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Soil bacterial diversity in the Arctic is not fundamentally different from that found in other biomes

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Summary

The severe environmental stresses of the Arctic may have promoted unique soil bacterial communities compared with those found in lower latitude environments. Here, we present a comprehensive analysis of the biogeography of soil bacterial communities in the Arctic using a high resolution bar-coded pyrosequencing technique. We also compared arctic soils with soils from a wide range of more temperate biomes to characterize variability in soil bacterial communities across the globe. We show that arctic soil bacterial community composition and diversity are structured according to local variation in soil pH rather than geographical proximity to neighboring sites, suggesting that local environmental heterogeneity is far more important than dispersal limitation in determining community-level differences. Furthermore, bacterial community composition had similar levels of variability, richness and phylogenetic diversity within arctic soils as across soils from a wide range of lower latitudes, strongly suggesting a common diversity structure within soil bacterial communities around the globe. These results contrast with the well-established latitudinal gradients in animal and plant diversity, suggesting that the controls on bacterial community distributions are fundamentally different from those observed for macroorganisms and that our biome definitions are not useful for predicting variability in soil bacterial communities across the globe.

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Introduction

The paradigm that 'Everything is everywhere, but the environment selects' for explaining microbial distributions (Baas Becking, 1934) has been supported by a range of studies indicating that microbial dispersal can be global (Finlay and Clarke, 1999; Finlay, 2002; Fenchel, 2003; Hubert *et al.*, 2009), and that microbial community composition is strongly influenced by contemporary site-specific environmental conditions (Crump *et al.*, 2004; Horner-Devine *et al.*, 2004; Fierer and Jackson, 2006; Lozupone and Knight, 2007; Cermeno and Falkowski, 2009). However, a recent review argues that historical factors such as dispersal limitation in the past (i.e. at a more primitive evolutionary stage) and changes in environmental conditions over time could result in significant biogeographical provincialism (i.e. endemism within microbial communities), and that the likelihood of such contingencies increases with spatial distance among communities (Martiny *et al.*, 2006). If dispersal limitation is the primary driver of biogeographical patterns, then geographic distance should be the best predictor of genetic divergence between communities and habitats in close proximity are more likely to share similar microbial taxa. These authors conclude that the relative importance of contemporary and historical factors in determining spatial patterning in microbial communities can only be evaluated through further studies that systematically sample and record data from various distances, habitats and environmental conditions.

Microbial communities in arctic tundra soils are exposed to particularly severe environmental stresses and thus these soils may be expected to harbor relatively

unique bacterial communities. However, few spatially comprehensive surveys of soil bacterial communities have been conducted, and it is not known if arctic soils harbor bacterial communities that are generally distinct from those found in more temperate environments. Here, we characterized bacterial community diversity and composition in soils collected from the Canadian, Alaskan and European Arctic to evaluate the relative influences of environmental heterogeneity and historical contingencies, and compared arctic soils with soils from a wide range of more temperate biomes to characterize variability in soil bacterial diversity and community structure across the globe. To the best of our knowledge, this is the first comprehensive study of the biogeography of soil bacterial communities in the Arctic, and may provide baseline information to characterize the impacts of future arctic warming (ACIA, 2005; IPCC, 2007).

Results

Across all soil samples, we obtained 107 879 quality sequences in total and 653–7653 sequences per sample (mean = 2103), and were able to classify 91.6% of those sequences. The dominant phyla across all the arctic soils were *Acidobacteria*, *Alphaproteobacteria*, *Actinobacteria*, *Betaproteobacteria* and *Bacteroidetes*, accounting for more than 83% of the bacterial sequences from each of the soils (Fig. 1, Table S1). In addition, the *Gammaproteobacteria*, *Verrucomicrobia*, *Gemmatimonadetes*, *Deltaproteobacteria* and *TM7* were present in most soils but at relatively low abundances, and 11 other rarer phyla were identified (Table S1).

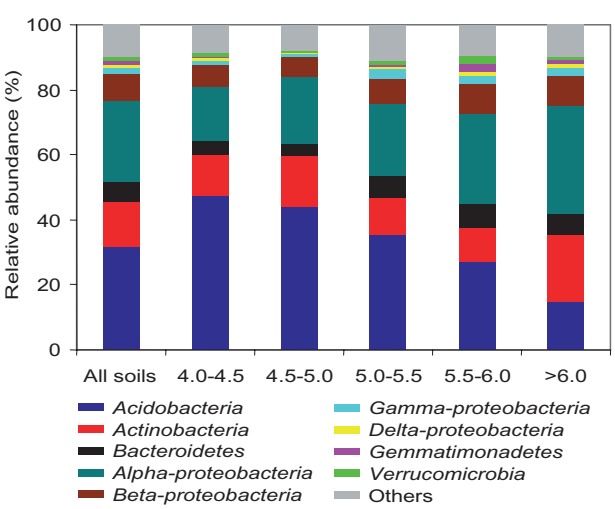

Fig. 1. Relative abundances of the dominant bacterial phyla in all soils combined, and in soils separated according to pH categories. Relative abundances are based on the proportional frequencies of those DNA sequences that could be classified at the phylum level.

The non-metric multidimensional scaling plots of the pairwise UniFrac distance ordinations clearly indicated significant variability in soil bacterial community composition across the Arctic that was strongly related to pH (Fig. 2). This interpretation was supported by correlation analyses between UniFrac distances and soil pH ($P < 0.001$), but no significant relationships to any of the other soil characteristics measured. Soil pH was the only significant predictor of UniFrac distances between communities, and addition of other variables (multivariate Mantel tests with pH plus other soil variables) did not increase the coefficient values. This influence of soil pH was evident even at a very coarse level of taxonomic resolution since the relative abundances of the dominant bacterial phyla (*Actinobacteria*, *Bacteroidetes*, *Acidobacteria, Alphaproteobacteria* and *Betaproteobacteria*) changed in a consistent manner across the soil pH gradient (Fig. 3). The strong influence of pH was also observed at the sub-phylum level (Table S3). For example, groups 1–3 of the phylum *Acidobacteria* decreased in relative abundance as soil pH increased while groups 4 and 6 showed the opposite pattern. The bacterial communities were highly variable in terms of both phylotype richness (Fig. 4A) and phylogenetic diversity (Fig. 4B) across the sample set. Each site contained 338–725 unique phylotypes within the 1000 randomly selected sequences per soil. Furthermore, Faith's index of phylogenetic diversity within the communities varied by a factor of ~2 among the sites. Regardless of the diversity metric employed, bacterial diversity was closely correlated with soil pH ($P < 0.0001$) (Fig. 4) and inversely correlated with soil C: N ratio ($P < 0.01$) but not with other soil and site characteristics ($P > 0.05$ in all cases) (Table S2). Together, these results strongly suggest that local soil pH is, directly or indirectly, a fundamental control on soil bacterial community composition and diversity among sites across the Arctic.

The pattern of differences in bacterial community composition (pairwise UniFrac distances) was not related to geographical distances between arctic sites ranging from 6 to 5500 km (Fig. 5). In addition, the UniFrac community distances among the pan-Arctic sites (i.e. those > 100 km apart each other) were not larger than those among individual sampling locations (0.02–0.1 km apart) within one site (Fig. S1). These results indicate that soils collected from distant locations did not necessarily harbor more distinct bacterial communities than those collected in close proximity to each other, and therefore that geographic distance among sites does not significantly influence soil bacterial community composition at this level of phylogenetic resolution.

We compared bacterial community composition and diversity in our arctic soils with those in 85 soils from a wide range of lower latitude biomes reported previously

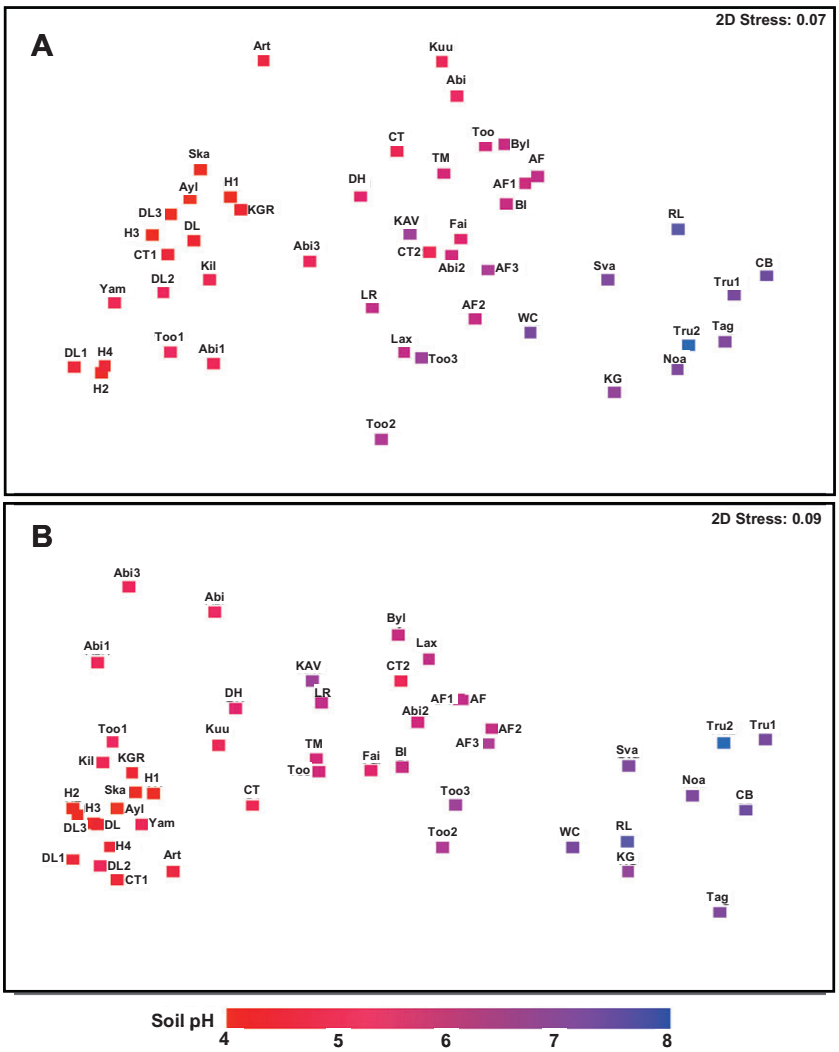

Fig. 2. Bacterial community compositional structure in soils across the Arctic as indicated by non-metric multi-dimensional scaling plots of the unweighted (A) and weighted (B) pairwise UniFrac community distances between sites. Sites have been color-coded according to soil pH gradient.

(Lauber *et al*., 2009). Visualization of the non-metric multidimensional scaling plots of the pairwise UniFrac distances ordinations clearly indicated that bacterial communities were as variable within arctic soils as across the lower latitude biome soils (Fig. 6). Likewise, both phylotype richness (Fig. 7A) and phylogenetic diversity (Fig. 7B) of the bacterial communities in our arctic soils were not significantly lower than in the lower latitude biome soils. Thus, even though environmental stresses may be particularly severe in arctic tundra, the compositional structure of arctic soil bacterial communities does not seem to be fundamentally distinct from that found in lower latitude biomes.

Discussion

The overriding importance of soil pH as a regional-scale control on soil bacterial community structure has recently been demonstrated using a variety of techniques (Fierer and Jackson, 2006; Hartman *et al*., 2008; Baker *et al*., 2009; Jesus *et al*., 2009; Jones *et al*., 2009; Lauber *et al*., 2009). In particular, recent studies have shown that bacterial communities in soils from a broad range of ecosystems across North and South America are strongly structured according to variation in soil pH (Fierer and Jackson, 2006; Lauber *et al*., 2009). By contrast, differences in other soil and site characteristics were poor predictors of bacterial community structure (Lauber *et al*., 2009), suggesting that variation in soil organic matter chemistry, vegetation type and environmental factors other than soil pH have relatively small impacts on the phylogenetic composition of soil bacterial communities. Together, these results strongly suggest that the distribution of bacterial phylotypes in terrestrial soil environments across the globe is largely determined by soil pH. We observed strong correlations between the relative abundances of the five most dominant phyla (*Actinobacteria*, *Bacteroidetes*, *Acidobacteria*, *Alphaproteobacteria* and

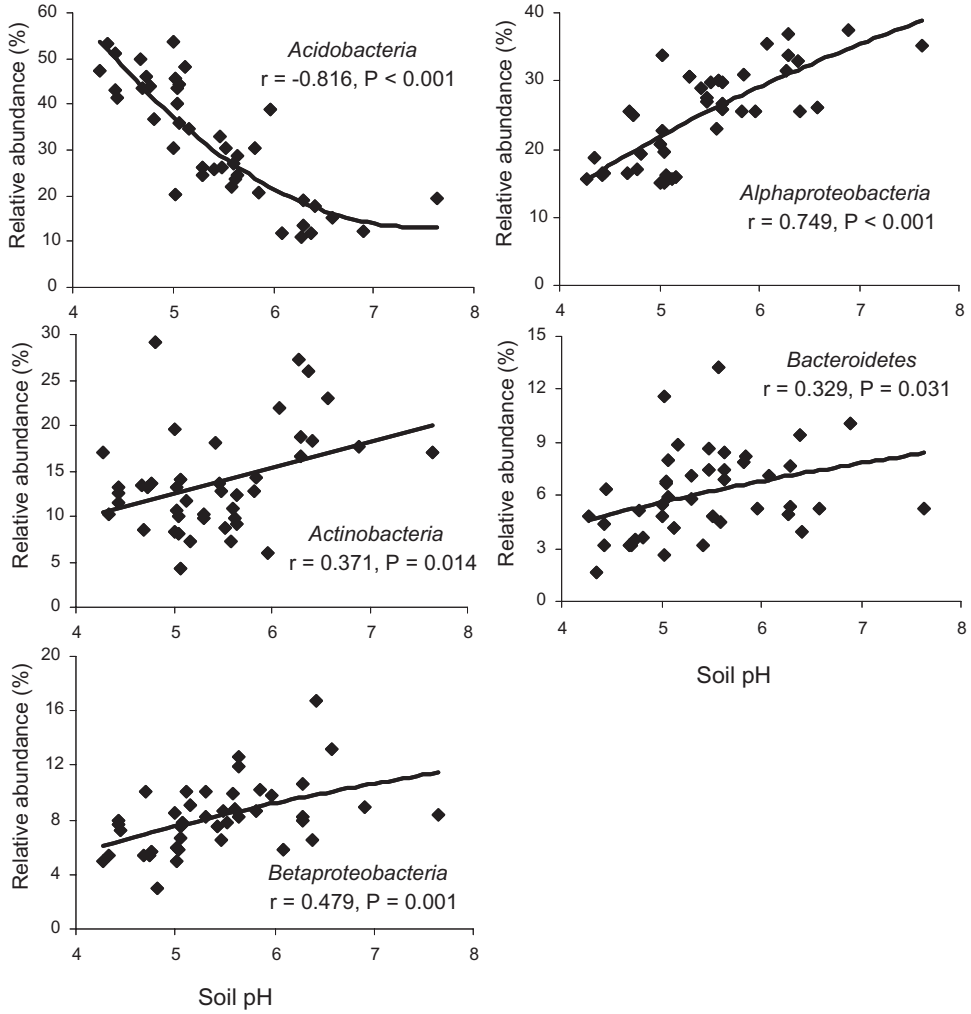

Fig. 3. Correlations between the relative abundances of the six dominant bacterial phyla and soil pH. Pearson correlations coefficients (*r*) are shown for each taxon with associated Bonferroni-corrected *P*-values.

Betaproteobacteria) and soil pH in arctic soils (Fig. 3), while no significant correlations were observed for *Alphaproteobacteria* and *Betaproteobacteria* in soils from lower latitude biomes (Lauber *et al*., 2009). Furthermore, phylotype richness and Faith's index of phylogenetic diversity of the bacterial communities were highest at pH ~6 in arctic soils (Fig. 4) while they were highest at pH ~7 in soils from those lower latitude biomes. These results indicate that although bacterial community composition is clearly strongly influenced by pH, the specific nature of the relationship may differ slightly between arctic and lower latitude soils.

Environmental heterogeneity and dispersal limitation are clearly both key determinants of the biogeographic patterns exhibited by animals and plants (Ganderton and Coker, 2005; Lomolino and Brown, 2006). Dispersal limitation is often considered less important for microorganisms (Fenchel *et al*., 1997; Finlay and Clarke, 1999; Finlay, 2002), resulting in biogeographic patterns that primarily reflect selection by contemporary environmental conditions (Baas Becking, 1934; de Wit and Bouvier, 2006). Martiny and colleagues (2006) have proposed that dispersal limitation and variation in past environmental conditions may also contribute to patterns of spatial variability in microbial communities, and may only become apparent in studies of spatial structure at continental or global-scales rather than over smaller scales. Our UniFrac distance data clearly indicate that the bacterial communities at each sampling location were fairly distinct from each other since ~55% of the sequences at each site were unique to that site (Fig. 7). Interestingly, this proportion of unique sequences (ranging from 335 to 657 per 1000 randomly selected sequences) in our arctic sites is very similar to values obtained for a wide range of other biomes (338–725 per 1000) using the same bar-coded pyrosequencing technique (Fig. 7., note that this compari-

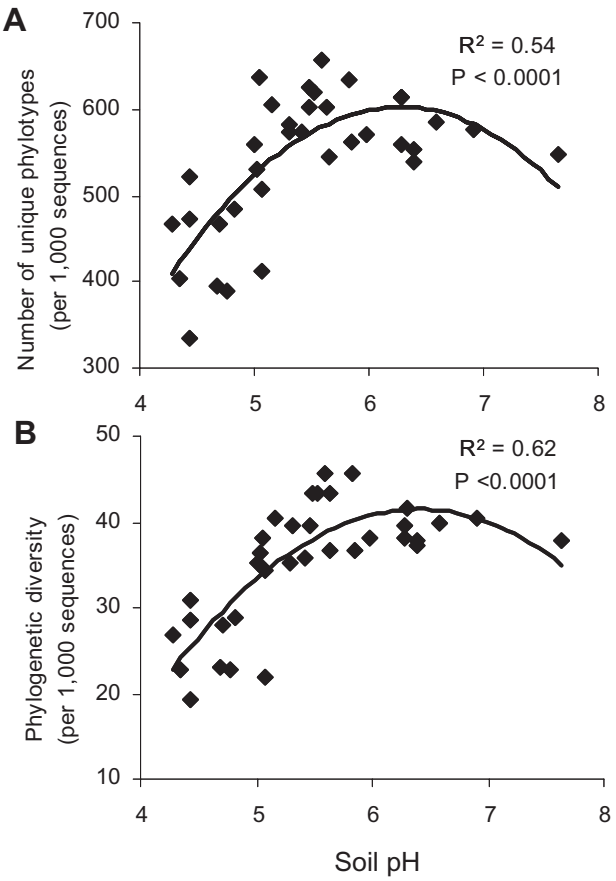

Fig. 4. Soil pH in relation to bacterial phylotype richness based on 97% sequence similarities (A) and to bacterial phylogenetic diversity using Faith's integrated index of phylogenetic breadth (B) in arctic tundra. Lines represent the best-fit quadratic models to the data. Diversity indices were calculated using random selections of 1000 sequences per soil sample.

son is based on proportional data to avoid effects of variability in sequencing depth on the biogeographical patterns observed). In conclusion, and perhaps not surprisingly, our high taxonomic resolution data indicate substantial 'endemism' (*sensu* Martiny) within the bacterial communities at each site, but nevertheless also many similarities in composition among sites.

Bacterial community similarities were much more closely related to site differences in soil pH than to differences in geographic proximity among sites that ranged from 0.02 to 5500 km apart. This pattern holds even if we compare soil bacterial communities from across a wide range of biomes (Fig. 6). Therefore, our results strongly suggest that soil bacterial community composition in arctic soils was determined much more by local environmental selection associated with variation in soil acidity than by dispersal limitation or other historical contingencies. While dispersal limitation may be important in structuring bacterial taxa at finer levels of taxonomic resolution (Cho and Tiedje, 2000; Papke *et al*., 2003; Green *et al*., 2004; Reche *et al*., 2005), it does not seem to have been important in structuring overall bacterial community composition across the arctic soils sampled here. Other researchers have found that dispersal limitation does not appear to be a dominant force structuring microbial communities in marine environments (Darling *et al*., 2000; Cermeno and Falkowski, 2009; Hubert *et al*., 2009; Patterson, 2009). Our results here suggest that dispersal limitations are also far less important than local environmental conditions in determining bacterial community-level differences in terrestrial soil environments.

The latitudinal diversity gradient is one of the most fundamental patterns in animal and plant biogeography. A wide range of plant and animal taxa increase in richness and phylogenetic diversity from the poles to the equator and many competing hypotheses have been proposed to explain the pattern (Lomolino and Brown, 2006). However, it is unknown if the latitudinal diversity gradient pattern is also evident in the biogeographical distributions of bacteria in terrestrial soil environments. We observed that bacterial communities were as variable within arctic soils as across the soils from a wide range of lower latitude biomes, and that richness and phylogenetic diversity levels were also similar (Fig. 7). Our results suggest that the compositional structure of arctic soil bacterial communities is not fundamentally distinct from that found

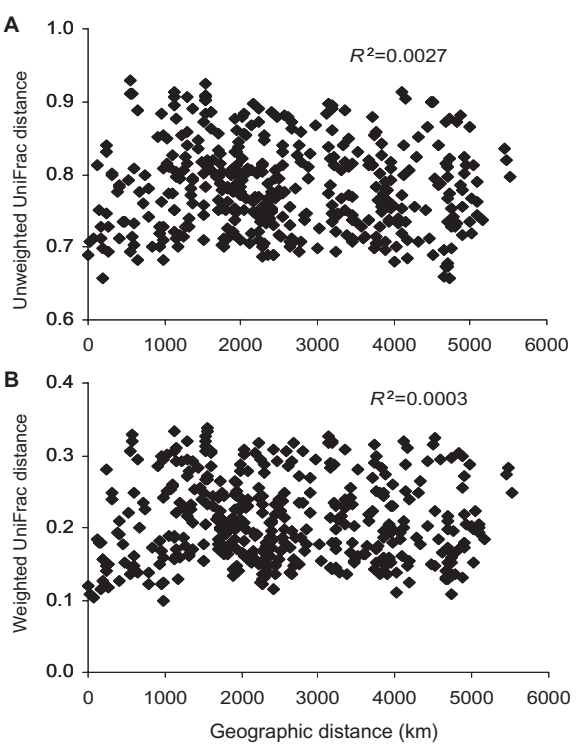

Fig. 5. Relationships between geographic distances and bacterial community distances as indicated by the unweighted (A) and weighted (B) pairwise UniFrac differences in phylotype composition between sites.

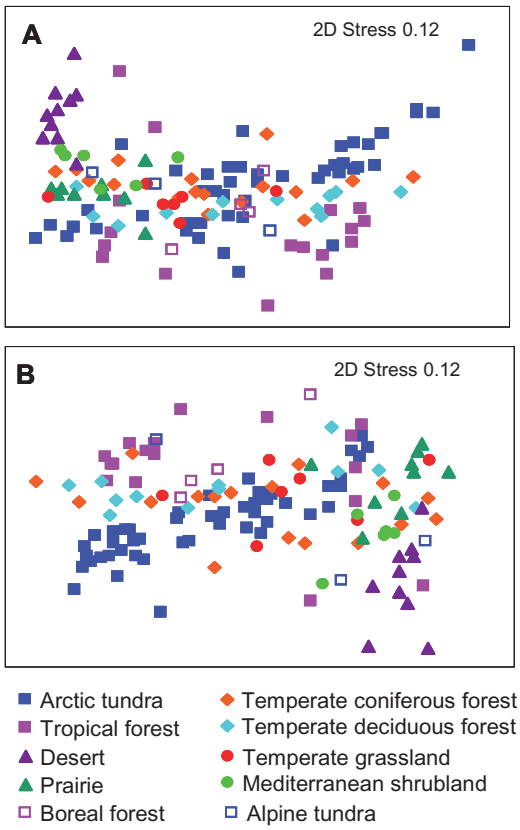

Fig. 6. Bacterial community compositional structure in arctic soils and in soils from a wide range of other lower latitude biomes as indicated by non-metric multi-dimensional scaling plots of the unweighted (A) and weighted (B) pairwise UniFrac distances between sites.

in lower latitude biomes, strongly suggesting a common pattern of phylogenetic variability among soil bacterial communities across the globe. Our finding that there is a near-complete absence of a latitudinal diversity gradient for soil bacteria agrees with other research on microscopic eukaryotes (Hillebrand and Azovsky, 2001), suggesting that microscopic organisms, in general, exhibit broad gradients in diversity that contrast with the latitudinal gradients commonly observed with plant and animal taxa. These results also suggest that the controls on bacterial community distributions are fundamentally different to those observed for animals and plants, and that our biome definitions are not useful for predicting variability in soil bacterial communities across the globe.

Experimental procedure

Site selection and soil sampling

Soil samples were collected from 29 heath tundra sites close to the top of exposed ridges in the Canadian, Alaskan and European Arctic in the summers of 2007 and 2008 (Table S4, Fig. S2). All sites (except 3: Ayl, Tru2, Yam) were located > 100 km apart from each other. At each site, soil samples were taken at three similar locations (20–100 m apart) from below dry heath vegetation in which at least one of the following plant species was common: *Empetrum* spp., *Cassiope* spp., or *Dryas* spp. Each sample (~12 cm × 12 cm in area, and 2–5 cm depth) of dark brown/black organic soil was cut out with a clean serrated knife and placed in a separate plastic bag. In addition, soil samples at the Daring Lake Canadian low arctic site were also collected from four similar well separated (0.4–1.2 km apart) patches of dry heath vegetation (minimum size ~100 m^2) (Chu and Grogan, 2010). All samples were shipped to Kingston, Canada as soon as possible where they were stored at –20°C until processing (within 4 weeks). Initial processing included removal of aboveground plant material and living roots prior to homogenizing the soil fraction of each sample and storing at –20°C prior to extracting soil DNA.

Soil nutrients and microbial biomass analyses

Soil pH was determined separately on each of the replicate soil samples for each site using a fresh soil to water ratio of 1:5 (AB15 pH meter, Accumet, Fisher Scientific). Total soil C and N contents for each replicate were determined by combustion (CNS-2000, LECO, St. Joseph, MI) on samples that had been dried at 65°C for 48 h and ground with a ball mill (Retsch PM 200 Planetary Ball Mill, Haan, Germany). Soil mineral N, dissolved organic C (DOC), dissolved organic N (DON) and microbial biomass C (MBC), biomass N (MBN) and biomass P (MBP) were determined as described before (Chu and Grogan, 2010).

Soil DNA extraction

We composited the replicate soil samples for each site and extracted DNA using the PowerSoil kit (MO BIO laboratories, Carlsbad, CA) according to the manufacturer's instructions. In addition, we investigated within-site variability by extracting DNA separately from each of the individual samples in a random selection of five of the pan-arctic sites, and in the samples from the four separate patches of dry heath from Daring Lake. Totally 47 DNA samples were used for bar-coded pyrosequencing including composited samples from each site (29 samples), individual samples within each of five randomly selected sites (14 samples) and the four samples from heath tundra at Daring Lake (4 samples).

Bar-coded pyrosequencing

The extracted DNA was diluted 100-fold with amplification, pooling and pyrosequencing performed as described previously (Fierer *et al.*, 2008; Lauber *et al.*, 2009). Briefly, a portion of the 16S small subunit ribosomal gene (region 27 to 338, *Escherichia coli* numbering) was amplified using a 27F primer with the Roche 454 'A' pyrosequencing adapter, while the 338R primer contained a 12-bp barcode sequence, a 'TC' linker and the Roche 454 'B' sequencing adapter. The targeted gene region has been shown to be the most appropriate for the accurate phylogenetic reconstruction of bacterial

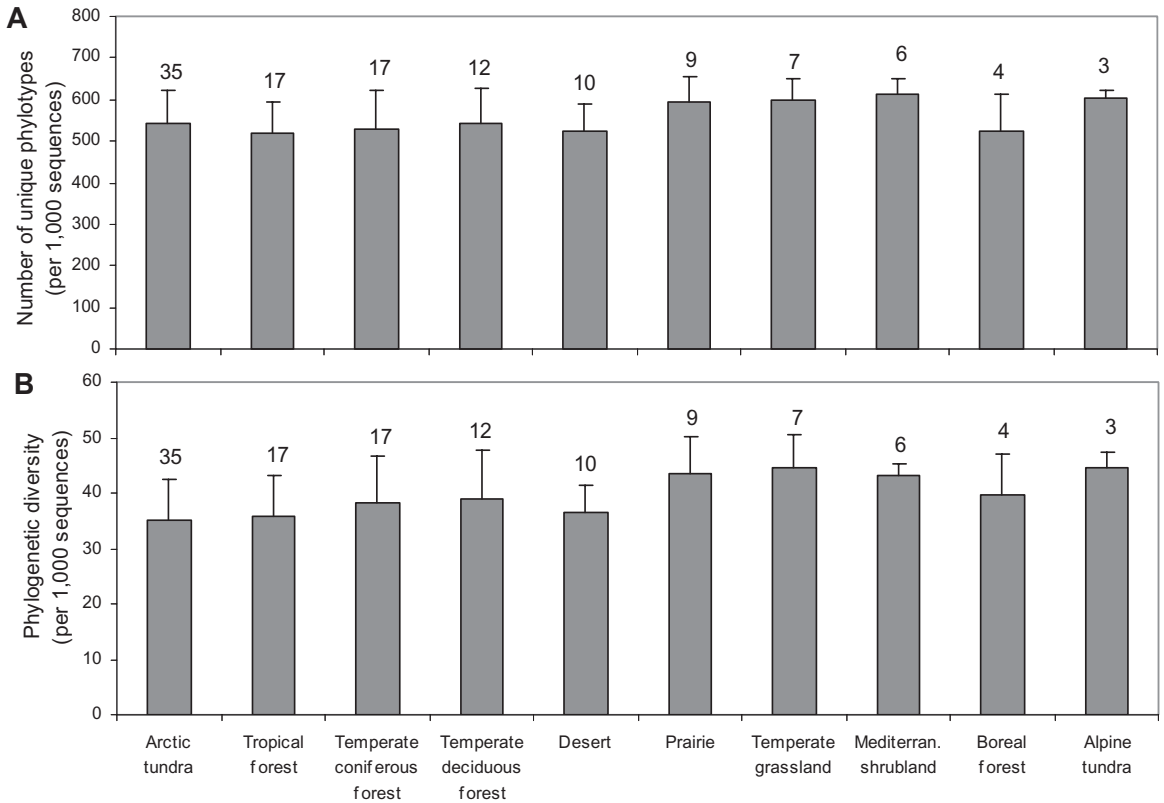

Fig. 7. Bacterial phylotype richness (A) and phylogenetic diversity (B) in arctic soils as compared with soils from a wide range of other biomes. Diversity indices were calculated using random selections of 1000 sequences per soil sample. The number of sampled sites is indicated above the columns.

sequences as other regions of the 16S rRNA can lead to significant misclassification of sequences (Liu *et al*., 2007). The error-correcting DNA barcodes allow one run of a massively parallel pyrosequencer to process thousands of samples simultaneously (Hamady *et al*., 2008). PCR reactions were conducted with 30 μM of each forward and reverse primer, 1.5 μl template DNA and 22.5 μl Platinum PCR SuperMix (Invitrogen, Carlsbad, CA). Each sample was amplified in triplicate, pooled and cleaned using the PCR clean up kit (MO BIO laboratories, Carlsbad, CA). An equal amount of PCR product for each sample was combined in a single tube and sent to the Environmental Genomics Core Facility at the University of South Carolina to be run on a Roche FLX 454 pyrosequencing machine.

Processing of pyrosequencing data

Data were processed following the procedure described previously (Fierer *et al*., 2008; Hamady *et al*., 2008; Lauber *et al*., 2009) using the Quantitative Insights Into Microbial Ecology (QIIME) pipeline (http://qiime.sourceforge.net). Briefly, low quality sequences were removed (those sequences < 200 bp in length) and the 12 bp barcode was examined in order to assign sequences to samples. Pyrosequencing data were processed using the QIIME pipeline (http://qiime.sourceforge.net). Phylotypes were identified using cdhit (Li and Godzik, 2006) and defined at the 97% sequence similarity level. A representative sequence from each phylotype was aligned using PyNAST (DeSantis *et al*., 2006; Caporaso *et al*., 2010) with a relaxed neighbor-joining tree built using fasttree (Price *et al*., 2009). Taxonomic identity of each phylotype was determined using the RDP Classifier (Wang *et al*., 2007). The difference in overall community composition between each pair of samples was determined from the neighbor-joining tree using the unweighted (i.e. presence or absence of taxa) and weighted (i.e. taking into account the relative abundances of taxa) UniFrac algorithm (Lozupone and Knight, 2005; Lozupone *et al*., 2006). UniFrac quantifies the fraction of unique branch lengths against the total branch length between pairs of communities from one phylogenetic dendogram, giving an estimate of the overall phylogenetic distance between each pair of communities. UniFrac provides a robust index of community distances because it integrates across levels of taxonomic resolution (Hamady and Knight, 2009).

Richness (i.e. number) of phylotypes was calculated at each site to compare community-level bacterial diversity at a single level of taxonomic resolution. We also estimated phylogenetic diversity using Faith's index (Faith, 1992) which provides an integrated index of the phylogenetic breadth across taxonomic levels. We obtained between 653 and 7653 quality sequences per sample for all 47 samples, with > 1000 sequences per sample from 35 of these samples. Using those 35 samples, we calculated both diversity metrics using

a randomly selected subset of 1000 sequences per soil to correct for differences in survey effort between samples This approach allows us to compare general diversity patterns among sites even though it is highly unlikely that we have surveyed the full extent of diversity in each community (Shaw *et al*., 2008). *Acidobacteria*, *Alphaproteobacteria*, *Actinobacteria*, *Betaproteobacteria* and *Bacteroidetes* were the most abundant groups of bacteria in the total sequence dataset and, for reasons of clarity, we refer to these five taxonomic groups as phyla, recognizing that we are using the term 'phyla' in a general manner.

Statistical analyses

Pairwise UniFrac distances calculated for total community analyses were visualized using non-metric multidimensional scaling plots as implemented in PRIMER v6 (Clarke and Warwick, 2001). Statistical analyses were performed in a similar manner to Lauber and colleagues (2008), and Fierer and Jackson (2006). Correlations between the diversity estimates and soil characteristics were tested for significance using SYSTAT 11.0. Best fit modeling of PD and individual phyla were performed in SigmaPlot using linear, polynomial (quadratic) and power law functions. ANOSIM analyses were conducted using PRIMER v6 (Clarke and Warwick, 2001), as were Mantel-type tests to test for correlations between UniFrac distances and soil characteristics. Rarefaction curves were produced using the QIIME toolkit (http://qiime.sourceforge.net).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Bacterial community distances in the pan-arctic soil samples and in soils 0.02–0.1 km apart within selected sites.
Fig. S2. Soil sampling sites across the Arctic. The red line indicates the extent of the arctic region as defined by the Arctic Human Development Report (ACIA, 2005).
Table S1. Relative average abundances of phyla classified with RDPII taxonomy across all soils and soils grouped into various pH categories (values represent % of total non-redundant sequences). Asterisks indicate sequences classified to the domain Bacteria, but not to a specific phylum.
Table S2. Correlations (R^2) between bacterial phylotype richness, phylogenetic diversity (PD) and soil and site characteristics. Values in bold indicate significant correlations ($P < 0.05$). DOC: dissolved organic carbon; DON; dissolved organic nitrogen: Avail. P: available P; MBC: soil microbial biomass C; MBN: soil microbial biomass N; MBP: soil microbial biomass P.
Table S3. Relative average abundances of phyla classified with RDPII taxonomy across all soils and soils grouped into various pH categories (values represent % of total non-redundant sequences). Asterisks indicate sequences within a phylum that were not classified to a specific class.
Table S4. Soil biogeochemical characteristics in the pan-arctic sites.

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