

Microbial Population and Distribution at a Mars Analog Alluvial Plain in Dyngjusedur, Iceland

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ABSTRACT

The limited nutrient availability, extreme temperatures, and desiccation of Arctic volcanic regions provide a unique opportunity to study environments with multiple similarities to extraterrestrial systems. Dyngjúsandur, Iceland, is a plain of nutrient-poor volcanic basaltic tephra shaped by alluvial and aeolian action sharing spectroscopic similarities to analogous geological features observed on Mars. To obtain spatial information at different scales, two regions of the Dyngjúsandur plain separated by 1 km and selected for their homogenous appearance were sampled in this study. Sampling schemes each consisted of nested triangular grids of samples beginning at the 0.1 m scale and increasing to the 100 m scale. Additional samples were recovered at 1 cm increments to a depth of 7 cm. Biological and geophysical analyses were performed including: 16S rRNA gene qPCR, DNA quantification, amplicon sequencing, moisture quantification, and separation of grain size fractions. The two sampling sites were found to have significantly different dsDNA content by *t*-test (p -value = 0.001) and Mann-Whitney *u*-test (p -value = 0.003). The DNA content (a proxy for biomass) showed the greatest variation at 10 m of sample separation, and both total dsDNA content and bacterial 16S rRNA gene copies showed significant correlations with sample grain size. Grain size distribution also appeared to influence the abundance of several bacterial phyla, with positive and negative correlations observed, though the same dominant phyla were observed across all samples studied. This work suggests that, in seemingly homogeneous environments undergoing aeolian resurfacing, the averages from a sample set collected at small spatial separation (1 m – 10 m) may be sufficient to define baseline levels of biomass present and the abundances of the most prominent phyla on a larger (100 m – 1 km) scale. However, sampling a larger site at smaller intervals (10 m) provides important characterization of site heterogeneity with diminishing information returns at increasingly smaller intervals (≤ 1 m).

INTRODUCTION

A goal of the Mars 2020 mission is to search for evidence of past life on the Martian surface. Such an undertaking requires the exploratory rover to be equipped with the analytical tools to analyze samples for potential biosignatures, then excavate and cache for potential future return to Earth. Onboard, the Mars 2020 rover carries a camera for field visualization (Mastcam-Z), sensors for identifying temperature, humidity, and mineral grain size and morphology (MEDA), a micro-focus X-ray fluorescence spectrometer for elemental chemistry (PIXL), and Raman spectrometers for mineralogical measurements and organic characterization (SHERLOC & SuperCam). In addition to these instruments, the Mars Reconnaissance Orbiter (MRO) has provided infrared spectroscopy measurements using the Compact Reconnaissance Imaging Spectrometer for Mars (CRISM), allowing for characterization of surface mineralogy in the search for water on Mars.¹⁻⁶ However, questions remain about the efficacy of these instruments for detecting or predicting biosignatures.⁷⁻⁹ When evaluating the instrument package of the Mars 2020 rover, and those of future missions, which *in-situ* measurement capabilities offer the greatest correlation with biomass and habitability assessments?

Constructing an instrument suite is only one part of achieving success when identifying signs of past life on Mars if present. The Mars 2020 rover is limited in the number of samples it can analyze and select for potential future return, increasing the importance of sample selection at the landing site.¹⁰ When characterizing a sampling location, factors such as moisture content, grain

size, and geochemistry of the sediment could result in vastly different habitability for various organisms, and heterogeneous distribution of any biomarkers might require large sampling sets to ensure collection of a theoretical sample that contains a biosignature.^{11, 12} Determining a sampling strategy informed by our best understanding of the likely distributions of and correlations between biosignatures and environmental parameters is therefore a primary concern, not just for Mars 2020 but for any landed planetary mission in search of biosignatures.

Field analog research is a primary way of testing instruments and sampling techniques in preparation for extraterrestrial missions.^{8, 13-15} With some key similarities to extraterrestrial terrains, analog field sites offer opportunities to test operational, technological, and scientific questions. As a result of its glacial and volcanic history and limited anthropogenic activity, Iceland has long been used as an analog for regions of the Martian surface with similar mineralogy and harsh environmental conditions.¹⁶⁻¹⁸ One such location is Dyngjúsandur, a plain in the Central Highlands of Iceland sculpted by a mix of alluvial and aeolian processes.¹⁹⁻²¹ Dyngjúsandur is largely composed of unconsolidated basaltic tephra, worn down to a fine sand, resulting in a location frequently disrupted by dust storms. Amidst the plains of black sand, larger chunks of lava are infrequently dispersed, resulting in an apparently open and relatively homogenous field site ideal for testing the spatial scale heterogeneity of nutrient-constrained native ecology. While the mineralogy of Dyngjúsandur has been investigated in other publications,¹⁹⁻²² the microbial abundance and composition at the site remains largely uncharacterized.²³

The Planetary Science and Technology from Analog Research (PSTAR)-funded Field Exploration and Life Detection Sampling through Planetary Analog Research (FELDSPAR) project is an international collaborative program aimed at testing operations and feasibility of a future Mars mission through field campaigns to various Icelandic lava fields.²²⁻²⁶ The FELDSPAR team visited the Dyngjúsandur sampling site annually starting in the summer of 2016, and this work identified relationships between the geophysical and environmental characteristics of the sandy plain and its biosignatures. To estimate microbial abundance at Dyngjúsandur, we analyzed total extracted DNA content as a bulk measurement given its ubiquitous use as genetic material by terrestrial organisms.²⁷ Quantitative polymerase chain reaction (qPCR) with universal 16S rRNA gene primers provides an additional bio-content measure with a specificity for prokaryotic organisms.²⁸ Environmental characteristics evaluated here include mass percentages of the moisture content and grain size fractions, detailed in methods. Biosignature abundances are important points of comparison for identifying shifts in habitability factors and, paired with 16S ribosomal ribonucleic acid (rRNA) gene amplicon sequencing, changes in the microbial community can also be observed. While these techniques enable both generality and specificity in terrestrial life detection, the highly evolved nature of the deoxyribonucleic acid (DNA) information storage system makes it an unsatisfactory biomarker on other planets. Here, we use abundant and diverse DNA as an indicator of habitability on Earth,^{29, 30} which could be assessed on other planetary bodies by the presence of ingredients needed to support life.²⁹⁻³¹ Terrestrial life will not likely identify the exact environmental factors that would make an environment habitable for theoretical extraterrestrial life, due to probable extreme differences in their evolution. However, some factors associated with universal needs of all theoretical life, such as a source of mass, a source of energy, and a relatively stable environment, may be identified successfully.²⁹ This thought process has led the current search for biosignatures to look for sources of liquid water and to advise sampling at depth, away from damaging radiation.^{29, 32} Examining broad patterns among terrestrial life may identify more factors that could be used to identify likely-habitable

environments, such as the small grain sizes that correlate with several biological data types in this work.

It is important to acknowledge that extracted DNA content is not the best means of estimating microbial biomass in many situations, since each cell has different quantities of DNA in its chromosome,³³ DNA from dead organisms will appear to be biomass despite it reflecting necromass,^{34, 35} and DNA concentrations neglect to account for RNA-based phages, which are an important component of the microbial community.³⁶ However, there is a correlation between environmental DNA and biomass, so this method of estimating biomass is not unusual.^{34, 37} While ribonucleic acid (RNA) concentrations would have provided excellent scientific insight into the microbial ecology dynamics within the phage community, sampling was not done with this in mind, so RNA has long since degraded in these samples. The sampling procedures were selected for several reasons, including an effort to keep sampling procedures as close to Martian missions as possible and a lack of confidence in the ability to extract even DNA from such oligotrophic samples. Since successful RNA extraction was not guaranteed from samples in such an extreme environment, preservation of the samples to enable this method was not a priority at the time.

To fully characterize a site, samples would need to be taken from each unique microenvironment within the region. However, identifying these microenvironments is challenging in sites that appear homogenous upon initial inspection, like the alluvial plains of Iceland or some Martian terrains, such as the northern Planitia. Therefore, a robust sampling strategy should be developed to obtain data that accurately represents the average environment and captures most of the variation present at a site without burdensome and resource-intensive over-sampling. Completely random sampling is only warranted when the regions of interest are truly homogenous,³⁸ and while Dyngjúsandur appears homogenous on the surface, past work has demonstrated variability within the plain.^{22, 24, 25} In a heterogeneous system, spatial autocorrelation must be considered, which describes the extent to which the distance between the samples affects their differences.³⁸ Since this site has not been well characterized previously, samples must be obtained in triplicate on multiple spatial scales to obtain “identical” replicates as well as replicates with sufficient distance to avoid autocorrelation. This will determine at what scale Dyngjúsandur has significant variation or autocorrelation effects. In this study, a nested triangular grid was used to satisfy this requirement. Biological and geochemical analyses were both performed on each sample to identify correlations between these variables, which were evaluated with statistical pairwise testing. More information on the geochemical characteristics of the site have been detailed in previous work.²²

Here, we characterize the Dyngjúsandur sampling site and the correlation of bulk biosignatures with environmental measurements and determine the spatial heterogeneity of biosignatures. Two analyses of bio-content were performed: total double stranded deoxyribonucleic acid (dsDNA) concentration by fluorescence assay and quantitative polymerase chain reaction (qPCR) with bacteria-focused primers. These general measures are intended to act as an estimate of biomass, and sequencing of the 16S rRNA gene amplicon was conducted to enable an estimate of biodiversity. The results of these assays were compared at each spatial scale and juxtaposed with grain size and moisture content to determine the most biologically predictive characteristics of this Mars analog site.

METHODS – DYNGJUSANDUR SAMPLES

Sampling: Nested Triangular Grids & Depth Profile

Sediment samples were recovered from a plain in Dyngjusandur, Iceland (64.92°N, 16.76°W) in June 2016. The sampling location was selected based on visual and morphological homogeneity, with a focus on sand sheets with relatively homogenous sediment with grain size maxima on the lapilli (~2mm diameter) scale (Figure 1). Sampling was performed using a series of nested triangles with edges of 0.1 m, 1 m, 10 m, and 100 m at two locations separated by 1 km hereafter referred to as D1 and D2 (Figure 2). These sites were chosen due to a high surface sand content (as compared to the large surface basaltic stones) with a 1 km separation between them. Sampling locations were marked using triangular tarps and flags and photographed aerially using a DJI Inspire 1 Quadcopter.

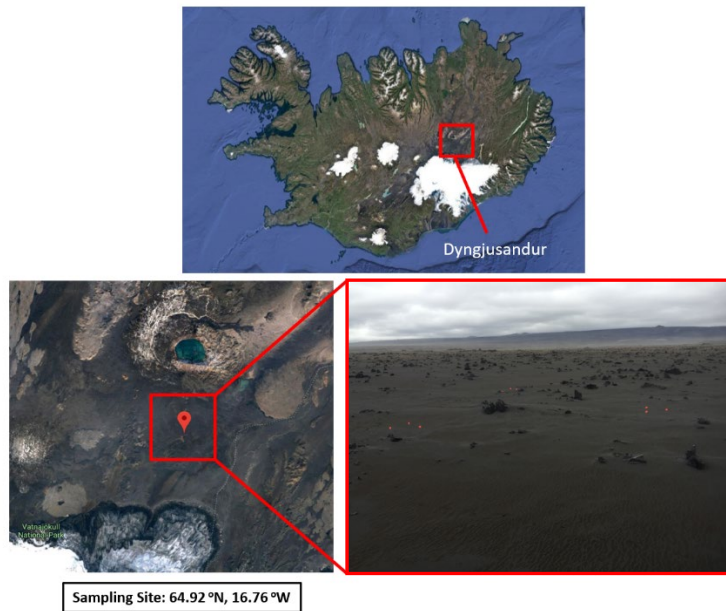


Figure 1. The Dyngjusandur field site. Dyngjusandur alluvial plain is located in the central highlands of Iceland, 16 km south of the Askja Caldera. The sand is composed of unconsolidated basaltic tephra, and while portions of the plains are morphologically homogenous, others are distributed with basaltic stone.

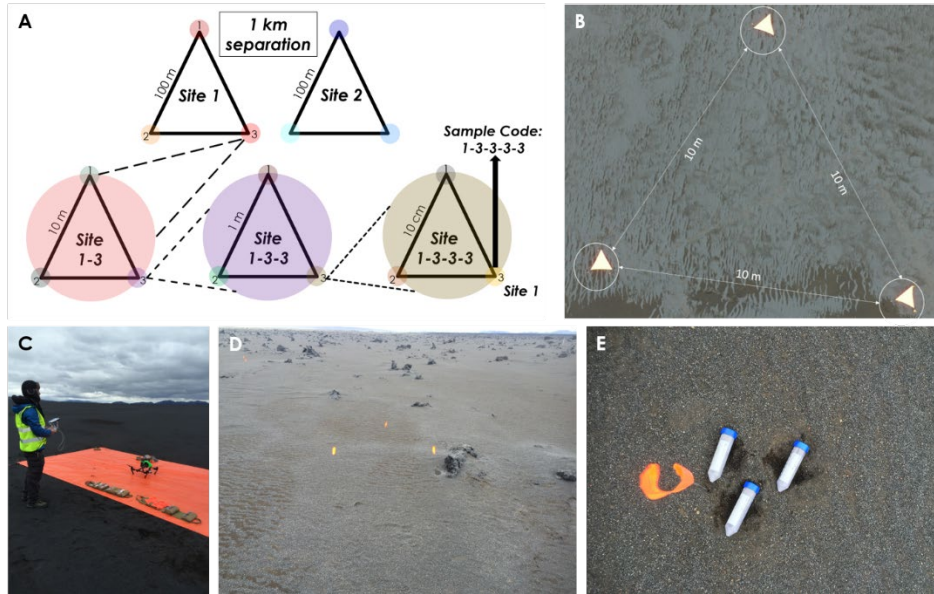


Figure 2. Nested Triangular Grids Sampling System. Two sampling sites were selected with a separation of 1 km. At each sampling site, a series of nested triangular grids was sampled to determine spatial heterogeneity of biomass. (A) The sampling schematic employed at Dyngjusandur. Each site was mapped into equilateral triangles, with the vertices separated by 100 m. Each corner of each triangle was then mapped into a smaller triangle, with distributions of 10 m, 1 m, and 0.1 m for a total of 162 samples. (B) A 10 m triangle from Site 1. Orange, triangular tarps with 1 m per side were placed at the corners of each 10 m triangle for visualization. (C) Aerial mapping of each site was obtained using a quadcopter for imaging. (D) The 1 m triangles prior to sample collection and aerial mapping were denoted in field by small orange flags. (E) Triplicate samples at 0.1 m spacing were recovered at the corners of each 1 m triangle after removing the top 1 cm of surface sediment.

Aerial photography was performed twice for each sampling location, first with flags marking the sampling locations and later with tarps that represented the sampling triangles. Following aerial photography with the flags, a spade was cleaned by rinsing with 70% isopropanol, wiping with a clean room cloth, and then the same spade was used to remove the top ~1 cm of sediment prior to sample collection. To minimize contamination, tarps were not used until after this sampling process. In addition to the samples collected on the surface, depth profile samples were recovered from a sampling site within 10 m of Site 1. These depth profiles comprised of seven samples total collected in 1 cm increments from the surface to a depth of 7 cm. Spectroscopic data was obtained for each location using a field portable visible near infrared (VNIR) ASD Fieldspec 4 field spectroradiometer (Analytical Spectra Devices, Boulder, CO) with high illumination contact probe (10 mm spot size, Model No. A 122300) containing a halogen source and a Bruker Tracer-IV SD portable X-ray fluorescence (pXRF) spectrometer with a 2 W Rh anode X-ray tube and a 10 mm² Silicon Drift Detector to collect secondary electrons. The pXRF had a voltage of 40 kV with an applied 44mA probe current and a total excitation area of 7 mm². Interpretation of spectroscopic data obtained the following year was presented in a companion paper.²² Sediment samples were deposited into sterile 50 mL Falcon conical tubes, and bagged for return to Georgia Tech.

The systematic sampling scheme was chosen to allow for ease of comparison between samples at different spatial scales. Triplicates are the minimum number of samples required for most statistical tests. Therefore, to accommodate the need to survey a large area and conduct statistical tests, acquiring three points of comparison at each spatial scale was determined to be optimal.^{22, 24-26}

All work, including sampling, was performed with an attempt to minimize anthropogenic contamination. Face masks, non-linting arm sleeves, and nitrile gloves were worn by those taking samples, and considerations were made to work downwind from sampling sites. Samples were returned to a field lab at the University of Akureyri where they were stored in -20 °C laboratory freezers until they were shipped under ambient conditions to Georgia Tech. Upon return to Georgia Tech, samples were stored in a -80 °C freezer until they were subject to characterization and bioassays. Apart from storage in frozen conditions whenever possible, no other preservation methods or agents were used in order to mimic the conditions of Martian missions wherever possible.

Sample Bulk Characterization (Moisture Content and Grain Size Analysis)

Sediment samples were defrosted in a room sterilized and prepared for biological analysis, and at least one gram of each was measured into glass scintillation vials, while the rest was reserved for future analyses, including the subsequently described DNA analyses. The vials were prepared in triplicate and weighed prior to the introduction of field sample. After obtaining the mass of the wet sample within the vial, sample vials were placed in an oven at 100 °C for 24 hours, and then weighed to determine the contribution of moisture to total dry sample mass. This process was repeated until consistent masses were observed on multiple days.

It should be noted that there was rain three days prior to sampling in this area and all samples were collected within a twelve-hour time span. Therefore, the moisture content data is likely influenced by the weather phenomena.

After moisture content was determined, grain size analysis was performed using dry sieving. The sieves captured grains at scales greater than 2000 µm, 850 µm, 425 µm, and less than 425 µm, selected to discriminate between fine, medium, and course sediments as per the Unified Soil Classification System (USCS).^{22, 23, 39} The sediment collected by each sieve was weighed to estimate the grain size composition for each location in the nested triangle.

Biological Assays (dsDNA Content, qPCR, and Amplicon Sequencing)

DNA was extracted from another subsample of the sediment samples using a DNeasy PowerLyzer PowerSoil Kit from Qiagen (Hilden, Germany). The standard protocol for the PowerLyzer kit proved insufficient for recovering DNA from our samples, and instead, an alternative PowerSoil Protocol for Low Biomass Soil was used as provided by Qiagen and adapted from Hale et al.⁴⁰ Successful extraction was confirmed using a Qubit dsDNA High Sensitivity Assay by Thermo Fisher (Waltham, MA), which quantifies double stranded DNA with a fluorescent dye and standard curve. A Qubit fluorimeter was used for fluorescence measurements.

Bacterial rRNA gene copies were determined for each sample using qPCR with standards provided in the FEMTO™ Bacterial DNA Quantification Kit (Zymo Research, Irvine, CA). Bacterial primers 515F (5'-GTG CCA GCM GCC GCG GTAA) and 806R (5'-GGA CTA CHV HHH TWT CTA AT) were used to target the V4 region of the 16S rRNA gene.⁴¹⁻⁴³ Samples were

run in triplicate on a CFX96TM Real-Time System (Bio-Rad, Hercules, CA), with 20 μ L reactions composed of 10 μ L 1x SsoAdvanced Universal SYBR[®] Green Supermix (Bio-Rad), 1 μ L of 10 μ M forward and reverse primer, 1 μ L of template DNA, and 8 μ L of water. Cycling conditions were 95 °C for 10 min; 40 cycles of 95 °C for 30 s, 50 °C for 30 s, and 72 °C for 1min followed by a final step of 72 °C for 7 min as recommended by the FEMTO kit.

A subset of extracts, one sample from each 1 m triangle at the D1 site, were prepared for 16S rRNA gene amplicon sequencing. Amplification of DNA was performed as outlined in Illumina's 16S Metagenomic Sequencing Library Preparation guide (15044223B), using the primers 341F (5'-CCT ACG GGN GGC WGC AG) and 785R (5'-GAC TAC HVG GGT ATC TAA TCC) to target the V3-V4 region of the 16S rRNA gene, which has shown excellent taxonomic coverage for bacteria and archaea.⁴⁴ Amplicons were sent to SeqMatic (Fremont, CA) for clean-up, indexing, and sequencing (S. Appendix 1). Sequences were processed using the DADA2 pipeline and analyzed using the Phyloseq package.^{45, 46} Taxonomic assignment was performed utilizing the Silva 138.1 database, which contains aligned and updated small and large subunit ribosomal gene sequences and their taxonomic assignments.^{47, 48} This database is one of the most widely used databases in amplicon sequencing work due to its wide breadth of data across all domains of life and consistent maintenance by the Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures in Bremen, Germany. Further analysis of the sequencing results will be explored further in future work.

Statistical Analysis

Pairwise *t*- and *u*-tests were performed using the R programming language (version 3.5.3) to compare moisture content, bacterial rRNA gene copies, and dsDNA content at each distance scale of the nested triangular grids.²⁵ The 1 m level involved the comparison of measurements using the corner 0.1 m sample at each 1 m triangle's apex as a grouping. Groupings were only compared within each parent 1 m triangle. The *p*-values obtained for each comparison were adjusted using a Bonferroni correction, and significant differences were identified as adjusted *p*-values less than or equal to 0.05.⁴⁹ The percentage of statistically significant differences across all triangles was determined by comparing the number of statistically significant differences to the total number of comparisons. This process was repeated for the 10 m spacing level using the 1 m triangle corners of each 10 m triangle as groupings, while the 100 m spacing level used the 10 m triangle corners as groupings. Sites 1 and 2 were analyzed as individual sites and as a greater combined site.

Correlation plots were generated using the corrplot package in R and Spearman's rank correlation coefficients were calculated. Sequencing reads were scaled to remove the least abundant amplicon sequencing variants (ASVs), and correlations between Phylum abundance and dsDNA content, bacterial rRNA gene copies, moisture content, and grain size were determined. Phyla demonstrating a positive or negative correlation with a parameter and a *p*-value less than 0.1 were included in a correlation plot. Correlations were also determined among dsDNA content, bacterial rRNA gene copies, moisture content, and grain size and presented in a separate correlation plot.

RESULTS

Data compiled into nine bar graphs representing bacterial rRNA gene copies, dsDNA content, and gravimetric moisture content at groupings of 0.1 m, 1 m, and 10 m are shown (Figure 3). The difference in biological characteristics between samples was quantified at each spatial separation using pairwise *t*-tests and *u*-tests to compare the within-group means and medians respectively. Two 100 m triangles separated by 1 km were sampled and analyzed as a single site. The two triangles were also considered as individual sites to distinguish trends at a smaller scale (Table 1).

Analysis of Combined Sites

As a combined site, variation was observed primarily at scales of 10 m and 100 m. For dsDNA content, both the *t*-test and *u*-test showed some statistical differences at the 100 m and 10 m levels. At 100 m and 10 m spacing, 16-33% of pairwise comparisons were statistically significantly different, while all comparisons between groups separated by 1 m were statistically similar. For bacterial rRNA gene copies and gravimetric moisture content, statistical differences between some sample sets separated by 10 m were observed, but not by 100 m. Both statistical tests revealed that in only 11% of comparisons between sample sets separated by 10 m were bacterial rRNA gene copies statistically different, and in 28% of comparisons between sample sets separated by 10 m was moisture content statistically different. Less than 2% of comparisons between sample sets separated by 1 m were considered statistically different.

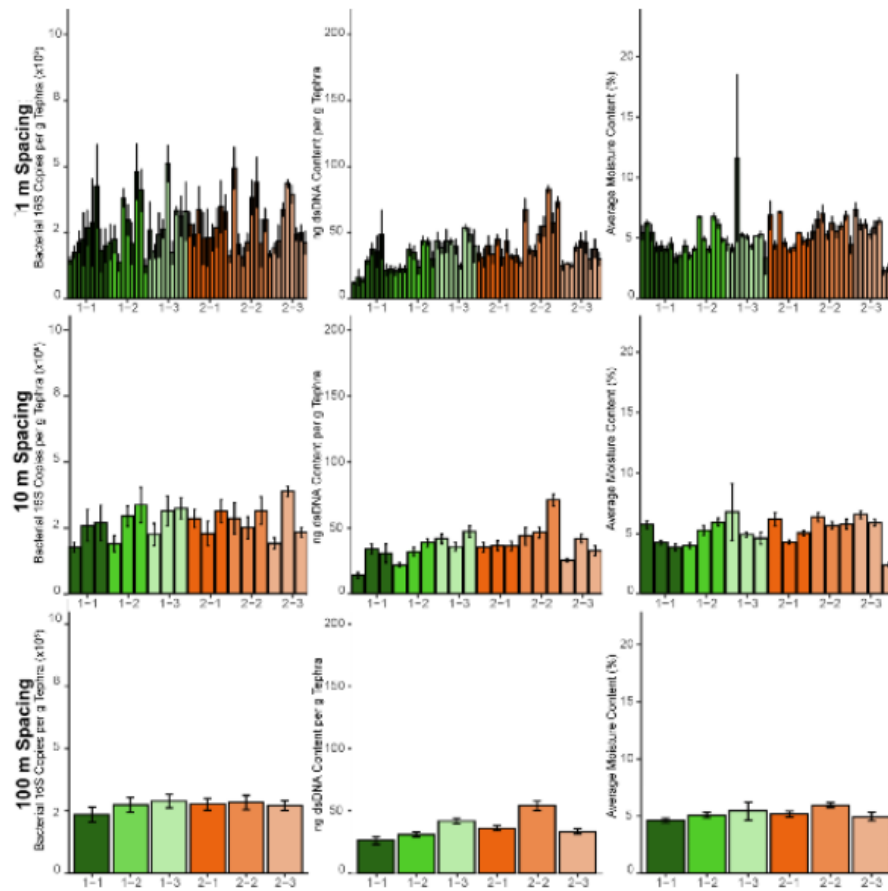


Figure 3. Dyngjusandur Characteristic Measurements. 16S rRNA gene copies, dsDNA content, and gravimetric moisture content at spatial distributions of 100 m, 10 m, and 1 m. D1 (green) and D2 (orange) are separated by 1 km and the shades of their respective colors represent the groups separated by 100 m. Three sub-samples of each sample at 1 m spacing were analyzed, thus error bars represent the heterogeneity of the sample. The measurements at the 1 m spacing were combined to yield the data presented for 10 m and 100 m spacing.

Table 1. Comparison of Differences Between Nested Triangles at Each Spatial Scale using Two Quantitative Tests

	Pairwise <i>t</i> -test			Pairwise Mann-Whitney <i>u</i> -test		
	Site 1			Site 1		
Separation	100 m	10 m	1 m	100 m	10 m	1 m
DNA Content	67%	22%	3.7%	67%	33%	0.0%
16S Gene Copies	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
% Moisture	0.0%	44%	3.7%	0.0%	44%	0.0%
	Site 2			Site 2		
	100 m	10 m	1 m	100 m	10 m	1 m

DNA Content	67%	33%	0.0%	67%	33%	0.0%
16S Gene Copies	0.0%	22%	0.0%	0.0%	22%	0.0%
% Moisture	0.0%	33%	0.0%	33%	22%	0.0%

*The table represents the percentage of comparisons between the triplicate measurements at each spatial scale that were statistically different from each other. A comparison was considered statistically different with $0.05 \geq p$.

Analysis of Individual Sites

Sites D1 and D2, which refer to the two 100 m triangles that were separated by 1 km, were analyzed individually (Table 1). In both sites, the 1 m scale showed less than 4% significant variation across each metric of measure based on the *t*-test and no statistically different comparisons based on the *u*-test. At the 10 m scale, the percentage of significant differences ranged from 22-44% when considering both tests for each metric except for 16S rRNA gene copies for Site 1, which showed no statistically significant differences between groupings. Only dsDNA content showed statistically significant differences at the 100 m level, with 67% different comparisons when comparing means and medians.

Variation at the 10 m scale ranged from 33-67% for each metric. Both tests showed no significant difference in comparisons at the 100 m scale for 16S rRNA gene copies, while gravimetric moisture content saw 33% significantly different comparisons at the 100 m scale based on medians in the *u*-test for Site 2. For both sites, dsDNA content demonstrated nearly the same percentage of statistically significant comparisons at each separation distance and for both pairwise tests.

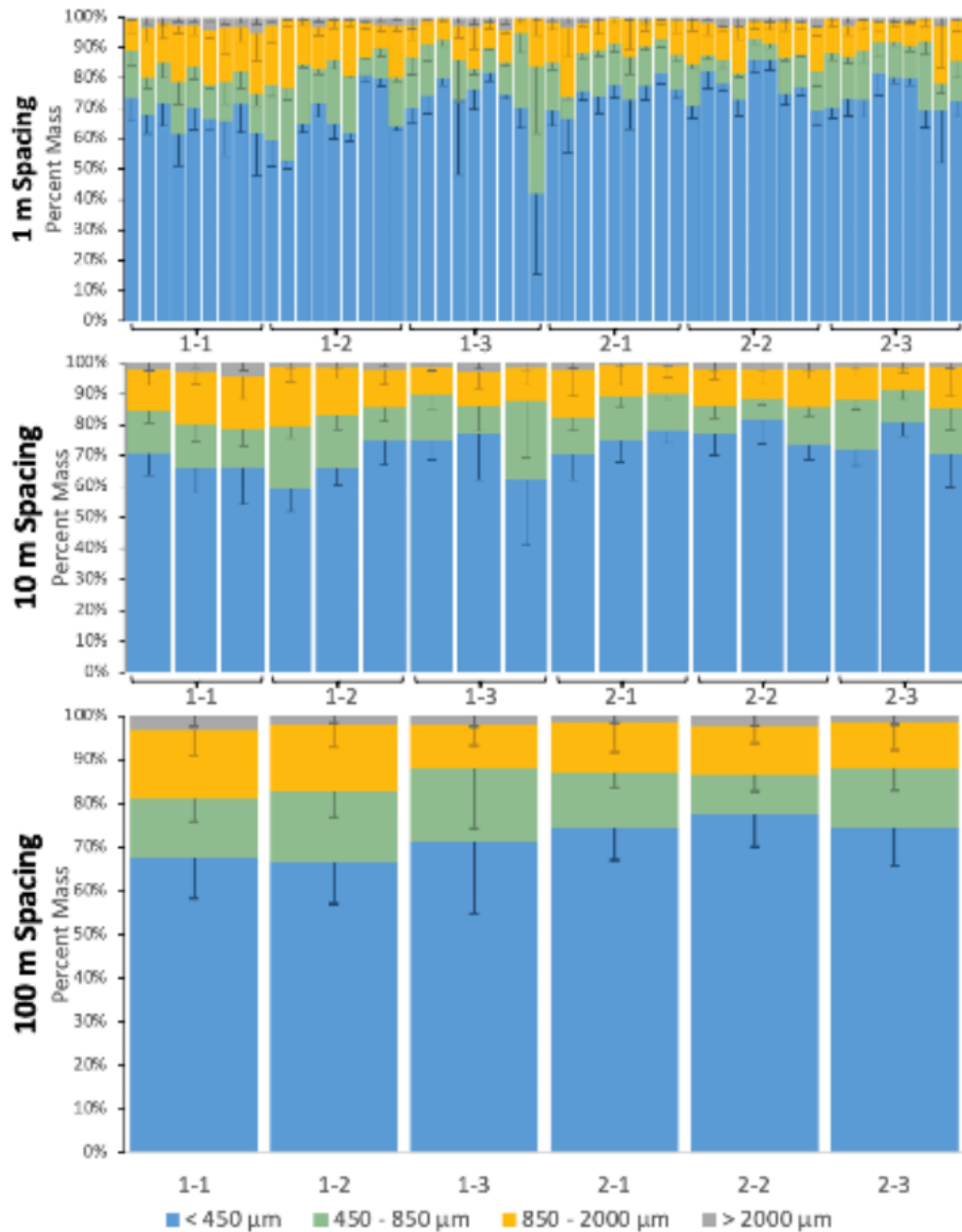


Figure 4. Dyngjusandur Grain Size Measurements. The grain sizes are represented as the percentage of total mass at spatial distributions of 100 m, 10 m, and 1 m. Three sub-samples of each sample at 1 m spacing were analyzed, thus error bars represent the heterogeneity of the sample. The measurements at the 1 m spacing were combined to yield the data presented for 10 m and 100 m spacing.

Correlations with Grain Size

343 Across all samples, the greatest proportion of each were grains less than 450 μm (dust),
344 with mid-sized grains (larger than 850 μm and 450 μm) representing the next most abundant
345 interval. Very little large sediment (larger than 2000 μm) was observed in all samples. The
346 percentage of each division by mass was compared with each sample's respective DNA content,
347 bacterial rRNA gene copies, and moisture content as seen in Figure 4. Across both sites, the grain
348 size fraction greater than 2000 μm represented an average of 1.96% ($\pm 1.62\%$ standard deviation)
349 per sample. The fraction ranging from 850-2000 μm represented an average of 12.29% ($\pm 5.85\%$
350 standard deviation) of each sample, while the fraction ranging from 425-850 μm represented an
351 average of 13.57% ($\pm 7.26\%$ standard deviation) of each sample. Finally, the fraction less than 425
352 μm was an average of 71.62% ($\pm 10.32\%$ standard deviation) of each sample (Figure 4).

353 To determine the relationship of each grain size to DNA content, bacterial rRNA gene
354 copies, and moisture content, a correlation matrix was made (Figure 5). A 90% confidence interval
355 was used to determine the significance of correlations and revealed that larger sediment was
356 inversely correlated with moisture content, bacterial rRNA gene copies, and dsDNA content. Both
357 16S rRNA gene copies and dsDNA content were strongly positively correlated, and a weak
358 positive correlation was observed between moisture content and dsDNA content. All three
359 variables, moisture, dsDNA, and 16S rRNA gene copies showed positive correlations with the dust
360 grain size fraction, and weak negative correlations with the mid-sized sediment fractions. The mid-
361 sized sediment fractions unsurprisingly displayed a strong negative correlation with the smallest
362 sediment size, and the grain size fraction between 850 - 2000 μm was positively correlated with
363 the largest sediment.

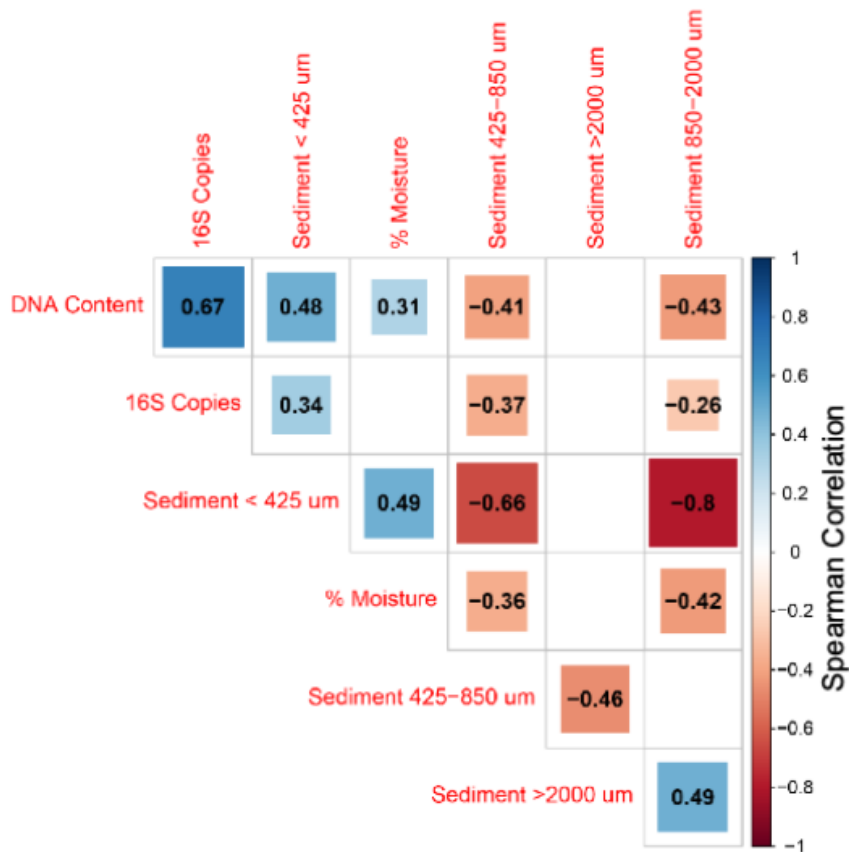


Figure 5. Spearman correlations between bacterial rRNA gene copies, dsDNA content, moisture content, and grain size. Blue represents positive correlations with 1 being the strongest, while red represents an inverse correlation with -1 being the strongest. Correlation coefficients are overlayed for statistically significant correlations, based on a 90% confidence interval. Empty boxes represent a lack of statistical significance.

Depth Profile: Biosignatures and Correlations

The 16S rRNA gene copies, dsDNA content, and gravimetric moisture content are shown in the samples taken at depths of 1 – 7 cm (Figure 6). Both DNA content and moisture content follow a similar trend of increasing beyond a depth of 1 cm. This trend is likely observed among the 16S rRNA gene copy data as well; however, the significance of the trend is questionable given the larger heterogeneity of these samples for this parameter. The difference in variation between the 16S rRNA gene copies and the dsDNA concentrations may be due to a significant portion of the dsDNA belonging to eukaryotic organisms, a DNA-phage community pressuring the bacterial community, or an artifact of the different measurements, since the proportion of 16S rRNA gene copies to total dsDNA tends to vary widely within microorganisms even of the same genus.⁵⁰ A large increase in DNA content is observed between the samples at depths of 2 cm and 3 cm, ~15 ng/g of DNA to ~30 ng/g, and the remaining samples never fall below 20 ng/g. Moisture content fluctuates but remains close to 5% at depths 2 cm and below. While the heterogeneity in 16S rRNA bacterial gene copies obscures trends, the deepest sample (7 cm) has the highest average number of copies of all the depth profile samples and is statistically different from samples taken in the top

4 cm. Samples taken from the top 2 cm were statistically different from the deepest sample based on a *t*-test comparison (*p*-value = 0.002), while samples taken from a depth of 3-4 cm were also significantly different with a slightly higher *p*-value (*p*-value = 0.02).

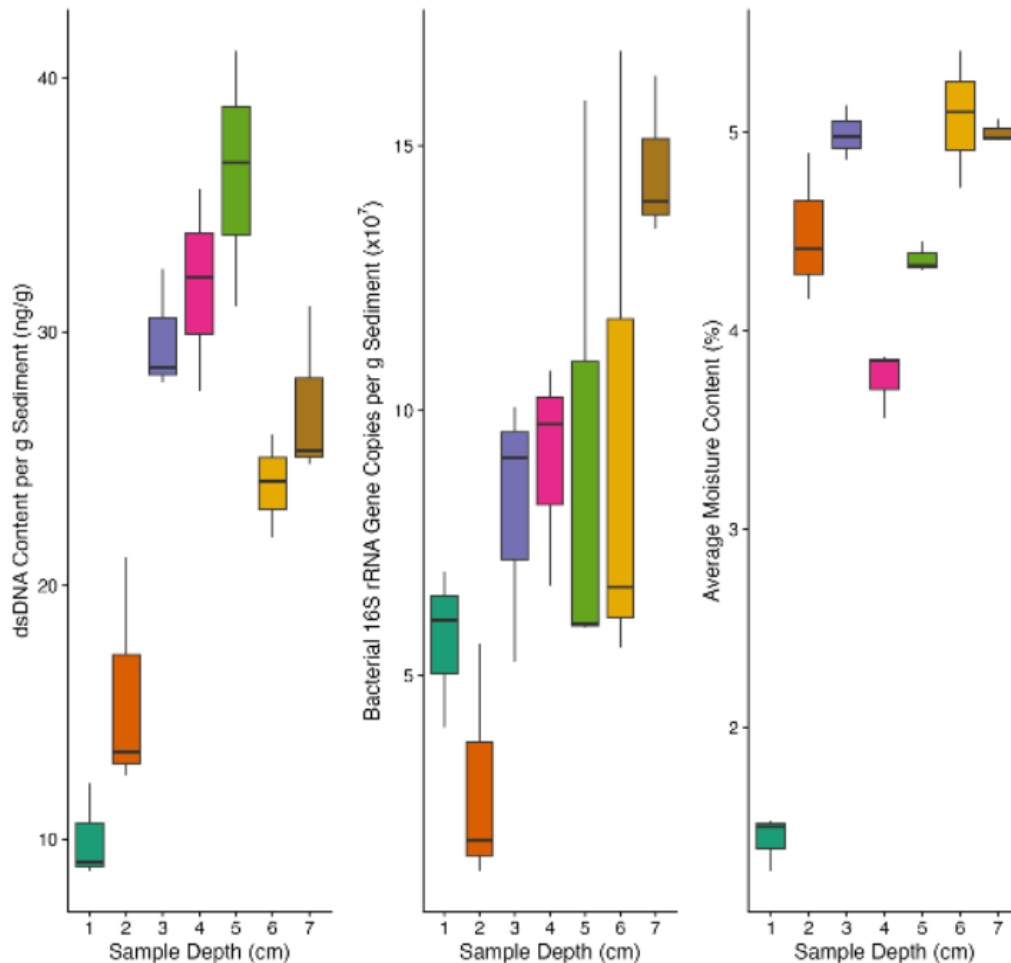


Figure 6. Dyngjusandur Depth Profile Measurements. *DNA content, 16S rRNA gene copies, and gravimetric moisture content from samples recovered from depths of 1-7 cm. Samples were taken in 1 cm increments. Triplicate sub-samples were analyzed for each data point.*

Grain size fractions followed a similar trend to the samples taken at varying spatial scales. The largest sediment (> 2000 μm) made up the smallest fraction of each sample, while the mid-sized sediment fractions (850-2000 μm and 425-850 μm) made up less than 25% of the samples respectively. The largest sediment fraction was made up of the smallest sediment (< 425 μm), with 50% composition across each sample.

Correlations were performed between the biosignature variables, moisture content, and grain size (Figure 7), and DNA content was shown to have a strong negative correlation with the largest sediment sizes. No other significant correlations were observed.

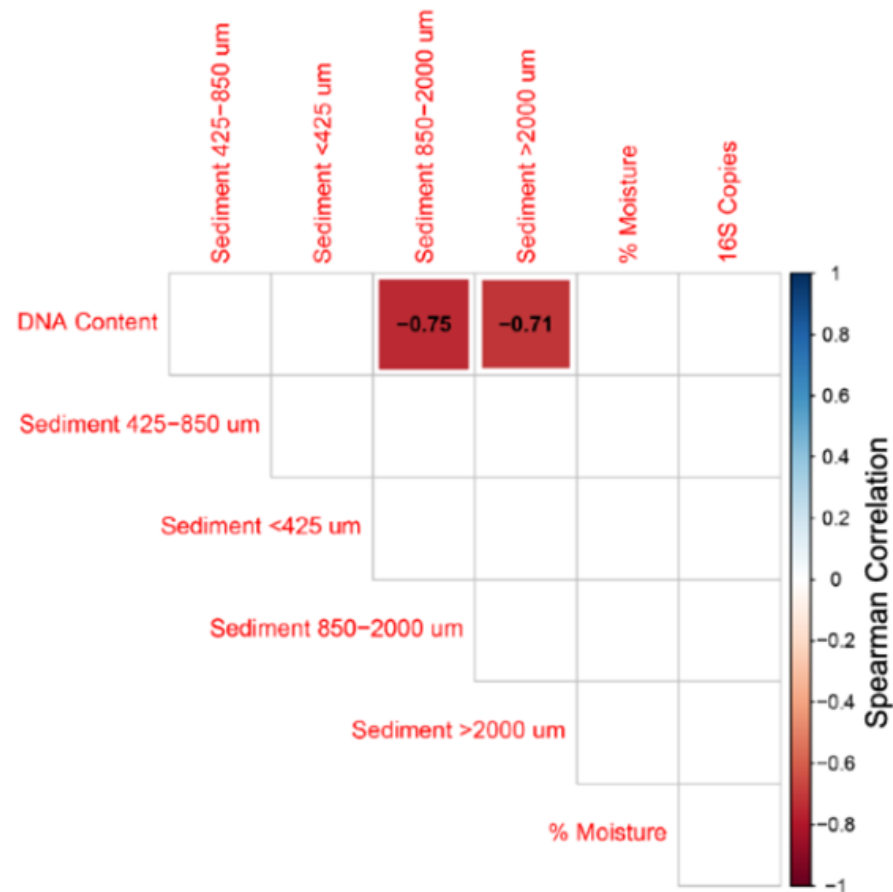


Figure 7. Depth Profile Spearman correlations between bacterial rRNA gene copies, dsDNA content, moisture content, and grain size. Blue represents positive correlations with 1 being the strongest, while red represents inverse correlation with -1 being the strongest. Correlation coefficients are overlaid for statistically significant correlations, based on a 90% confidence interval. Empty boxes represent a lack of statistical significance.

16S rRNA Gene Amplicon Sequencing

After processing, 4465 ASVs representing putative individual bacterial or archaeal species were uncovered across all samples, and all phyla representing less than 1% of the total abundance were grouped together (Figure 8). Eleven phyla with abundances greater than 1% were observed in the nine samples: Acidobacteriota, Actinobacteriota, Bacteroidota, Bdellovibrionota, Chloroflexi, Gemmatimonadota, Myxococcota, Patescibacteria, Plantomycetota, Proteobacteria, and Verrucomicrobiota. Of the abundant phyla, Actinobacteria, Proteobacteria, and Acidobacteria each had an average abundance greater than 10%, with shares of 37%, 23%, and 13% respectively.

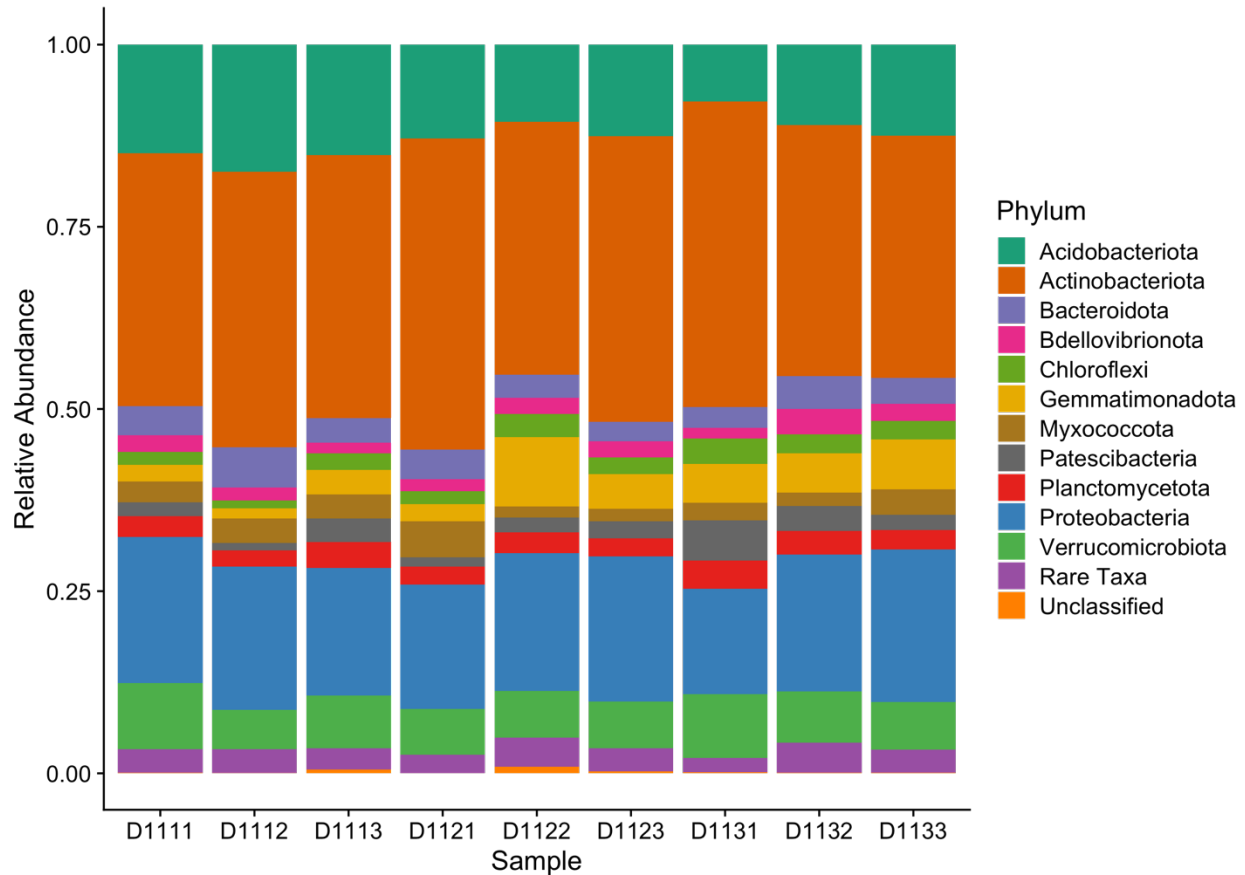


Figure 8. Abundant Sequences in Dyngjusandur Samples. Sequencing results from one sample from each 1 m triangular grid from Site D1, representing the phyla with greater than 1% abundance. Of the eleven most abundant phyla, Actinobacteriota, Proteobacteria, and Acidobacteriota each accounted for more than 10% of the total population.

While the most abundant phyla have mostly consistent relative abundances, the minor phyla show more variation. This is particularly evident in Gemmatimonadota, Myxococcota, and Patescibacteria, which change significantly in relative abundance for each sample. Of course, examining the phyla does not capture the diversity of the ASVs, since those are a much more specific taxonomic classification, so to examine variability in the ASVs, three alpha diversity metrics were calculated for each of the three groups separated by 10 m (Figure 9).

Overall, observed diversity, which is the total number of ASVs, closely follows the trend identified by the Chao diversity metric, which gives more weight to the singletons and doubletons, or ASVs that are only found once or twice in the samples. While the trends are similar, Chao diversity metrics are much higher overall, indicating there are many ASVs that were found in very low abundance. However, all groups are statistically similar to each other for the Observed and Chao diversity metrics. For Shannon diversity, groups 2 and 3 are statistically significantly different from each other (p -value = 0.046), indicating that the richness and evenness of the ASVs is higher in group 3 than group 2.

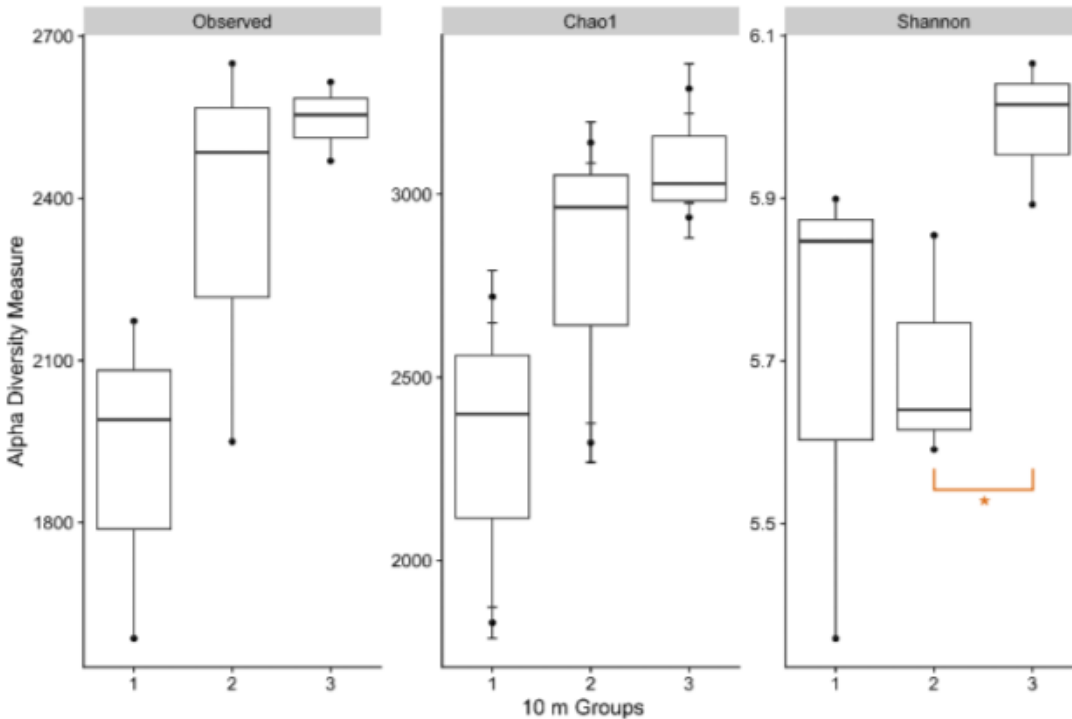


Figure 9. Alpha Diversity at Dynjgusandur. Three alpha diversity metrics were used to provide comparisons for the total number of ASVs (Observed), the number of rare ASVs (Chao1), and the richness and evenness of the samples (Shannon). The * indicates two groups are statistically significantly different (p -value < 0.05) from each other.

Sequencing Correlations

Correlations were observed between phylum abundance and dsDNA content, bacterial rRNA gene copies, gravimetric moisture content, and grain size (Figure 6). A strong positive correlation was observed between 16S rRNA gene copies and Patescibacteria and a weak positive correlation was observed between DNA content and Cyanobacteria. Rokubacteria had negative correlations with both moisture content and DNA content. However, the smaller grain size fractions demonstrated the strongest correlations with the abundances of sequences from different phyla. The sediment fraction smaller than 850 μ m and larger than 450 μ m demonstrated strong positive correlations with Acidobacteria, Armatimonadetes, and Abditibacteriota, and strong negative correlations with Chloroflexi, Cyanobacteria, Gemmatimonadetes, and Patescibacteria. The finest sediment size fraction, less than 450 μ m, showed a strong positive correlation with Cyanobacteria, and strong negative correlations with Rokubacteria and Actinobacteria.

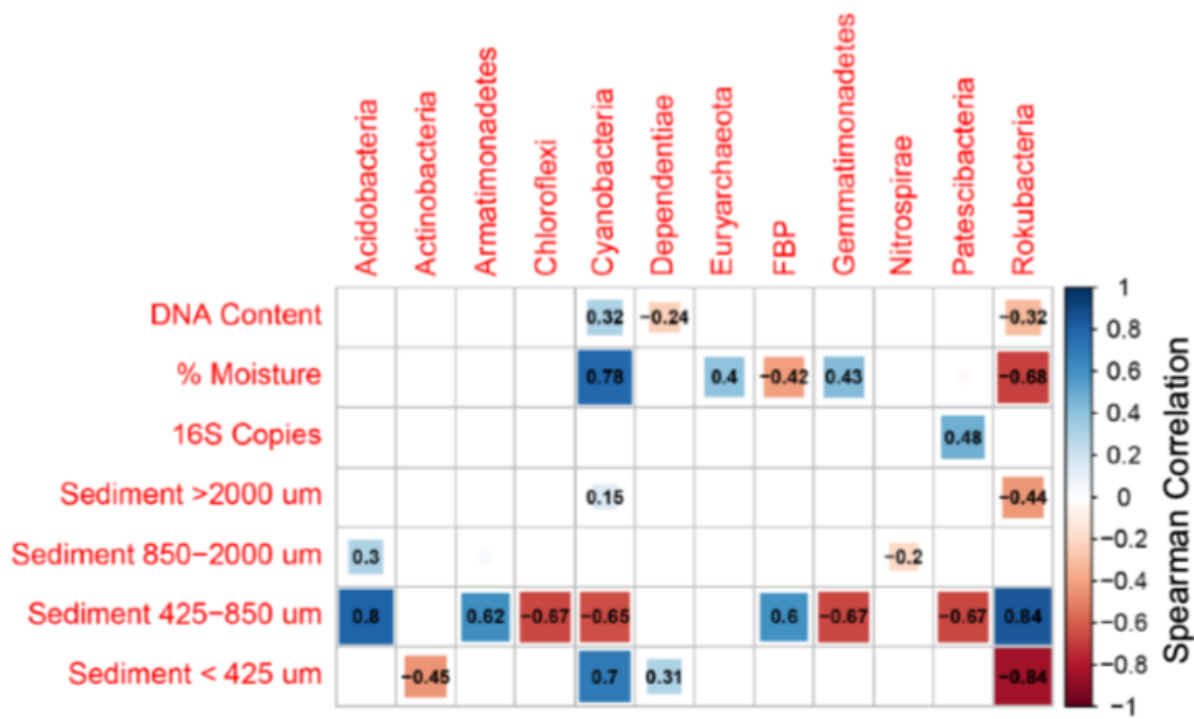


Figure 9. Spearman correlations between phyla and primary measures. Phyla demonstrating a significant correlation (p -value less than 0.1) with dsDNA content, bacterial rRNA gene copies, moisture content, or grain size were included in the plot above. Shades of blue represent a positive correlation with 1 being the strongest, and shades of red represent a negative correlation with -1 being the strongest. Correlation coefficients are overlaid for statistically significant correlations, based on a 90% confidence interval. Empty boxes represent a lack of statistical significance.

DISCUSSION

Spatial Influences

Characterizing the impacts of spatial scale and environmental factors on bulk biomass is a key step towards understanding how biosignatures may be distributed at Mars analog sites. These results suggest that visually homogenous sampling sites can vary dramatically in biosignature and geochemical measurements at different spatial scales (Figure 1). Across both D1 and D2, the smallest grouping, 1 m, yielded less than 5% statistically different comparisons for each metric. Comparing 1 m triangles separated by 10 m, however, resulted in 22-44% statistically different comparisons for D1, and 22-33% comparisons for D2. The pairwise t -tests and u -tests were consistent for all sets of comparisons except for moisture content at D2 with 100 m separation. These tests were selected to determine if two sets of samples that are separated at a certain distance have significantly different characteristics. Each test has a different underlying assumption about the distribution of the data; the Welch's t -test assumes there is a normal distribution of the data, while the Mann-Whitney u -test does not use this assumption. This sample set has insufficient data points to determine whether the distribution is normal, so both tests are used. The differences

between the two tests at 100 m separation most likely indicates that the underlying population of biosignatures is not normally distributed at this scale. This is not unexpected and highlights the need to understand the assumptions underlying different statistical models and to test them when possible.²⁵ This data suggests that distributions in environmental data should not be assumed to be normal and that, when possible, sampling in triplicate at close scales (within a region that would be considered “identical”) to assess the heterogeneity of a site should be performed.

The larger percentage of significant differences at the 10 m grouping compared to the other spatial scales points toward environmental shifts influencing biosignature measurements when moving beyond the relative closeness of the 1 m scale. The 10 m scale was found to exhibit significant variability in geochemical analyses in a companion paper,²² strengthening the conclusion that sampling at larger distances would not capture sufficient variability to characterize the site. While the geochemical differences may have influenced the significant differences in biosignature measurements seen here, the companion paper addressed Icelandic sites beyond just Dyngjúsandur, suggesting the environmental variability found here is not unique to this location.²²

A positive correlation between dsDNA content and moisture content was observed, which may suggest that moisture content is an influencing factor for this microbial distribution, but the rain prior to sampling makes this conclusion tenuous. A significant positive correlation between 16S rRNA gene copies and dust and negative correlations with the mid-sized sediment fractions are observed, indicating the influence of grain size on the community (Figure 4). Similar correlations were also observed between moisture content and these grain size fractions, which is likely a result of a higher surface area for the water to adhere to in the smaller grain sizes. The finest grain size fractions appear to have the most significant impact on microbial colonization, while the large fractions demonstrate a negative trend for both biosignatures and moisture capacity, likely due to the smaller surface area on the large grains relative to their volume. This is consistent with literature that has found important relationships between microbes and the mineral surfaces that they colonize.¹² In general, different minerals have been shown to attract certain types of microbes due to the nutrients (iron, phosphorous, sodium, etc.) that can be extracted.¹² While few studies have examined the effects of grain size on microbial communities in a directly comparable way, overall trends indicate that the higher surface area associated with smaller grains should allow a greater number of microbes to colonize the minerals.¹²

Interestingly, the differences observed between groups of samples separated by 10 m were often not observed in groups separated by 100 m for both sites and both statistical tests. For D2, 16S rRNA gene copies show statistically significant differences in 22% of the comparisons made between the groups separated by 10 m, but there are no statistically significant differences between sample groups separated by 100 m. Similarly, there were statistically significant differences in gravimetric moisture content at D1 between groups separated by 10 m (44% of comparisons), but there are again no statistically significant differences between sample groups separated by 100 m. However, homogeneity was not a hard rule at the 100 m scale. For dsDNA content at both sites, the percentage of significantly different comparisons increased from 10 m to 100 m, changing from 22-33% to 67%. The magnitude of the percentage increase may be inflated due to the limited number of comparisons available at the 100 m scale (3 comparisons), but this highlights that one of three 10 m triangles at D1 had significantly more or less microbial colonization in comparison to its counterparts. This observation is maintained when considering the pairwise *t*-test results for

16S rRNA gene copies at both sites, which maintain 67% different comparisons from 10 m to 100 m, showing that a single 10 m triangle had significantly different microbial colonization than its neighboring corners. These cases suggest the importance of recovering a multitude of samples from a sampling site given that biomass can vary significantly even within a visibly homogenous environment. This observation is consistent with other work, which recommends at least 27 samples for three sets of triplicate collections at three locations with the same material.¹¹

Aeolian Resurfacing

Samples taken at depths several centimeters below the surface were shown to contain more dsDNA and 16S rRNA gene copies than samples taken closer to the surface (Figure 4). Given the consistent and frequent resurfacing of the Dyngjúsandur plains by wind action, sediment exhumed closer to the surface is likely to primarily contain organisms robust enough to withstand the turbulent conditions and resettling.⁵¹⁻⁵⁴ The heterogeneity observed for samples taken at depths of 5-6 cm may be due to a shift in community composition towards organisms less specialized for surviving in windy surface conditions, resulting in a higher variability in the qPCR measurements (Figure 5). Sequencing of these samples would provide greater insight into the shifts in community composition hinted at by this bulk biosignature data. While moisture content did not directly correlate to individual shifts in bulk biosignatures (Figure 5), moisture significantly increased after the first 1 cm of depth, mirroring the trends observed for the biosignatures quantified here. However, it did not increase above approximately 5%, which was consistent with the surface sediment samples recovered for the spatial study. There was likely not enough variation in the moisture content within these samples due to the precipitation shortly preceding sample collection. This may obscure trends, leading to the lack of significant correlations between moisture content and the other variables.

The grain size fractions recovered from the depth profile closely mirror the trends observed during the spatial study, with smaller grain sizes making up the bulk of each sample. Again, the largest grain size composed the smallest fraction of each sample. Correlation tests also suggest grain size continues to have an impact on bulk biomass, with DNA content showing strong negative correlations with the two largest sediment sizes. This trend could be influenced by the DNA extraction method, which uses bead tubes to disrupt the sample. It is possible this method is less efficient for larger grain sizes; however, the larger grain sizes may also provide less surface area for microbial growth, resulting in respectively diminished DNA content among these fractions.^{22, 55}

On the surface, moisture content and the small grain size fraction (425 – 800 μm) are inversely correlated (Figure 5), suggesting that small basalt grain sizes do not hold onto moisture well. However, the dust fraction (<425 μm) correlates positively with moisture content, implying that only grain sizes below 425 μm are small enough for basalt to begin retaining water at the surface. At depth, neither of these correlations are seen, which may be due to the smaller sample size of the depth profile or the fact that the recent weather phenomena caused water saturation at depth. Water content, bacterial rRNA gene copies, and dsDNA increase with depth but do not correlate significantly with each other. Since the phyla tend to have significant but opposite correlations with moisture content and the small grain size fraction at the surface (Figure 9), it's possible that trends among the phyla at depth are similar, but the lack of sequencing data obscures

trends between biological variables and the environmental variables. It's also possible that the likely saturation of the moisture content at depth due to the recent precipitation obscures trends between biomass and moisture content or the small grain size fractions that are normally there.

Microbial Community Impacts

The phyla uncovered from the D1 samples can provide a greater understanding of microbial distribution at the Dyngjusandur alluvial plane. At D1, clear variation is observed at the 10 m scale for dsDNA content and 16S rRNA gene copies, and interrogating the 100 m grouping reveals one of the corner 10 m triangles (D1-1) to have significantly less dsDNA content than its counterparts. Despite differences in these measurements, amplicon sequencing suggests that the community across D1 is relatively homogenous, with the same three phyla (Proteobacteria, Acidobacteria, and Actinobacteria) comprising over 70% of the community of each sample on average (Figure 8) and only one diversity metric (Shannon) revealing significantly different diversity between two of the 10 m groups (D1-2 and D1-3). Searching for correlations between biosignature measurements and phyla revealed few strong correlations. DNA content showed a positive correlation with Cyanobacteria, and negative correlations with Dependitiae and Rokubacteria. Moisture content showed a strong positive correlation with Cyanobacteria and a strong negative correlation with Rokubacteria.

Here, however, the impact of grain size fractions on microbial abundance is most pronounced, with the fraction between 425-850 μm showing both strong positive and negative correlations with several phyla. Positive correlations observed with this fraction include Acidobacteria, Armatimonadetes, Abditibacteriota, and Rokubacteria, and negative correlations were observed between Chloroflexi, Cyanobacteria, Gemmatimonadetes, and Patescibacteria. The importance of the 425-850 μm fraction was also documented in another FELDSPAR publication by Rader et al., finding that the rarer microorganisms were influenced by shifts in the abundance of this fraction in addition to mineral characteristics.²³ Previous studies, as noted by Rader et al., suggest that surface qualities of the sediment, such as concave areas and crevices, could provide protective environment from weathering, while other factors such as water retention, porosity, and mineral availability may also be influential.^{54, 56, 57} The grain size fraction less than 450 μm showed negative correlations with Actinobacteria and Rokubacteria, and a positive correlation with Cyanobacteria. The contrasting correlations displayed by these fractions is unsurprising given the strong negative correlation these fractions shared, but it suggests that the grain size of a sampling site could play a critical role in predicting the types of organisms in a sample. Even when bulk biomass fails to distinguish two sites, community composition may be variable, which could be predicted by grain size distribution.

Analyses of bacterial abundances or diversity as they correlate with grain size in Martian analog sites are rare, but the localization of cells on specific minerals has been observed. In basaltic glass samples, cell abundances were significantly greater on weathered palagonite surfaces; the unweathered glass had very few cells associated with it.⁵⁸ Obsidian glass, which weathers less readily, showed abundant microbial growth only on altered regions, specifically iron oxide crystals.⁵⁸ These localized biofilms were unique to areas where water could come in contact with the rock: the exposed or weathered regions.⁵⁸ This implies that volcanic rocks which have undergone greater weathering, which are often associated with smaller grain sizes, are more

suitable for microbial colonization. The tendency of certain taxa to colonize specific minerals has also been observed, which may indicate that the correlations observed between the phyla and grain sizes here are caused by the inclination of each of these phyla to colonize specific minerals that may be exposed or partitioned differently between each grain size.¹²

The environmental variables that correlate most often and strongly with the phyla are moisture content and the small grain size fraction (425 – 800 μm) data (Figure 9). The phyla that are correlated with the most measured environmental variables here are Cyanobacteria and Rokubacteria, which have an opposite relationship with the small grain size fraction and moisture content data. To explore this relationship, a few key traits for each phylum are outlined briefly here.

Rokubacteria are significantly inversely correlated with moisture content, DNA content, the large grain size fraction ($> 2000 \mu\text{m}$) and the dust fraction. Their only significant positive correlation is with the small grain size fraction. Rokubacteria is a relatively new phylum, so not much is known about it, but thus far the members of this phylum have been found in a wide variety of terrestrial samples and contain mixotrophic metabolisms.⁵⁹ Rokubacteria appear to have diverse metabolic pathways, many of which are associated with synthesizing secondary metabolites, and significant genetic variation among members of the phylum.^{59, 60} Within an agricultural setting, significant positive correlations between Rokubacteria and nitrogen and phosphorus imply that the phylum is able to increase concentrations or quality of those essential nutrients.⁶⁰ Combined with the positive correlation between the small grain sizes in this data, it's possible the secondary metabolites are used to chelate and extract various nutrients (phosphorus, iron, other metals) from the rocks with weathered surfaces, but not the dust fraction which may have lost most of its valuable nutrients.

In contrast, Cyanobacteria are significantly positively correlated with moisture content, DNA content, the large grain size fraction, and the dust fraction, and they have a significant negative correlation with the small grain size fraction. This phylum is much better understood in the literature and is thought to be the first photosynthetic organism which initiated the Great Oxidation Event.⁶¹ Since Cyanobacteria are often found in marine samples, it's possible the strong correlations with dust and water content are related to its familiarity with or even preference for aqueous environments, though this phylum is also very diverse and found frequently in terrestrial environments.^{61, 62} Cyanobacteria are phototrophic organisms,⁶² so it's also possible the correlations with the grain size fractions are related to the grains' exposure to sunlight. Dyngjúsandur is very windy, so the dust fraction is often subject to aeolian resurfacing and would therefore receive more sunlight than heavier fractions. The large grain size fraction has a weak, but significant correlation with Cyanobacteria, which could be explained by the bacteria colonizing the exposed surface of the large grains.

Implications for Astrobiology and Site Selection

Analyzing the microbiota and raw biomass of planetary analog environments with respect to geophysical characteristics and spatial scale provides critical characterization for future extraterrestrial missions in search of life and for further terrestrial field studies. Missions like the Mars 2020 Perseverance Rover and campaigns to remote terrestrial environments are limited in

their sampling capacity, and this work presents important insight into necessary considerations for producing a sampling strategy for these missions. These results suggest that sample separation, grain size fractions, and depth are important factors for identifying bulk biomass on an otherwise visually homogenous plain.

Sampling Dyngjúsandur at 1 m of separation yielded few significantly different comparisons among moisture, dsDNA content, and 16S rRNA gene copies, suggesting a higher degree of homogeneity as samples sharing such close clustering. However, comparing these samples with those collected 10 m away yielded a much higher percentage of significant comparisons, while sampling at 100 m separation saw these differences mostly averaged out. The two sampling sites were compared, 1 km of separation, and both *t*-test and *u*-test showed statistically significant comparisons. These results imply an ideal separation range for sample gathering with site characterization in mind. Spatially tight clusters (sub 1 m) provide little characterization of a larger sampling site, while clusters separated by longer distances (10 m) covered a greater diversity of bulk biomass, 16S rRNA gene copies, and moisture measures represented by the high percentage of statistically significant comparisons. The lack of variability among samples separated by 100 m suggests that a rough characterization of a site's biomass may be possible with a smaller set of samples, although the finer details of a site, like geophysical relationships, will be lost without more comprehensive sampling.

The aeolian action at Dyngjúsandur likely amplifies the impacts of sample depth on bulk biomass due to the near constant turnover of the top layers of sediment. The depth profile analysis shows significant differences between the top levels of sediment and the bottom levels when comparing dsDNA content. This result supports the hypothesis that upper levels of sediment are composed of a unique selection of the native biodiversity, primarily organisms robust enough to survive frequent weathering. This observation has implications for future Mars missions, an extraterrestrial target home to sediment storms like those observed at Dyngjúsandur, and where sampling at depth has long been postulated to be highly important.⁶³ At Dyngjúsandur, the majority of biomass was observed at depths of 3 cm and below. In comparison, Mars has additional factors influencing the anticipated depth profile of potential biosignatures, including persistent exposure to ionizing radiation, likely increasing optimal sampling depth significantly.⁶⁴⁻⁶⁶ To optimize for preservation of organics and reduce UV radiation, a sampling depth of 5 cm has been previously suggested.³² Sequencing of the Dyngjúsandur samples would provide valuable details about shifts in community composition with respect to sediment depth, and additional geochemical measurements taken for each sample, such as pH, total organic carbon, and total nitrogen, would rigorously characterize the influence of environmental factors on life in Mars analog samples.

Despite this work focusing on terrestrial biosignatures, we do not necessarily expect potential extraterrestrial life to conform to our traditional understanding of Earth-based biology. Rather, this work characterizes the qualities life adopts under extreme environmental pressures and the factors that must be considered when establishing an extraterrestrial or terrestrial sampling plan. Microbial association with the geophysical parameters analyzed here is most frequently statistically significant when looking at Spearman correlations between taxa prevalence and the abundance of smaller grain sizes. This association between taxa and smaller grain sizes could be due to the increased surface area-to-volume ratio, which may impact mineral fractionation, mineral exposure, and porosity. Therefore, smaller sediment fractions should be prioritized when sampling

from regions like Dyngjúsandur. Spatial sampling has revealed that significant variation in biomass within visually homogenous sites occurs at the 10 m scale, so the most thorough characterization of a site would require sampling within 10 m separation. Sampling at depth is also recommended in barren, windy environments, as biosignatures are more abundant at least 3 cm below the surface. Therefore, based on this data, ideal sampling in visually homogenous alluvial extraterrestrial plains may be best at separations of 10 m, at depths of greater than 3 cm, and with focus on the smaller grain size fractions. While this proposed sampling scheme may be unrealistically resource-intensive for some Martian instrument suites, enhanced spatial sampling with less resource-intensive instruments could inform those with fewer available analyses.

Conclusions

Generally, systematic sampling at extraterrestrial environments has been neglected in favor of seeking visually interesting samples. While this is efficient and minimizes the collection of “repeat” measurements from similar samples, geophysical and biological heterogeneity at Dyngjúsandur, Iceland has shown significant geophysical and biological variation within visually similar samples. Since Dyngjúsandur is an alluvial plain analogous to regions on Mars, extraterrestrial sampling can be informed by these findings. Systematic spatial sampling that accounts for significant variation at the 10 m scale is recommended, when possible, for organic and geophysical analyses, and biosignatures should be sought among smaller grain sizes at depth. The alluvial plains on Earth may not reveal what can be found on Mars, but the trends identified at this analog site can be used to inform sampling schemes designed to fully characterize regions or locate biosignatures on our neighboring planet.

AUTHOR DISCLOSURE & CONFIRMATION

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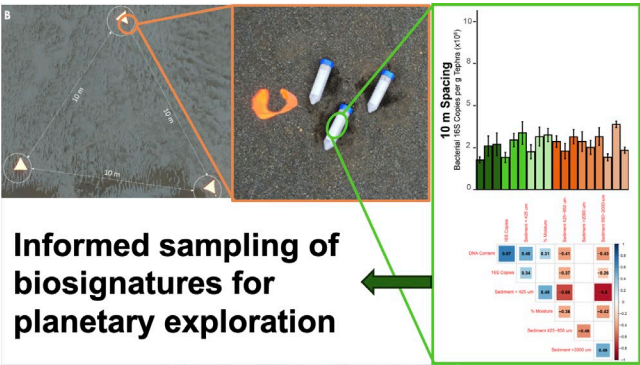
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Microbial population and distribution at a Mars Analog Alluvial Plain in Dyngjúsandur, Iceland

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