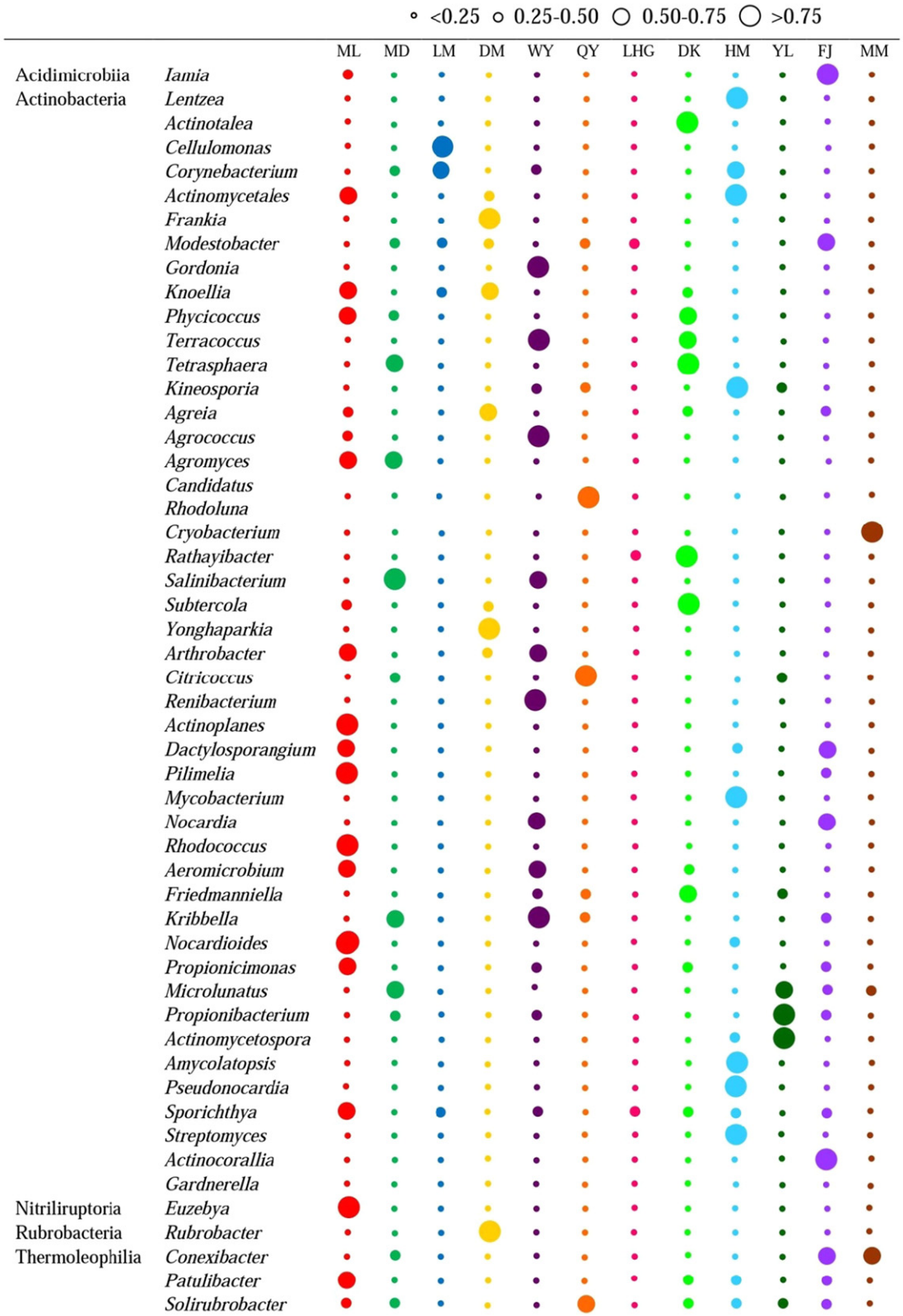

Figure 7. The indicator genera in the forelands of the different glaciers. The size of each circle defines the association strength (indicator value) of a genera with the different glaciers: 0–0.25: not characteristic; 0.25–0.5: weakly characteristic; 0.5–0.75: characteristic; and 0.75–1.0: strongly characteristic.

soils. The relative abundances of the different phyla were different as the soil developed in a glacier foreland (Jangid *et al* 2013, Rime *et al* 2015, Wu *et al* 2012), and the alpha diversity increased with the development of soils in a glacier foreland (Rime *et al* 2015, Schutte *et al* 2010, Wu *et al* 2012). Although we selected samples from the terminus of all the glaciers, the time that the soils were exposed was not same for the

different glaciers because the rates of glacial retreat rate were different in different areas of the Earth (Vaughan *et al* 2013, Yao *et al* 2012). Stochastic events could be another explanation (Dini-Andreote *et al* 2015, Martiny *et al* 2003). Dini-Andreote *et al* reported that the initial community establishment was be primarily dominated by stochastic events, and therefore, different actinobacterial communities formed in different places.

Although the relative abundance and the alpha diversity of Actinobacteria were not indicators of biogeography, the actinobacterial community structure did demonstrate biogeographic separation (table 2). When we analysed the biogeographic patterns of the community structure, the structure of the smaller communities was less affected by biogeography (figures 4 and 6). The biogeographic effect was greater for the class Actinobacteria than for the classes Acidimicrobiia and Thermoleohilia. In general, the research on the biogeography of Actinobacteria is limited. Newton *et al* (2007) found that in 18 lakes, the Actinobacteria acI Lineage community did not show a biogeographic pattern; the authors hypothesised that their focus on a single bacterial lineage only could explain the absence of a biogeographic pattern. Based on our results (figure 6), this hypothesis was correct. Based on the analysis of indicator species, each genus had a biogeographic identification, and the effect was stronger when the actinobacterial community contained more members (figure 7).

Recently, the evidence has continued to increase that microbial communities have biogeographical patterns (Martiny *et al* 2011, Hazard *et al* 2013, Liu *et al* 2014, Rysanek *et al* 2015). In many studies, the bacterial community changed with distance, but these changes were not completely consistent. In King *et al* (2010), the bacterial community dissimilarity was autocorrelated with a distance within 240 m, on the south side of the Green Lakes Valley Watershed in the USA. However, there were no correlations between 240 m and 2000 m. A significant positive spatial autocorrelation of the distribution of the genotypes was observed among distances of $<$197 km (Cho and Tiedje 2000). According to our results, the actinobacterial community did not show geographical isolation in Asia ($<$2148 km) (figure 6). At the scale of the continents, the biogeographic effects were significantly correlated with the distance among the sites (figure 6). We believe that the bacteria have a biogeographic pattern and that the community structure is simultaneously affected by distance and other environmental factors (Xiong *et al* 2012). However, the effects of the two types of factors, the distance and the other environmental factors, were different at different scales. In addition to some previous research, the dissimilarity of the bacteria increased with distance in this study (Martiny *et al* 2011, Rysanek *et al* 2015, Xiong *et al* 2012). However, the soil nutrient heterogeneity did not increase with distance. When the distance increased to some threshold, the dissimilarity caused by the effect of the spatial heterogeneity was greater than that of the soil nutrient heterogeneity in some types of environment. This relation was in contrast to the conclusion of Fierer and Jackson (2006) that microbial biogeography was controlled primarily by edaphic variables, which could explain why the dissimilarity of the bacteria did not change with the distance in some regions. The climate factors were affected by the geographic position, and the climate significantly influenced the bacterial community (Angel *et al* 2010, Bahl *et al* 2011). Our sample locations were all located in the glacier forelands, which reduced the influences of the climate (figure 3).

The sites near the glacier termini were in the beginning stage of primary succession in the glacier forelands and were more easily affected by exotic species (Martiny *et al* 2003, Dini-Andreote *et al* 2015). Many of the glaciers were located in cold, high-elevation environments that were linked with the upper atmosphere via the movement of cold air masses (Darcy *et al* 2011). Many Actinobacteria form spores that could be spread through the high-elevation air current, which is convenient for the dispersal of Actinobacteria. With this type of dispersal, the idea of Gast (2015) would be supported as to why they were not globally ubiquitous. The geographical barriers and the local adaptations affected the dispersal (Papke and Ward 2004). The dispersal ability may dilute the effects of vicariant events, but dispersal alone does not obliterate all the distributional patterns in time and space (Dolan 2006). The most abundant and dominant species are predicted to have higher rates of dispersal and levels of ubiquity (Finlay 2002). Our results were in approximate accord with this prediction. However, there were a few exceptions. Of the four genera with the highest mean relative abundance, *Gardnerella* was found only in the Antarctic, whereas *Arthrobacter* was found at half of the sites. *Pseudonocardia* and *Salinibacterium* met this prediction.

5. Conclusions

The actinobacteria phylum was one of the dominant phylum in forefields of glaciers. The continental scale investigation of biogreography actinobacterial communities in glacier forefileds showed that the dissimilarity of the actinobacterial communities increased with increasing geographic distance. And the effect of geography was remarkable when the distance exceeded a certain continent-level threshold. In other world, the communities were significantly different on the separate continents. In addition, the communities with greater diversity or higher abundace were more strongly affected by geographic distance.

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