

北京城区PM_{2.5}各组分污染特征及来源分析

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白洋淀冬季沉积物好氧反硝化菌垂向分布特征及群落构建

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摘要: 为了探究白洋淀冬季沉积物好氧反硝化菌群落垂向分布特征、关键物种和群落构建过程, 结合好氧反硝化功能基因 (*napA*) 高通量测序技术, 进行了微生物多样性分析、物种差异分析、关键物种识别和群落构建过程研究. 结果表明, 该时期白洋淀沉积物高通量测序得到13 845个 OTUs, 共分为10个门类, 其中第一大门类为变形菌门, 达到29.03%~94.46%, 从表层到底层呈下降趋势; 占比前二的纲为 β -Proteobacteria 和 γ -Proteobacteria; 占比前三的属为 *Cupriavidus*、*Aeromonas* 和 *Thauera*. 微生物 α 多样性显示垂向分组间表层沉积物 Chao1 指数最大为 $3\,327.67 \pm 621.28$, 明显高于底层 ($2\,193.96 \pm 455.57$); 中层沉积物 Simpson 指数最大为 0.97 ± 0.013 , 明显高于表层 (0.94 ± 0.029). 主成分分析和 Venn 图显示表层和底层间差异性最显著, Adonis 分析表明垂向间存在极其显著差异 ($P < 0.001$); 随机森林分析和网络分析的关键物种有交叉相同的物种 (*Bordetella*), 但差异贡献程度最高的物种不同, 分别为 *Ferrimonas* 和 unassigned; 中性群落模型 (NCM) 结果显示从表层到底层解释率逐渐增大, 整个淀区解释率最大 ($R^2 = 0.655$), 表、中和底层的标准化随机率 (NST) 分别为 0.29 ± 0.31 、 0.56 ± 0.35 和 0.88 ± 0.21 , 呈现极其显著差异 ($P < 0.001$); NCM 和 NST 结果表明由表层到底层随机性选择过程主导程度呈现加强趋势. 综上, 通过对该时期沉积物好氧反硝化菌群垂向分布特征和群落构建过程进行研究, 可为低温好氧反硝化菌的筛选提供技术支持.

关键词: 白洋淀; 冬季; 沉积物; 好氧反硝化菌; 垂向分布; 群落构建

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Vertical Distribution Characteristics and Community Construction of Aerobic Denitrification Bacteria from the Sediments of Baiyangdian Lake During the Winter Freezing Period

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Abstract: To explore the vertical distribution characteristics, key species identification, and community construction of aerobic denitrification bacteria from the sediments of Baiyangdian Lake during the winter freezing period, a MiSeq high-throughput sequencing technique based on *napA* was used. Moreover, microbial diversity analysis, species difference analysis, key species identification, and community construction were carried out. The results showed that high-throughput sequencing obtained 13 845 OTUs, which were divided into 10 phyla; Proteobacteria accounted for the largest proportion with 29.03%-94.46% and showed a decreasing trend from surface sediments to bottom sediments. The top two classes were β -Proteobacteria and γ -Proteobacteria, and the top three genera were *Cupriavidus*, *Aeromonas*, and *Thauera*. The α -diversity showed that the maximum Chao1 index of surface sediments was $3\,327.67 \pm 621.28$, which was significantly higher than that of bottom sediments ($2\,193.96 \pm 455.57$), and the maximum Simpson index of middle sediments was 0.97 ± 0.013 , which was significantly higher than that of surface sediments (0.94 ± 0.029). The principal coordinates analysis and Venn diagrams revealed that there were significant differences between surface sediments and bottom sediments. Adonis analysis showed significant differences in vertical distribution ($P < 0.001$). The random forest and network analyses had the same key species, such as *Bordetella*, but the species with the highest difference contribution degree differed (*Ferrimonas* and unassigned, respectively). The neutral community model (NCM) showed that the interpretation rate increased gradually from surface sediments to bottom sediments, and the whole area was the largest ($R^2 = 0.655$). The normalized stochasticity ratios (NST) were respectively 0.29 ± 0.31 , 0.56 ± 0.35 , and 0.88 ± 0.21 and showed significant differences ($P < 0.001$). NCM and NST showed that the dominant degree of random selection process showed a strengthening trend from surface sediments to bottom sediments. Considering all results of this study, the vertical distribution characteristics of aerobic denitrification bacteria in sediments during this period can provide technical support for the screening of low-temperature aerobic denitrification bacteria.

Key words: Baiyangdian Lake; winter; sediment; aerobic denitrification; vertical distribution; community construction

白洋淀作为我国华北地区最大的淡水湖泊, 目前存在的主要环境问题是富营养化^[1], 同时, 沉积物中赋存大量氮磷营养盐等污染物^[2], 由于水-沉积

物界面环境因素的变化, 导致氮磷污染物向上覆水扩散^[3,4], 因此对沉积物中污染物的治理也应重视. 天然水体大多呈现好氧状态, 其中氮素作为富营养

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化的主要污染物,因此,如何在好氧条件下实现生物脱氮是白洋淀水体实现自我修复的关键问题。

由于白洋淀地区冬季漫长而寒冷的气候特征,导致白洋淀水体微生物活性降低、水生植物代谢减弱和自净脱氮效果降低,同时上游接纳污水厂尾水的河流因低温影响会有总氮偏高的特征;由于实现低温条件下高效稳定的生物脱氮较为困难,因此部分好氧反硝化菌可在低温条件下脱氮的特征引起了关注.有研究分别从冬水田^[5]、养殖水体^[6]、松花江^[7]和水稻土壤^[8]等系统中分离出耐冷好氧反硝化菌.比如,蔡茜等^[5]的研究在冬水田中分离出1株耐冷碱蒙氏假单胞菌 H97,在 15℃ 下总氮去除速率达 $0.81 \text{ mg} \cdot (\text{L} \cdot \text{h})^{-1}$; Yang 等^[9]的研究在实验室生物反应器中分离出1株紫色杆菌 M-11,在 2℃ 下硝氮去除率达 89%; Kou 等^[10]的研究在低温条件下混合培养好氧反硝化菌处理微污染水体,硝酸盐氮去除率高于 65%.但目前大多研究仅处于实验室培养基环境下,针对天然环境下的研究却鲜见报道,可能是由于天然环境下高效菌筛选困难且对天然环境的认识不足,因此进一步进行天然环境下该时期好氧反硝化菌的群落结构以及关键物种的研究十分必要.群落构建过程的研究对如何维持群落稳定^[11]和调节群落结构^[12]发挥着重要作用,目前大多研究依据 16S rRNA 技术进行微生物群落的研究,但针对功能菌群落结构与群落构建过程的研究还较少^[13],因此明确该时期好氧反硝化菌群落构建过程^[14]十分重要.此研究不仅有助于进一步认识冬季天然环境下的氮循环微生物特征和群落构建过程,还有助于为将来适用于低温环境的高效菌筛选策略的制定和白洋淀周边污水厂污水脱氮的研究提供理论支持。

本文选取白洋淀冬季冰封期的沉积物样品,结合好氧反硝化菌功能基因 (*napA*) 的高通量测序技术分析该时期沉积物好氧反硝化菌群垂向分布特征;同时分析好氧反硝化菌群落差异和关键物种,明确该时期群落构建过程,以期定向筛选适合白洋淀冬季冰封期水体特征的低温好氧反硝化菌提供技术支持。

1 材料与方法

1.1 样品采集及测定

白洋淀是华北地区最大的淡水湖泊,位于河北省雄安新区,地理位置为 $38^{\circ}43' \sim 39^{\circ}02' \text{N}$ 、 $115^{\circ}38' \sim 116^{\circ}07' \text{E}$,总面积为 366 km^2 .结合前期研究^[1,4]和现场调研,本文选取 15 个采样点,分别为藻荇淀 (S1)、烧车淀 (S2)、文化苑 (S3)、鸳鸯岛 (S4)、枣

林庄 (S5)、平阳淀 (S6)、滂王淀 (S7)、鲋鲊淀 (S8)、端村 (S9)、白沟引河 (S10)、瀑河 (S11)、萍河 (S12)、唐河 (S13)、府河 (S14) 和潞笼河 (S15),具体采样点如图 1 所示,依据历史承载功能,白洋淀被划分为 5 个典型淀区, S1 为自然区 (AN), S2 ~ S4 为旅游区 (TA), S5 ~ S7 为生活区 (LA), S8 和 S9 为养殖区 (BA), S10 ~ S15 为入淀区 (EA). 2019 年 1 月采集沉积物样品,每个采样点分别采集表层 (0 ~ 2 cm, S)、中层 (2 ~ 4 cm, M) 和底层 (4 ~ 6 cm, B) 的沉积物样品,进行冬季沉积物好氧反硝化菌垂向分布特征分析及群落构建过程的研究。

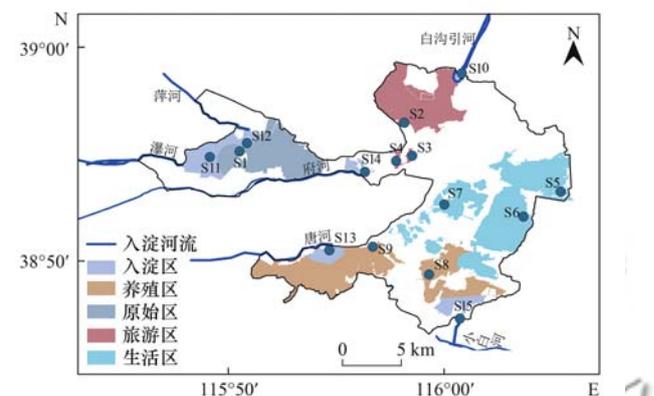


图 1 白洋淀冬季沉积物采样点示意

Fig. 1 Sampling sites of Baiyangdian Lake sediments during winter

1.2 DNA 提取与 PCR 扩增

提取沉积物样品中 DNA 并采用 NanoDrop 进行定量,用 1.2% 琼脂糖凝胶电泳检测 DNA 提取质量,并进行高通量测序.有研究表明,可通过 *napA* 功能基因来研究好氧反硝化菌群落特征^[15],因此利用提取的总 DNA 样本对沉积物的 *napA* 基因进行 PCR 扩增^[16],并由派森诺生物科技有限公司进行高通量测序,进而分析好氧反硝化菌群落垂向分布特征. PCR 扩增后进行测序工作,并采用 QIIME 得到有效数据。

1.3 微生物生物信息分析

利用 R 语言 QIIME2 软件对微生物群落的 α 多样性进行分析,菌群丰富度^[17]选用 Chao1 指数来评估,菌群的多样性^[18]选用辛普森指数 (Simpson 指数) 和香农指数 (Shannon 指数) 来表征,菌群的均匀度以 Pielou 指数来表征,测序深度^[19]以覆盖率指数 (Coverage) 来表征;利用 R 语言进行主成分分析 (principal component analysis, PCA)^[20] 和 Venn 图来研究采样点垂向沉积物的好氧反硝化菌群落的差异,并利用 Adonis 分析来研究垂向间菌群群落在统计学上的差异;利用 QIIME2 软件选用随机森林^[21] 算法确定垂向各分组间标志物种,利用 R 语言 igraph 包完成网络分析^[22] 进一步确定垂向各分组

间关键物种. 利用 R 语言完成中性群落模型 (NCM)^[23] 和标准化随机率 (NST)^[24], 明确确定性和随机过程在好氧反硝化菌群落构建中的相对重要性.

1.4 统计分析

由 R 和 Origin 软件完成本文所需绘图, 由 SPSS 23 完成数据统计分析. 其中 $P < 0.05$ 以“*”表示, 说明存在显著差异; $0.001 < P < 0.01$ 以“**”表示, 说明存在极显著差异; $P < 0.001$ 以“***”表示, 说明存在极其显著差异.

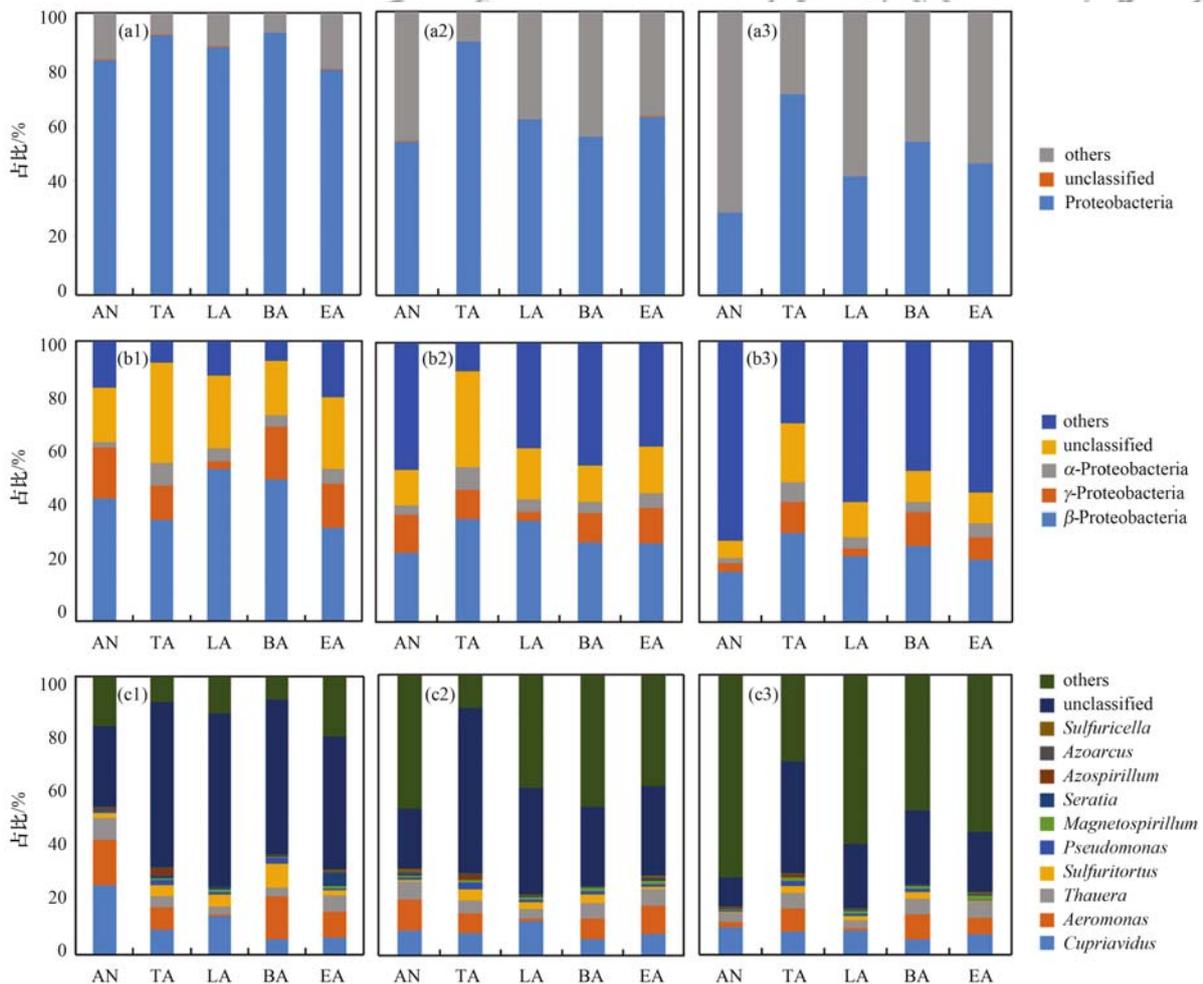
2 结果与讨论

2.1 微生物群落组成

为更深入分析冬季好氧反硝化菌群落组成, 此部分将进行垂向和水平两方面的分析. 结果显示该时期好氧反硝化菌属于 13 845 个 OTUs, 10 个门类 163 个属, 图 2 分别展示了菌群丰度较高门、纲和属的占比, 菌群丰度低于 0.1% 的物种归类为 others.

在门水平上, 10 个门类分别为变形菌门、放线菌门、拟杆菌门、厚壁菌门、蓝藻菌门、浮霉菌门、硝化螺旋菌门、异常球菌-栖热菌门、脊索动物和节肢动物. 如图 2(a1)~2(a3) 所示, 第一大门类为变形菌门 (Proteobacteria), 占比为 29.03%~94.46%, 变形菌门占比随着沉积物层深增加呈下降趋势, 其中旅游区各层深变形菌门占比明显高于其他淀区, 自然区减少最多, 从表层处的 83.22% 降低到底层处的 29.03%, 这与周石磊等^[25] 关于白洋淀春季沉积物变形菌门的变化趋势一致. 有研究发现, 变形菌门在碳和氮代谢过程中具有重要作用^[26], 放线菌门在降解有机物过程中起到主要作用^[27,28], 拟杆菌门主要参与硝化反应过程^[29], 厚壁菌门主要促进植物残留物的降解^[30]. 综上, 在门水平上, 变形菌门占比从表层到底层呈下降趋势, 其中旅游区减少缓慢, 自然区减少快速, 且各典型淀区间变形菌门占比存在差异.

图 2(b1)~2(b3) 为沉积物纲水平的菌群结



(a1) 门水平-表层, (a2) 门水平-中层, (a3) 门水平-底层; (b1) 纲水平-表层, (b2) 纲水平-中层, (b3) 纲水平-底层; (c1) 属水平-表层, (c2) 属水平-中层, (c3) 属水平-底层

图 2 白洋淀冬季沉积物好氧反硝化菌群门、纲和属组成分析

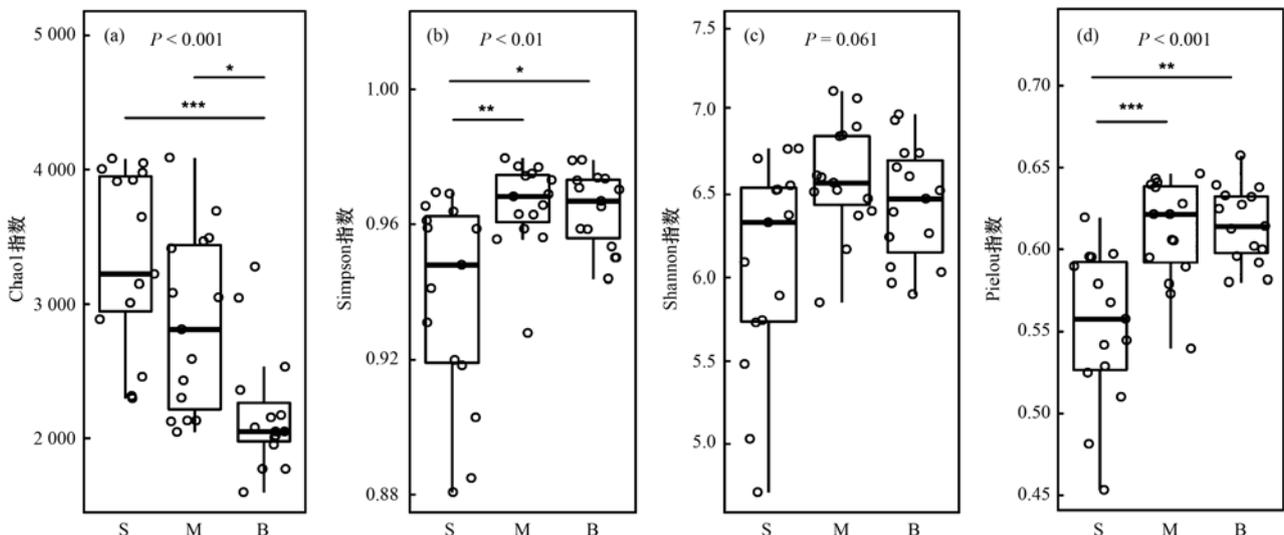
构, β -Proteobacteria 是第一大纲, 占比为 16.78% ~ 63.67%, 且随着沉积物层深增加呈下降趋势, 其中生活区占比减少最快, 入淀区减少最缓慢, 有研究发现 β -Proteobacteria 大多具有脱氮特性^[31]; γ -Proteobacteria 为第二大纲, 占比为 2.31% ~ 34.23%, 自然区和入淀区占比随着沉积物层深增加呈下降趋势, 其余淀区呈现下降后增加的趋势, 且研究发现 γ -Proteobacteria 在反硝化过程中发挥关键作用^[32]; α -Proteobacteria 为第三大纲, 占比为 1.31% ~ 15.43%, 其在氮磷代谢过程中发挥着重要作用^[33]. 综上, 在纲水平上, β -Proteobacteria 和 γ -Proteobacteria 占比从表层到底层呈下降趋势, 各典型淀区在纲水平的占比各不相同, 水平和垂向分组间均存在一定差异.

图 2(c1) ~ 2(c3) 为沉积物属水平的菌群结构, 其中占比前 10 的属包括: *Cupriavidus*、*Aeromonas*、*Thauera*、*Sulfuritortus*、*Pseudomonas*、*Magnetospirillum*、*Serratia*、*Azospirillum*、*Azoarcus* 和 *Sulfuricella*, 未分类的占比也较高, 可能与白洋淀沉积物中微生物研究较少有关. *Cupriavidus* 是第一大纲, 在表层自然区占比最高, 表、中和底层养殖区和入淀区占比均较低; *Cupriavidus* 属于 β -Proteobacteria 纲且具有脱氮特性^[31]. *Aeromonas* 在表层自然区和养殖区占比最大, 且从表到底层占比减少快速, 生活区各层 *Aeromonas* 占比最低; 研究表明其可在低温条件下进行高效异养硝化-好氧反硝化^[34]. *Thauera* 在表层自然区占比最高, 其余淀区各层深占比相差较小, 且研究表明其能够利用芳烃作为碳源进行反硝化^[35]. 同时研究发现 *Pseudomonas* 作为典型的好氧反硝化菌广泛存在于

污水废水系统和自然环境中^[36], 且具有耐冷嗜碱好氧反硝化作用^[5,34]. 综上, 在属水平上, 各典型淀区间好氧反硝化菌群差异性明显高于纲水平, 但在水平和垂向间好氧反硝化菌群的差异并不显著.

2.2 微生物 α 多样性分析

图 3 为各采样点沉积物垂向分组的好氧反硝化菌群 α 多样性指数. Chao1 指数反映微生物群落的丰富度, 表层 Chao1 指数值最大为 $3\,327.67 \pm 621.28$, 表明表层微生物群落最丰富, 菌群丰度最高; 且 Chao1 指数从表层到底层呈现随着采样深度增加而降低的趋势, 并且在垂向间均存在极其显著差异 ($P < 0.001$). Simpson 指数和 Shannon 指数反映微生物群落的多样性, 中层 Simpson 指数和 Shannon 指数值最大为 0.97 ± 0.013 和 6.59 ± 0.325 , 表明中层微生物群落多样性最高, 表层 Simpson 指数和 Shannon 指数值最小为 0.94 ± 0.029 和 6.09 ± 0.619 ; Simpson 指数和 Shannon 指数从表层到底层呈现先升后降的趋势, 并且 Simpson 指数在垂向间存在极显著差异 ($P < 0.01$), 而 Shannon 指数无显著差异. Pielou 指数反映菌群的均匀度, 底层菌群的均匀度最大为 0.62 ± 0.022 , Pielou 指数从表层到底层呈现随着采样点深度增加而增大趋势, 且在垂向间均存在极其显著差异 ($P < 0.001$). 采样点覆盖率指数变化范围为 0.983 ~ 0.995, 表明有足够测序深度, 且从表到底覆盖率指数不断增大. 综上, 白洋淀垂向上好氧反硝化菌群 α 多样性存在差异, 且表层沉积物微生物丰富度明显高于底层, 中层沉积物微生物多样性明显高于表层.



* 表示组间存在显著差异; ** 表示组间存在极显著差异; *** 表示组间存在极其显著差异

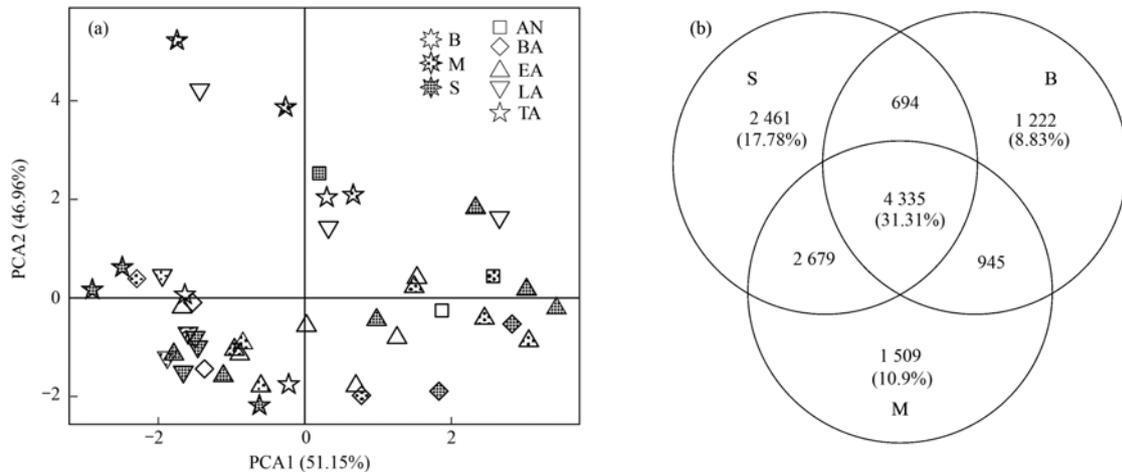
图 3 白洋淀冬季不同层沉积物好氧反硝化菌群生物多样性指数

2.3 微生物群落差异分析

2.3.1 主成分分析

通过主成分分析该时期垂向及典型淀区间沉积物好氧反硝化菌的差异,如图 4(a)所示,PCA1 和 PCA2 分别解释了总体变化的 51.15% 和 46.96%, 总共解释了整体变化的 98.11%。根据垂向分组显示,表、中和底层在 4 个象限均有分布,但表层多数采样点分布于三、四象限,中层多数采样点分布于二、三象限,底层多数采样点分布于—、三、四象限,表、中和底层间存在一定差异,可能是由于不同

层存在的环境差异引起的。根据淀区分组显示,生活区采样点主要集中于第三象限,旅游区采样点主要分布于第二、三象限,自然区主要分布于—、四象限,入淀区主要分布于—、三、四象限,养殖区采样点主要分布于第三、四象限,5 个典型淀区存在显著差异,可能是由于不同淀区环境因素差异引起的^[37]。通过 Adonis 分析各采样点的好氧反硝化菌群落结构的差异性,结果显示 $P < 0.001$, 表明了白洋淀冬季冰封期好氧反硝化菌群落结构在垂向间存在极其显著差异。



(b). 括号中数值为此部分占全部 OTUs 种类的百分数

图 4 白洋淀冬季不同层沉积物好氧反硝化菌的主坐标分析和韦恩图

Fig. 4 PCoA and Venn analysis of aerobic denitrification bacteria from sediments of different layers of Baiyangdian Lake during winter

2.3.2 Venn 图分析

使用 Venn 图分析该时期垂向间沉积物好氧反硝化菌群的差异,图 4(b) 每个椭圆代表不同层深,椭圆间的重叠区域指示分组间共有的 OTUs,每个区块的数字指示该区所包含的 OTUs 数目.图 4(b) 所示共存在的 OTUs 种类有 4 335 个,表、中和底层独有的 OTUs 种类分别为 2 461、1 509 和 1 222 个,表层 OTUs 种类明显高于中、底层;结合 α 多样性分析结果,微生物丰富度越高,OTUs 种类越多,这一结论与寇文伯等^[38]对鄱阳湖菌群研究结果一致,但微生物多样性指数越高,OTUs 种类越少,这一结果与其结论相反.相邻两层共有 OTUs 数目高于非相邻层,其中表层和中层共有的 OTUs 种类最多(2 679 个),表层和底层共有的 OTUs 种类最少(694 个),由于各分层间环境状况的差异引起 OTUs 种类存在较大差异,与靳燕等^[39]关于北运河浮游细菌研究中环境因子对 OTUs 种类有较大影响的结论一致.综上,该时期沉积物的好氧反硝化菌群在垂向上存在显著差异。

2.4 微生物标志物种分析

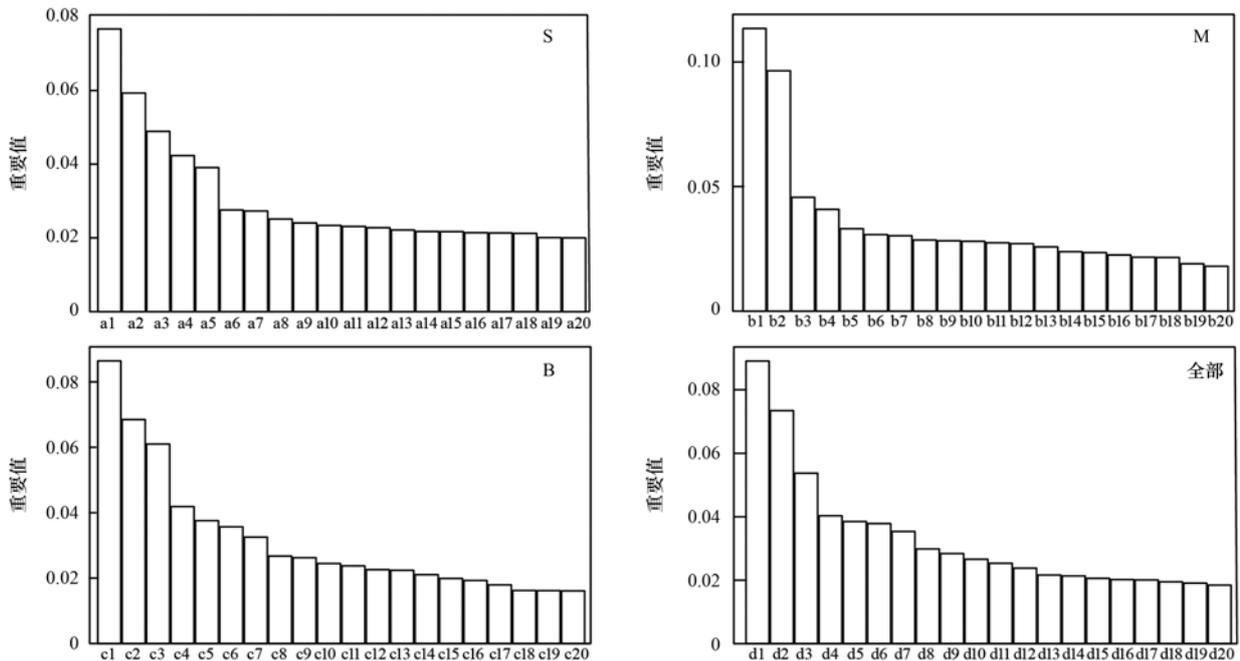
2.4.1 随机森林分析

通过随机森林分析出垂向分组间的标志物种,

图 5 分别为沉积物表层、中层、底层和整个淀区属水平重要性前 20 的菌群,重要性越强的物种对组间差异的贡献越大,此物种即为组间差异的标志物种.表层中, *Dechloromonas* 贡献最高,其次为 *Sulfuricurvum*; 中层、底层和整个淀区中, *Ferrimonas* 贡献最高,最新研究表明 *Ferrimonas* 在对变化环境的适应性反应中发挥相关作用^[40]; 中层中 *Desulfosaricina* 贡献次之,底层中 *Campylobacter* 贡献次之.表、中和底层与整个淀区相同的标志物种有 6 个,分别为 *Ferrimonas*、*Achromobacter*、*Azoarcus*、*Bordetella*、*Sulfuritortus* 和 *Azospirillum*, 其中所占比例前 10 的菌属有 3 个,分别为 *Azoarcus*、*Sulfuritortus* 和 *Azospirillum*, 因此菌属所占比例对标志物种存在明显影响.结果表明 *Ferrimonas* 对组间差异贡献最大。

2.4.2 网络分析

依据 Z_i 值和 P_i 值将所有节点划分为 4 类: 普通节点、模块核心、网络核心和连接点,当 $Z_i < 2.5$, $P_i \leq 0.62$ 时为普通节点,其余均为网络中的关键节点.图 6 所示,表层关键物种有 35 个,其中 unassigned 占比为 80%,其余为变形菌门,分别属于



a1. *Dechloromonas*, a2. *Sulfuricurvum*, a3. *Aeromonas*, a4. *Ferrimonas*, a5. *Bordetella*, a6. *Edwardsiella*, a7. *Terasakiella*, a8. *Citrobacter*, a9. *Sulfuricella*, a10. *Burkholderia*, a11. *Saccharophagus*, a12. *Bradyrhizobium*, a13. *Azospirillum*, a14. *Azoarcus*, a15. *Sulfuritortus*, a16. *Achromobacter*, a17. *Magnetospirillum*, a18. *Chelatococcus*, a19. *Sulfuritalea*, a20. *Paracoccus*; b1. *Ferrimonas*, b2. *Desulfosarcina*, b3. *Comamonas*, b4. *Chelatococcus*, b5. *Achromobacter*, b6. *Sulfurivermis*, b7. *Paracoccus*, b8. *Oceanimonas*, b9. *Azospirillum*, b10. *Sulfuritortus*, b11. *Dechloromonas*, b12. *Sulfuricurvum*, b13. *Thauera*, b14. *Pseudomonas*, b15. *Bordetella*, b16. *Rhodobacter*, b17. *Burkholderia*, b18. *Homo*, b19. *Azoarcus*, b20. *Aminobacter*; c1. *Aminobacter*, c2. *Campylobacter*, c3. *Aeromonas*, c4. *Bradyrhizobium*, c5. *Sulfuritortus*, c6. *Bordetella*, c7. *Achromobacter*, c8. *Sulfuricurvum*, c9. *Thauera*, c10. *Azoarcus*, c11. *Agrobacterium*, c12. *Thioalkalivibrio*, c13. *Homo*, c14. *Arcobacter*, c15. *Pseudomonas*, c16. *Shewanella*, c17. *Azospirillum*, c18. *Sinorhizobium*, c19. *Rhizobium*, c20. *Oceanithermus*; d1. *Ferrimonas*, d2. *Aeromonas*, d3. *Achromobacter*, d4. *Azoarcus*, d5. *Bordetella*, d6. *Sulfurivermis*, d7. *Sulfuritortus*, d8. *Bradyrhizobium*, d9. *Pseudomonas*, d10. *Azospirillum*, d11. *Chelatococcus*, d12. *Rhodobacter*, d13. *Paracoccus*, d14. *Edwardsiella*, d15. *Dechloromonas*, d16. *Sinorhizobium*, d17. *Thioalkalivibrio*, d18. *Comamonas*, d19. *Yersinia*, d20. *Rhizobium*

图5 白洋淀冬季不同层沉积物好氧反硝化菌随机森林分析重要性前20的属

Fig. 5 Top 20 genera of random forest analysis of aerobic denitrification bacteria from sediments of different layers of Baiyangdian Lake during winter

Saccharophagus、*Thauera*、*Bordetella* 和 unclassified. 中层关键物种有 9 个, unassigned 占比为 88.9%, 其余为 unclassified. 底层关键物种有 10 个, unassigned 占比为 90%, 其余为 unclassified. 组间共有关键物种有 8 个, 表层独有关键物种最多为 27 个, 中层无独有关键物种. 整个淀区关键物种有 9 个, 与中层关键物种完全相同. 其中 *Thauera* 为第三大菌属, 为表层独有关键物种, 可能与其所占比例远高于中层和底层有关, Wang 等^[41] 最新分离的 *Thauera* 菌属具有同时去除铵、亚硝酸盐和硝酸盐的能力. 综上, unassigned 对空间分组差异性贡献最大, *Saccharophagus*、*Thauera* 和 *Bordetella* 对空间分组差异性贡献最小, *Bordetella* 与随机森林分析的标志物种相同, 属于 β -Proteobacteria 且具有脱氮特性^[42].

应用 Erdos-Renyi 模型建立随机网络, 进一步验证微生物网络的拓扑特征是否有意义. 以图密度、平均路径长度、聚类系数等指标作为衡量标准^[43], 可评估网络之间拓扑特征的差异程度, 以反映微生

物互作的频率、复杂性以及环境异质性等. 如表 1 所示, 表、中和底层的节点数和边数均小于或等于整个淀区的, 因此整个淀区物种完全包含各层深所含的沉积物物种. 表层、中层、底层和整个淀区的微生物网络节点数、边数和图密度与随机网络相同, 且其余微生物网络的拓扑指数值均大于随机网络的拓扑指数值^[44]. 因此, 微生物网络的拓扑特征是有意义的.

2.5 微生物群落构建

为了明确确定性和随机过程在好氧反硝化菌群落构建中的相对重要性, 同时通过中性群落模型 (NCM) 和标准化随机率 (NST) 进行分析. 如图 7 所示, 使用 NCM 预测了该时期表层、中层、底层和整个淀区数据集相结合的亚群落中 OTU 出现频率与其相对丰度之间的关系, 表、中和底层的解释率 (R^2) 逐渐变大, 整个淀区中解释率最高, $R^2 = 0.655$, 表明随机过程在不同水文机制下对好氧反硝化菌群落的形成都非常重要; 并且好氧反硝化菌群

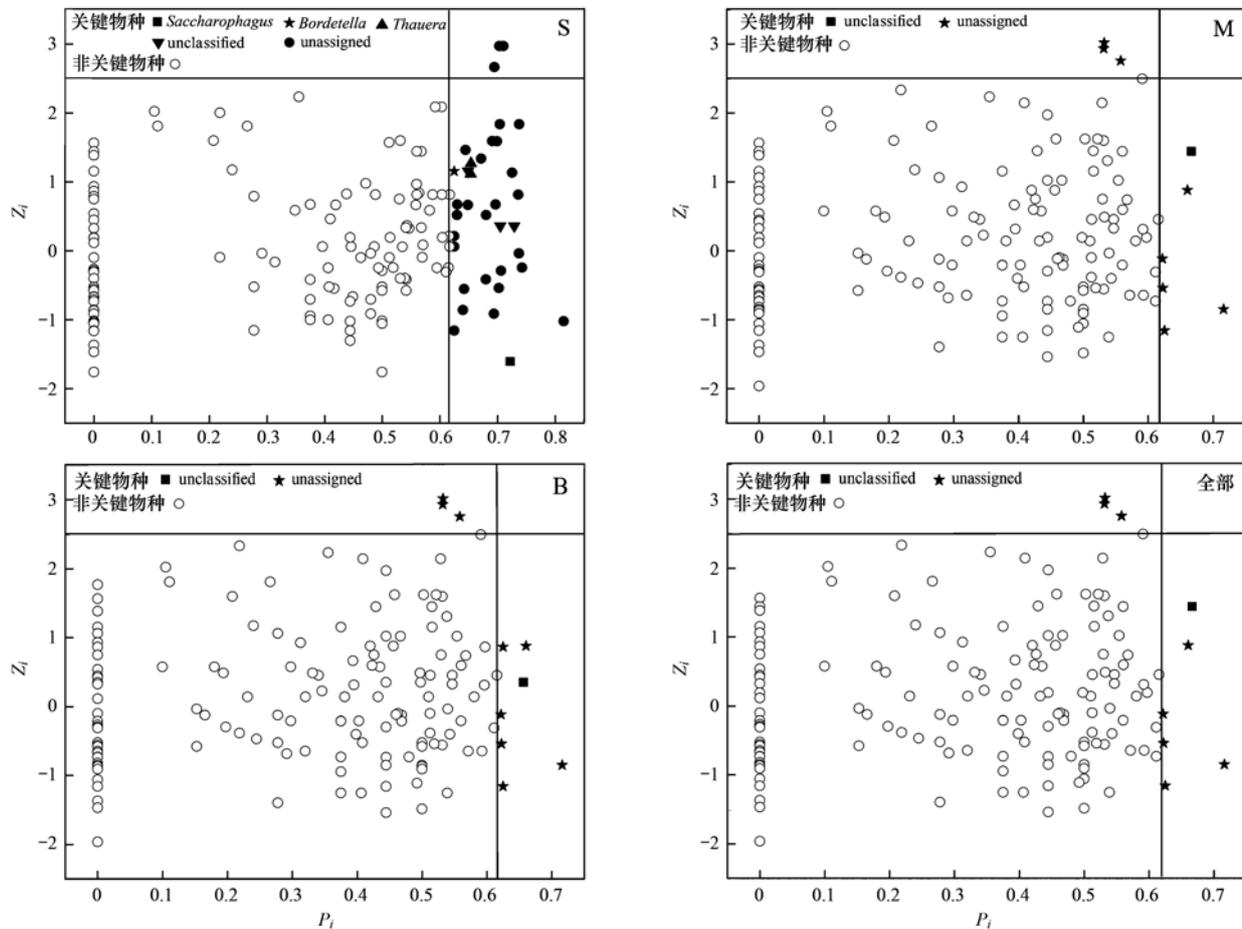


图 6 白洋淀冬季不同层沉积物好氧反硝化菌关键物种散点图

Fig. 6 A scatter diagram of key species of aerobic denitrification bacteria from sediments of different layers of Baiyangdian Lake during winter

表 1 白洋淀冬季不同层沉积物好氧反硝化菌网络分析拓扑指数

Table 1 Topological index of network analysis of aerobic denitrification bacteria from sediments of different layers of Baiyangdian Lake during winter

拓扑指数	微生物网络				随机网络			
	S	M	B	全部	S	M	B	全部
节点	283	285	282	285	283	285	282	285
边	1 409	1 414	1 409	1 414	1 409	1 414	1 409	1 414
图密度	0.035	0.035	0.036	0.035	0.035	0.035	0.036	0.035
模块度	0.382	0.374	0.373	0.374	0.286	0.287	0.286	0.286
网络直径	6.030	6.030	6.030	6.030	4.800	4.100	4.600	4.800
网络平均度	20.020	20.253	20.454	20.253	10.943	10.898	10.971	10.925
平均路径长度	3.131	3.132	3.111	3.132	2.699	2.704	2.695	2.704
聚类系数	0.455	0.452	0.453	0.452	0.035	0.034	0.037	0.035
介数中心性	615 314	625 759	601 680	625 759	167 781	183 017	173 625	192 004

在表层的 $N \times m$ 值最高, $N \times m$ 值为 11 207 (其中 $N = 14 587$, $m = 0.768$), 表明表层好氧反硝化菌群的物种扩散高于中层和底层^[45], 可能是由于表层直接与上覆水接触, 增强了表层物种扩散程度, 这与 Wan 等^[46] 的研究指出疏浚后细菌群落受随机性过程影响更大的结果一致. 如图 8 所示, 使用 NST 评估确定性和随机过程在群落构建中的相对重要性^[47], 表层好氧反硝化菌的 NST 值为 0.29 ± 0.31 , 分布在 50% 边界线以下, 表明表层确定性选择过程主导着该时期好氧反硝化菌群落构建; 底层好氧反硝化菌的 NST 值为 0.88 ± 0.21 , 分布在 50% 边界线以上, 表明底层随机

性选择过程主导着该时期好氧反硝化菌群落构建; 中层好氧反硝化菌的 NST 值为 0.56 ± 0.35 , 大部分分布在 50% 边界线以上, 表明中层随机性选择过程对该时期好氧反硝化菌群落的影响更大, 且表、中和底层呈现极其显著差异 ($P < 0.001$).

综上, 中性群落模型和标准化随机率结果均显示从表层到底层好氧反硝化菌群落构建确定性选择影响逐渐减小, 随机性选择影响逐渐增大. 这可能由于表层与上覆水接触, 因而导致表层可变性变强, 受确定性选择影响更大; 而中层和底层所接触的间隙水可变性较小, 因而随机性选择占主导. 一方面, 微

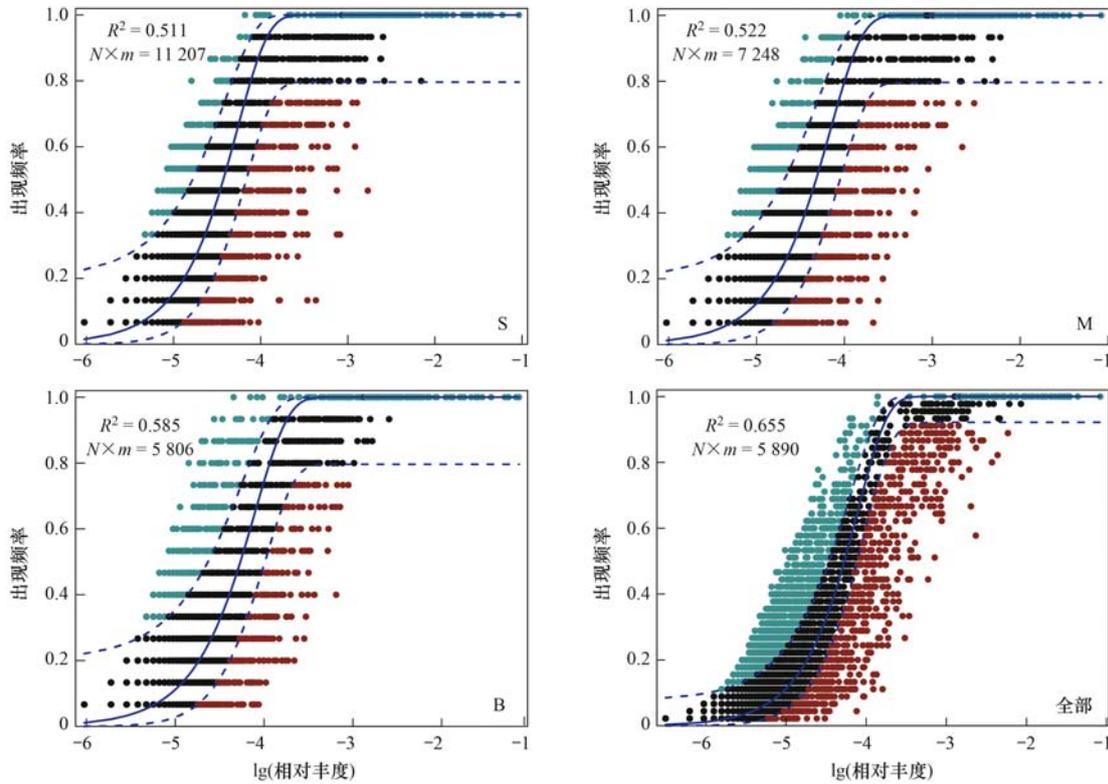


图7 白洋淀冬季不同层沉积物好氧反硝化菌的中性群落模型

Fig. 7 NCM analysis of aerobic denitrification bacteria from sediments of different layers of Baiyangdian Lake during winter

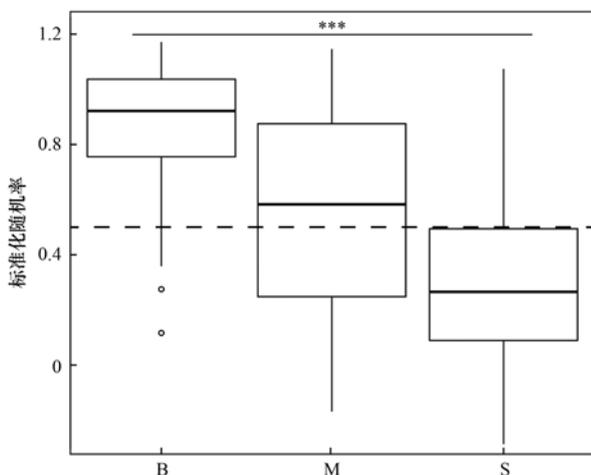
生物多样性讨论表明,从表层到底层微生物丰富度逐渐减小(S: $3\ 327.67 \pm 621.28$; M: $2\ 861.95 \pm 635.78$; B: $2\ 193.96 \pm 45.57$),更高的物种丰富度促进了菌群间的相互作用^[48],增加了从底层到表层群落构建过程确定性选择的影响,因而从表层到底层随机性选择影响逐渐增大.另一方面,与随机网络相比,微生物网络结构的存在暗示了群落构建中确

定性过程的存在,从表层到底层模块度逐渐减小(S:0.382; M:0.374; B:0.373)与随机性选择逐渐加强相吻合. Li等^[49]关于土壤真菌的研究结果表明随土层深度增加,确定性过程减少,随机性过程增加,这与本文结论相一致.因此,微生物多样性和网络分析结果与中性群落模型和标准化随机率分析结果相一致,从表层到底层群落构建过程随机性选择影响逐渐增大.

3 结论

(1)白洋淀冬季冰封期沉积物中好氧反硝化菌群属于10个门类163个属,属于13 845个OTUs,第一大门类为变形菌门,占比为29.03%~94.46%,随着沉积物层深增加呈下降趋势;第一大纲为β-Proteobacteria,占比为16.78%~63.67%;占比前三的属分别为*Cupriavidus*、*Aermonas*和*Thauera*.

(2)白洋淀冬季冰封期好氧反硝化菌群α多样性在垂向上存在差异,且沉积物表层微生物丰富度明显高于底层,沉积物中层微生物多样性指数明显高于表层.主成分分析和Venn分析表明,表层和中层存在差异较小,表层和底层差异最明显,且非相邻层沉积物的差异显著高于相邻层沉积物.通过Adonis分析表明该时期好氧反硝化菌群垂向间存在极其显著差异($P < 0.001$).



虚线表示50%分界线;***表示组间存在极其显著差异;圆点为底层的异常值

图8 白洋淀冬季不同层沉积物好氧反硝化菌的标准化随机率分析

Fig. 8 NST analysis of aerobic denitrification bacteria from sediments of different layers of Baiyangdian Lake during winter

(3) 随机森林分析表明, *Ferrimonas* 在垂向分组间贡献程度最高; 网络分析表明, unassigned 对垂向分组差异性贡献最大, *Saccharophagus*、*Thauera* 和 *Bordetella* 对垂向分组差异性贡献最小. 随机森林分析和网络分析的标志物种有交叉相同的物种 (*Bordetella*), 但差异贡献程度最高的物种不同.

(4) 通过中性群落模型(NCM)和标准化随机率(NST)分析, 表明表层确定性选择过程主导着该时期好氧反硝化菌群落构建, 而底层随机性选择过程占主导, 从表层到底层随机性选择过程主导程度逐渐增强, 且表层好氧反硝化菌群的物种扩散高于中层和底层. 标准化随机率结果表明, 表、中和底层呈现极其显著差异($P < 0.001$).

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