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滇池水中细菌和古菌氮代谢功能基因的空间分布

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摘要: 氮代谢在滇池水生态系统氮素循环和转化过程中起到重要的作用, 不仅真核生物参与氮素转化, 原核生物作为氮素循环的主要驱动者, 在氮素生物化学循环中的作用更不容忽视。基于 16S rDNA 高通量测序技术, 监测滇池草海和外海区域 13 个点位, 分析滇池水中原核生物氮循环功能关键基因的分布特征。结果发现, 滇池水中细菌 35 门, 427 属, 主要以变形菌门和拟杆菌门为优势门类; 古菌 14 门, 61 属, 主要以广古菌门为优势门类; β 多样性指数显示滇池整体细菌丰富度指数高于古菌, 草海细菌多样性指数高于外海。PICRUSt 功能解析表明细菌和古菌具有功能上的丰富性, 细菌中有 35 个参与氮代谢的 KO 通路, 涉及氮异化硝酸盐还原基因 *nirB*、一氧化氮还原酶基因 *norB* 和硝酸还原酶基因 *nasK* 等关键基因; 古菌中有 23 个参与氮代谢的 KO 通路, 涉及固氮酶基因 *nifH*、*nifK* 和 *nifD*, 古菌固氮酶基因拷贝数显著高于其它氮代谢基因, 草海中古菌氮代谢能力整体高于外海, 滇池水中古菌比细菌固氮潜能更大。本研究从原核生物氮循环中功能基因的角度, 探讨滇池不同区域水中细菌和古菌氮循环差异, 为进一步揭示氮循环机制, 解决氮素污染引起的富营养化提供理论参考。

关键词: 滇池; 氮代谢; 原核生物; 空间分布; 功能基因

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Spatial Distribution of Nitrogen Metabolism Functional Genes of Eubacteria and Archaeobacteria in Dianchi Lake

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Abstract: Nitrogen metabolism plays an important role in the nitrogen cycle and transformation in Dianchi Lake. Not only do eukaryotes participate in nitrogen transformation but prokaryotes, as the main drivers of the nitrogen cycle, also play an extremely important role in the nitrogen cycle. Based on 16S rDNA high-throughput sequencing technology, 13 sites in Caohai and Waihai of Dianchi Lake were monitored, and PICRUSt function analysis method was adopted to analyze the microbial community diversity and key genes of nitrogen metabolism in Dianchi Lake. Bacteria belonging to 35 phyla and 427 genera were found in Dianchi Lake water and mainly included Proteobacteria and Bacteroidetes. Archaea had 14 phyla and 61 genera and mainly belonged to Euryarchaeota. The overall bacterial richness index of Dianchi Lake was higher than that of archaea, and the bacterial diversity index of Caohai was higher than that of Waihai. Functional prediction showed functional richness of bacteria and archaea. There were 35 KO pathways involved in nitrogen metabolism in bacteria, including key genes such as nitrogenous nitrate-reducing gene *nirB*, nitric oxide reductase gene *norB* in denitrification, and nitroreductase gene *nasK*. There were 23 KO pathways involved in nitrogen metabolism in archaea, involving *nifH*, *nifK*, and *nifD* nitrogenase genes in nitrogen fixation. The copy number of nitrogenase genes was significantly higher than that of other nitrogenase genes. The copy number of nitrogen-fixing genes of archaea was higher than that of bacteria, the nitrogen metabolism capacity of archaea in Caohai was higher than that in Waihai, and the potential of nitrogen-fixation of archaea in Dianchi Lake water was higher than that of bacteria. From the perspective of community structure and function prediction of bacteria and archaea, this study discussed the differences of nitrogen cycle in bacteria and archaea in different areas of Dianchi Lake and provided a decision basis for water environment management in Dianchi Lake.

Key words: Dianchi Lake; nitrogen metabolism; prokaryote; spatial distribution; functional genes

水生态系统的氮素循环是一个复杂的生物化学过程, 细菌和古菌是微生物氮素循环中的主要参与者, 在维持生态系统结构和功能稳定, 能量流动和物质循环转化过程中起着核心作用^[1]。细菌和古菌的群落结构因不同区域地理气候特征影响呈现时空差异性^[2,3], 细菌和古菌的功能特性及其在生物地球化学循环中的作用, 在一定程度上能够反映水生态系统的状况^[4-8]。滇池是云贵高原地区最大的淡水

湖泊, 近年来滇池正处于由中度富营养向轻度富营养转化的关键时期^[9,10], 氮含量过高是滇池水循环中长期面临的水环境问题^[11]。以微生物为主导的氮

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代谢是地球氮循环的主要驱动力^[12,13],对于水环境中氮素循环转化起到了决定性的作用^[14].因此,要全面了解滇池水生生态系统状况,揭示滇池氮素的生物地球化学循环机制,对滇池水中细菌和古菌群落结构组成及功能的研究显得尤为重要^[15,16].

随着分子生物学技术的推陈出新,方便快捷经济可靠的微生物检测技术和方法被越来越多的研究学者所接受^[17~19].高通量测序技术能够获得全面的微生物群落信息,其包含的 PICRUSt 软件能够更高效准确地解析微生物功能信息^[20,21],该技术已在淡水生态系统和海洋生态系统中得到良好的应用^[22,23].目前,研究人员在滇池开展了大量关于微生物的研究工作,初步探究了滇池细菌群落组成的时空分布特征和影响因素^[24,25],然而针对滇池水中细菌和古菌氮代谢过程的研究却鲜见报道.因此,本研究选取滇池草海和外海两个典型区域样品,基于微生物学角度,采用 16S rDNA 高通量测序技术研究滇池水中细菌和古菌群落组成,预测参与氮循环的细菌和古菌功能基因,分析滇池不同点位氮循环功能差异,以期为进一步揭示氮循环机制,解决氮素污染引起的富营养化提供理论参考.

1 材料与方法

1.1 研究区概况

滇池位于云南省昆明市,流域面积约为 2 920 km²,是我国最为重要的高原湖泊之一.滇池南北长度约 39.4 km,东西宽度约 12.7 km,周长为 161.6 km^[26].滇池湖体东北部有障壁沙坝,将湖体分成南北两个部分,沙坝以北称为草海,离市区较近,面积约 10 km²,占滇池湖体总面积的 3%,是昆明市西部区域纳污河道的过水流域;沙坝以南称为外海,是滇池的主体部分,面积约 289 km²,占滇池湖体总面积的 97%^[27].

1.2 研究方法

1.2.1 样品采集

根据高原湖泊滇池水文特征,于 2018 年 1 月在滇池的草海和外海区域采集表层水样品.水样选择在滇池表层 0.5 m 处用采水器采集,同时取 3 个平行样品.采样共设置 13 个采样点,由北向南依次为,草海 3 个采样点,外海 10 个采样点,采样点位置如图 1.

1.2.2 水中理化参数测定

野外采集现场进行了水温及溶解氧浓度检测,其余水中理化指标检测带回实验室进行.水样经 0.45 μm 滤膜过滤后,进行水中理化参数的测定.溶解性总磷(DTP)采用过硫酸钾法测定^[28],采用碱性

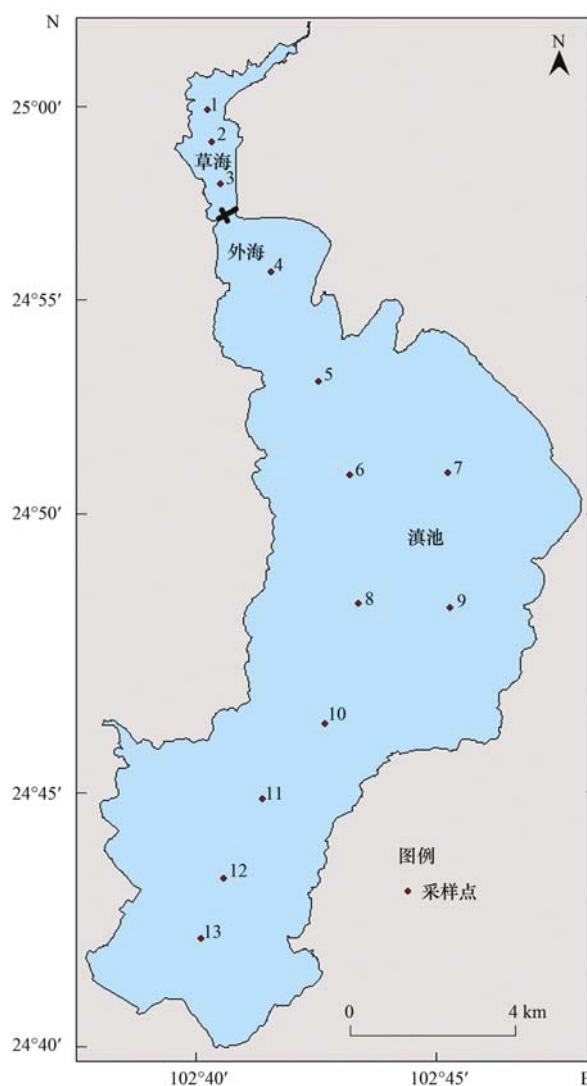


图 1 滇池采样点示意

Fig. 1 Sampling sites in Dianchi Lake

过硫酸钾消解法测溶解性总氮(DTN),氨氮(NH_4^+-N)通过纳氏试剂法测定,硝态氮(NO_3^--N)测定通过紫外分光光度法^[29].DON 通过 DTN 与 NH_4^+-N 和 NO_3^--N 浓度差所得.

1.2.3 细菌和古菌群落结构和功能解析

将滇池每个点位现场采集的 1 000 mL 水样置于聚乙烯塑料桶中,带回实验室,用于 16S rDNA 细菌和古菌高通量测序分析.水样通过 0.22 μm 滤膜后用于水中细菌和古菌 DNA 提取.细菌的 PCR 扩增所用的引物已经融合了 MiSeq 测序平台的 V3-V4 通用引物,引物分别为 341F 引物和 805R 引物,341F 引物:CCCTACACGACGCTCTTCCGATCTG (barcode) CCTACGGGNGGCWGCAG; 805R 引物:GACTGGAG TTCCTTGGCACCCGAGAATTCCAGACTACHVGGGT ATCTAATCC.古菌引用槽式 PCR 扩增有三轮,第一轮使用 M-340F, GU1ST-1000R 引物扩增:古 1st-340F: CCCTAYGGGGYGCASCAG; 古 1st-1000R: GGCCATGCACYWCYTCTC. PCR 结束后进行第二

轮扩增. 第二轮使用第一轮 PCR 产物进行扩增, PCR 所用的引物已经融合了测序平台的 V3-V4 通用引物. 349F 引物: CCCTACACGACGCTCTTCC GATCTN (barcode) GYGCASCAGKCGMGAAG; 806R 引物: GACTGGAGTTCCTTGGCAGCCGAGAATTCCA GGACTACVSGGTATCTAAT. 第三轮扩增, 引入 Illumina 桥式 PCR 兼容引物, PCR 扩增后进行上机测试^[30]. 数据预处理后去除嵌合体及非特异性扩增序列, 最终得到细菌和古菌丰度, 最后通过 PICRUSt 软件进行基因解释分析, 利用 QIIME 获得的 closed OTU-table 与 KEGG 数据库进行比对, 获得水中细菌和古菌功能信息^[31].

1.2.4 数据统计分析

采用 R 语言 gplots package 建立滇池水中细菌和古菌属水平物种丰度图, 同时基于 PICRUSt 功能分类结果, 通过 STAMP 软件, 采用 Welch's t-test 方法, 比较草海和外海水中微生物存在显著差异的功能分类.

2 结果与讨论

2.1 滇池氮磷浓度的分布特征

对滇池 13 个点位水中理化参数指标进行整理分析如表 1. 滇池草海和外海区域水中 DTN 浓度存在显著差异, 草海水中 DTN 平均浓度为 $1.98 \text{ mg} \cdot \text{L}^{-1}$, 草海水中 $\text{NH}_4^+ \text{-N}$ 和 $\text{NO}_3^- \text{-N}$ 浓度分别为 $0.12 \text{ mg} \cdot \text{L}^{-1}$ 和 $1.20 \text{ mg} \cdot \text{L}^{-1}$, 占草海 DTN 的质量分数分

别为 6% 和 62%, DON 占 DTN 的 32%. 外海水中 DTN 平均浓度为 $1.41 \text{ mg} \cdot \text{L}^{-1}$, 外海水中 $\text{NH}_4^+ \text{-N}$ 和 $\text{NO}_3^- \text{-N}$ 浓度分别为 $0.10 \text{ mg} \cdot \text{L}^{-1}$ 和 $0.19 \text{ mg} \cdot \text{L}^{-1}$, 占外海 DTN 的质量分数分别为 7% 和 13%, DON 占 DTN 的 80%, DON 是外海水中氮的重要形态, 占有较高的比重. 草海和外海水中 DTP 浓度分别为 $0.06 \text{ mg} \cdot \text{L}^{-1}$ 和 $0.09 \text{ mg} \cdot \text{L}^{-1}$, 草海和外海水中 DTP 浓度在 $P < 0.05$ 水平上无显著性差异. 草海水中 DO 浓度平均值为 $11.62 \text{ mg} \cdot \text{L}^{-1}$, 外海水中 DO 浓度平均值为 $8.71 \text{ mg} \cdot \text{L}^{-1}$, 外海水中 DO 浓度显著低于草海水中 DO 浓度. 草海和外海区域水温平均浓度变化范围在 $11.7 \sim 12.7^\circ\text{C}$ 之间, 滇池平均水温为 12.2°C , 滇池整体表层水温变化不大.

综合来看, 根据《地表水环境质量标准》(GB 38382-2002), 滇池溶解氧含量高, 符合 I 类地表水标准. 草海总氮浓度为 V 类地表水标准, 外海总氮浓度达到 IV 类地表水标准, 草海和外海总磷浓度符合 IV 类地表水标准. 滇池氮磷污染仍较为严重, 但水质状况已有所改善^[11, 32]. 水中营养盐浓度的变化不仅能改变微生物的丰度水平还能显著影响微生物的群落功能^[33]. 董志颖^[22]的研究表明, 氮的输入影响了固氮、异化硝酸盐还原、反硝化、异化硝酸盐还原到铵和同化硝酸盐还原相关基因的相对丰度, 氮源输入影响了细菌群落代谢潜力. 目前滇池湖体水质状况整体趋稳向好, 对入水中氮素循环的深入了解将有助于滇池水环境改善, 增速滇池水循环的健康发展.

表 1 滇池水中理化参数指标¹⁾

Table 1 Physical and chemical parameters in Dianchi Lake

项目	DTN / $\text{mg} \cdot \text{L}^{-1}$	$\text{NH}_4^+ \text{-N}$ / $\text{mg} \cdot \text{L}^{-1}$	$\text{NO}_3^- \text{-N}$ / $\text{mg} \cdot \text{L}^{-1}$	DTP / $\text{mg} \cdot \text{L}^{-1}$	DO / $\text{mg} \cdot \text{L}^{-1}$	水温 / $^\circ\text{C}$
草海 (CH)	$1.98 \pm 0.03\text{a}$	$0.12 \pm 0.02\text{a}$	$1.20 \pm 0.04\text{a}$	$0.06 \pm 0.02\text{a}$	$11.62 \pm 0.12\text{a}$	$12.7 \pm 0.11\text{a}$
外海 (WH)	$1.41 \pm 0.05\text{b}$	$0.10 \pm 0.03\text{a}$	$0.19 \pm 0.02\text{b}$	$0.09 \pm 0.02\text{a}$	$8.71 \pm 0.08\text{b}$	$11.7 \pm 0.16\text{a}$

1) 数据为不同区域样品的平均值 $\pm$ 标准差 (草海, $n=3$; 外海, $n=10$); 同一列相同字母表示差异不显著, 不同字母表示差异显著 ($P < 0.05$)

2.2 滇池水中细菌和古菌群落结构特征

滇池水中细菌和古菌的群落结构组成如图 2. 在滇池水中样品中共获得 35 门、75 纲、143 目、274 科和 427 属细菌群落组成, 细菌群落组成在门水平上主要以变形菌门 (Proteobacteria) 和拟杆菌门 (Bacteroidetes) 为优势门类, 变形菌门和拟杆菌门占总细菌群落组成的 90% 以上. 在细菌属水平上, 主要以假单胞菌属 (*Pseudomonas*)、黄杆菌属 (*Flavobacterium*) 和不动杆菌属 (*Acinetobacter*) 为优势属, 如图 2(a) 和 2(c). 古菌共获得 14 门、19 纲、25 目、31 科和 61 属, 古菌群落组成主要以广古菌门 (Euryarchaeota) 为优势门类, 其次为泉古菌门 (Crenarchaeota). 在古菌属水平上, 主要以甲烷丝状

菌属 (*Methanothrix*)、甲烷细菌属 (*Methanobacterium*) 和甲烷绳菌属 (*Methanolinea*) 等为优势属类, 如图 2(b) 和 2(d). 滇池细菌和古菌的聚类分析, 如图 2(c) 和 2(d), 在相似性水平上, 除 13 号点位外, 草海 (1~3 号) 和外海 (4~12 号) 样品分成两大组, 结果表明不同点位中属水平下细菌和古菌的群落结构存在一定差异.

对水中细菌和古菌微生物多样性进行分析如表 2. 高通量测序分析共获得细菌优质序列总数为 57 260, 聚类后 OTU 总数为 1 205, 样品文库覆盖率达到 0.992; 古菌优质序列总数为 85 009, 聚类后 OTU 总数为 335, 样品文库覆盖率达到 0.999, 表明细菌和古菌测序数据合理, 能够代表样品中物种的

表 2 滇池水中细菌和古菌多样性

Table 2 Richness and diversity of bacteria and archaea in Dianchi Lake

类别	区域	点位	序列总数	OTU	Shannon 指数	Simpson 指数	ACE 指数	Chao1 指数	盖度
细菌	草海	1	42 099	613	3.45	0.067	1 503	1 047	0.993
		2	55 504	601	3.89	0.072	1 324	1 047	0.995
		3	53 224	2 834	4.39	0.076	3 113	2 995	0.990
		4	53 385	923	2.97	0.120	2 772	1 853	0.991
		5	58 698	1 972	3.52	0.120	4 410	3 189	0.984
		6	67 448	1 054	2.27	0.301	2 432	1 916	0.992
	外海	7	62 609	1 093	3.20	0.100	2 522	1 923	0.991
		8	62 124	850	2.80	0.134	2 057	1 600	0.993
		9	59 386	897	2.74	0.195	1 993	1 412	0.993
		10	59 693	745	2.51	0.214	1 718	1 238	0.994
		11	62 277	869	2.89	0.119	2 065	1 437	0.993
		12	50 040	733	2.40	0.213	1 843	1 282	0.993
		13	57 905	2493	3.28	0.115	3 281	3 038	0.986
	平均值		57 260	1 205	3.08	0.150	2 387	1 844	0.992
古菌	草海	1	91 503	322	2.91	0.115	521	408	0.998
		2	97 559	245	2.95	0.082	441	360	0.999
		3	103 403	483	3.19	0.100	902	685	0.998
		4	72 642	394	3.17	0.086	770	589	0.998
		5	107 492	421	2.61	0.152	521	492	0.999
		6	65 390	290	2.91	0.118	412	460	0.999
	外海	7	75 556	315	2.67	0.143	562	439	0.998
		8	86 473	383	3.14	0.086	451	463	0.999
		9	79 256	263	2.97	0.090	382	380	0.999
		10	85 696	390	2.78	0.145	605	588	0.998
		11	92 091	343	2.79	0.132	732	566	0.998
		12	74 654	312	3.20	0.086	394	376	0.999
		13	73 398	191	1.60	0.428	232	215	0.999
	平均值		85 009	335	2.84	0.136	530	463	0.999

中细菌多样性指数,滇池所有水中样品中细菌丰度指数高于古菌丰度指数.

2.3 滇池水中细菌和古菌功能分类

PICRUSt 能较为准确地给出功能基因的存在及其丰度情况.通过 PICRUSt 对滇池水中细菌和古菌功能构成进行分析,从而获得滇池不同区域之间微生物功能上差异.基于 KEGG 数据对比样品中的微生物功能类别,共获得 6 大类功能信息,包括代谢 (metabolism)、人类疾病 (human diseases)、有机系统 (organismal systems)、遗传信息过程 (genetic information processing)、细胞进化过程 (cellular processes) 和环境信息 (environmental information processing).草海 (CH) 样品中细菌和古菌总功能基因的丰度比例均略高于外海 (WH) 样品中总功能基因的丰度比例.氨基酸代谢功能 (amino acid metabolism)、碳水化合物代谢功能 (carbohydrate metabolism) 以及膜运输功能 (membrane transport) 在细菌功能组成中所占丰度比例较高 [图 3(a)].氨基酸代谢功能 (amino acid metabolism)、碳水化合物代谢功能 (carbohydrate metabolism) 以及能量代谢功

能 (energy metabolism) 在古菌功能组成中所占比例较高 [图 3(b)].基于 PICRUSt 功能三级分类结果,在显著性水平 $P < 0.05$ 水平上,比较草海和外海存在差异的功能丰度比例及 95% 置信区间内的功能丰度的差异比例,草海和外海样品中存在显著差异的功能丰度如图 3(c) 所示.根据细菌三级功能分类,草海和外海细菌代谢功能基因存在显著差异,脂多糖生物合成蛋白质代谢基因所占的丰度比例比其他代谢功能基因更大.根据古菌功能基因三级功能分类,在 $P < 0.05$ 水平上类固醇激素生物合成功能基因 (steroid hormone biosynthesis) 在草海和外海样品中存在显著差异.草海和外海样品在某些与微生物代谢功能相关的基因上表现出了显著差异性.

2.4 滇池水中细菌和古菌氮代谢

滇池水中氮污染情况存在显著差异,因此进一步研究了滇池水中细菌和古菌参与氮代谢途径的基因 (K00910).为了研究滇池水中细菌和古菌参与氮代谢途径的基因,将滇池水中细菌和古菌的功能基因解释的结果与 KEGG 数据库中氮代谢直系同源基因进行对比,以结果中具有基因拷贝数的氮代谢

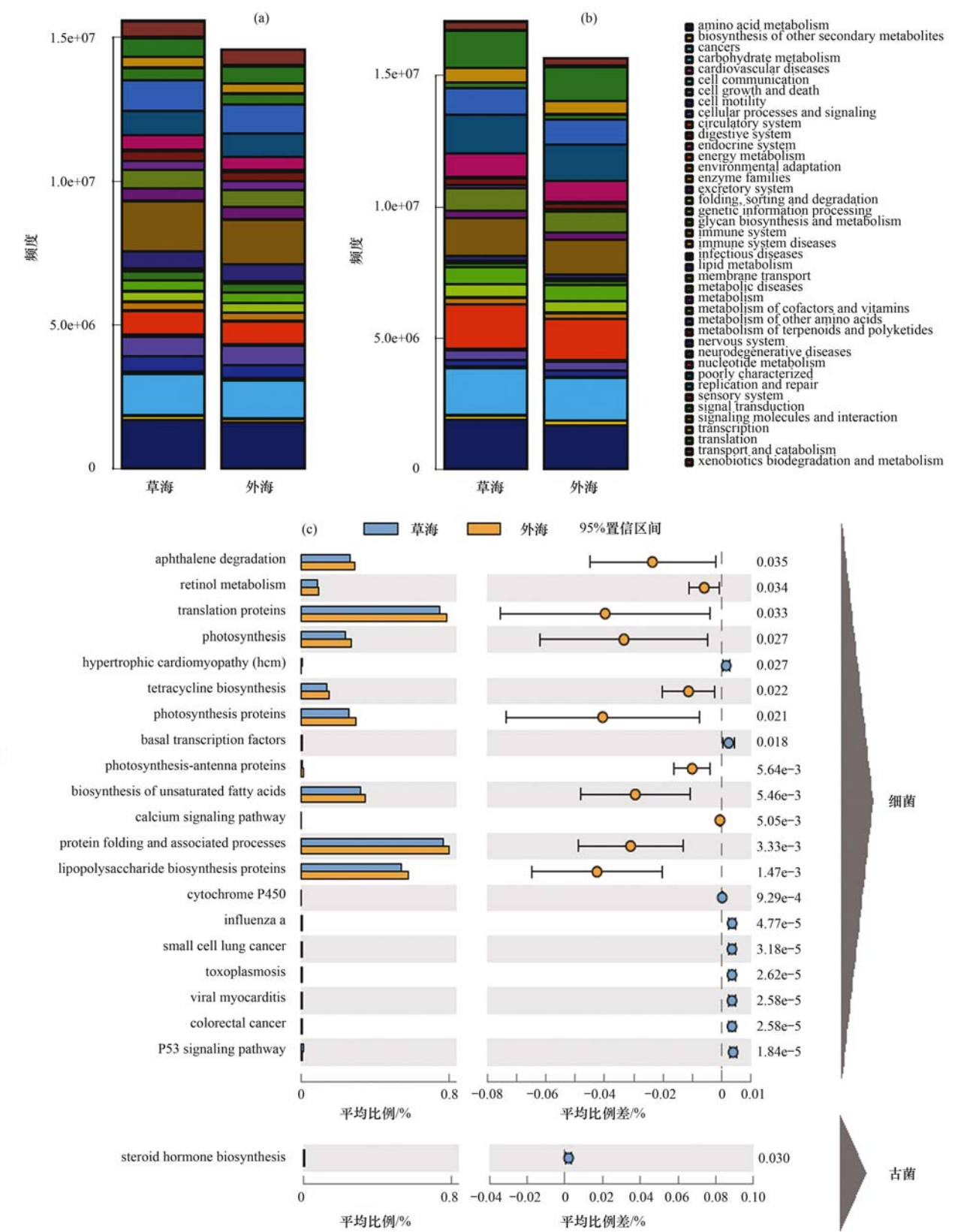


图3 KEGG 功能基因组成及差异

Fig. 3 Composition and differences of KEGG functional genes

通路基因进行分析,结果如图4和图5. 功能基因中共有35个细菌氮代谢功能基因和23个古菌氮代谢功能基因具有数值,表现出丰富的氮代谢能力^[7,21]. 在细菌氮代谢基因拷贝数聚类分析中,在0.97的相似性水平上,外海北部区域与滇池其他区域分成两

个部分. 在古菌氮代谢基因拷贝数聚类分析中,在0.81相似性水平上,滇池南部13号采样点与滇池其他区域分成两个部分. 结果表明,在滇池不同区域水中细菌和古菌的氮代谢具有差异.

根据氮在氮循环中的不同价位变化,将氮循环

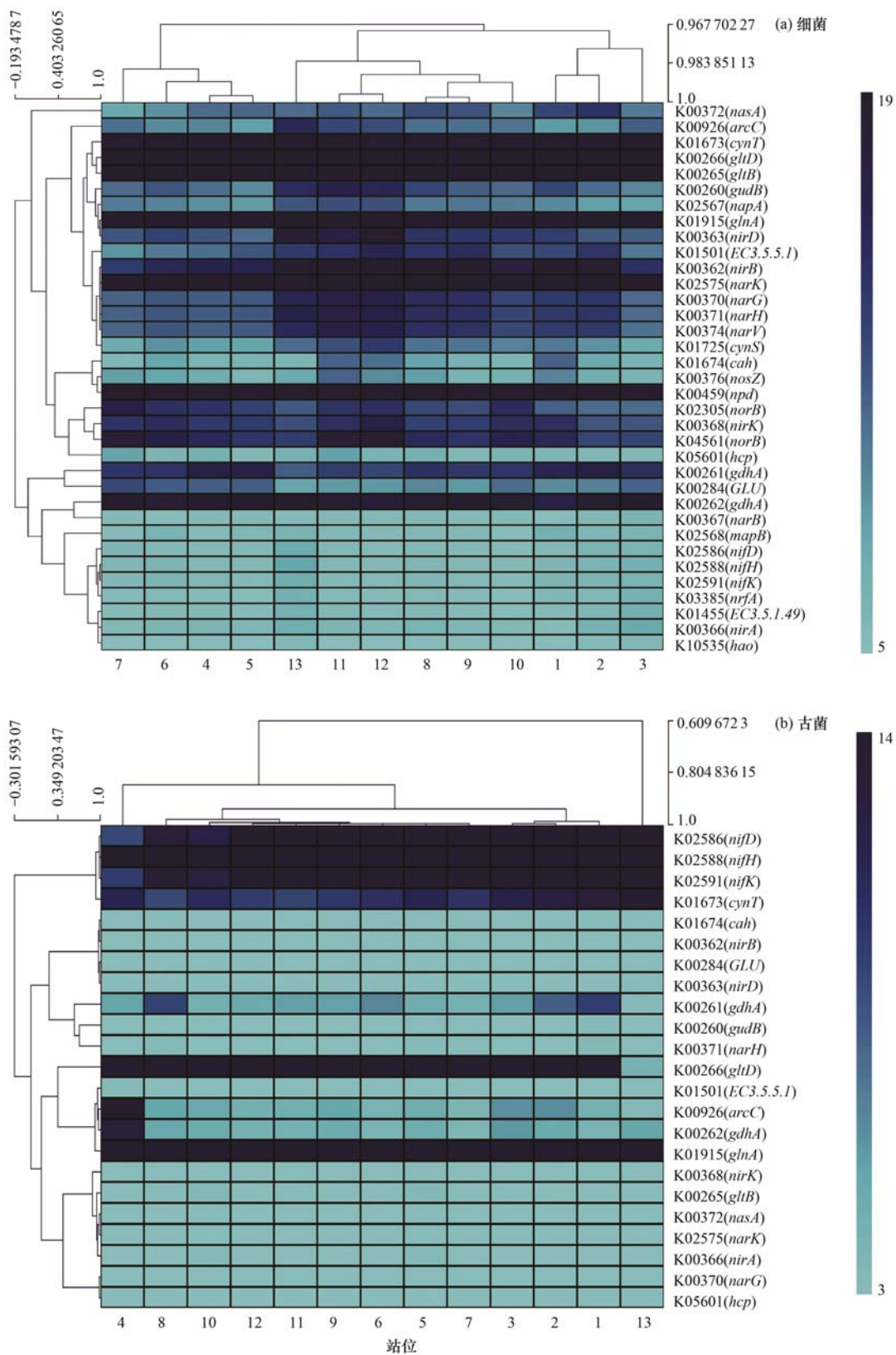


图 4 细菌和古菌氮代谢通路基因热图

Fig. 4 Heatmap of nitrogen metabolism pathway in bacteria and archaea

中的代谢通路依次进行关键基因丰度分析,从而了解不同代谢通路中各基因所做的贡献.在细菌中氮异化硝酸盐还原过程中,亚硝酸盐还原酶基因 *nirB* 最为丰富,滇池外海中 *nirB* 基因拷贝数高于草海,

其次是基因 *nirD* 和 *narL*,异化还原酶基因 *nrfA* 所含基因拷贝数最少.在氮同化硝酸盐还原过程中,硝酸还原酶基因 *nasK* 拷贝数高于基因 *nirA*、*nasB* 和 *narB* 基因.亚硝酸盐同化还原酶基因 *nirA* 被认为是

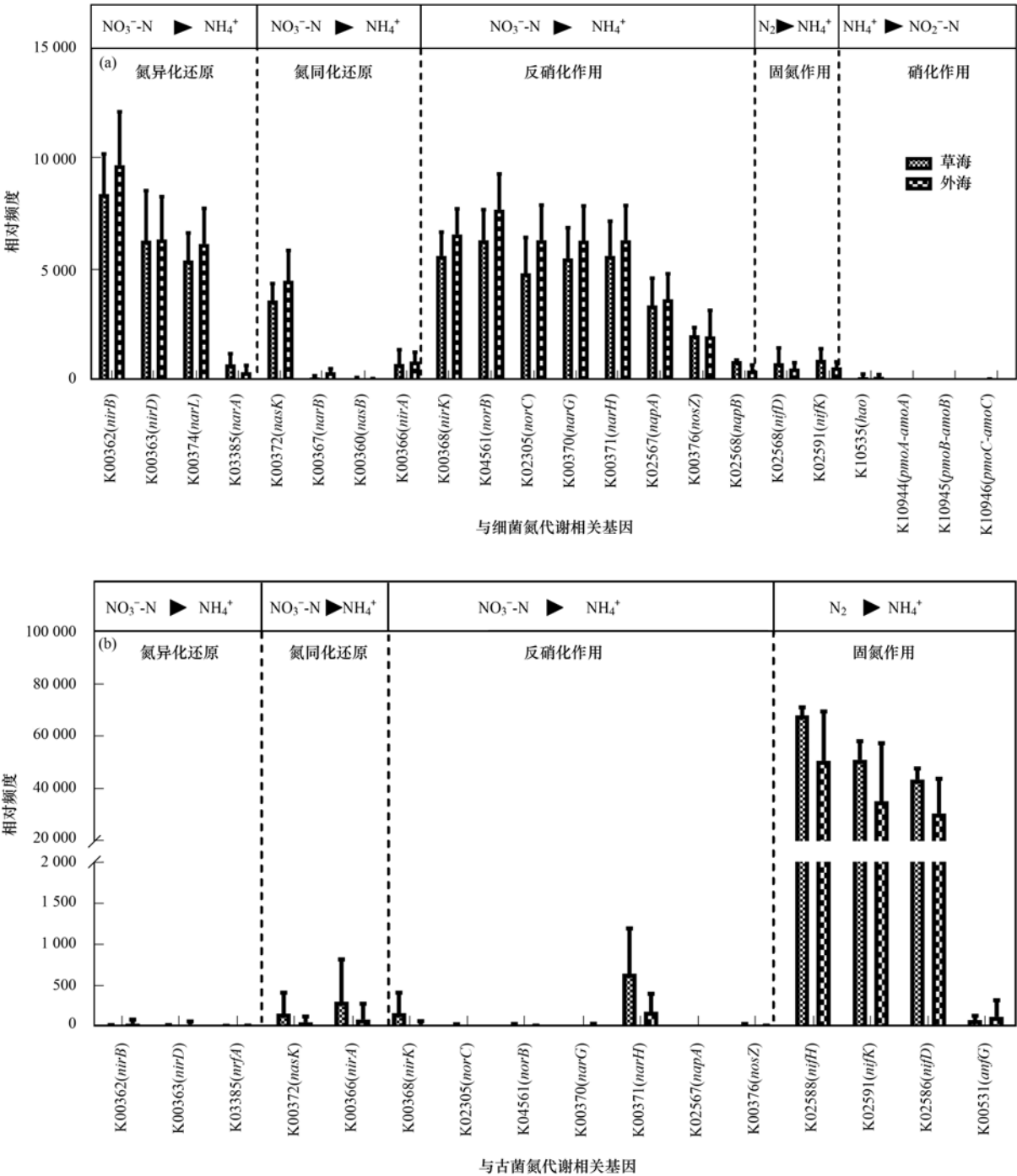


图5 细菌和古菌氮代谢途径及关键丰度差异

Fig. 5 Nitrogen metabolism pathway and gene copy number in bacteria and archaea

导致全球污水处理厂硝酸盐吸收减少的主导基因,在滇池水中细菌硝酸盐吸收中,也起到了一定的作用.反硝化作用中一氧化氮还原酶基因 *norB* 丰度最高,其次是硝酸还原酶基因 *narG*,亚硝酸还原酶基因 *nirK*、*norC* 和 *narH* 基因,反硝化作用途径的氧化亚氮还原酶的编码基因 *nosZ*、异化还原酶基因 *napA* 和 *napB* 基因与同途径基因呈现显著差异.硝化作用基因显著低于上述氮代谢中的其他基因.古菌氮循环过程中,固氮酶基因 *nifH*、*nifK* 和 *nifD* 在固氮中起重要作用,古菌固氮作用中固氮酶基因拷贝数远高

于细菌中固氮基因拷贝数.针对于 PICRUSt 基因预测古菌与细菌固氮酶基因的研究较少.固氮酶是一种催化 N_2 还原的功能恒定蛋白,存在于古细菌和细菌的许多系统发育谱系中^[34].大多数生物固氮是由分布在细菌和古细菌中的含钼固氮酶催化的.尽管从各种细菌和古细菌中纯化出来的钼固氮酶的生化特性和结构非常相似,但是重氮营养菌之间合成、组装和维持其活性的遗传要求却大不相同.在固氮细菌和古细菌中,使重氮营养生长所需的 *nif* 基因的互补序列差异很大^[35].

3 结论

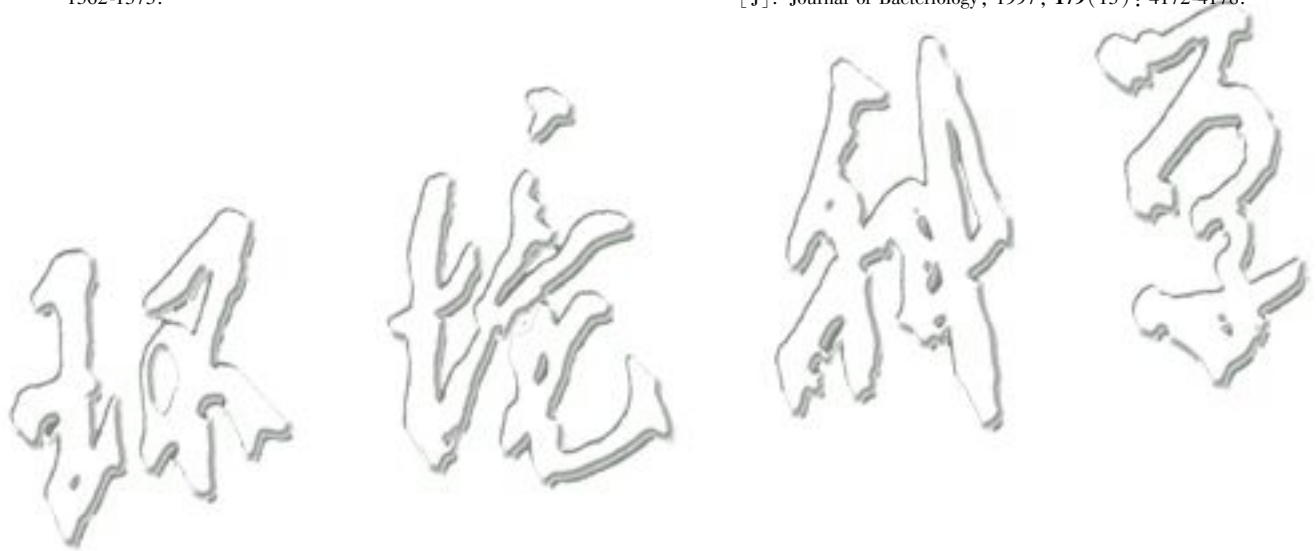
(1)滇池水中细菌主要以变形菌门和拟杆菌门为优势门类,古菌主要以广古菌门为优势门类.滇池全湖细菌丰富度指数高于古菌丰富度指数,草海中细菌多样性指数高于外海中细菌多样性指数.

(2)PICRUSt 功能解析出滇池水中细菌和古菌功能上的丰富性,草海中古菌氮代谢能力整体高于外海,滇池水中古菌比细菌固氮潜能更大.

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