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模拟升温对冰川前缘地微生物种群的影响

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摘要: 由于全球变暖影响, 冰川处于不断退缩状态. 本研究以天山乌鲁木齐河源 1 号冰川前缘地 3 个不同退缩年代的土样为研究对象, 设置 2 个温度处理, 分别为 5°C 与 15°C, 通过 150d 室内培养实验, 探讨升温对冰川前缘地微生物种群的影响. 结果表明, 在原始样品中, 随土壤样品退缩年代的增加, 土壤总碳氮含量增加, 微生物的数量及 α 多样性增加. 150d 培养实验结果表明: 细菌、古菌拷贝数随升温发生变化, 但改变未达显著水平. 此外, 升温改变微生物群落结构, 且对不同样点微生物群落结构影响不同. 通过对升温后变化显著的优势 OTUs 进行分析, 退缩年代较短的样点对升温响应更为明显, 主要表现为 *Thiobacillus* 属相对丰度的升高. 结果表明, 冰川前缘地微生物对变暖响应的土壤异质性, 其结果可为高山冰川地区升温下微生物的特征变化提供参考信息.

关键词: 冰川前缘; 微生物群落; 升温; 微宇宙; 高通量测序

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Effect of Simulated Warming on Microbial Community in Glacier Forefield

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Abstract: Glaciers are constantly retreating because of global warming. In this study, three soil samples along the forefield of Urumqi Glacier No. 1 were collected. The effects of warming on the microbial community in the glacier forefield were investigated through a 150-day laboratory experiment. In this experiment, two temperature treatments were performed at 5°C and 15°C. The results showed that with increasing deglaciation age, the concentrations of carbon and nitrogen increased and the abundance and alpha diversity of microbial communities increased in the original samples. The 150-day laboratory experiment indicated that warming insignificantly changed the copy number of archaea and bacteria. Furthermore, it changed the microbial community composition, and the changes varied in different sampling sites. Based on the analysis of abundant OTUs changing significantly with warming, the sampling sites with shorter deglaciation age had stronger response with warming, representing an increase in the abundance of genus *Thiobacillus*. Furthermore, these results revealed that warming caused different effects on microbes along glacier forefield and thus, it could provide important characteristics of the microbial community with warming in alpine glacier regions.

Key words: glacier forefield; microbial community; warming; microcosm; high-throughput sequencing

自 1880 ~ 2012 年, 全球平均气温已上升 0.85°C, 这种升温趋势将持续下去^[1]. 冰川是对温度变化的敏感区, 变暖进程直接导致冰川消融, 径流量增加, 海平面上升等一系列现象. 冰川覆盖 10% 的陆地面积, 储存全球 70% 的淡水, 蕴藏着巨大的生物资源, 是全球生物圈的重要生态系统之一^[2-4]. 全球变暖条件下, 高山冰川不断退缩, 新暴露的土壤及微生物使冰川前缘地成为研究微生物原生演替及物质循环的理想实验地^[5-7].

已有研究主要集中在随冰川退缩年代改变的生物及非生物因子的变化. 微生物作为冰川地区的先锋生物, 促进土壤的发育, 积极参与碳氮等元素的生物地球化学循环, 并为后续植物的生长提供物质基础^[8]. 目前已发现 Proteobacteria、Bacteroidetes、Actinobacteria、Acidobacteria 及 Cyanobacteria 等微生

物广泛存在于冰川前缘地中^[6,9-11]. 有研究表明, 随着退缩年代的增加, 土壤碳氮含量增加, 植被覆盖率上升, 土壤 pH 值下降, 微生物生物量及多样性增加^[6,12]. 同时, 微生物群落结构发生变化, 优势种群的相对丰度改变^[13]. 由于全球变暖导致的土壤温度的升高能够通过改变微生物影响碳元素循环过程, 进一步诱导土壤中碳素释放至大气中^[14-16]. 因此, 研究升温条件下冰川前缘地微生物群落的变化特征对于理解碳反馈过程具有重要意义.

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在本文中以天山一号冰川前缘地为研究对象,采集不同退缩年代的土壤,以高通量测序及荧光定量技术对冰川前缘地微生物种类和数量进行分析。同时,设置两个不同温度,通过揭示升温条件下土壤微生物群落组成及其变化规律,以期为科学评价升温过程中微生物的变化提供参考,这对于了解和预测未来冰川前缘地生态系统将如何发展是十分必要的。

1 材料与方法

1.1 采样地概况及样品采集

天山乌鲁木齐河源 1 号冰川(天山 1 号冰川, 43°07'N, 86°48'E)位于新疆维吾尔自治区乌鲁木齐县境内,是天山中段北坡干旱地区的固体水库、绿洲摇篮及生产、生活的主要水资源之一。其平均年降水量及年均温分别为 478.1 mm 及 -4.7℃。

2017 年 11 月,在天山 1 号冰川西支前缘地采集土壤样品(0~20 cm),置于 -20℃ 冰箱中保存。冰川于 1993 年末退缩成两支,1993 年以前,整条冰川的退缩速度为 4.5 m·a⁻¹,1993~2004 年,东西支的退缩速度分别为 3.5 m·a⁻¹及 5.8 m·a⁻¹[17]。沿冰川退缩方向按照 5 点 3 重复的方法采集样品,根据土样与冰川末端的距离,3 个采样点的退缩年代分别为 0、15 和 31 a。

1.2 土壤理化性质的测定

有机碳及总氮用元素分析仪进行测量。DOC、NO₃⁻ 和 NH₄⁺ 通过水溶液的滤液进行测量。土壤容重用环刀法测量。土壤 pH 用 pH 计对土壤水溶液进行测量(水土比为 2.5:1)。土壤湿度及田间持水量(WHC)通过烘干法测定。

1.3 微宇宙培养实验

取 15 g 新鲜土壤(调节至 60% WHC)置于 60 mL 血清瓶中,用胶塞压好铝盖置于培养箱在 5℃ 及 15℃ 条件下培养。培养前,对采样点重复进行混合,较大石头及土壤大颗粒通过 2 mm 筛子除去。培养体系充入合成空气(20% O₂ 及 80% N₂),用于模拟表层土的空气状况。150d 培养实验结束后,进行土壤样品采集,共 18 个样品。

1.4 DNA 的提取、扩增及高通量测序

土壤 DNA 的提取试剂盒为 Power Soil DNA Isolation Kits(MoBio Laboratories, Carlsbad, USA),具体操作参考说明书。利用 Nanodrop 2000 检测 DNA 的质量。对 16S rRNA 基因的 V4 高可变区进行扩增确定微生物群落组成,引物为 515F(5'-GTGCCAGCMGCCGCGGTAA-3')和 806R(5'-GGACTAC HVGGGTWTCTAAT-3')。PCR 扩增产物经过 2% 琼

脂糖凝胶电泳验证后切胶回收,利用 GeneJET Gel Extraction Kit(Thermo scientific, Delaware, USA)纯化产物。随后使用 Ion Plus Fragment Library Kit 48 rxns(Thermo scientific, Delaware, USA)进行文库构建,使用 Ion S5TMXL 进行上机测序。

1.5 荧光定量 PCR

利用试剂盒 SYBR[®] Premix Ex Taq[™] II (Tli RNaseH Plus)(Takara, Dalian, China)对冰川前缘地提取出的 DNA 进行定量。古菌定量所用引物为: A806F(5'-ATTAGATACCCSBGTAGTCC-3')^[18] 和 A958R(5'-YCCGCGCTTG AMTCCAATT-3')^[19];细菌的引物为: BAC 27F(5'-AGAGTTTGATCCTGGC TCAG-3')^[20] 和 EUB 338R(5'-GCTGCCTCCCGTAG GAGT-3')^[21]。最终得到样品 DNA 以每克干土的拷贝数为单位。

1.6 统计分析

对测序下机数据进行质量过滤。去除序列首尾两端的 barcode 和前后端引物后,拼接序列,去除低质量片段及片段长度 < 200 bp 的序列,仅保留长度范围在 245~260 bp 内的序列。利用 UPARSE^[22] 用于去除嵌合体,在 97% 的相似度水平进行聚类并得到 OTU,对所有样本中 count 小于 10 的 OTU 进行删除,避免具有低丰度的高可变性的 OTU 对于差异结果的干扰。随后采用 Greengene 数据库进行物种注释。

α 多样性选用 Shannon 指数, β 多样性选用基于 Bray-Curtis 距离的主坐标分析进行表征。OTU 水平上的相对丰度的差异由 DESeq2 进行检验,并对其中相对丰度较高(>0.5% of rarefied reads)且发生显著改变的 OTUs 进行进一步注释分析。

2 结果与分析

2.1 土壤理化性质

本研究所选取的天山 1 号冰川前缘地 3 个采样点的理化性质见表 1。3 个样地的土壤均呈碱性(7.91~8.17)。有机碳及总氮含量分别为 2.93~6.16 g·kg⁻¹和 0.11~0.32 g·kg⁻¹,在 C 点达到最大值,且两个指标随退缩年代的增加而上升。而 C:N 则具有相反的趋势(范围为 19.13~26.84)。土壤湿度、土壤容重、DOC 及 NH₄⁺ 最大值均出现在 A 点,最小值为 B 点。NO₃⁻ 则在 B 点达到最高,为 3.23 mg·kg⁻¹。

2.2 升温对微生物的影响

2.2.1 升温对微生物数量的影响

对冰川前缘地 16S rRNA 基因拷贝数进行定量分析,结果见图 1(5℃ 条件培养下样品简称为 5A、

表 1 天山 1 号冰川前缘地 3 个采样点的环境指标¹⁾

Table 1 Environmental parameters along the Urumqi Glacier No. 1 forefield

采样点	退缩时 间/a	土壤湿度 /%	土壤容重 /g·cm ⁻³	100% WHC/%	有机碳 /g·kg ⁻¹	总氮 /g·kg ⁻¹	DOC /mg·kg ⁻¹	NH ₄ ⁺ /mg·kg ⁻¹	NO ₃ ⁻ /mg·kg ⁻¹	C:N	pH
A	0	10.67 ± 0.86a	1.41 ± 0.04a	12.30 ± 1.22b	2.93 ± 0.04b	0.11 ± 0.02b	25.64 ± 2.55a	1.28 ± 0.10a	0.86 ± 0.15c	26.84 ± 4.86a	8.17 ± 0.30a
B	15	4.88 ± 0.07c	1.16 ± 0.03b	20.59 ± 1.66a	6.03 ± 0.05a	0.28 ± 0.00a	20.05 ± 1.41b	1.16 ± 0.10a	3.23 ± 0.26a	21.74 ± 0.33a	7.94 ± 0.14a
C	31	5.85 ± 0.26b	1.23 ± 0.06b	22.19 ± 3.19a	6.16 ± 0.05a	0.32 ± 0.03a	23.60 ± 1.93a	1.26 ± 0.09a	2.04 ± 0.18b	19.13 ± 1.55a	7.91 ± 0.13a

1)表中不同字母表示差异达到 0.05 的显著水平 ($P < 0.05$)

5B 和 5C, 15℃ 条件培养下样品简称为 15A、15B 和 15C, 下同). 各样地中细菌拷贝数均显著高于古菌拷贝数 ($P < 0.05$), 细菌在 5℃ 的拷贝数 (以干土计, 下同) 为 $1.72 \times 10^8 \sim 1.56 \times 10^9$ copies·g⁻¹, 古菌拷贝数为 $7.92 \times 10^3 \sim 1.73 \times 10^7$ copies·g⁻¹. 其在 15℃ 的细菌及古菌拷贝数分别为 $1.29 \times 10^8 \sim 1.41 \times 10^9$ copies·g⁻¹ 与 $4.21 \times 10^4 \sim 2.27 \times 10^7$ copies·g⁻¹. 随退缩年代的增加, 古菌及细菌拷贝数增加. 升温 10℃, 细菌拷贝数下降, 古菌拷贝数上升, 但变化均未通过显著性检验.

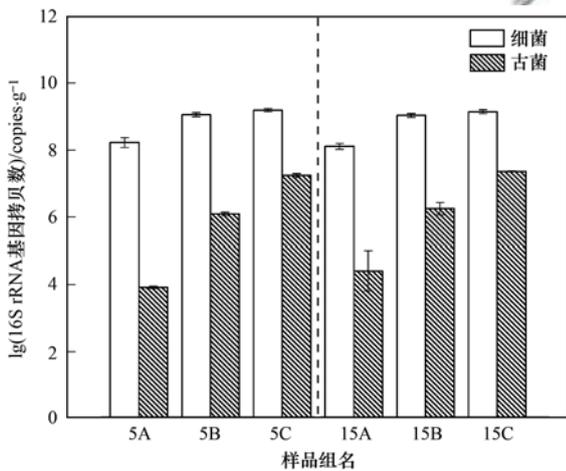


图 1 不同温度下微生物数量

Fig. 1 Microbial abundance under different temperatures

2.2.2 升温对微生物多样性的影响

对冰川前缘地不同退缩年代的 3 个土壤样点的 α 多样性进行比较 (图 2). 结果显示, 不同采样点的 α 多样性存在差异, 整体为随退缩年代的增加而增加. 同时, 为研究微生物种群结构的差异, 基于 Bray-Curtis 距离对微生物进行主坐标分析 (图 3), Bray-Curtis 距离越近, 表明两个群落的物种组成相似性越高. 不同采样点在图 3 中的距离较远, 证明不同采样点微生物群落结构差异明显. 比较 5℃ 与 15℃ 条件下微生物群落 α 多样性及 β 多样性, 未发现明显升温作用影响. 与 B 和 C 点相比, 升温对 A 点微生物群落结构的改变更为明显.

2.2.3 升温对微生物群落结构的影响

质量控制步骤过后, 所有样品中检测到基于 16S rRNA 序列 1 080 317 条 (每个处理 3 个重复), 其

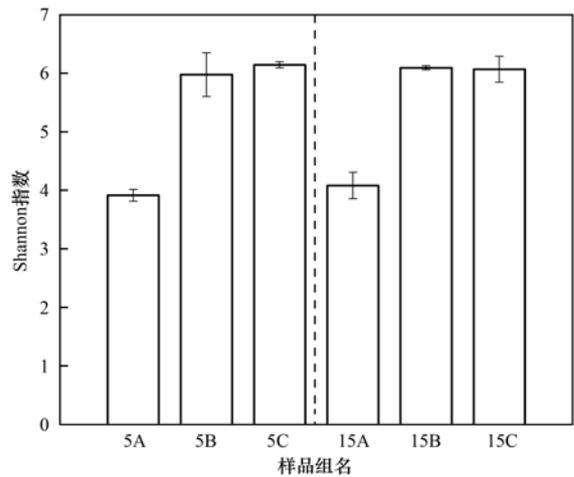


图 2 不同温度下的 Shannon 指数

Fig. 2 Shannon index under different temperatures

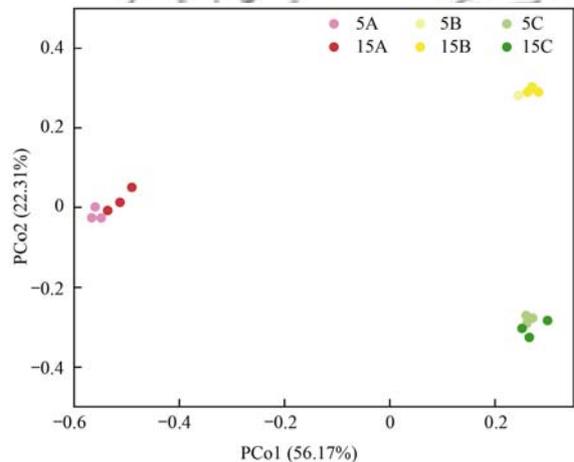


图 3 不同温度下微生物基于 Bray-Curtis 距离的主坐标分析

Fig. 3 Principal coordinate analysis based on the Bray-Curtis distance of microbial communities under different temperatures

中仅包含 0.01% ~ 1.57% 的古菌. 通过与数据库的比对, 共产生 3194 个 OTU. 由于土壤发育年份不同, 微生物的优势种群发生变化 (图 4). 总体上, 冰川前缘地土壤的优势种群为变形菌门 (Proteobacteria)、放线菌门 (Actinobacteria) 和拟杆菌门 (Bacteroidetes), 占各样本微生物群落总量的 61% 以上. A 点的种群多样性较低, 优势种群的相对丰度总和可达 99% 以上. 随退缩年代的增加, 芽单胞菌门 (Gemmatimonadetes) 相对丰度随之增加.

基于 OTU 水平研究升温对微生物优势种群相对丰度的影响, 图 5 为 A、B 和 C 采样点中达显著变

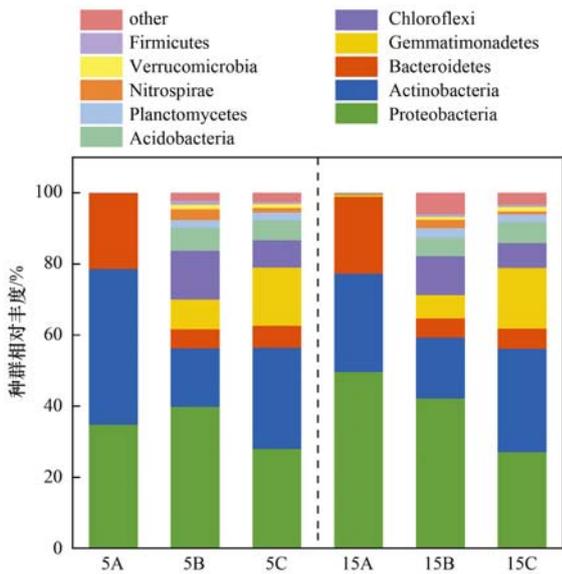


图 4 不同温度下微生物群落组成
Fig. 4 Microbial community composition under different temperatures

化的 OTU 进行 \log_2 转换后的变化倍数,柱状图上各点代表 15°C 时 OTU 相对丰度的占比,其中黑点代表相对丰度占比 > 0.5% 的 OTU.

A 点的种群结构较为简单,且相较于 B 和 C 点变化更为明显.在门水平上,主要表现为升温后 Proteobacteria 相对丰度的上升及 Actinobacteria 相对

丰度的下降.在 OTU 水平上,354 个 OTU 产生变化,其中 30 个 OTU 变化达到显著水平且均随升温呈现上升趋势.相对丰度 > 0.5% 的 OTU_598、OTU_5263 及 OTU_11548 均为 *Thiobacillus* 属 (Proteobacteria,表 2).该属为嗜温菌,主要包括一些好氧或兼性细菌^[23].

B 点在门水平上,表现为升温后 Proteobacteria 相对丰度的上升.在 OTU 水平上,1 020 个 OTU 产生变化,其中 55 个 OTU 的变化达到显著水平且均随升温呈现上升或下降趋势.相对丰度 > 0.5% 的 OTU_13、OTU_27 及 OTU_54 均属 Proteobacteria 且相对丰度均随升温而上升.其中 OTU_13 为 *Thiobacillus* 属. OTU_27 (*Thiotrichaceae*) 与硫沉积过程相关. OTU_54 属 Xanthomonadales 目,该目主要为嗜温菌,为严格需氧微生物^[23].

C 点在门水平随升温变化不明显,在 OTU 水平上,1 058 个 OTU 产生变化,其中 24 个 OTU 的变化达到显著水平.相对丰度最高的 OTU 达 0.41%,属 Nitrospirae 门.与 B 点类似,所属 Chloroflexi 及 Gemmatimonadetes 的变化显著的 OTU 随升温相对丰度增加.同时, Nitrospirae 与 Acidobacteria 中发生显著变化的 OTU 随升温相对丰度下降.

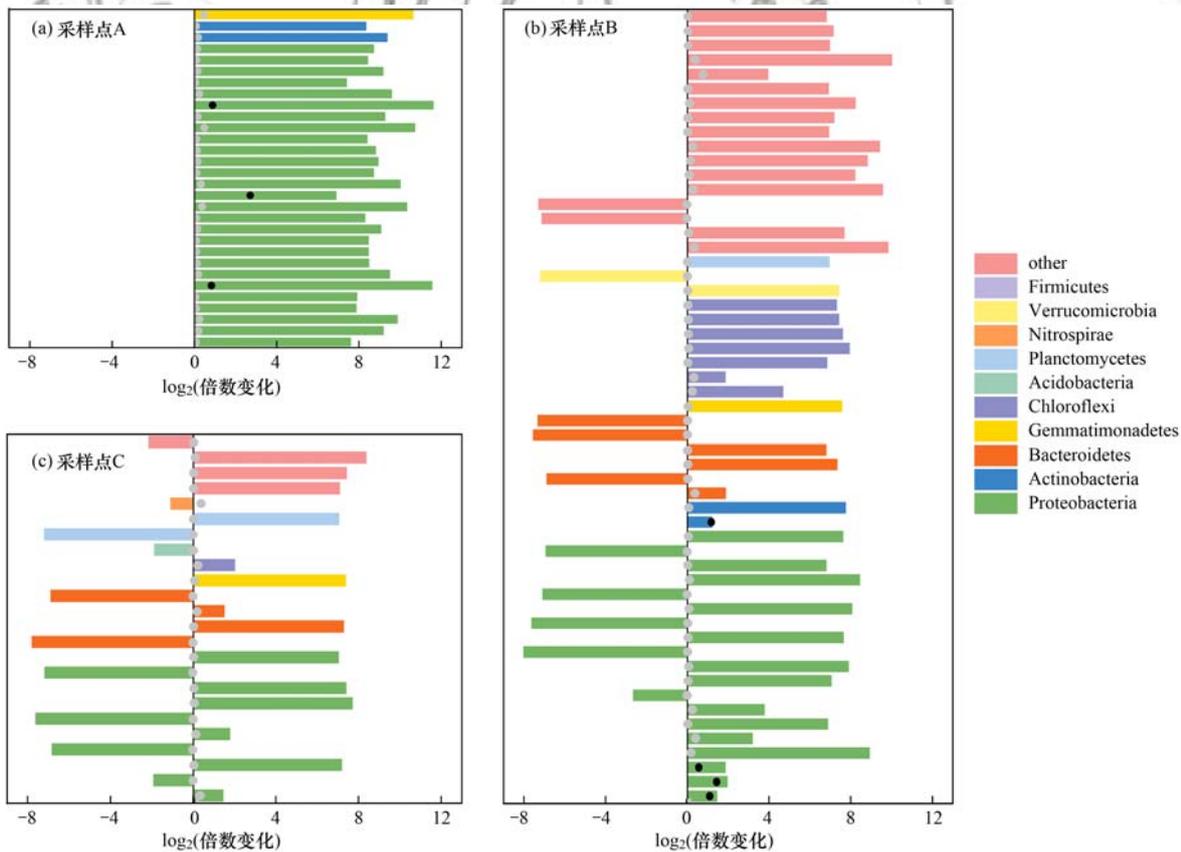


图 5 OTU 水平上微生物相对丰度的变化倍数

Fig. 5 Fold change of microbial relative abundance at the OTU level

表 2 升温后变化显著的优势 OTUs

Table 2 Significant changes in abundant OTUs with warming

采样点	OTU ID	相对丰度/%	界	门	纲	目	科	属	种
A	OTU_598	0.83	Bacteria	Proteobacteria	Betaproteobacteria	Hydrogenophiales	Hydrogenophilaceae	<i>Thiobacillus</i>	unclassified
	OTU_5263	2.72	Bacteria	Proteobacteria	Betaproteobacteria	Hydrogenophiales	Hydrogenophilaceae	<i>Thiobacillus</i>	unclassified
	OTU_11548	0.89	Bacteria	Proteobacteria	Betaproteobacteria	Hydrogenophiales	Hydrogenophilaceae	<i>Thiobacillus</i>	unclassified
B	OTU_13	1.10	Bacteria	Proteobacteria	Betaproteobacteria	Hydrogenophiales	Hydrogenophilaceae	<i>Thiobacillus</i>	unclassified
	OTU_27	1.44	Bacteria	Proteobacteria	Gammaproteobacteria	Thiotrichales	Thiotrichaceae	unclassified	unclassified
	OTU_54	0.56	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Sinobacteraceae	unclassified	unclassified
	OTU_1690	1.17	Bacteria	Actinobacteria	Actinobacteria	Actinomycetales	Nocardiodaceae	unclassified	unclassified

3 讨论

本研究中土壤碳氮含量及其变化趋势与其他冰川前缘地一致^[24,25]。细菌、古菌拷贝数随冰川退缩年代的增加而增加,且细菌数量远高于古菌数量,在 A 点可高达 10^4 倍,这与天山一号冰川前缘地功能微生物及可培养微生物的变化趋势相同。其研究表明,微生物数量增加趋势与土壤碳氮含量的升高及 pH 的降低相关^[26,27]。微生物演替与土壤发育过程同时发生,在退缩年代较久的地区,冰川前缘地营养的累积及微生物与土壤的相互作用更强,并且增加趋势在有植被覆盖的地区更为明显^[8]。微宇宙实验发现升温改变冰川前缘地细菌、古菌拷贝数,但并未达到显著水平。Blankinship 等^[28]对 75 个模拟气候变化的研究总结表明,在干冷地区,升温将降低微生物数量。而 Chen 等^[29]的研究结果则与之相反,升温增加 7.6% 微生物数量,且在寒冷地区的增加作用更为显著。不同的结果可能与土壤性质、升温方式及持续时间、微生物数量测量手段等因素紧密相关。

由于降水(雨、雪)、水沉积(云、雾、冰雹)、风沉积和灰尘沉积等作用沉降及迁移的营养元素及微生物使冰川前缘地微生物种群具有高度相似性^[30]。相较于 A 点, B 和 C 点的微生物群落结构更为类似,这可能与 A 点为新暴露土壤有关。随退缩年代增加,微生物群落多样性增加,更多微生物定殖并参与碳氮等元素循环过程。Proteobacteria 是天山一号冰川前缘地微生物的优势种群,与其他高山冰川中的结果相同^[6,9]。Proteobacteria 具有多种代谢途径,包括光养自养,光合异养及化能自养等^[31],使其能够广泛存在于各种生态环境中。随退缩年代的增加而导致的 Proteobacteria 相对丰度的减少可能与一些适应低温及寡营养的微生物的相对丰度的减少相关^[32]。Actinobacteria、Bacteroidetes 相对丰度随退缩年代的变化可能与土壤 pH 的变化相关^[5,32]。

微生物在冰川前缘地的物质循环中起着重要的作用,通过升温可以改变其群落结构组成,从而改变其功能。通过主坐标分析,可知 150 d 的室内升温实

验对退缩年代较短的 A 点影响最明显。在对 Damma 冰川的研究中发现,退缩年代较短的位点碳稳定机制较为薄弱,会对气候变化迅速发生适应行为^[25],这可能解释 A 点更为明显的微生物群落的变化及 OTU 水平上 A 和 B 点显著变化的优势 OTU。DeAngelis 等^[33]的长期升温实验显著增加 Proteobacteria 的相对丰度,并认为可将其产生显著变化的微生物作为升温指示物种,这与本研究中升温后变化显著的优势 OTU 一致。升温可能造成嗜冷微生物的死亡,本研究中表现为微生物对变暖条件的热适应性,即 A 点及 B 点中嗜温属相对丰度的增加。并且需氧微生物相对丰度的增加与微宇宙实验中有氧条件相关。此外,升温可能导致易降解碳的减少,改变土壤营养条件,从而改变微生物群落组成^[34]。长期的培养实验及模型预测表明,未来碳释放速率将取决于温度、碳质量等因素^[35]。然而,微生物可以通过调整其群落组成,降低呼吸作用对温度的敏感性,保持土壤碳库的稳定,进一步调整对外部环境的反馈作用^[16]。因此,研究升温后微生物群落的变化有助于人们理解未来全球变暖条件下元素循环过程。

4 结论

(1) 原始样品中,随冰川退缩年代的增加,土壤总碳氮含量增加,微生物数量及其种群多样性增加。

(2) 150 d 微宇宙实验表明,升温对微生物数量及多样性改变不显著,但对微生物群落结构影响显著,对退缩年代较短的样点的微生物群落结构影响更为明显。

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