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ARTICLE

Archaeal ammonia oxidizers respond to soil factors at smaller spatial scales than the overall archaeal community does in a high Arctic polar oasis

Samiran Banerjee, Nabla Kennedy, Alan E. Richardson, Keith N. Egger, and Steven D. Siciliano

Abstract: Archaea are ubiquitous and highly abundant in Arctic soils. Because of their oligotrophic nature, archaea play an important role in biogeochemical processes in nutrient-limited Arctic soils. With the existing knowledge of high archaeal abundance and functional potential in Arctic soils, this study employed terminal restriction fragment length polymorphism (t-RFLP) profiling and geostatistical analysis to explore spatial dependency and edaphic determinants of the overall archaeal (ARC) and ammonia-oxidizing archaeal (AOA) communities in a high Arctic polar oasis soil. ARC communities were spatially dependent at the 2–5 m scale ($P < 0.05$), whereas AOA communities were dependent at the ~1 m scale ($P < 0.0001$). Soil moisture, pH, and total carbon content were key edaphic factors driving both the ARC and AOA community structure. However, AOA evenness had simultaneous correlations with dissolved organic nitrogen and mineral nitrogen, indicating a possible niche differentiation for AOA in which dry mineral and wet organic soil microsites support different AOA genotypes. Richness, evenness, and diversity indices of both ARC and AOA communities showed high spatial dependency along the landscape and resembled scaling of edaphic factors. The spatial link between archaeal community structure and soil resources found in this study has implications for predictive understanding of archaea-driven processes in polar oases.

Key words: archaea, t-RFLP, 16S rRNA, *amoA*, spatial scale.

Résumé : Les archéens sont omniprésents et fort abondants dans les sols de l'Arctique. De par leur nature oligotrophe, les archéens jouent un rôle important dans les processus biogéochimiques des sols pauvres en nutriments de l'Arctique. En partant du fait que les archéens sont abondants et font preuve d'un important potentiel fonctionnel dans les sols de l'Arctique, la présente étude a employé le profilage par t-RFLP (« terminal restriction fragment length polymorphism ») et l'analyse géostatistique afin d'explorer la dépendance spatiale et les déterminants édaphiques de communautés généralement archéennes (ARC) et archéennes oxydant l'ammoniac (AOA) dans un sol polaire d'une oasis du Haut-Arctique. Les communautés générales étaient spatialement dépendantes à des échelles de 2–5 m ($P < 0,05$) tandis que les communautés d'AO étaient dépendantes à une échelle de ~1 m ($P < 0,0001$). L'humidité, le pH et la teneur en carbone total du sol étaient des facteurs édaphiques cruciaux influençant la structure communautaire des ARC et des AOA. Or, l'homogénéité des AOA était en corrélation simultanée avec l'azote organique dissous et l'azote minéral, laissant croire à une différenciation possible des niches des AOA qui se traduirait par des microsites de sol de types minéraux et organiques humides abritant des génotypes d'AOA distincts. Les indices de richesse, d'homogénéité et de diversité des communautés d'ARC et d'AOA ont présenté une dépendance spatiale élevée d'un bout à l'autre du paysage terrestre et ressemblaient à une mise à l'échelle des facteurs édaphiques. Le lien spatial entre la structure communautaire archéenne et les ressources des sols qu'on a établi dans la présente étude a des ramifications dans l'analyse prospective des processus régis par les archéens dans les oasis polaires. [Traduit par la Rédaction]

Mots-clés : archéens, t-RFLP, ARNr 16S, *amoA*, échelle spatiale.

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Introduction

Archaea are ubiquitous and able to thrive in harsh environmental conditions (DeLong 1992; DeLong et al. 1994; Francis et al. 2005), which makes them particularly relevant to Arctic ecosystems. Previous studies have found a high abundance of archaeal 16S rRNA genes (up to 10^{10} copies·(g soil)$^{-1}$) in Arctic soils (Banerjee et al. 2011*b*). While archaea play important roles in many global biogeochemical cycles, including carbon, nitrogen (N), and sulfur (Offre et al. 2013), their role in ammonia oxidation has received much attention, with studies reporting considerably higher ammonia-oxidizing archaeal (AOA) community abundance than their bacterial counterparts (Leininger et al. 2006). The AOA can comprise up to 10% of the total prokaryotic community in soil (Hatzenpichler 2012; Zhalnina et al. 2012) and previous reports have found between 10^5 and 10^7 AOA gene copies in Arctic soils (Banerjee and Siciliano 2012; Alves et al. 2013). The oligotrophic nature of AOA (Erguder et al. 2009; Hatzenpichler 2012) makes them important for nutrient-limited ecosystems such as Arctic polar oases, where AOA have been shown to drive ammonia oxidation potential (Banerjee and Siciliano 2012).

Polar oases are important ecological units of Arctic and Antarctic soils that represent isolated and relatively small areas with localized climatic conditions within a prevailing polar desert. Characteristics of soil archaeal communities in polar oases may be unique, as oases benefit from relatively favourable temperature and longer hours of insolation, unlike the surrounding polar desert (Muc et al. 1989). The Truelove polar oasis has been the subject of extensive ammonia oxidation research with regards to its link to nitrous oxide emissions from these N-limited soils (Ma et al. 2007; Siciliano et al. 2009; Banerjee and Siciliano 2012). At Truelove, the dominant mechanism of nitrous oxide release appears to be the result of nitrifier denitrification in which nitrifying organisms outcompete denitrifiers for available nitrate (Ma et al. 2007; Siciliano et al. 2009). Since AOA dominate among ammonia-oxidizing prokaryotes in these polar oases soils (Banerjee and Siciliano 2012), studying the overall archaeal (ARC) community and AOA community structures in relation to soil resources is critical to our understanding of archaea-driven soil processes.

Arctic soils are heterogeneous and spatially structured between the 5 and 40 m scale, depending on soil type (Banerjee et al. 2011*a*). Thus, soil resources may also structure spatial distribution of archaeal communities at various spatial scales in different Arctic ecosystems. However, our knowledge regarding the structure and spatial scaling of archaeal communities in polar oasis soils is limited and questions remain as to what scale are community characteristics, such as richness, evenness, and diversity, spatially dependent for ARC and AOA. Spatial heterogeneity in microbial habitats is critical for the microbial ecosystems because it allows simultaneous co-existence of species in communities (Ettema and Wardle 2002). Moreover, microbial spatial structure has implications for ecosystem processes, and it can reveal how combinations of several communities or microhabitats function together at the field scale or at a larger scale (Franklin and Mills 2007). Thus, spatial patterns of archaeal community properties can reveal their substrate preferences, niche partitioning, and nutrient-acquisition strategies in polar oases soils. Using terminal restriction fragment length polymorphism (t-RFLP) profiling and geostatistics, this study characterized multi-scale spatial structure of ARC and AOA richness, evenness, and diversity in a high Arctic polar oasis, and explored whether spatial scaling of archaeal communities reflects the scaling of their edaphic determinants. AOA have a high affinity for N (Hatzenpichler 2012), and as such, a diverse AOA community would acquire N from different sources in N-limited polar oases soils. Thus, our first hypothesis was AOA diversity indices are strongly associated with organic and mineral N contents. Moreover, since AOA communities are functionally distinct and known for niche differentiation (Zhalnina et al. 2012), our second hypothesis was AOA community characteristics are structured at smaller spatial scales than are those of ARC communities.

Materials and methods

Study site and soil sampling

This study was conducted at Truelove Lowland site (75°40′N, 84°35′W). This coastal lowland is situated on the northeastern coast of Devon Island and it covers an area of 43 km² of Devon Island's total 55 000 km² area (Lev and King 1999; Ma et al. 2007). It is a polar oasis on Devon Island in the Canadian Arctic Archipelago. The mean annual air temperature is approximately –16 °C, with the highest recorded daily temperature of 21 °C in July and the lowest monthly temperature of –45 °C in January (Environment Canada 2011). The total annual precipitation is about 185 mm with 36 mm as rain (Environment Canada 2011). The topography of Truelove Lowland is characterized by a series of raised beach crest ridges, lower foreslopes, and wet sedge meadows with Regosolic Static Cryosols, Brunisolic Eutric Turbic Cryosols, and Gleysolic Turbic Cryosols soils, respectively (Lev and King 1999; Ma et al. 2007). Three parallel transects (300 m each; 2 m distance between each of the transects) were established in the third week of July. A total of 93 soil samples were collected from 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). A fine-scale sampling scheme may miss patterns occurring on broader scales, whereas a large-scale sampling design may not capture fine scale dynamics (Franklin and Mills 2007). Thus, variable lag distance design, i.e., adjacent steps separated by a repeated sequence, is a useful sampling design for characterizing multiscale patterns in an ecosystem (Fortin et al. 1989).

We opted for this design to simultaneously capture the fine- (0–1 m), medium- (1–10 m), and large- (10–300 m) scale spatial patterns. Approximately 250 g of soil samples were collected at 1–10 cm depth using a hand trowel and were sieved with a 4.75 mm sieve. Between samples, sieves and hand trowels were sterilized with 95% ethanol and dried before use.

Soil analyses

In the laboratory, soil gravimetric moisture, pH, extractable ammonium (NH_4^+) and nitrate (NO_3^-), total organic carbon, total carbon, total nitrogen, dissolved organic carbon, and dissolved organic nitrogen (DON) contents were measured as described previously (Banerjee et al. 2011*b*). Soil DNA was extracted from 0.5 g of samples according to the method described by Griffiths et al. (2000). We performed t-RFLP of archaeal 16S rRNA and *amoA* on 93 samples. The archaeal 16S gene was amplified using the primers Arch21F (5′-TTCCGGTTGATCCYGCCGGA-3′) and Arch958R (5′-YCCGGCGTTGAMTCCAATT-3′) (DeLong 1992). The archaeal *amoA* gene was amplified using the primers Arch-amoAF (5′-STAATGGTCTGGCTTAGACG-3′) and Arch-amoAR (5′-GCGGCCATCCATCTGTATGT-3′) (Francis et al. 2005). Each 30 μL PCR reaction contained 0.5 μL of DNA (diluted 1:20), 1× PCR buffer, 0.2 mmol/L dNTPs, 2 mmol/L $MgCl_2$, 0.4 μmol/L each primer, and 0.7 U Platinum *Taq* DNA Polymerase (Invitrogen Life Technologies). Both the forward primers were labeled with WellRED fluorescent dye D4 (Integrated DNA Technologies). PCR success and amplicon quality was assessed by 1% agarose gel electrophoresis and visualized by staining with ethidium bromide. Bands of expected size (930 and 635 bp for 16S and *amoA*, respectively) were cleaned, and restriction digest was performed on amplicons to prepare them for t-RFLP analysis. For each reaction, 5 μL of PCR product was digested with 2.5 U of *Alu*I (for 16S archaea) or *Msp*I (for AOA) enzyme, 1 μg of bovine serum albumin, and 1× of the corresponding buffer (Promega). Digested fragments were desalted by ethanol precipitation and resuspended in 8 μL of ultrapure water (Integrated DNA Technologies). Fragments were prepared for analysis as suggested by the manufacturer for the Beckman Coulter CEQ8000 Fragment Analysis System (Beckman Coulter Inc.). A 1.5 μL volume of digested PCR product was combined with 38 μL of Sample Loading Solution (Beckman Coulter Inc.) and 0.5 μL of 600 bp size standard. Fragment lengths were determined by electrophoresis using a Beckman Coulter (CEQ8000) automated sequencer, version 6.0.2. Analysis of fragment profiles was performed using the Beckman Coulter fragment analysis package 8000, version 8.0.52, fragment analysis algorithm version 2.2.1.

Statistical analyses

Richness, Pielou's evenness, Shannon index, and inverse Simpson index were calculated in PRIMER-E version 6 (PRIMER-E, Plymouth, UK). PERMANOVA and canonical analysis of principal coordinates (CAP) (Anderson and Willis 2003) were performed using Euclidian resemblance matrix of soil properties and second-order distance matrix of ARC and AOA operational taxonomic unit (OTU) matrix with 999 permutations in PRIMER-E. To assess the spatial structures of ARC and AOA communities, CAP analysis was conducted by constraining OTU matrix against spatial distance classes (i.e., transect positions). Edaphic factors with a correlation of greater than 0.4 were overlaid as vectors on the CAP plots. Spearman Rank correlations between soil properties and diversity indices of AOA were calculated in SPSS version 20 (IBM SPSS Statistics, Armonk, New York). Spatial variability was assessed using geostatistical analyses in GS+ version 10.0 (Gamma Design Software, Plainwell, Michigan, USA). Spatial variability was determined by calculating the semivariance, which is half of the average squared difference between the components of a data pair (Goovaerts 1998). Data pairs were arranged in lag distance classes on the basis of the distance between sampling locations. For positive spatial autocorrelation, semivariance increases with distance, indicating that samples taken at nearby points will likely be more similar than those taken further apart (Franklin and Mills 2007). The key parameters of a semivariogram (a plot of semivariance and lag distance) are range, sill, and nugget (Fig. 1). The range of a semivariogram highlights the zone of spatial dependency, i.e., the lag distance at which the semivariance value becomes highest, whereas sill is the maximum variability of a variable. Nugget variance is the random variability due to experimental error. The spatial dependence (SPD) was calculated as SPD = $C/(C + C_0)$, where C is the structural variance, C_0 is the nugget, and $C + C_0$ is the sill. Thus, structural variance is the amount of variance resulting from spatial structure, i.e., the difference between sill and nugget (Goovaerts 1998). Values of SPD vary from 0 (no spatial dependence) to 1 (high spatial dependence). All semivariograms were calculated with a minimum of 30 sample pairs per lag class

Fig. 1. An empirical semivariogram showing nugget, sill, and range. Range indicates the area of spatial dependency, i.e., the lag distance at which the semivariance value becomes highest, whereas sill is the maximum variability of a variable. Nugget variance is the random variability due to experimental error.

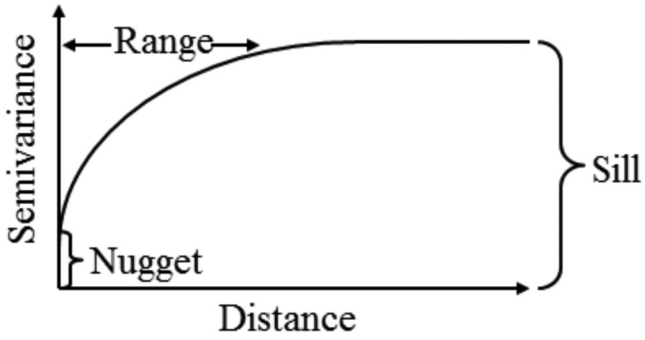
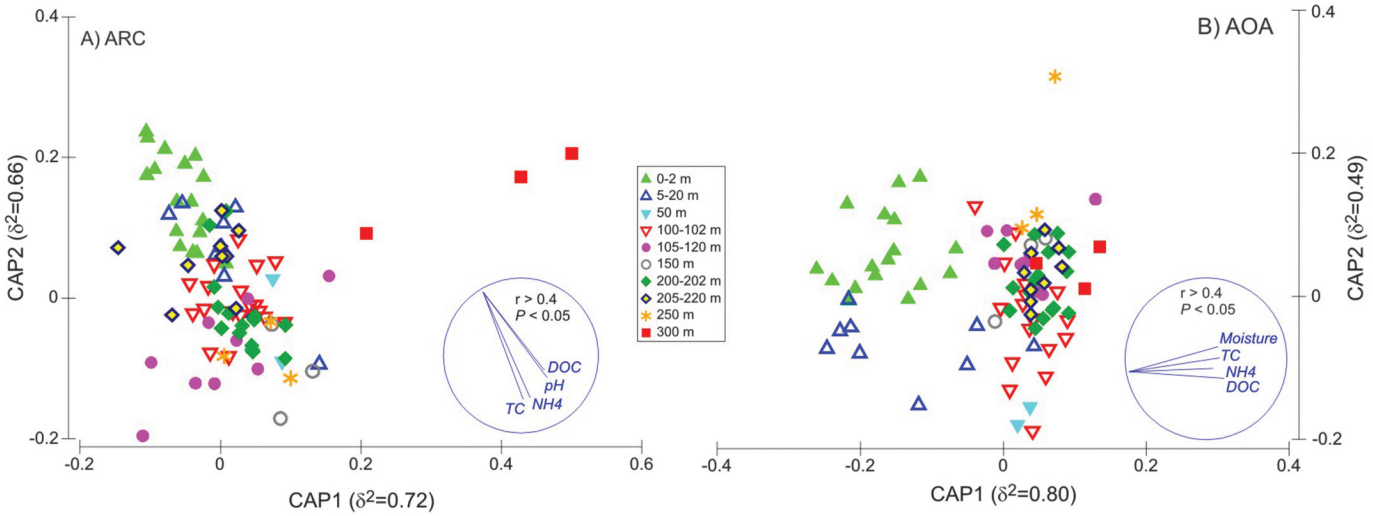


Fig. 2. Canonical analysis of principal coordinates (CAP) of a Bray–Curtis similarity matrix of t-RFLP profiles showing clustering of (A) overall archaeal (ARC) community and (B) ammonia-oxidizing archaeal (AOA) community at Truelove Lowland. CAP was performed with a second-order distance matrix of archaeal communities ordinated against landscape positions using 999 permutations. Only edaphic vectors with correlations >0.4 ($P < 0.05$) are included in the plots. TC, total carbon; TOC, total organic carbon.



(Journel and Huijbregts 1978). Gaussian, spherical, or exponential models were fitted to the semivariograms using the least-squares method in GS+. Semivariance was computed up to 300 m with the *Autofit* option in GS+; however, semivariograms were shown up to specific distances for clarity of patterns near origin. Spatial pattern near origin is critical for semivariograms, as it highlights the nugget effect (Goovaerts 1998). Since archaeal community characteristics were spatially dependent at small scales, final semivariograms were shown at smaller scales without compromising the structure of semivariogram. Final semivariograms were selected by considering goodness-of-fit and assessing residual sum of squares and R^2 values.

Results and discussion

The CAP analysis revealed structuring of ARC and AOA communities at different spatial scales in Truelove Lowland (Fig. 2). The ARC communities formed significant ($P < 0.001$) clusters at individual spatial distance, particularly at small scales, such as 0–2, 100–102, and 200–202 m (Fig. 2A). On the other hand, AOA communities also formed significant ($P < 0.001$) clusters, with AOA profiles at the 0–20 m scale in a separate group (Fig. 2B). This indicates that AOA communities are spatially structured at small spatial scales and there is a possible niche partitioning of AOA genotypes. The observation that communities at the same spatial distance but on different transects formed separate clusters on CAP plot indicates differences in the AOA community structure even at the 2 m distance (lateral distance between 2 transects).

The effect of spatial distance on archaeal communities was also supported by PERMANOVA results, which showed significant effects on ARC ($P < 0.05$) and AOA ($P < 0.001$; $n = 93$) distribution. Truelove Lowland has a distinctive topography that offers a range of slope conditions, such as level elevated crests of raised beaches, foreslopes, backslopes, and wet sedge meadows (Lev and King 1999). This unique topography results in spatial heterogeneity of soil resources at various landscape positions (Banerjee et al. 2011*a*, 2011*b*). The effects of spatial distance on archaeal community structure found in this study are consistent with a previous report (Siciliano et al. 2009) that showed a similar effect on bacterial community structure in Truelove Lowland soils.

Soil moisture, pH, and carbon content have been shown to influence archaeal abundance and community structure in various ecosystems (Erguder et al. 2009; Zhalnina et al. 2012). This study demonstrates that both ARC and AOA communities in polar oasis soils are also structured by moisture, pH, and TC content (Fig. 2). Additionally, we found that total N was important for ARC communities, and that DON and C:N were important for AOA communities. Drivers of differences in AOA communities also emerged when correlations between soil properties and diversity indices were assessed (Table 1; Supplementary Fig. 1[1]). Soil DON and NH_4^+ contents significantly ($P < 0.01$; $n = 93$) correlated with AOA evenness and diversity, supporting our first hypothesis. Unlike their bacterial counterparts, archaeal ammonia oxidizers depend on organic N sources in soil (Hatzenpichler

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjm-2015-0669.

Table 1. Spearman rank correlations between soil properties and diversity indices of archaeal *amoA*.

	Evenness	Shannon	invSimpson
Moisture	−0.340**	−0.345**	−0.375**
NH_4^+	−0.377**	0.333**	0.371**
NO_3^-	−0.232*	NS	−0.212*
DOC	−0.243*	0.212*	−0.240*
DON	−0.454**	−0.344**	−0.336**
TC	−0.363**	0.289**	−0.338**
TN	0.319**	−0.260*	0.303**

Note: *, Significant at $P < 0.05$ level ($n = 93$); **, significant at $P < 0.01$ level ($n = 93$); NS, not significant; NH_4^+, extractable ammonium; NO_3^-, extractable nitrate; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; TC, total carbon; TN, total nitrogen. Soil pH, TOC content, and species richness did not show any significant correlations.

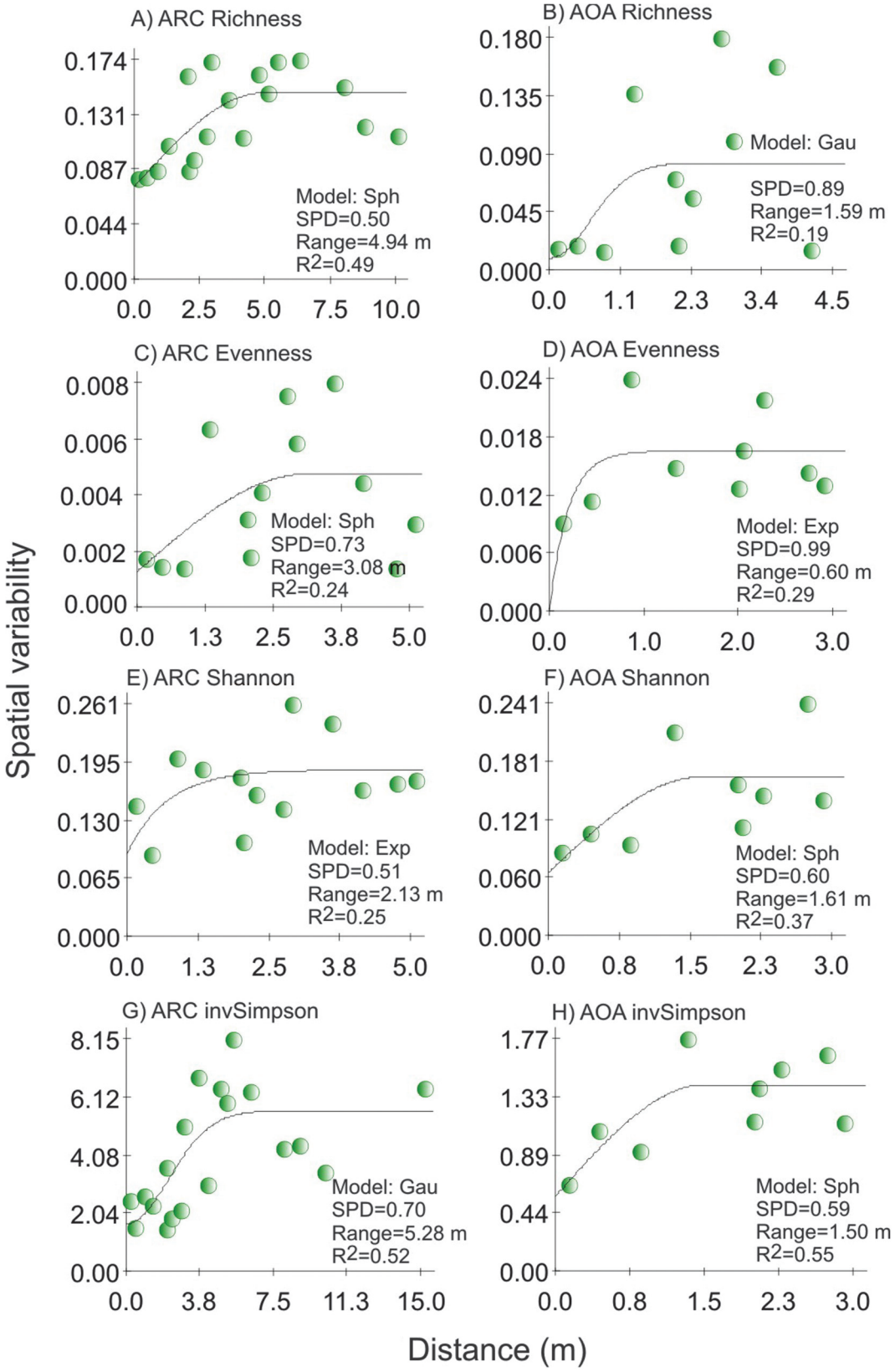
2012; Zhalnina et al. 2012), particularly in environments such as the Arctic where N is limited. Thus, our results support Alves et al. (2013), who found a strong relationship between DON and AOA communities in Arctic soils. The simultaneous correlations between AOA evenness and soil moisture, organic N, and mineral N indicate a possible niche differentiation of AOA communities whereby dry mineral and wet organic soil microsites harbour different AOA genotypes (Hatzenpichler 2012; Alves et al. 2013). The consistent relationships between AOA evenness and edaphic factors indicate that evenness is a better index than richness for interpreting t-RFLP community data (Blackwood et al. 2007). Nonetheless, C:N ratio was the only factor that correlated ($P < 0.05$; $n = 93$) with ARC diversity indices and no significant correlations were found between soil resources and AOA richness (data not shown). The lack of correlations for ARC indices and significant correlations for AOA can be ascribed to the fact that ARC communities are involved in a wide range of soil processes and as such are functionally diverse, whereas AOA communities involved in ammonia oxidation are functionally similar and are governed by key edaphic factors. Nonetheless, there was no significant correlation between soil pH and AOA diversity indices. AOA communities have remarkable ecological and phylogenetic diversity (Erguder et al. 2009), and AOA activity is largely dominant in low pH soils (Nicol et al. 2008). Soil pH is a major determinant of AOA particularly in acidic soils (Zhalnina et al. 2012), and thus, we posit that the lack of correlation found in this study is attributable to consistently neutral pH (pH = 7.54, Banerjee et al. 2011*a*) in Truelove oasis soils.

Semivariance analysis revealed that both ARC and AOA communities are highly spatially dependent but function at different scales (Fig. 3). For example, diversity indices of both communities had SPD consistently higher than 0.5, indicating high spatial dependency. However, while ARC communities were spatially structured at the 2–5 m scale, AOA communities were structured at the ~1 m scale, supporting our second hypothesis. Within each community, there were no considerable differences in the SPD and range of various diversity indices. Knowledge of spatial autocorrelation is particularly important in microbial ecology, as it can reveal the extent to which similarity of microbial community properties is dependent on spatial separation distance (Legendre 1993). The small spatial scales of ARC and AOA (1–5 m) communities found in this study were somewhat consistent with our previous report (Banerjee et al. 2011*b*), which found archaeal abundance in Truelove Lowland soils was spatially autocorrelated at 1.2 m. The transects for soil sampling were separated by a lateral distance of 2 m, and thus, the small spatial range of AOA communities explains the separate clustering of AOA on CAP plots formed at the similar landscape position but on different transects (i.e., 2 or 4 m from each other). Semivariance analysis is one of the most robust and commonly used methods for quantitatively describing spatial variation and modelling microbial spatial dependence (Goovaerts 1998; Ettema and Wardle 2002; Franklin and Mills 2007). Spatial range in a semivariogram reflects the distance up to which a property is spatially autocorrelated, and a longer range indicates strong spatial similarity owing to homogeneity in soil resources (Ettema and Wardle 2002). This suggests that edaphic factors controlling archaeal distribution in polar oasis soils are highly heterogeneous. Indeed, our previous report also found that soil properties at Truelove Lowland were spatially dependent at the <10 m scale, with moisture and pH operating at ~1 m (Banerjee et al. 2011*a*). The small range of spatial structure observed in this study suggests that relatively small changes in edaphic factors such as moisture and DON that control AOA distribution result in large changes in the evenness of AOA genotypes. Thus, the variable-lag-distance approach employed here reveals a consistency in spatial scaling of archaeal communities and their edaphic drivers. The consistency in spatial scaling of archaeal communities and their edaphic determinants found using t-RFLP profiling highlights the validity of this technique in an era of high-throughput sequencing (van Dorst et al. 2014). More importantly, it reinforces the usefulness of t-RFLP as a tool for rapid assessment of a large number of samples when less depth of community coverage is warranted.

Conclusions

Linking microbial patterns to underlying drivers is a central goal in microbial ecology. Microbial spatial scaling has critical importance in ecology, as it can reveal the factors controlling a microbial property at different scales. This study demonstrates that ARC and AOA communities are structured at the 2–5 and ~1 m spatial scales, respectively, resembling their edaphic controls in polar oasis soils. The smaller scales of AOA spatial structure and simultaneous associations with DON and mineral N indicate a possible niche partitioning of AOA

Fig. 3. Semivariograms showing spatial characteristics of diversity indices of overall archaeal (ARC) community and ammonia-oxidizing (AOA) archaeal community at Truelove Lowland. Spatial variability (semivariance) was calculated using spherical (Sph), Gaussian (Gau), and exponential (Exp) models. SPD indicates spatial dependence, and range indicates the zone of spatial dependency. All semivariograms were computed up to 300 m distance; however, the semivariograms are shown up to specific distance for clarity of spatial patterns near origin. All R^2 values were statistically significant at $P < 0.05$.



genotypes. Nonetheless, richness, evenness, and diversity of ARC and AOA communities have high spatial dependency. The consistent relationships between AOA evenness and soil properties suggest that evenness is a better index than richness for interpreting t-RFLP community data. Overall, we report spatial characteristics of archaeal communities in polar oasis soils and demonstrate a consistency in spatial scaling of AOA diversity and the edaphic drivers.

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