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Evidence of High Microbial Abundance and Spatial Dependency in Three Arctic Soil Ecosystems

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Microbial spatial heterogeneity has significant implications for ecological processes. Although microbial spatial patterns have been investigated agricultural and pristine soil ecosystems, little information is available on microbial spatial scaling in Arctic soils and how it is correlated with soil resources. In this comprehensive study, we assessed microbial abundance in 279 soil samples collected from three Canadian Arctic ecosystems and elucidated microbial spatial heterogeneity from fine (10 cm) to large (300 m) scales. Our results demonstrate that the abundance of archaeal 16S rRNA, bacterial 16S rRNA, and fungal 18S rRNA ITS gene copies (10^8–10^{11}, 10^8–10^{10}, and 10^8–10^{10} per gram of dry soil, respectively) in Arctic soils is similar to agricultural and pristine soils. Microbial spatial distribution is well structured in Arctic soils and shows high spatial dependency (0.50–0.99) at the scale of measurement of the experiment. The spatial range of microbial distribution is regularly <3 m which may be attributed to the periglacial processes such as thermokarst, cryoturbation, and gelifluction. Microbial spatial distribution is significantly ($P < 0.01$) correlated to the soil moisture, pH, dissolved organic C, dissolved organic N, total organic C, and total N content; however, the correlation is more consistent in Histels than Orthels or Turbels.

Abbreviations: DOC, dissolved organic carbon; DON, dissolved organic nitrogen; SP, spatial dependency; SPD, proportion of total variability that is spatially dependent; TOC, total organic carbon; TN, total nitrogen.

Permafrost-affected soils encompass about 26% of world's and 40% of Canada's total land area (Bockheim and Tarnocai, 1998). Extremely low temperature, long winter, short growing season, and regular cryoturbation typify the uniqueness of these ecosystems. Similar to other ecosystems (Van Der Heijden et al., 2008), soil microbial communities play a key role in Arctic soils. Soils in Canadian Arctic ecosystems are predominantly Orthels, Turbels, and Histels. Microbial communities and their associations with soil properties may vary in different types of Gelisolic ecosystems. Spatial variability is an integral quality of soil properties and in many cases this variability is nonrandom (Goovaerts, 1997). Soil spatial heterogeneity results from variations in pedologic and geologic soil forming factors, soil physicochemical and ecological processes (Ettema and Wardle, 2002). Spatial dependency (SPD) of soil properties diminishes with increasing distance between points in space. Owing to the inherent variability of soil physicochemical properties soil microbial abundance may also vary across multiple spatial scales. The awareness of microbial spatial variability has increased considerably in the last 10 yr. Microbial spatial patterns have been studied in agricultural (Franklin and Mills, 2003; Grundmann and Debouzie, 2000; Nunan et al., 2002), forest (Morris, 1999; Saetre and Baath, 2000), and grassland (Nicol et al., 2003; Ritz et al., 2004) soils. However, to our knowledge, no study has elucidated microbial spatial variability in high Arctic ecosystems. Microbial spatial structure has significant functional implications for ecosystem processes. Microbially driven ecosystem functions are exhibited at multiple spatial scales and understanding of microbial spatial distribution/structure is critical to substantiate how combinations of several

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communities or microhabitats function together at field scale or larger scale pertinent to researchers (Franklin and Mills, 2007). Our objective in this study was to examine the overall abundance and spatial dependency of archaeal, bacterial, and fungal populations in various types of Gelisol in Canadian Arctic ecosystems.

MATERIALS AND METHODS

Three Arctic sites were selected for this study: Truelove Lowland, Simpson Lake, and Ross Point. Covering an area of 43 km^2, the Truelove Lowland (75°40′ N, 84°35′ W) is located on the northeastern coast of Devon Island; it has been the subject of extensive historical scientific expeditions (Lev and King, 1999; Paré and Bedard-Haughn, 2011; Siciliano et al., 2009) and the topography and soil types are well documented. Simpson Lake (68°35′ N, 91°57′ W) is situated in the middle of the Boothia Peninsula; the upperslope positions are likely comprised of Orthels whereas lowerslope positions are likely Turbels. Ross Point (68°31′ N, 111°10′ W) site is situated in the south port of Victoria Island, the second largest island in the Canadian Arctic Archipelago. The soils at this research site are predominantly Histels. The three research sites selected in this study encompass 7° in latitude and 27° in longitude of Canadian Arctic. Furthermore, the sites consist of a polar oasis (Truelove Lowland), a Histel ecosystem (Ross Point) and a Orthel/Turbel ecosystem (Simpson Lake), and thus represent the diversity of Canadian permafrost ecosystem. At each site, soil samples were collected along three parallel transects (300 m each; 2 m lateral distance) at 31 points (0, 0.1, 0.2, 0.5,1, 2, 5, 10, 20, 50, 100, 100.1, 100.2, 100.5, 101, 102, 105, 110, 120, 150, 200, 200.1, 200.2, 200.5, 201, 202, 205, 210, 220, 250, 300 m). In total 93 soil samples were collected from each site and 279 soil samples were collected from three sites.

At each sampling point, approximately 250 g of soil sample was collected. For spatial comparison, we aimed to use the same design at three research sites. In contrast with Simpson Lake and Ross Point, a 300 by 300 m grid design was not possible to establish at Truelove Lowland. Moreover, fine scale patterns may not be captured with a grid design due to its even lag distance (minimum 2 m). Variable (irregular) sampling design, adjacent steps separated by a repeated sequence, is a particularly useful design for substantiating multiscale patterns in an ecosystem (Fortin et al., 1989). Therefore, in this study, we specifically employed the aforementioned variable-lag-distance transect approach to simultaneously capture the fine (0–1 m), medium (1–10 m), and large (10–300 m) scale spatial patterns of microbial communities in three Gelisolic ecosystems.

Soil gravimetric water content (θ_g) was calculated by measuring the weight loss of 5 g soil samples after they were dried for 24 h at 105°C and the water content expressed as percentage of dry soil mass (Gardner, 1986). Soil pH was measured using 5 g soil in a 1:1 soil/water (deionized) mixture with an Accumet pH meter (Accumet 925, Fischer Scientific, Hanover Park, IL). The dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) contents were measured using TOC-VCPN analyzer (Shimadzu Scientific Instruments, Columbia, MD). Various concentrations of potassium hydrogen phthalate (0–200 mg L^{-1}) and potassium nitrate (0–20 mg L^{-1}) were used as standards for total dissolved organic C and total dissolved N analyses, respectively. A 12-mL aliquot of the diluted (1:10) soil extracts was analyzed. The amount of DON in soil was determined by subtracting the mineral N content (sum of exchangeable NH_4^+ and NO_3^- content) from dissolved total N content. Total organic carbon (TOC) content was determined by combustion (at 840°C and 1100°C, respectively) using the Leco CR-12 Carbon Analyzer (LECO Corp., St. Joseph, MI) (Wang and Anderson, 1998). Soil total N (% mass) was determined by dry combustion using a Leco CNS-2000 elemental analyzer (Wright and Bailey, 2001). For Truelove Lowland and Simpson Lake samples, a soil standard of known concentration (5.17% C, 0.441% N) was used to calibrate the instrument. However, a plant standard of known concentration (42.9% C, 2.59% N) was used for Ross Point soils because of high soil organic matter content. For each soil sample, 0.2 g of air-dried, ball-ground subsample was analyzed.

DNA extraction from soils was performed according to the method described by Griffiths et al. (2000) with the modification that DNA samples were precipitated in Polyethylene Glycol overnight and RNase was not added after extraction. However, no RNA contamination was found when DNA samples were examined using agarose gel electrophoresis and RNase treatment. We measured the variability in DNA extraction efficiency as it may vary with soil organic matter content. DNA extraction variability was not considerable. The number of bacterial 16S rRNA, archaeal 16S rRNA, and fungal 18S rRNA gene copies present in the soil DNA extracts were determined by quantitative real-time PCR using the QuantiTect SYBR Green PCR Master Mix, an ABI 7500 real-time polymeerase chain reaction (PCR) machine (Applied Biosystems, Foster City, CA), and bacterial (Ovreas et al., 1997), archaeal (Coolen et al., 2004), and fungal (Gardes and Bruns, 1993) specific primers. Each 20 μL reaction contained 10 μL of master mix, 10 pmol of the primers, 6 μL sterilized mili-Q water, and 2 μL (20–50 ng) template DNA (1:10 diluted). Standard curves ($r^2 > 0.99$) were generated by preparing standards from purified PCR product from one of the soil DNA extracts. The amplification efficiency of the genes was between 80 and 100%. The specificity of the amplified products was examined by melting curve analysis. Amplification inhibition effects were evaluated by measuring gene abundance on three different dilutions of representative samples and selecting the dilution that minimizes the inhibition (Dumonceaux et al., 2006).

The Anderson–Darling test and Levene's test were performed using Minitab 11 (Minitab Inc., State College, PA) to check for normal distribution and homoscedasticity. Non-normally distributed variables were log or square-root transformed. Spearman rank correlations were calculated using SPSS 16.0 software (SPSS Inc. Chicago, IL). The degree of spatial heterogeneity was assessed by semivariance analysis. Semivariance (Eq. [1]), γ(h), can be defined as half of the average squared difference between the components of a data pair:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{\alpha=1}^{N(h)} [z(x_k) - z(x_k + h)]^2 \qquad [1]$$

where $z(x_k)$ is the property, $z(x_k+h)$ is the value at h lag distance and $N(h)$ is the number of data pairs for a given distance (Goovaerts, 1997). The key features of a semivariogram are nugget variance, sill, and range. Nugget variance (the intercept of the semivariance at $h = 0$) indicates the stochastic variation resulted from experimental error or variation at scales smaller than the minimum sampling lag distance. Sill is the maximum variability attained by a variable whereas range indicates the zone of SPD (i.e., the lag distance at which the semivariance value reaches

maximum). The SPD indicates what proportion of the total variability is spatially dependent and it was calculated by: $C/(C + C_0)$, where C is the structural variance, C_0 is the nugget, and $C+C_0$ is the sill. The value of SPD is unit-less and ranges between 0 indicating no spatial dependency and 1 indicating highest spatial dependency with no nugget variance. Each lag class comprised of a minimum of 30 pairs of comparisons as recommended by Journel and Huijbregts (1978). Various models such as spherical, exponential, Gaussian, linear were fitted to the raw semivariograms and the best-fitted model was selected on the basis of lowest residual sum of squares and highest coefficient of determination (Goovaerts, 1997). Geostatistical analyses were performed using GS+ version 9.0 (Gamma Design Software, Plainwell, MI).

RESULTS AND DISCUSSION

Microbial communities in permafrost ecosystems are confronted with extreme environmental conditions such as prolonged subzero temperature, freeze–thaw cycles, desiccation, and starvation (Wagner, 2008). Despite these conditions, the overall size of bacterial, archaeal, and fungal populations in these Arctic soil ecosystems (Table 1) resembles that of grassland (10^9–10^{11}; Jenkins et al., 2009), agricultural (10^9–10^{10}; He et al., 2007), and forest (10^8–10^9; Kemnitz et al., 2007) soils. The results of this study are also in line with Stres et al. (2010) who noted high (10^8) prevalence of Bacterial 16S rRNA gene copies in alpine soils. In the active layer of Canadian High Arctic permafrost ecosystems, however, Yergeau et al. (2010) and Wilhelm et al. (2011) reported relatively low abundance of fungal (8.60×10^4) and archaeal (1.49×10^4 and 3.68×10^4, respectively) ribosomal gene copies. Although, the reported bacterial 16S rRNA gene abundance (3.05×10^7 and 3.81×10^7, respectively) is somewhat similar to this study, the overall microbial abundance is considerably higher at the three Arctic ecosystems studied here. In particular, Truelove Lowland had considerably larger microbial populations than the other two sites. It should be noted that Truelove Lowland is a polar oasis in the middle of a vast polar desert. It is an animal-hotspot thus grazing, accumulation of fecal matter, and dead animal body parts may favor microbial activity making this site ecologically dynamic and unique. Important factors such as snow cover, temperature, wind speed, and most importantly water and nutrient availability vary along the mesotopographic gradients in Arctic ecosystems (Billings, 1973; Giblin et al., 1991). At Truelove Lowland, transects for soil sampling were laid out on backslope (area behind raised beach crest) and snow accumulation is considerably higher in backslope area due to wind protection (Giblin et al., 1991). Presence of snowbank in this area may have caused higher microbial abundance. This is in agreement with Zinger et al. (2009) who found high microbial diversity owing to variation in topography and differential snow cover.

The value of SPD and range indicates the degree and distance of spatial autocorrelation of an attribute, respectively. Except, bacterial 16S abundance at Simpson Lake, microbial abundances were spatially autocorrelated and demonstrated strong spatial structures (Fig. 1). The value of SPD between 0.5 and 1 indicates high spatial dependency and autocorrelation. The high SPD (0.50–0.99) of microbial communities in Gelisols is comparable to grassland (0.33–0.85; Ritz et al., 2004), agricultural (0.42–1.0; Philippot et al., 2009), and forest (0.41–0.93; Saetre and Baath, 2000) soils. The r^2 value of a semivariogram reflects how clearly the experimental model incorporates the spatial variability and demarcates it from the stochastic nugget variability to show the spatial structure. The r^2 values of the semivariograms ranged between 0.49 to 0.99, indicating high fit. Gaussian is the best fitted model to the semivariograms in this study. The semivariance in Gaussian model reaches the sill asymptotically (Goovaerts, 1997) which indicates a comparatively smoother transition or gradient of the spatial patterns. Ecologically, this implies that the niches of Gelisolic microbial communities smoothly merge into one another as the soil properties change across the landscape. Range of a semivariogram indicates the distance up to which spatial autocorrelation of a particular attribute persists. Thus, longer range reflects strong spatial autocorrelation and homogeneity in soil resources. The degree and range of microbial spatial dependency are intrinsically associated with soil physicochemical attributes and soil types (Bragato and Primavera, 1998). Banerjee et al. (2011) showed that soil physicochemical properties at Truelove Lowland and Simpson Lake are spatially well structured but the spatial range of soil physical properties is considerably smaller than Histels of Ross Point. While the spatial range at Truelove Lowland is approximately 10 m, spatial autocorrelation diminishes beyond 1 m for most soil attributes at Simpson Lake. On the other hand, the zone of spatial dependence of soil attributes is approximately 40 m in Histels of Ross Point. In contrast to Truelove and Simpson Lake, the Histels at Ross Point is more homogeneous (i.e., devoid of periglacial processes such as cryoturbation, gelifluction, frost

Table 1. Overall microbial abundance (copy number g^{-1} dry soil) and soil attributes at three Arctic ecosystems: Truelove Lowland, Simpson Lake, and Ross Point.

Soil and microbial attributes	Truelove Lowland†	Simpson Lake	Ross Point
Bacterial 16S rRNA	$2.9 \times 10^{10}(2.8 \times 10^9)$	$4.2 \times 10^8(7.1 \times 10^7)$	$1.5\times 10^9(2.5 \times 10^8)$
Archaeal 16S rRNA	$2.7 \times 10^{11}(1.8 \times 10^{10})$	$5.5 \times 10^8(1.0 \times 10^8)$	$7.9\times 10^8(1.4 \times 10^8)$
Fungal 18S rRNA ITS	$5.9 \times 10^{10}(8.5 \times 10^8)$	$2.2 \times 10^8(4.6 \times 10^7)$	$7.7\times 10^8(1.5 \times 10^8)$
θ_g	25 (1.7)	20 (1.4)	61 (5.6)
pH	7.5 (0.013)	5.5 (0.029)	7.6 (0.040)
DOC‡, mg kg^{-1} dry soil	7.4 (0.24)	380 (42)	1900 (160)
DON, mg kg^{-1} dry soil	1.6 (0.14)	54 (4.5)	190 (18)
TOC, % weight	3.3 (0.27)	1.2 (0.16)	16 (1.1)
TN, % weight	0.37 (0.023)	0.099 (0.012)	1.1 (0.068)

† Mean values (n = 93) of different variables for three sites. Standard errors are shown in parentheses.
‡ DOC, dissolved organic carbon; DON, dissolved organic nitrogen; TOC, total organic carbon; TN, total nitrogen.

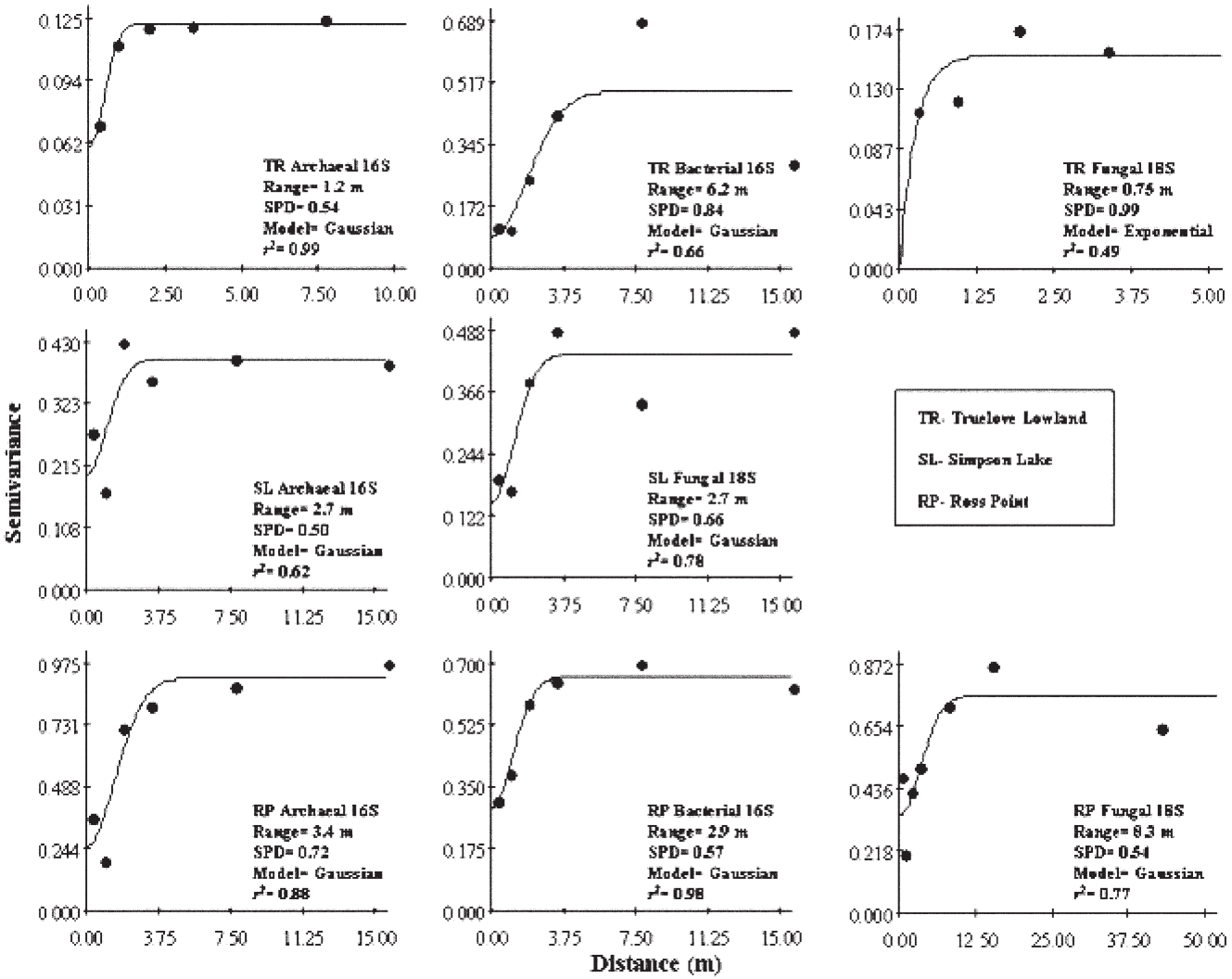

Fig. 1. Semivariograms showing spatial variability of archaeal 16S rRNA, bacterial 16S rRNA, and fungal 18S rRNA ITS gene abundance at three Arctic ecosystems: Truelove Lowland (TR), Simpson Lake (SL), and Ross Point (RP). Range indicates the zone of spatial dependency. Spatial dependency (SPD) was calculated by: $C/(C + C_0)$, where C is the structural variance, C_0 is the nugget, and $C+C_0$ is the sill. Various models (Gaussian, exponential etc.) were fitted (solid line) to the experimental semivariograms. Spatial dependency was considered from fine (10 cm) to large scale (300 m) but no dependency was found beyond 10 m distance. The semivariograms are shown up to specific lag distance for clarity of the spatial patterns near origin. The abundance of bacterial 16S rRNA genes was spatially independent at Simpson Lake.

stirring, and mounding). Since these periglacial processes create irregular soil horizon, movement of soil mass, and redistribution of organic matter (Bockheim and Tarnocai, 1998), they change the spatial nature of soil properties creating high spatial heterogeneity. Thus the range of spatial autocorrelation at Ross Point is considerably larger than the other two sites.

In a low Arctic tundra landscape, Stewart et al. (2011a, 2011b) noted the importance of soil moisture, nutrient availability, and microclimate conditions in structuring the small-scale spatial variation of N fixation by cyanobacteria. Using semivariogram analysis in an alpine ecosystem, King et al. (2010) found high spatial autocorrelation of bacterial abundance and community composition. Similar results were also observed by Zinger et al. (2009) who reported high spatial variation of bacterial and fungal communities in alpine ecosystems and highlighted the importance of snow cover, which is also congruent with the present study. In a series of alpine landscapes, Zinger et al. (2011) recently reported that nonrandom spatial patterns of crenarchaeal, bacterial, and fungal communities are strongly associated with soil variables and plan community composition. In this study, consistently high correlations ($P < 0.01$) were observed between the tested soil attributes and microbial abundance at all three sites with Spearman rank correlations as high as 0.93 (Table 2). The importance of soil pH in influencing microbial communities and ecological processes is well recognized in non-Arctic soils (Cuhel et al., 2010). Chu et al. (2010) noted that soil pH is a predominant factor structuring bacterial abundance and community composition in Arctic soil ecosystems. Similarly, in alpine ecosystems, soil pH is one of the key factors shaping bacterial communities (King et al., 2010; Zinger et al., 2011). The present study is in agreement with this finding and it further extends the notion to report not only bacterial but archaeal and fungal abundance are also significantly correlated to soil pH. Nonetheless, Chu et al. (2010) did not find any significant correlations between bacterial communities and soil moisture, DOC, DON, and soil C content. Typically

Table 2. Spearman rank correlations between soil properties and the abundance of archaeal 16S rRNA (Archaea), bacterial 16S rRNA (Bacteria), and fungal 18S rRNA ITS (Fungi) at three Arctic ecosystems: Truelove Lowland (TR), Simpson Lake (SL), and Ross Point (RP).

Microbial abundance	θ_g			pH			DOC†			DON			TOC			TN		
	TR	SL	RP	TR	SL	RP	TR	SL	RP	TR	SL	RP	TR	SL	RP	TR	SL	RP
Archaea	ns‡	ns	0.85**	–0.38**	ns	–0.77**	ns	ns	0.81**	0.22*	ns	0.84**	ns	ns	0.93**	ns	ns	0.71**
Bacteria	ns	0.52**	0.34**	ns	ns	–0.26**	0.28**	0.60**	0.25*	ns	0.63**	0.30**	ns	0.48**	0.29**	ns	0.43**	ns
Fungi	ns	0.38**	0.48**	–0.27*	ns	–0.44**	ns	0.31**	0.42**	ns	0.36**	0.44**	ns	0.25*	0.49**	ns	0.24*	0.35**

* Correlations significant at $P < 0.05$.

** Correlations significant at $P < 0.01$.

† DOC, dissolved organic carbon; DON, dissolved organic nitrogen; TOC, total organic carbon; TN, total nitrogen.

‡ ns, nonsignificant.

soil moisture is highly correlated with other soil attributes and microbial communities in Arctic ecosystems (Banerjee et al., 2011; Bardgett et al., 2007). Similarly in this study, consistently high correlations were found between soil moisture and microbial abundance at Simpson Lake and Ross Point. Dissolved organic carbon and DON pools in soil act as a conduit between aquatic and terrestrial ecosystems and play a critical role by offering substrates for microbial populations (Wickland et al., 2007). The importance of DOC and DON for soil ecological processes of Arctic ecosystems is well recognized with reports showing significant correlations between dissolved organic matter and microbial abundance and processes (Buckeridge et al., 2010; Chu and Grogan, 2010). This study also found strong significant correlations (r = 0.25–0.84; $P < 0.01$) between microbial prevalence and DOC and DON content. Significant association between microbial abundance and C content observed in this study is in line with Stres et al. (2010) who found that soil C alone can explain more than 70% variability in microbial abundance patterns in an alpine ecosystem.

The correlation pattern, that is, the strength of associations between microbial parameters and soil resources differed considerably between three habitats. Correlations observed for the homogenous Histels at Ross Point were comparatively higher than Simpson Lake and Truelove. For example, soil archaeal populations at Simpson showed no correlation with the tested soil properties; on the other hand, at Ross Point, the relationships between archaeal population and soil properties were comparatively stronger (>0.7) than bacterial populations. The aforementioned patterns can be attributed to different regulating factors and differential niche selection of bacteria and archaea in soil (Schleper, 2010). Nonetheless, relatively few significant correlations were found at Truelove Lowland. As soil spatial dependency operates at small scales at Truelove Lowland, it is possible that microbial communities and soil properties may be correlated at finer scale, that is, <0.2 m, that our transect design was unable to capture. Owing to the periglacial processes, permafrost soils experience pronounced small-scale variation (change in organic and inorganic compounds, microtopography, and microclimate) which thereby influences the abundance, diversity, and distribution of microbial communities (Wagner, 2008). For example, in sites with large-scale physical processes, the relationships between bacterial and archaeal abundance and tested soil attributes were highly consistent (i.e., Ross Point) compared to sites with finer scale physical processes (Truelove Lowland) so the spatial dependency of these microbial communities was linked to the scale of physical processes occurring at each site.

Overall we show consistently high abundance of archaeal, bacterial, and fungal gene copies across 7° in latitude and 27° in longitude of the Canadian Arctic. Microbial communities are spatially well structured and the zone of spatial dependency varies between the types of Gelisols with the Histels of Ross Point having a much larger spatial dependency compared to the two Orthel/Turbel Gelisolic ecosystems. However, in spite of the high microbial abundance found in the present study microbial diversity may be low, which may underestimate the spatial heterogeneity. Future studies will assess spatial patterns of microbial diversity and will determine if this difference in spatial dependency holds across multiple sites.

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