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黄山土壤细菌群落和酶活性海拔分布特征

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摘要: 黄山具有保存较完整的生态系统及明显的地势高差,为研究中亚热带森林生态系统土壤微生物群落海拔分布格局提供天然场所. 本研究在黄山景区 670~1 870 m 按每 100 m 的间隔采集土样,利用 Illumina MiSeq 高通量测序技术分析土壤细菌群落结构及多样性的海拔变化特征,同时测定相关土壤理化性质和土壤酶活性. 结果表明:①土壤全氮、碱解氮、全钾和总有机碳含量均存在显著海拔差异(P<0.01),且总体上随着海拔升高而增加;土壤蔗糖酶活性存在显著海拔差异(P<0.01),且总体上随海拔升高而增强,但酸性磷酸酶和脲酶活性无显著海拔分异(P>0.05);②将 12 个海拔梯度分为高中低3组(低海拔 670~875 m;中海拔 1 080~1 370 m;高海拔1 460~1 780 m),发现土壤细菌 OTU 数目:中海拔 > 低海拔 > 高海拔,但是高、中、低海拔的差异不明显;③在 875~1 370 m 小范围海拔内,土壤细菌群落多样性沿海拔呈单峰模式分布;而在 670~1 780 m 整个海拔范围内,土壤细菌群落多样性无明显海拔分布模式;④所有样地中,相对丰度大于 3%的优势菌门共 7 个,优势菌目共 15 个;⑤相关性热图分析表明,土壤 pH 对不同海拔土壤细菌群落结构差异性影响最大. Pearson 相关性分析和偏 Mantel 分析表明,细菌群落 α 多样性 (P<0.01)和 β 多样性 (偏 Mantel r=0.560, P=0.001)主要受土壤 pH 影响. 因此,土壤 pH 是决定黄山不同海拔土壤细菌群落结构及多样性的主要环境因子.

关键词:黄山;细菌群落结构;Illumina 高通量测序;土壤 pH;土壤酶活性

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Elevational Distribution Characteristics of Soil Bacterial Community and Enzyme Activities in Mount Huangshan

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Abstract: Mount Huangshan has a well-preserved ecosystem and obvious differences in vertical geography, which provide a natural laboratory for studying the altitudinal distribution patterns of soil microbial communities in a mid-subtropical forest ecosystem. The soil bacterial community structure and diversity of the samples collected every 100 m from 670 to 1870 m on the south slope of Mount Huangshan were examined using Illumina MiSeq high-throughput sequencing technology. The soil physicochemical properties and soil enzyme activities of the samples were also measured to explore the relationship between bacterial communities and soil properties as well as enzyme activities. The results showed that ① The contents of soil total nitrogen, available nitrogen, total potassium, and total organic carbon were significantly different across the altitudes (P < 0.01) and generally increased as altitude increased. The soil sucrase activities across altitudes were significantly different (P < 0.01), and generally increased as altitude increased. However, there was no significant difference in acid phosphatase and urease activities between different altitudes (P > 0.05). 2 The 12 elevational gradients were divided into three groups: low altitude (670-875 m), medium altitude (1080-1370 m), and high altitude (1 460-1 780 m). The OTUs in low altitude sites were greater than in high altitude sites but lower compared to medium altitude sites. However, the differences in OTUs across altitude sites were not significant. 3 The soil bacterial community diversity showed a unimodal pattern in a small range of altitudes from 875-1 370 m, although no apparent trend was observed at the altitudes from 670-1 780 m. 4 There were 7 dominant phyla and 15 dominant orders with a relative abundance of more than 3% in all soil samples. 5 Correlation heat map analysis between the top 15 bacterial phyla and soil physicochemical properties as well as enzyme activities showed that soil pH had the greatest effect on the differences in soil bacterial community structure across the different altitudes. Pearson correlation analysis and Partial Mantel test also showed that bacterial community α -diversity (P < 0.01) and β -diversity (Partial Mantel r = 0.560, P = 0.001) were mainly affected by soil pH. Consequently, soil pH was the key environmental factor determining the soil bacterial community structure and diversity across the different altitudes on Mount Huangshan.

Key words: Mount Huangshan; bacterial community structure; Illumina high-throughput sequencing; soil pH; soil enzyme activity

山地生态系统是陆地系统组成部分之一,具有重要的生态系统功能^[1].在山地生态系统中,植物、土壤、气候等环境条件随海拔梯度发生剧烈变化,为研究生物群落海拔分布格局及其对环境变化的响应提供天然实验室^[2].迄今为止,动植物的海拔生物多样性分布模式已经被广泛研究,表现为在

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低或中海拔多样性最高[1]. 土壤微生物在生物地球 化学循环和生态系统功能维持中起着重要作用[3], 但是对其海拔分布格局的研究仍落后于动植物[4]. 目前已有研究表明土壤微生物多样性的海拔分布模 式有递减式[5]、驼峰式[6]、下凹式[7]、阶梯式[1] 等, 也有研究发现土壤微生物呈无明显海拔分布模 式[8], 所有的这些研究都集中在一个较大的垂直间 隔和对比鲜明的生态系统. 此外, 还有一些学者研 究了较小尺度海拔范围内的土壤微生物,发现土壤 微生物在这些较小海拔范围内多具有明显的海拔分 布模式[9~11]. 可见, 目前在海拔梯度上没有统一的 微生物多样性分布模式[11].

关于微生物群落分布格局, Bass-Becking^[12]和 De Wit 等[13] 认为"微生物无处不在, 但受环境选 择",虽然所有的微生物是世界性分布,但是特定的 环境中大多数物种只是潜在的; 而扩散限制假说则 认为微生物生物地理学和大型生物相似. 存在着生 物地理学模式[14,15],但实际上往往是这两大观点的 综合作用. 近年来研究结果显示. 土壤微生物群落的 分布与土壤 pH^[16]、土壤养分含量^[3]、植被类型^[17]、 海拔[6]等环境因子密切相关, 支持微生物群落空间 分布的环境选择作用. 因此, 在研究土壤微生物群落 空间分布格局的形成和维持机制时,应同时考虑当 下环境因素(土壤理化性质)和历史因素(海拔)[10].

黄山位于我国安徽省南部黄山市境内, 地处我 国南北植物区系交替地带, 具有特殊的地理环境和 局部小气候, 形成了明显的植被和土壤山地垂直分 带[18],是研究微生物群落海拔分布特征的理想场 所. 近年来, 国内外学者对该区域的动植物^[18,19]和 土壤真菌[20]等方面进行了研究, 但是对土壤细菌 海拔分布状况的研究较少, 因此, 本文分析了黄山 670~1780 m 整个海拔梯度范围内的土壤细菌群落 结构特征及其土壤环境影响因素, 以期为黄山土壤 生态系统物种多样性的认识和保护提供依据.

材料与方法

1.1 研究区概况

黄山(118°01′~118°17′E, 30°01′~30°18′N) 位于安徽省南部, 主峰莲花峰高1864 m, 景区面积 为154 km², 地处中亚热带区, 全山年均气温 7.8℃, 年均降雨量 2394.5 mm. 黄山植被海拔差异 明显, 植被类型主要是喜暖性针叶林、常绿落叶阔 叶混交林和山顶矮林草甸[18]. 黄山土壤的海拔分 布也较明显, 自下而上为黄红壤、黄壤、暗黄棕壤、 酸性棕壤,且局部分布着山地草甸土和山地草甸沼 泽土[19].

1.2 样品采集

2017年10月,在黄山景区内沿温泉、云谷寺、 光明顶一线的南坡进行采样,按约每100 m 的海拔 间隔设置一块样地,样地基本情况见图 1 和表 1. 采样时尽量避开人为扰动较大的区域, 每块样地分 别设置 3 个 20 m×20 m 的样方. 去除地表覆盖物 后,在每个样方内用直径38 mm 的土钻按S型采集 10 个表层 10 cm 深的土样, 混匀后装入无菌自封

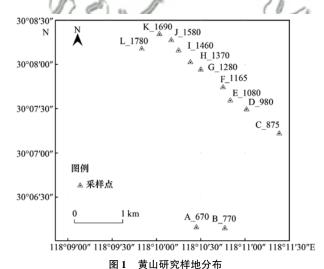


Fig. 1 Distribution of sampling sites in Mount Huangshan

表 1 样地概况

Table 1 Basic condition of sampling sites

海拔/m	编号	经度/(°)	纬度/(°)	坡度/(°)	坡向/(°)	植被类型	土壤类型
670	A	118. 174	30. 103	22	SW198	针阔混交林	黄壤
770	В	118. 180	30. 103	28	SE138	针阔混交林	黄壤
875	C	118. 190	30. 120	25	SE155	常绿阔叶林	黄壤
980	D	118. 184	30. 125	22	SE165	常绿落叶阔叶混交林	黄棕壤
1 080	E	118. 181	30. 127	20	SE159	常绿落叶阔叶混交林	黄棕壤
1 165	F	118. 179	30. 129	30	SW190	常绿落叶阔叶混交林	黄棕壤
1 280	G	118. 175	30. 132	21	SE166	常绿落叶阔叶混交林	黄棕壤
1 370	Н	118. 173	30. 134	22	SE170	常绿落叶阔叶混交林	黄棕壤
1 460	I	118. 171	30. 136	20	SE150	常绿落叶阔叶混交林	黄棕壤
1 580	J	118. 169	30. 138	28	SE166	落叶阔叶林	黄棕壤
1 690	K	118. 167	30. 139	19	SE155	山地矮林	棕壤
1 780	L	118. 164	30. 136	22	NW310	山地草甸	草甸土

袋,用冰盒运回实验室.剔除根系、石块等杂物后,将土样分为两份:一份保存于-80℃超低温冰箱用于土壤 DNA 提取;一份风干后用于土壤理化性质和酶活性测定.

1.3 分析方法

1.3.1 土壤理化性质的测定

土壤含水率(SM)用烘干法测定;土壤容重(BD)用环刀法测定;土壤pH用电位法测定,水土比2.5:1;全氮(TN)用半微量凯氏定氮法测定;碱解氮(AN)用碱解扩散法测定;全磷(TP)用酸溶-钼锑抗比色法测定;有效磷(AP)用双酸浸提-钼锑抗比色法测定;全钾(TK)用氢氧化钠碱熔-火焰光度法测定;有效钾(AK)用乙酸铵浸提-火焰光度法测定;总有机碳(TOC)用重铬酸钾氧化外加热法测定^[21].

1.3.2 土壤酶的测定

土壤酸性磷酸酶(ACP)活性用磷酸苯二钠比色 法测定,取 5 g 风干土加入 2.5 mL 甲苯摇匀 15 min 后,加入 20 mL 0.5% 磷酸苯二钠,于 37℃下培养 24 h,酶活性以 24 h 后 1 g 土中释放出来的酚毫克数表示;土壤脲酶(UE)活性用靛酚蓝比色法测定,取 5 g 风干土加入 1 mL 甲苯,反应 15 min 后再加入 10 mL 10% 尿素液和 20 mL 柠檬酸盐缓冲液(pH 6.7)于 37℃培养 24 h,酶活性以 24 h 后 1 g 土中 NH₄⁺-N的毫克数表示;土壤蔗糖酶(SC)活性用3,5-二硝基水杨酸比色法测定,取 5 g 风干土加入 15 mL 8% 蔗糖溶液、5 mL 磷酸缓冲(pH 5.5)和 5 滴甲苯,混匀后于 37℃培养 24 h,定时取样后加入 3,5-二硝基水杨酸,沸水浴加热 5 min,酶活性以 24 h 后 1 g 土中葡萄糖毫克数表示 [22].

1.3.3 土壤 DNA 提取和高通量测序

用 E. Z. N. A. soil 试剂盒 (Omega Bio-tek, USA)提取土壤总 DNA. 对 V3 ~ V4 区进行 PCR 扩增, 引物为 338F (ACTCCTACGGGAGGCAGCAG)和 806R (GGACTACHVGGGTWTCTAAT). PCR 反应体系为 20 μL: 5 × FastPfu 缓冲液 4 μL, 2.5 mmol·L⁻¹ dNTPs 2μL, 正负向引物各 (5 μmol·L⁻¹) 0.8 μL, FastPfu 聚合酶 0.4 μL, DNA 模板 1 μL. PCR 扩增程序为: 95℃ 预变性 3 min; 27 个循环 (95℃变性 30 s, 55℃ 退火 30 s, 72℃ 延伸 30 s); 72℃延伸 10 min. 扩增后用 2% 琼脂糖凝胶回收 PCR 产物,用 AxyPrep DNA 凝胶回收试剂盒 (Axygen Biosciences, USA)纯化, Tris_HCl 洗脱, 2% 琼脂糖电泳检测. PCR 产物用 QuantiFluor™-ST 蓝色荧光定量系统(Promega, USA)检测定量. 在上海美吉生物医药科技有限公司 Illumina Miseq

PE300 平台进行高通量测序.

1.3.4 序列数据分析

原始序列用 Trimmomatic 软件进行质控,用 FLASH 软件进行拼接:用 UPARSE 7.1 软件进行聚类,按 97%的相似度对序列进行聚类获得操作分类单元(OTU).用 RDP Classifier 2.2 对序列进行物种分类注释,比对 Silva 数据库(SSU128),置信度阈值为 70%.按最小样本序列数统一抽取38 702条有效序列来研究土壤细菌群落结构.

1.4 数据分析

用 SPSS 20.0 进行单因素方差分析,Duncan 法用于显著性检验,显著性水平为 P < 0.05. 用 R 软件生成 Venn 图,用于统计高、中、低海拔样本中所共有和独有的 OTU 数目. 用 Mothur 1.30.1 计算土壤细菌群落的 α 多样性指数,包括谱系多样性 PD 指数、Shannon 指数、Simpson 指数、Chaol 指数、ACE 指数和 Good's 物种覆盖度. 用 R 软件pheatmap 包绘制丰度前 15 细菌门与各土壤理化性质和酶活性的 Spearman 相关性热图. 用 Pearson 相关分析检验细菌群落 α 多样性 (Chaol 和 PD 指数)与土壤理化性质和酶活性之间的相关性. 基于unweighted UniFrac 群落距离算法和 Bray-Curtis 环境因子距离算法,用 Mantel 和偏 Mantel 检验 670~1870 m 细菌 β 多样性和环境因子的关系 (permutations = 999).

2 结果与分析

2.1 土壤理化性质及酶活性的海拔变化特征

2.1.1 土壤理化性质

如表2所示,不同海拔土壤含水率差异显著, 最高海拔1780 m 的土壤平均含水率最大,为 65.50%;而不同海拔土壤容重无显著差异,最低 海拔 670 m 处的土壤容重最大, 为 1. 27 g·cm⁻³. 黄 山土壤均为酸性,海拔1370 m的土壤酸性最强 (pH 4.10), 与 670 m (pH 5.31)、1080 m (pH 5.78) 和1165 m(pH 5.64) 存在显著差异. 不同海 拔土壤养分之间存在不同程度的显著性差异. 土壤 全氮和碱解氮含量总体上随海拔升高而增大; 1690 m 高山矮林的土壤全氮和碱解氮含量最高且明显高 于其他海拔, 分别是 7.27 g·kg⁻¹和 574.05 mg·kg⁻¹. 不同海拔土壤全磷和有效磷含量存在显 著差异, 但无明显海拔变化规律, 且 1690 m 的土壤 全磷和有效磷含量最高,分别为 0.80 g·kg⁻¹和 4.35 mg·kg⁻¹. 土壤全钾含量随海拔升高而显著增 大, 但有效钾含量无明显的海拔分布规律. 各海拔 之间的土壤有机碳含量存在显著差异,有机碳含量

总体上随海拔升高而增加.

2.1.2 土壤酶活性

不同海拔土壤蔗糖酶活性差异显著,而不同海拔土壤酸性磷酸酶、脲酶活性无显著差异(表2). 土壤蔗糖酶活性总体上随海拔升高而增强,1690 m 山地 矮 林 的 蔗 糖 酶 平 均 活 性 最 高, 达 89.39 mg·(g·d)⁻¹. 最低海拔 670 m 的土壤酸性磷酸酶、 脲酶和蔗糖酶活性均最低. 土壤理化性质和酶活性的相关性分析(表3)表明, 土壤酸性磷酸酶活性只与土壤有效钾含量显著相关; 土壤脲酶活性与土壤碱解氮、有效磷含量均显著正相关; 土壤蔗糖酶活性与土壤含水率、全氮、碱解氮、全磷、全钾和总有机碳含量均显著正相关, 与土壤容重显著负相关.

表 2 不同海拔土壤理化性质和酶活性1)

Table 2	Soil	physicocl	hemical	properties	and soil	enzyme	activities	across	different	altitudes

海拔	SM	BD	-H	TN	AN	TP	AP	TK	AK	TOC	ACP	UE	SC
/m	/%	$/g \cdot cm^{-3}$	рН	$/g \cdot kg^{-1}$	$/mg \cdot kg^{-1}$	$/g \cdot kg^{-1}$	/mg·kg - 1	/g•kg - 1	$/mg \cdot kg^{-1}$	$/g \cdot kg^{-1}$	/mg•(g•d)	-1/mg•(g•d) -1	$/\text{mg} \cdot (\text{g} \cdot \text{d})^{-1}$
670	27. 95 с	1. 27	5. 31 ab	1.68 d	143. 27 e	0.32 cd	1. 94 d	17.90 de	137. 10 a	25. 45 e	1.85	0. 52	5.58 d
770	44.07 abc	0.85	$4.76~\mathrm{bc}$	2. 20 d	$205.\;29\;\mathrm{de}$	$0.\ 27\ \mathrm{cd}$	$2.\ 15\ \mathrm{cd}$	16.41 e	87. 43 cde	$25.\;82~\mathrm{e}$	2. 34	0.94	$17.24~\mathrm{cd}$
875	$29.42~\mathrm{bc}$	0.92	4.54 с	$3.08~\mathrm{cd}$	$240.\;68\;\deg$	$0.33~\mathrm{cd}$	3.43 abcd	$23.\;32\;\mathrm{cde}$	55. 62 f	$44.\ 15\ \mathrm{de}$	2. 24	1.24	$27.59~\mathrm{bcd}$
980	43.47 abc	0.74	4. 21 c	5.78 ab	$425.\;7\;\mathrm{bc}$	0.55 b	$3.56~\mathrm{abc}$	$28.46~\mathrm{c}$	97. 53 bcd	68. 99 abo	2. 11	1.01	43.14 bcd
1 080	28.31 c	0.84	5. 78 a	$3.00~\mathrm{cd}$	$204.\;37\;\deg$	0. 25 d	$2.50\mathrm{bcd}$	30. 12 с	62.73 ef	$48.\;01\;\mathrm{cd}$	2. 17	0.84	$38.54~\mathrm{bcd}$
1 165	24. 97 c	0.88	5.64 a	5.16 b	$323.43 \mathrm{bcd}$	$0.44~\mathrm{bc}$	$2.78\mathrm{bcd}$	30.00 с	96.09 bcd	$78.\;61~\mathrm{ab}$	2. 30	0.70	31. 85 bcd
1 280	42.84 abc	0.78	$4.81~\mathrm{bc}$	$4.33~\mathrm{bc}$	$335.\;14\;\mathrm{bcd}$	$0.41\mathrm{bcd}$	$2.36\mathrm{cd}$	30.66 с	111. 12 abc	66.71 bc	2. 15	0.74	36.88 bcd
1 370	$29.69~\mathrm{bc}$	1.01	4. 10 c	5.50 b	462. 50 ab	0.57 b	3. 34 abcd	25. 51 cd	104. 91 bcd	75. 41 ab	2.08	0.79	39.04 bcd
1 460	49.60 abc	0.73	4.55 c	5.37 b	430.69 bc	0.55 b	4.04 ab	31. 49 с	97. 84 bcd	61. 27 bcd	2.09	1.14	37.65 bcd
1 580	32.72 be	0.90	$4.73~\mathrm{bc}$	$4.16~\mathrm{bc}$	308. 59 cd	0.45 bc	$2.69\mathrm{bcd}$	39.66 b	74. 45 def	$48.\;19\;\mathrm{cd}$	2. 23	0.81	50.17 bc
1 690	54.03 ab	0.78	4.48 c	7. 27 a	574. 05 a	0.80 a	4. 35 a	31.57 с	127. 50 ab	89.66 a	2.00	1.06	89. 39 a
1 780	65.50 a	0.81	$4.\;82~\mathrm{bc}$	5.05 b	416. 72 bc	$0.42\mathrm{bcd}$	2.31 cd	50.06 a	93. 50 cde	58. 26 bed	2. 21	0.85	60.42 ab
F	2. 90	1. 96	5.66	8. 92	8. 27	8. 40	2. 75	12.77	5. 72	8. 63	1. 99	2.09	3. 15
P	*//	NS	**	**	11/2/		*	** 🗸	1 60	n "	NS	NS	(* *

1) * * 表示 $P \le 0.01$, * 表示 0.01 < $P \le 0.05$, NS 表示 P > 0.05; 同一列数据不同小写字母表示差异显著; SM 为含水率, BD 为容重, TN 为全氮, AN 为碱解氮, TP 为全磷, AP 为有效磷, TK 为全钾, AK 为有效钾, TOC 为总有机碳, ACP 为酸性磷酸酶, UE 为脲酶, SC 为蔗糖酶, 下同

表 3 土壤理化性质和酶活性 Pearson 相关性1

Table 3 Pearson correlation between soil enzyme activities

\ //	and soil physico	chemical propertie	es
项目	ACP	UE	SC
SM	0.07	0. 20	0. 44 **
BD	-0.19	-0.22	-0.39 *
рН	0.05	-0.28	-0.23
TN	-0.08	0.30	0. 57 **
AN	-0.10	0. 34 *	0. 58 **
TP	-0.20	0. 32	0. 50 **
AP	-0.22	0. 62 **	0. 21
TK	0.03	-0.07	0. 46 **
AK	-0.42 *	-0.25	0.06
TOC	-0.06	0. 17	0. 53 **

1) * * 表示在 0.01 水平(双尾)上显著相关, * 表示在 0.05 水平 (双尾)上显著相关, 下同

2.2 16S rRNA 测序结果与多样性分析

本研究中,优化序列共2043838条,最多69355条,最少49151条.将12个海拔梯度分为3组:低海拔A~D、中海拔E~H和高海拔I~L(图2).低海拔共有4305个OTU,中海拔共有4750个OTU,高海拔共有4445个OTU.低海拔和中海拔共有的OTU为4237个,低海拔和高海拔共有的OTU为3978个,高海拔和中海拔共有的OTU为4154个.低海拔特有的

OTU 为 122 个,中海拔特有的 OTU 为 251 个,高海拔特有的 OTU 为 65 个.3 组的 OTU 数一共为5 023 个,它们共有的 OTU 为3 892个.

单因素方差分析表明, $670 \sim 1.780$ m 各海拔梯度之间的 Shannon 指数差异显著 (F = 2.43, P = 0.03), 其余各指数差异均不显著 (P > 0.05). PD 指数、Shannon 指数和 Simpson 指数能反映各样品

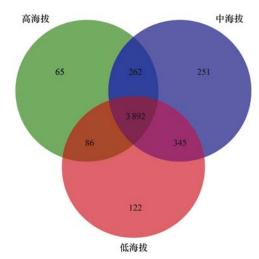


图 2 不同海拔土壤样品细菌 OTU 数量韦恩图

Fig. 2 Venn diagram of OTU number from soil samples at different altitudes

土壤微生物群落多样性. 海拔1 165 m 处的 Shannon 指数最大, Simpson 指数最小; 875 m 处的 Shannon 指数最小, Simpson 指数仅次于最大均值(770 m), 说明1 165 m 的细菌群落多样性最高, 875 m 的多样性最低. Chao1 和 ACE 指数反映群落丰富度. 1 165 m 处 Chao1 和 ACE 指数最大, 875 m 处的 Chao1 和 ACE 指数最小, 说明1 165 m 的土壤细菌总数和菌群丰富度最高. 覆盖度值越高, 样本中序列被测出

的概率越高,没有被测出的概率越低,反映测序结果是否代表样本中微生物的真实情况^[23].各海拔土壤样品测序的覆盖度为98.26%~98.65%,说明本次测序结果能充分反映供试土样微生物的真实情况.在670~1780 m整个海拔范围内,土壤细菌群落多样性无明显海拔分布规律;875~1370 m小海拔范围内,细菌群落多样性沿海拔梯度先增高后降低,呈单峰模式(表4).

表 4 细菌群落 α 多样性指数

Table 4	The α	diversity	indices	of	bacterial	communities

海拔/m	PD 指数	Shannon 指数	Simpson 指数	Chao1 指数	ACE 指数	覆盖度/%
670	175. 45	6. 58	0. 005 39	3 189	3 162	98. 38
770	152. 31	6. 17	0.00796	2 788	2 790	98. 48
875	133. 04	5. 95	0.00764	2 522	2 485	98. 60
980	147. 06	6. 17	0.00654	2 776	2 741	98. 47
1 080	173. 56	6. 59	0.00472	3 140	3 088	98. 44
1 165	194. 92	6. 81	0.003 58	3 457	3 462	98. 26
1 280	155. 00	6. 28	0.005 66	2 785	2 736	98. 55
1 370	138. 89	6. 11	0.00645	2 549	2 554	98. 61
1 460	160. 23	6. 29	0.00633	2 919	2 925	98. 40
1 580	164. 61	6. 40	0.00487	3 091	3 044	98. 31
1 690	150. 62	6. 32	0.005 31	2 694	2 658	98. 63
1 780	148. 80	6. 25	0. 005 48	2 605	2 594	98. 65

2.3 细菌群落结构

本次测序共得到34门、85 纲、171 目、328 科、557 属. 相对丰度大于3%的优势细菌门共7个[图3(a)],分别是变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)、放线菌(Actinobacteria)、绿弯菌门(Chloroflexi)、浮霉菌门(Planctomycetes)、疣微菌门(Verrucomicrobia)和硝化螺旋菌门(Nitrospirae). 其中,变形菌门(34.09%~

42.71%)、酸杆菌门(20.48%~42.71%)、放线菌门(9.69%~15.89%)、绿弯菌门(8.50%~15.50%)相对丰度较大.相较于其他海拔,1780m的变形菌门(34.09%)和放线菌门(9.69%)相对丰度最低,绿弯菌门(15.50%)和浮霉菌门(7.06%)相对丰度最高.

各海拔土壤细菌目中相对丰度大于 3% 的有 15 个「图 3 (b)]. 其中,根瘤菌目(Rhizobiales,

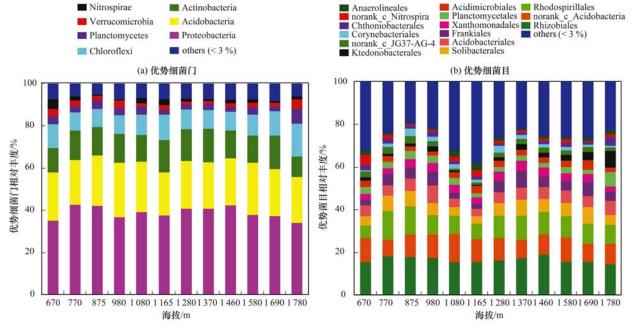


图 3 优势细菌门和优势细菌目相对丰度

Fig. 3 Relative abundance of dominant bacterial phyla and dominant bacterial orders

14.50% ~ 19.21%)、红螺旋菌目(Rhodospirillales, 6.06% ~ 13.42%)、酸杆菌门下的未定种类(norank_c_Acidobacteria, 7.81% ~ 13.26%)和Solibacterales(3.45% ~ 7.77%)以及酸杆菌目(Acidobacteriales, 3.42% ~ 8.32%)、弗兰克氏菌目(Frankiales, 2.60% ~ 7.90%)的相对丰度较大. 黄单胞杆菌目(Xanthomonadales)在1370 m的相对丰度最高(4.65%). 纤线杆菌目(Ktedonobacterales, 7.97%)和浮霉状菌目(Planctomycetales, 6.80%)在1780 m的相对丰度最高. 醋微菌目(Acidimicrobiales)在1690 m的相对丰度最高(4.56%).

2.4 土壤性质和酶活性对细菌群落的影响

2.4.1 细菌群落结构与土壤性质及酶活性的相关性

土壤环境因子 pH、全氮 TN、总有机碳 TOC 与 土壤细菌群落结构之间存在密切相关关系[16]. 如 图 4 所示, 土壤 pH 与硝化螺旋菌门(R = 0.766)、 Latescibacteria (R = 0.855) 及拟杆菌门 (Bacteroidetes, R = 0.427) 呈极显著正相关关系(P<0.01), 与绿弯菌门呈显著正相关关系(R= 0.422, P < 0.05); 与厚壁菌门(Firmicutes, R = -0.832)和衣原体门(Chlamydiae, R = -0.494)呈 极显著负相关关系(P<0.01),与酸杆菌门呈显著 负相关关系(R = -0.355, P < 0.05). 土壤 TN 与 厚壁菌门呈极显著正相关关系(R=0.477, P< (0.01),与放线菌门(R = 0.338)、衣原体菌门(R =0.361)和 Saccharibacteria(R=0.384)呈显著正相关 关系(P < 0.05);与硝化螺旋菌门(R = -0.407)和 Latescibacteria (R = -0.398) 呈显著负相关关系(P<0.05). 土壤 TOC 与放线菌门呈极显著正相关关 系(R=0.456, P<0.01), 与厚壁菌门(R=0.374) 及 Saccharibacteria (R = 0.402) 呈显著正相关关系 (P<0.05);与硝化螺旋菌门呈极显著负相关关系 (R = -0.435, P < 0.01), 与 Latescibacteria 呈显著 负相关关系(R = -0.384, P < 0.05). 上述结果表 明,土壤 pH 和碳氮养分含量对硝化菌门、厚壁菌 门和 Latescibacteria 这 3 类菌群的影响均显著. 环 境因子聚类分析表明, 土壤 pH 单独聚为一类, 对 不同海拔土壤细菌群落结构差异性影响最大. 硝化 螺旋菌门、芽单胞菌门(Gemmatimonadetes)、厚壁 菌门和衣原体菌门这些菌群主要起固氮和固碳作 用[24],与脲酶和蔗糖酶活性显著相关(P < 0.05).

2.4.2 细菌群落多样性与土壤性质及酶活性的相关性

Pearson 相关性分析(表 5)表明,在 670~

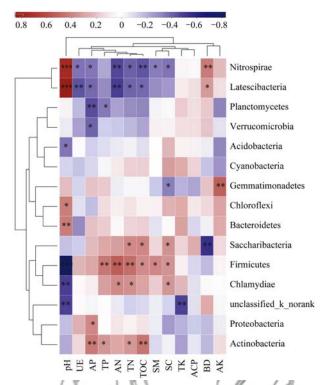


图 4 总丰度前 15 细菌门与土壤理化性质及酶活性相关性热图 Fig. 4 Correlation heat map of the top 15 bacterial phyla and soil physicochemical properties as well as enzyme activities

1780 m, 土壤含水率和 pH 对土壤细菌群落谱系多样性(PD 指数)及丰富度(Chao1 指数)的影响均达显著水平(P<0.05). 而在 875~1370 m 相对较小的海拔范围内, 土壤 pH 和全钾是影响菌群谱系多样性及丰富度的主要环境因子(P<0.01). 蔗糖酶和脲酶与微生物数量有关[22], 本研究结果表明细菌群落丰富度与脲酶活性显著相关(P<0.05), 与蔗糖酶活性无显著相关关系(P>0.05).

表 5 土壤理化性质及酶活性与细菌群落多样性 Pearson 相关性

Table 5 Pearson correlation between α-diversity indices and soil physicochemical properties as well as enzyme activities

	1	1		
项目 -	670 ~ 1	1 780 m	875 ~ 1	370 м
坝日 -	PD 指数	Chao1 指数	PD 指数	Chaol 指数
SM	-0.38 *	-0.46 **	-0.35	-0.40
BD	0.25	0. 29	0.07	0. 13
pН	0. 74 **	0. 69 **	0. 75 **	0. 69 **
TN	-0.22	-0.26	-0.17	-0.20
AN	-0.32	-0.36 *	-0.33	-0.35
TP	-0.16	-0.18	-0.28	-0.29
AP	-0.22	-0.19	-0.42	-0.37
TK	0.10	0.07	0. 67 **	0. 67 **
AK	0. 21	0. 15	0. 21	0. 17
TOC	-0.17	-0.23	-0.09	-0.16
ACP	0.05	0.04	0.34	0.30
UE	-0.42 **	-0.38 *	-0.60 **	-0.55 **
SC	-0.25	-0.30	-0.14	-0.18
•			•	

Mantel 分析(表 6)表明,670~1780 m 海拔范围内,土壤细菌群落与海拔、土壤 pH 和碳氮含量

具有显著相关性(P<0.05). 偏 Mantel 分析表明, 土壤 pH 对细菌 β 多样性在该海拔范围内的分布模式的贡献率最大.

表 6 细菌群落与环境因子的 Mantel 和偏 Mantel 检验

Table 6 Mantel and Partial Mantel test between bacterial

•.•	1		1	c .
communities	and	environment	a I	tactors

项目	Mante	1 检验	偏 Mantel 检验		
坝目	r	P	r	P	
海拔	0. 167	0.009	0. 082	0.059	
SM	0.087	0. 105	0.076	0.094	
BD	0.017	0.767	0.001	0.476	
pН	0.679	0.001	0. 560	0.001	
TN	0. 167	0.008	0. 019	0. 331	
AN	0. 205	0.004	0. 141	0.009	
TP	0.064	0. 202	-0.021	0.632	
AP	0.055	0.303	0. 047	0. 196	
TK	0.055	0.359	- 0. 054	0.805	
AK	0.058	0.342	0. 043	0. 204	
TOC	0.112	0.029	- 0. 009	0. 539	

3 讨论

3.1 不同海拔土壤理化性质及酶活性特征

随着海拔梯度的变化,土壤类型、植被类型、 气候等发生变化,从而造成土壤理化性质与养分供 应情况的海拔差异[25]. 本研究发现, 土壤含水率呈 显著海拔差异,且1780 m 草甸土的含水率最大,而 土壤容重无显著海拔差异. 海拔升高导致气温下 降、降雨量增大、空气湿度增加, 使土壤水分蒸发 减弱, 因此土壤含水量随海拔升高而增大[3]. 草甸 土表层草甸植物覆盖度较高, 根系较集中, 使表层 水分渗透力较差[26],从而导致草甸土含水率较高. 本研究中土壤全氮、碱解氮、全钾和总有机碳含量 总体上随着海拔升高而增加. 秦松等[27] 的研究结 果也证明, 有机质、氮、磷、钾元素与海拔显著正 相关. 此外, 地形对土壤理化性质的影响也较明 显,海拔是主导因素,坡度坡向等微地形条件造成 山体起伏, 对土壤质地影响较大[28]. 黄山明显的海 拔差异和特殊的地形条件,导致土壤理化性质存在 不同程度的海拔差异.

土壤酶活性与土壤性质、土壤类型等环境条件密切相关,被广泛作为土壤质量和土壤生物活性的重要指标^[29].本研究发现土壤蔗糖酶活性存在显著海拔差异,且该酶活性总体上随着海拔升高而增强;而土壤酸性磷酸酶和脲酶活性无显著海拔差异,且该两种酶活性无明显的海拔分布特征(表2). Chang 等^[30]研究了600~1400 m 的人工毛竹林下土壤,发现土壤脲酶和酸性磷酸酶活性均随海拔升高而增强.曹瑞等^[31]研究了川西1563~3994 m 的5种不同海拔生态系统土壤,发现随着海拔升

高, 有机层(0~15 cm)土壤蔗糖酶、脲酶和酸性磷 酸酶活性均呈现出先增加后减少再增加的海拔变化 趋势, 且存在显著的海拔差异. 也有研究表明多数 土壤酶活性沿海拔无显著变化情况[32]. 说明土壤 酶活性的海拔分布情况因地而异. 本研究发现, 土 壤脲酶和蔗糖酶与土壤养分之间存在显著正相关关 系(表3),符合前人研究结果[10,33].磷酸酶参与磷 酸单酯的水解[34],与土壤有机质、全氮、速效磷含 量密切相关. 但是本研究未发现酸性磷酸酶与土壤 碳、氮、磷显著相关(表3). 将670 m的平均土壤 有机质、全氮、全磷和有效磷的数据剔除后,与平 均酸性磷酸酶活性做 Pearson 双尾相关性检验, 发 现平均土壤有机质(P=0.022)、全氮(P=0.007)、 全磷(P=0.004)及有效磷(P=0.009)含量与酸性 磷酸酶活性显著相关,可能是因为670 m处的土壤 养分含量较其他海拔偏低.

3.2 不同海拔土壤细菌群落结构及多样性

本研究利用 Illumina 高通量测序技术对黄山不 同海拔土壤细菌群落组成进行探究, 发现随着海拔 升高, 土壤细菌 OTU 数目: 中海拔 > 低海拔 > 高海 拔;但从整体来看高、中、低海拔的差异不明显, 细菌 OTU 组成重叠情况较明显, 共有 OTU 数高达 3892. 本研究中, 变形菌门、酸杆菌门和放线菌门 在各海拔土壤细菌群落中占绝对优势. Zhang 等[35] 研究沿海拔梯度常绿阔叶林、落叶阔叶林、针叶林 和亚高山灌从这4种植被类型下的土壤细菌群落, 发现酸杆菌门、放线菌门、变形菌门和疣微菌门占 主要优势,与本研究结果相似.变形菌门、酸杆菌 门、放线菌门和疣微菌门主要起有机质分解作 用[24], 本区 670~1 780 m 植被类型从针阔混交林 过渡到山地草甸, 地表凋落物较多, 土壤养分较丰 富,因此土壤中分解有机质的微生物更具优势.就 目水平而言, 本研究发现1780 m 的细菌目相对丰 度与其他海拔差异较大,可能是因为1780 m 的植 被是草本植物,而其他海拔样地的植被是木本植 物. 已有研究证明, 相较于其他植被类型, 天然草 地的土壤细菌群落最丰富, 植被类型对土壤理化性 质影响较大,这种影响作用是基于植物凋落物及根 系分泌物的不同,从而影响土壤微生物群落 组成[36].

揭示山地生态系统中群落演替和群落聚集的驱动力和机制对预测土壤生态服务功能对气候变化的响应至关重要^[37].本研究发现,土壤细菌群落多样性在 670~1 780 m海拔范围内呈无明显海拔分布模式,在 875~1 370 m小海拔范围内呈单峰状分布.同时,在 670~1 780 m海拔范围内,与细菌群

落 α 多样性显著相关的环境因子土壤含水率、pH和碱解氮含量均无明显海拔分布模式;在 875~1370 m范围内,土壤 pH值和全钾含量总体上先增大后减小(表 2 和表 5).本研究首次揭示了黄山景区内土壤细菌群落的海拔分布模式,该研究结果与前人研究结果类似.有研究发现,长白山北坡 530~2200 m不同海拔的土壤细菌群落多样性呈无明显规律;但是长白山苔原2000~2500 m的土壤细菌群落谱系多样性随海拔梯度呈单峰模式,土壤碳氮含量是该细菌多样性海拔分布模式的主要影响因子^[9,16]. Han等^[10]研究了长白山原始红松林 699~1177 m土壤细菌群落多样性及组成结构,发现细菌多样性随着海拔上升呈驼峰状曲线变化,并推测可能的原因是土壤含水率和地上植被组成.

3.3 土壤细菌群落与土壤性质及酶活性的关系

本研究表明, 土壤 pH 对酸杆菌门、绿弯菌门 和硝化螺旋菌门等优势菌群均影响显著, 且 pH 单 独聚为一类,对不同海拔菌群结构差异性影响最大 (图4). Pearson 相关性分析(表5)表明 pH 对菌群 α 多样性的影响极显著(P < 0.01), 且影响作用明 显大于其他环境因子(相关系数最大). 偏 Mantel 分析表明细菌 β 多样性不受海拔地形因子的影响, 主要受土壤 pH 影响(表6). 因此, 土壤 pH 是影响 黄山土壤细菌群落海拔分布的主要环境因子. 近年 来大量研究表明, 土壤 pH 是影响细菌群落的最关 键因子. 土壤 pH 虽然不改变细菌群落本身, 但是 直接或间接地和其他土壤变量, 如土壤养分可有效 性、含水量等相互作用,从而对土壤细菌群落分 布、组成和多样性等产生影响. Siles 等[33]的研究 发现, 土壤 pH 和土壤细菌丰富度无相关关系, 但 是和细菌群落结构及多样性显著相关. Shen 等[16] 的研究证明, 土壤 pH 是长白山土壤细菌群落沿海 拔空间分布的决定因素. Lauber 等[39]研究 88 份来 自美国南北的土壤, 发现土壤 pH 值与细菌群落组 成、谱系多样性均显著相关, 从而证明土壤 pH 对 陆地范围内的土壤细菌群落结构起决定作用. 本研 究证明,除了土壤 pH 外,土壤氮含量、含水率等其 他土壤化学性质也与细菌群落密切相关. Liu 等[11] 研究卧龙保护区3000~3945 m 土壤细菌群落,发 现土壤pH、全氮和含水量与整个细菌群落关系密 切. Ren 等[2]研究了太白山北坡不同海拔土壤细菌 群落,发现土壤细菌群落和土壤含水量及容重显著 相关.

土壤酶是由微生物或根系通过水解或氧化降解 特定的有机化合物而合成的^[40],气候和土壤因子 直接和间接地与森林类型相关,从而显著影响土壤 酶活性^[34],因此土壤性质、土壤酶、土壤微生物三者之间密切相关.已有研究证明土壤酸性磷酸酶、脲酶活性与土壤细菌群落密切相关^[38].马转转等^[41]的研究表明,土壤细菌群落的丰富度指数与土壤脲酶活性显著正相关,均匀度指数与土壤蔗糖酶活性显著正相关,土壤脲酶活性是该研究区内细菌群落组成与结构的重要驱动因子之一.而本研究发现土壤脲酶、蔗糖酶活性与细菌群落结构组成和多样性密切相关,而酸性磷酸酶与细菌群落无显著相关关系(图 4 和表 5). Xiao等^[42]的研究发现,福建天宝岩自然保护区1 125~1 520 m森林土壤酸性磷酸酶活性为 0.504~0.637 mg·(g·24 h)⁻¹.因此,推测可能的原因是本研究区各海拔的土壤酸性磷酸酶含量均较高,无明显的海拔分布差异.

此外,土壤细菌群落组成和多样性对海拔高度的响应不能解释为对海拔的简单响应,可能是由于土壤有机质含量、温度等多种因素之间的相互作用所致^[43].本研究区内,随着海拔梯度升高森林植被类型也发生变化(表1).已有研究证明,土壤性质特别是pH对土壤细菌群落起主要影响作用,植被起间接影响作用^[44].本研究虽未直接研究地上植被对土壤细菌群落的影响,但是不能排除植被通过改变土壤pH和氮含量等间接影响土壤细菌群落.然而,本研究结果证明土壤pH是影响黄山细菌群落的主要环境因子,进一步说明环境选择作用^[45]显著影响该海拔梯度内的土壤细菌群落.

4 结论

- (1) 黄山 670~1780 m 存在保存较为完整的森林生态系统,该海拔范围内土壤含水率、pH 和养分含量均存在显著差异. 土壤蔗糖酶活性存在极显著海拔差异,而土壤酸性磷酸酶和脲酶活性无明显海拔差异.
- (2) 黄山土壤细菌 OTU 数目: 中海拔 > 低海拔 > 高海拔, 但从整体来看高、中、低海拔的差异不明显, 细菌 OTU 组成重叠情况较明显. 各海拔样地共有 7 个优势细菌门和 15 个优势细菌目. 1 780 m草甸土的土壤细菌目相对丰度与其他海拔的差异较大.
- (3)在875~1370 m 小海拔范围内,土壤细菌群落多样性呈单峰式海拔分布模式;而在670~1780 m 整个海拔范围内,土壤细菌群落多样性无明显海拔分布模式.土壤 pH 是影响黄山土壤细菌群落海拔分布的主要土壤环境因子,说明环境选择作用显著影响该研究区域土壤细菌群落.

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