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# 金沙江丰富类和稀有类浮游真核微生物的分布特征与影响因素

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摘要:浮游真核微生物通常由少数丰富类和大量稀有类组成,二者在维持水生生态系统健康稳定方面具有重要作用.目前对大型筑坝河流中这两类真核微生物的生物地理分布模式所知甚少.以我国西南梯级水电开发河流金沙江为研究区域,对比分析丰富类和稀有类浮游真核微生物在不同河段的分布特征,解析影响两类微生物空间分布的主导因素.结果表明,相比上游自然河段,金沙江浮游真核微生物的α多样性在梯级大坝河段显著升高,稀有类的α多样性增长比高于丰富类.浮游真核丰富类和稀有类微生物的群落组成在不同河段间存在显著差异,其中 Vermamoeba 属等优势属的相对丰度在两河段间同样存在明显差异.影响丰富类和稀有类浮游真核微生物群落组成的关键地化因子有海拔和 pH 等,两类微生物群落相似性与地理距离和环境异质性均符合距离衰减关系,其群落构建均受扩散限制和环境筛选共同影响;方差分解分析和偏 Mantel 检验结果显示扩散限制是影响丰富类和稀有类分布的主要驱动因素.研究结果为我国西南缺资料区水电开发河流中微生物的地理分布模式和生态响应提供数据支持.

关键词:浮游真核微生物;稀有类;地理分布模式;扩散限制;金沙江 中图分类号: X172 文献标识码: A 文章编号: 0250-3301(2023)07-3864-08 **DOI**: 10.13227/j. hjkx. 202207269

# Distribution Characteristics and Influencing Factors of Abundant and Rare Planktonic Microeukaryotes in Jinsha River

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Abstract: Planktonic microeukaryotes are usually composed of a few abundant species and a large number of rare species, which play an important role in maintaining the health and stability of aquatic ecosystems. At present, little is known about the biogeographical distribution patterns of these two groups of microeukaryotes in large damming rivers. This study analyzed the distribution patterns of abundant and rare planktonic microeukaryotes and the dominant factors affecting their spatial distributions in the Jinsha River, one of the largest rivers in southwestern China that is strongly regulated by cascade dams. The results showed that the alpha diversity of planktonic microeukaryotes in the Jinsha River was higher in the cascade dam reach than that in the upstream natural reach, and the increase in alpha diversity of rare species was larger than that of rich species. There were significant differences in microbial community composition among different river sections, and the relative abundances of the dominant genera such as Vermamoeba shared by them were also significantly different between the two river sections. The results of distance decay analysis revealed that the geographic distribution patterns of rare and abundant taxa were jointly influenced by environmental heterogeneity and dispersal limitation, and the results of variance decomposition analysis and partial Mantel further indicated that dispersal limitation was the dominant ecological process. The results provided data support for the distribution and ecological response of microorganisms in rivers in the areas lacking data in Southwest China.

Key words: planktonic microeukaryotes; rare taxa; biogeographic pattern; dispersal limitation; Jinsha River

真核微生物形态大小各异,分布广泛,具有高度的多样性,在生物地球化学循环和能量流动方面发挥着重要作用<sup>[1,2]</sup>.多数微生物通常由少数丰富类和大量稀有类组成,丰富类是生态系统中生物量的主要贡献者,而稀有类则是维持生态系统多样性和稳定性的重要类群<sup>[3,4]</sup>.研究丰富类和稀有类的分布特征与影响因素对认识水域生态系统的功能具有重要意义<sup>[4]</sup>.环境筛选(与环境异质性相关)和扩散限制(与地理距离相关)是影响微生物群落组成的关键生态学过程<sup>[5]</sup>.这两个过程在微生物群落构建中通常共同发挥作用,但在不同生态系统或环境介质中,各自的作用强度不同<sup>[6]</sup>.已有河流微生物生

态学相关研究重点解析了浮游细菌的沿程生态演替 规律和群落建成机制<sup>[7,8]</sup>,但丰富类和稀有类浮游 真核微生物在大型河流的地理分布模式及影响因素 仍不甚了解.

金沙江是我国西南地区最重要的大型河流之一,也是微生物信息资料缺乏区<sup>[9]</sup>.由于金沙江等西南河流的自然环境条件复杂,同时受到水电开发

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等强人类活动影响,是典型的生态脆弱区[10,11].已有研究以细菌为主要微生物类群,开展了西南河流微生物的初步普查,重点阐释了澜沧江等河流中浮游细菌的群落组成及时空变化规律[12~14].然而,目前对西南河流浮游真核微生物信息仍十分匮乏,其对梯级水电开发的响应更不清楚.解析金沙江浮游真核微生物的地理分布模式,对于补充西南缺资料区数据信息、认识西南河流的生物生境特征及响应规律具有重要意义.本研究利用 18S rRNA 基因扩增子测序技术,对比分析丰富类和稀有类浮游真核微生物在不同河段的分布特征,解析影响两类微生物空间分布的主导因素,以期为我国西南河流微生物的分布规律和生态响应提供数据支持.

#### 1 材料与方法

#### 1.1 样品采集与地化因子测定

研究区域范围覆盖金沙江干流河长2 279 km, 海拔范围为3 441~250 m. 共布设 49 个采样点(图 1),包括上游河段采样点共 13 个(N1~N13),其中 N13 位于梨园(LY)水库变动回水区以外,不受水库 蓄水影响;中下游河段采样点共 36 个(LY.1至 CJD).金沙江上游主要为自然流态河段,定名为"上 游自然河段";中下游人类活动的影响主要是梯级 大坝的建设,定名为"梯级大坝河段".

于2019年9月进行现场观测和水体样品采集. 使用GPSMAP62s(Garmin, KS, USA)现场记录每个采样点的经度、纬度和海拔,使用便携式HQ40d多参数水质分析仪(Hach, CO, USA)测量水温

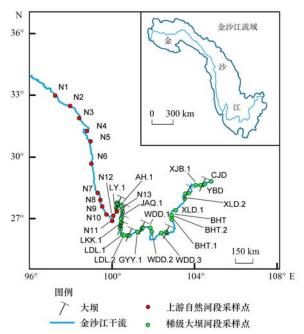


图 1 金沙江 49 个采样点位分布示意

Fig. 1 Distribution of the 49 sampling sites along the Jinsha River

(T)、电导率(Ec)、pH 值和溶解氧(DO);使用便携式 2100P 浊度仪(Hach, CO, USA) 现场测定水体浊度. 在每个采样点采集 3 份表层水样, 共获得 147份水样. 采集的水样分两部分, 一部分水样用 0. 22  $\mu$ m 孔径的聚碳酸酯滤膜过滤收集浮游微生物;另一部分水样运送回实验室, 参照 Xue 等[15]的方法, 测定水样的 pH、电导率(Ec)、总有机碳(TOC)、硝氮(NO $_3^-$ )、氨氮(NH $_4^+$ )、有效磷(AP)、总氮(TN)和总磷(TP)等理化指标. 采样点信息及水体理化性质数据已在 Chen 等[6] 研究中详细列出.

#### 1.2 DNA 提取和高通量测序

使用 PowerWater DNA 提取试剂盒(MoBio, CA, USA)提取水样中微生物 DNA,具体方法参照 试剂盒说明书. 根据 Xue 等[15] 的方法,选取带 barcode 的特异性引物 528F(5'-GCGGTAATTCCAG CTCCAA-3') 和 706R (5'-AATCCRAGAATTTCACC TCT-3'),对 18S rRNA 基因的 V4 高变区进行 PCR 扩增.参照 Liu 等[16]的方法构建基因文库,将各样 品的 PCR 产物以等量(mol)混合,使用 Illumina MiSeq PE250 平台(Illumina, San Diego, CA, USA) 进行双端测序. 使用 QIIME2(v. 1.8.0) 平台切除序 列的引物片段,弃去未匹配引物的序列.使用 DADA2 算法对原始数据进行质量过滤,将过滤后的 高质量序列按照100%的相似性聚类成扩增子序列 变异体(ASV). 选择每个 ASV 中出现频数最高的序 列,在Silva数据库中采用RDP分类器对ASV代表 序列进行比对注释. 最后以序列最少的样本为标准 将 ASV 均一化处理,最大限度消除由于测序量不同 而导致的偏差. 参照 Zhang 等[17]的方法,从测序得 到的真核生物数据集中排除了后生动物等多细胞动 物的 ASVs. 参照 Mo 等[18]的方法,将平均相对丰度 大于 0.1% 的 ASV 界定为丰富类,将平均相对丰度 小于 0.001% 的 ASV 界定为稀有类.

#### 1.3 数据分析

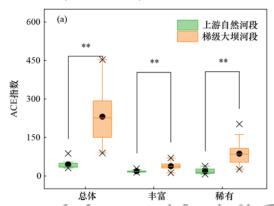
使用 R 3.5.1 软件的"vegan"程序包进行以下分析:①计算样品的浮游真核微生物 α 多样性指数 (ACE 指数和 Shannon 指数);②基于样品间 Bray-Curtis 距离计算浮游真核微生物的 β 多样性,并采用非度量多维尺度分析(NMDS)可视化不同样品间真核微生物的群落结构差异;③使用相似性分析(ANOSIM)方法检测各样品间群落组成差异的显著性;④进行 Mantel 检验,分析单个环境因素或地理因素与浮游真核微生物群落相似性的相关性;⑤基于欧式距离计算环境差异性矩阵,用于距离衰减分析;⑥通过方差分解分析(VPA)计算地理距离和环境因素对浮游真核微生物群落结构变异的解释率.

其中基于地理距离的空间变量使用主轴邻距法 (PCNM)进行计算; ⑦用偏 Mantel 检验确定所有的 环境因素或地理距离的共同作用与群落结构是否显 著相关. 利用 PASSAGE2 软件(www. passagesoftware. net)对群落相似性、地理距离和环 境差异性矩阵进行线性化.

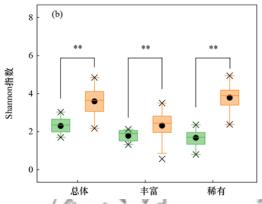
#### 结果与分析

#### 2.1 浮游真核微生物的 α 多样性

如图 2 所示, α 多样性 (ACE 指数和 Shannon



指数)分析结果表明,浮游真核微生物总体、丰富类 和稀有类的 α 多样性在不同河段间(上游自然河段 和梯级大坝河段)存在显著差异性(ACE 指数:P< 0.01; Shannon 指数: P < 0.01). 相比上游自然河 段,梯级大坝河段总体、丰富类和稀有类的 ACE 指 数平均值分别增加了 412%、104% 和 374% 「图 2 (a)], Shannon 指数平均值分别增加了 56.5%、 30.0% 和 126% 「图 2(b)]. 稀有类 ACE 指数和 Shannon 指数平均值在梯级大坝河段的增加幅度均 高于丰富类.



箱体内的横线表示数据中值,实心圆表示数据平均值,叉号表示数据最大值和最小值; \*\* 表示 P < 0.01

#### 图 2 金沙江浮游真核微生物的 ACE 指数和 Shannon 指数

Fig. 2 ACE index and Shannon index of planktonic microeukaryotes in the Jinsha River

#### 2.2 浮游真核微生物的群落组成

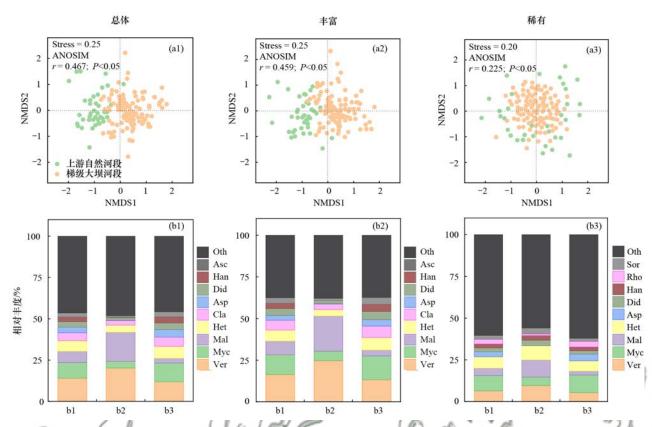
浮游真核微生物总体、丰富类和稀有类的 NMDS 分析结果如图 3(a) 所示, 总体和丰富类的上 游自然河段(N1~N9)和多数梯级大坝河段(AH.1 至 CJD) 样点明显分开, 而稀有类的梯级大坝河段样 点相比上游自然河段分布较为聚集. ANOSIM 分析 结果显示,总体、丰富类和稀有类浮游真核微生物 的群落组成在两个河段间均呈现出显著差异(P< 0.05),稀有类(r=0.225)在河段间的差异性小于 丰富类(r=0.459).

图 3(b)显示了金沙江浮游真核微生物优势属 的相对丰度,总体和丰富类的优势属相同,主要包 括 Vermamoeba、麦克属(Mychonastes)、马拉色菌 属(Malassezia)、Heteromita、曲霉菌属(Aspergillus) 和亚隔孢壳属(Didymella),这些优势属在总体和 丰富类中的总相对丰度占比均高于50%.除与总 体和丰富类共有的优势属外,稀有类的优势属还 有 Rhogostoma 和 Sorodiplophrys. 相比上游自然河 段,不同浮游真核微生物类群的 Vermamoeba 属和 马拉色属在梯级大坝河段的相对丰度均较低;例 如,总体、丰富类和稀有类的 Vermamoeba 属在梯 级大坝河段的相对丰度分别为11.8%、13.3%和 5.3%, 明显低于上游自然河段(总体: 20.1%; 丰

富类:24.7%;稀有类9.5%).相反,总体、丰富类 和稀有类的麦克属在上游自然河段的相对丰度分 别为 4.2%、5.7% 和 5.1%,均低于梯级大坝河段 (总体:11.4%; 丰富类:14.3%; 稀有类: 10.6%).可见,丰富类和稀有类真核微生物的主 要优势属相对丰度在不同河段间表现出相似

规律. 2.3 地化因子与浮游真核微生物群落组成的相关性 Mantel 分析结果显示(表1),总体、丰富类和

稀有类与海拔、地理距离、水温、pH、TP、DO、Ec 和 NO; 等地化因子均具有显著相关性(P < 0.05), 说明浮游真核微生物的群落组成可能受多种地理因 素和环境因素共同影响.海拔(总体:r=0.35;丰 富:r=0.35; 稀有:r=0.08)、地理距离(总体:r= 0.39; 丰富:r=0.39; 稀有:r=0.09)和TP(总体:r =0.32; 丰富:r=0.30; 稀有:r=0.08) 与浮游真核 微生物群落的相关性较高,推测为影响程度较大的 地化因子. 丰富类和稀有类的影响因子也存在一定 差异, 例如丰富类与 DOC 无显著相关性 (P> 0.05), 而稀有类与 DOC 显著相关(P<0.05); 稀有 类与浊度无显著相关性(P>0.05),但丰富类与浊 度有显著相关性(P<0.05),且稀有类的相关系数 r 值均较低.



(a) NMDS,(b) 优势属的相对丰度; Ver: Vermamoeba 属, Myc: Mychonastes 麦克属, Mal: Malassezia 马拉色菌属, Het: Heteromita 属, Cla: Cladospori 属, Asp: Asp: Aspergillus 曲霉菌属, Did: Didymella 亚隔孢壳属, Han: Hannaella 属, Asc: Ascochyta 壳二孢属, Rho: Rhogostoma 属, Sor: Sorodiplophrys 属, Oth: others 其他; b1 表示全河段, b2 表示上游自然河段, b3 表示梯级大坝河段

#### 图 3 金沙江浮游真核微生物的 NMDS 分析和优势属的相对丰度

Fig. 3 NMDS analysis of planktonic microeukaryotes and relative abundances of their dominant genera in the Jinsha River

#### 表 1 Mantel 检验分析显示地化因子对浮游真核微生物群落的影响

Table 1	Mantel tests showing the	effects of geochemical	factors on planktonic	micro eukaryotic community

此化四マ	É	体	丰1	富类	稀	有类
地化因子	r	P	r	P	r	P
海拔	0.35	0.001	0. 35	0.001	0. 08	0. 001
距离	0.39	0.001	0.39	0.001	0.09	0.001
水温	0. 25	0.001	0. 26	0.001	0.06	0.001
浊度	0.08	0.015	0.09	0.018	0. 02	0. 121
DO	0.08	0.011	0.08	0.017	0.05	0.002
Ec	0. 23	0.001	0. 23	0.001	0. 07	0.001
рН	0. 24	0.001	0. 23	0.001	0.06	0.002
DOC	0.07	0. 021	0.05	0. 118	0. 04	0.020
TP	0.32	0.001	0.30	0.001	0.08	0.001
TN	0.01	0. 334	0.01	0.418	-0.01	0. 701
SRP	-0.05	0. 891	-0.06	0. 901	0. 01	0. 188
NH <sub>4</sub> <sup>+</sup>	-0.01	0. 813	-0.01	0. 539	0. 01	0. 207
$NO_3^-$	0. 12	0.001	0. 11	0.002	0.05	0. 001

## 2.4 地理距离和环境异质性对浮游真核微生物群落组成的影响

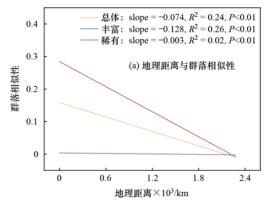
距离衰减分析表明[图 4(a)和 4(b)],总体、丰富类和稀有类浮游真核微生物的群落相似性与地理距离和环境异质性之间均存在显著的负相关关系(P<0.01),符合距离衰减关系,说明其群落结构受扩散限制和环境筛选共同影响.在表征距离衰减关

系的线性回归方程中,地理距离和环境异质性对稀有类回归方程的斜率(衰减率)分别为 0.003 和 0.005,明显低于丰富类的 0.128 和 0.179,说明稀有类受环境筛选和扩散限制的影响较小.

方差分解分析(VPA)结果显示[图 5(a)],丰富类和稀有类的群落差异性分别由环境异质性和地理距离共同解释了30.6%和20.2%,稀有类的未解

释率为 79.8%,高于丰富类的 69.4%;丰富类和稀有类分别由地理距离单独解释了 14.9% 和 10.2%,高于环境异质性的 11.1% 和 6.66%.如图 5(b)所示,偏 Mantel 检验结果表明,总体、丰富类和稀有类浮游真核群落组成受环境异质性和地理距离共同影

响(P<0.05),且三者与地理距离(总体:r=0.363;丰富:r=0.368;稀有:r=0.098)的相关性均高于环境异质性(总体:r=0.098;丰富:r=0.073;稀有:r=0.032),说明扩散限制可能是影响浮游真核微生物群落的主导过程.



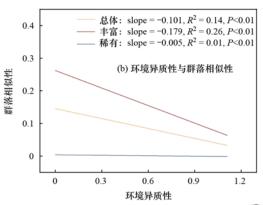
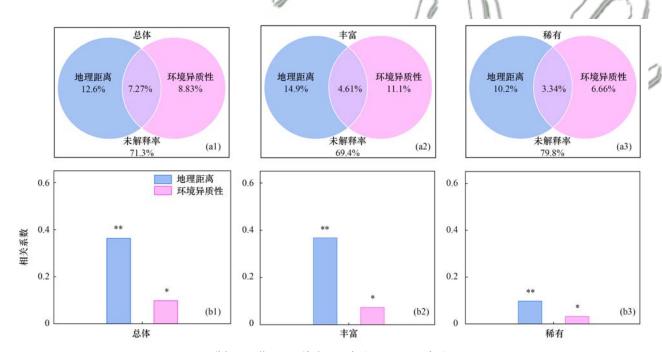


图 4 金沙江浮游真核微生物群落相似性与地理距离和环境异质性的距离衰减关系

Fig. 4 Distance decay relationships between similarity of planktonic microeukaryotic community and geographic distance and environmental heterogeneity in the Jinsha River



(a) VPA 分析,(b)偏 Mantel 检验; \*\* 表示 P < 0.01, \* 表示 P < 0.05

图 5 金沙江浮游真核微生物的 VPA 分析和偏 Mantel 检验 Fig. 5 VPA analysis and partial Mantel test of planktonic microeukaryotes in the Jinsha River

#### 3 讨论

本研究中浮游真核微生物的 α 多样性表现为 梯级大坝河段较上游自然河段显著增加[图 2(a)和 2(b)]. 这种梯级大坝河段 α 多样性的提高可能有 如下 3 点原因:①大坝的修建阻碍了河流的连通性,使大坝前方形成新的河流汇流点,因此微生物多样性在大坝河段显著升高<sup>[19]</sup>,而笔者的研究结果验证 了这一点;②有文献表明携带不同微生物群落的环

境介质的混合将产生新的微生物群落,即"群落融合"<sup>[20]</sup>,金沙江大坝蓄水后库区内水位上升,增加了与河岸带土壤的交互作用范围,进而将沿河土壤中的微生物物种带入水体,这种不同环境介质的微生物群落融合,是梯级大坝河段浮游真核微生物多样性增加的可能原因之一;③金沙江下游水体的 TP 等营养物指标高于上游,表明下游营养物质较上游更为丰富<sup>[6]</sup>,基于"多个体假说",资源的高效获取会导致个体数量的增加<sup>[21]</sup>,导致微生物的α多样性

提高. 同时, 笔者发现浮游真核微生物稀有类的 α 多样性在梯级大坝河段的增加幅度高于丰富类. 这可能与丰富类和稀有类在生态功能及环境适应性等方面的差异性有关, 也支持了稀有类群是微生物多样性的主要贡献者这一观点<sup>[22]</sup>. 由于稀有类较高的α 多样性, 增加了群落的功能冗余, 从而提高了微生物对河流筑坝带来的变化环境的耐受能力<sup>[15,23,24]</sup>.

金沙江浮游真核微生物的群落组成在不同河段 间存在显著差异[图 3(a)]. 本研究区域覆盖 2 279 km河段,海拔变幅3 191 m,沿程地形地貌从 上游的高山峡谷到中下游的盆地,浮游真核微生物 在河段间的空间差异特征,可能与大河流域的土地 利用类型、地貌特征、海拔等地理地质因素密切相 关[25,26]. 如 Liu 等[27] 发现长江流域浮游细菌群落的 空间差异与土地利用类型密切相关,同一地形的细 菌群落趋向于彼此相似,而所在地形类型不同的细 菌群落之间存在明显差异; Chen 等[6] 发现海拔和 地理距离是金沙江细菌和真菌在河段间差异性的主 导驱动因素. 另一方面金沙江因修建梯级大坝带来 水温、pH、DO 和营养盐等水体理化性质的变 化<sup>[28,29]</sup>. 而水温、pH、DO 和营养盐等环境因素对 控制水体中微生物的群落组成有重要作用[30-32]. 如 水温和 pH 会直接或间接影响真核微生物的生长和 新陈代谢<sup>[33,34]</sup>. Mental 结果表明金沙江浮游真核微 生物群落组成与海拔和地理距离等地理因素和水 温、pH、DO 和 TP 等环境因素均显著相关(表1). 根据 NMDS 和 ANOSIM 的分析结果,笔者发现相比 于丰富类,稀有类河段间群落组成差异性较小[图3 (a)],且与多种地化因子的相关性均较低(表1). 这可能与两类微生物对环境变化的敏感性有关. 通 常丰富类群在环境中更活跃,对环境变化高度敏感; 而稀有类在环境中多数处于休眠状态,这种生态策 略使其对环境变化的耐受性更强[35,36].

金沙江浮游真核微生物的物种注释与相对丰度 分析显示,麦克属和 Vermamoeba 属为主要优势属, 均属于河流、湖泊等水域生态系统中常见的真核微 生物<sup>[37-39]</sup>.其中,麦克属作为典型的绿藻纲微型生物,其有着各种潜在碳浓缩机制,为不同环境下的碳 同化提供了更多的可能<sup>[40]</sup>.由于金沙江梯级大坝河 段水体中的无机碳含量如碳酸根等低于上游自然河 段水体<sup>[29]</sup>,而麦克属独有的高适应性碳同化能力, 增强了其在碳源较为枯竭条件下的竞争能力,使其 得以大量繁殖,这为麦克属在梯级大坝河段相对丰 度较高的现象提供了解释. Vermamoeba 属是一种肉 足纲的变形虫,可以作为宿主细胞支持其他微生物 的生长繁殖,使其他微生物免受不利环境的干扰,而 宿主细胞往往会裂解死亡<sup>[37]</sup>. 这种对其他微生物的保护机制可能是 Vermamoeba 属在梯级大坝河段相对丰度较低的原因. 同时笔者发现稀有类的优势属相对丰度占比较丰富类有所下降,推测原因有 2 点:①稀有类对降水和营养波动等偶发事件有明显响应,导致部分物种在压力条件下保持低增长率;②低丰度的稀有物种在竞争中被其他丰富物种在营养物质获取等方面抑制,导致负频率依赖现象<sup>[41]</sup>.

揭示微生物群落的构建和组装机制是当前微生 物生态学的研究重点[41~43]. 本研究发现金沙江浮游 真核微生物丰富类和稀有类的群落构建受到环境筛 选和扩散限制的共同作用(图 4 和图 5). 偏 Mantel 和 VPA 结果表明,相比于环境筛选,扩散限制是丰 富类和稀有类真核微生物群落构建的主导驱动过 程. 扩散限制和环境筛选对微生物群落构建的相对 贡献,与研究区域的空间尺度有关[18,44]. Wu 等[44] 研究表明,真菌的地理分布模式在大区域尺度上 (1000~4000 km)受扩散限制影响较强,而环境异 质性对在较小尺度(<1000 km)的真菌变异解释率 较高. 笔者在金沙江的研究区域空间距离超过 2000 km,扩散限制在大尺度空间中微生物的群落 构建可能发挥主导作用.此外,河流筑坝形成的物理 阻隔,导致蓄水区微生物种群的空间隔离,极大地限 制了微生物沿河流的流动和扩散,提高了扩散限制 对真核微生物群落构建的影响权重[25].另一方面, 根据"尺寸-可塑性"假说,扩散限制的影响会随微生 物体型的增加而增加[45]. 而相比细菌、古菌等微生 物类群,真核微生物体型较大,这使得它们更容易受 到大坝河段的扩散限制的影响[46]. 同时基于 VPA 结果,笔者发现总体、丰富类和稀有类的未解释率 均较高,且稀有类的未解释率高于丰富类.未解释率 均较高的原因可能与微生物之间的相互作用、未监 测到的环境因素或生物因素有关[8,47]. 而稀有类比 丰富类更高的未解释率,则可能是因为稀有类占据 了狭窄的生态位,经常与其他物种发生相互作用,例 如竞争等[41].

#### 4 结论

- (1)金沙江浮游真核微生物的 α 多样性在梯级 大坝河段显著提高,相比丰富类,稀有类的增加幅度 更为明显.
- (2)丰富类和稀有类浮游真核微生物群落组成在上游自然河段和梯级大坝河段之间均差异显著,且两类微生物的 Vermamoeba 属等优势属相对丰度在不同河段间表现出类似规律.
  - (3)海拔、pH 等是影响丰富类和稀有类浮游真

核微生物群落组成的关键地化因子,两类微生物的 地理分布受扩散限制和环境筛选共同影响,其中扩 散限制是两类微生物群落构建的主导生态学过程. 参考文献:

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