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专论与综述

土壤微生物群落对全球气候变化响应的研究进展

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摘　要：全球气候变化对陆地生态系统过程和功能产生重要影响，土壤微生物群落在陆地生态系统几乎所有的生物地球化学循环过程起到关键作用。本文针对气候变化对土壤微生物的影响研究结果，主要从土壤微生物活性(土壤呼吸与酶活性)和微生物群落结构对大气 CO_2 升高、增温、降水变化、氮沉降等全球变化单因子和多因子的直接或间接响应进行综述，并进一步阐述参与土壤碳氮循环过程的功能微生物对气候变化的响应机制与适应规律。全球变化因子改变了土壤微生物的群落组成，呈现降低、增加和无影响 3 种效应，且不同功能微生物也呈现不同的敏感性。多个全球变化因子对土壤微生物群落结构的交互效应可能存在加性、协同、拮抗作用，产生加和的、相互促进或抵消的整体效果。然而，目前对多种全球变化因子如三因子或四因子的组合作用，以及多因子的高阶交互作用研究较少；已有的研究地理分布不均匀，且时间和空间大尺度的研究不足；缺乏综合生态系统模型对全球变化的影响进行模拟和预测。最后指出今后的研究发展方向：进行多种全球变化因子、长时间、多生态系统点位、大空间尺度的土壤微生物群落动态研究；探究多种全球变化因子的高阶交互作用；建立综合响应的生态系统模型，精确全球气候变化及其交互作用对土壤微生物群落影响的估算。这将有助于准确预测未来全球气候变化情景下生态系统尤其是土壤微生物生态系统的响应，为生态系统的可持续发展提供科学基础。

关键词：土壤微生物群落；气候变化；增温；大气 CO_2 浓度升高；氮沉降；降水变化；交互作用

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Responses of soil microbial community to global climate change: a review

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Abstract: Global climate change affects the processes and functions of terrestrial ecosystems where soil microbial community plays a crucial role in almost all of the biogeochemical cycles. Here, we reviewed the direct and indirect responses of soil microbial activities (e.g., soil respiration and enzyme activities) and community structure to individual and multiple global change factors, including elevated CO_2 concentration, warming, altered precipitation, and nitrogen deposition. Besides, we summarized the mechanisms for the adaptation of soil microbial community and the responses of functional microorganisms involved in soil carbon and nitrogen cycle to climate change. Generally, these global change factors may have positive, negative, or insignificant effects on soil microbial communities, and different functional microorganisms also showed different sensitivity to them. Moreover, the interactive effect of multiple global change factors on soil microbial community structure may be additive, synergistic, or antagonistic. However, there is a paucity of research on the combined effects of multiple global change factors, such as three, four, and even more factors. In addition, the distribution of the studied areas is uneven, and studies involving various ecosystems with large spatial and temporal scale are scarce. No comprehensive ecosystem model is available to simulate and predict the effects of global change on soil microbial communities. Finally, we summarized the research trends: (1) dynamic monitoring of soil microbial communities in multiple ecosystems in large spatial scale for a long time involving multiple global change factors, (2) the interaction of multiple global change factors, and (3) development of comprehensive ecosystem model to accurately estimate the impact of global climate change and factors' interaction on soil microbial community. These will help to accurately predict the response of ecosystem, especially soil microbial ecosystems, under future global climate change scenarios, and lay a basis for the sustainable development of ecosystems.

Keywords: soil microbial community; climate change; warming; elevated CO_2 concentration; N deposition; altered precipitation; interaction

联合国政府间气候变化专门委员会(Intergovernmental Panel on Climate Change, IPCC)第六次会议报告指出：2019 年大气二氧化碳(CO_2)含量达到 200 万年来的最高值，甲烷(CH_4)和氧化亚氮(N_2O)是 80 万年来的最高值，2019 年全球大气中 CO_2、CH_4 和 N_2O 的体积浓度分别达到 409.9、1 866.3 和 332.1 nL/L，与 1750 年相比分别增长了 47.3%、157.8%和 23.0%[1]。全球变暖是不争的事实。1850–2019 年，地表平均气温升高了 1.09 (0.95−1.20) ℃；降水格局也发生着变化，高纬度地区降水量明显增加，热带陆地区域干湿季节降水量差异增大；季风

降水预计将在中长期内持续增加，尤其在南亚和东南亚、东亚和西非地区[1]。氮沉降是元素氮以气体形式或通过干沉降或湿沉降从大气进入生物圈的过程，人为源氮沉降主要来源于全球化石燃料燃烧排放的氮氧化物和农业化肥中使用的氮等[2]，20 世纪 90 年代中期，全球氮沉降总量为每年 103 Tg，预计 2050 年将达每年 195 Tg[3]。

土壤是陆地生态系统的重要组成部分，也是陆生生物赖以生存的物质基础。土壤具有特殊的物理结构和复杂的化学成分，是微生物的理想栖息地，也是微生物最丰富多样的环境介质[4]。仅 1 g 的土壤中就包含多达 10 亿个细菌，由成千上万的分类单元组成[5]。土壤微生物群落在陆地生态系统几乎所有生物地球化学过程中发挥着关键作用，如有机物分解、养分循环、温室气体排放等[6-8]。土壤微生物群落组成、多样性、丰度及其功能与土壤理化性质、植被特征及气候等因素密切相关[9]。全球变化因子及其相互作用通过调节土壤微生物群落来影响生态系统功能[10-11]。然而，一旦某些气候生态位狭窄物种的生存环境受到气候变化的影响，可能导致多样性下降甚至物种灭绝[12]。微生物群落多样性、组成与功能对全球变化的响应和反馈是微生物生态学的前沿问题。大多数关于全球变化对土壤微生物群落的影响研究多集中于单一全球变化因子产生的正效应、负效应或中性效应，而全球变化往往包含着多因子的变化，这种多因子的交互作用不可忽视[4,13]。

本文对现有全球气候变化背景下土壤微生物群落结构的响应进行综述，探讨土壤微生物群落结构对 CO_2 浓度升高、气候变暖、降水变化、氮增多单因子和多因子交互作用的响应和反馈，以期为预测全球气候变化对土壤生态系统功能的影响、土壤管理和可持续发展提供依据。

1 全球变化单因子对土壤微生物群落和功能的影响

全球变化因子对土壤微生物群落组成、丰富度和功能等产生直接或间接的影响，而且土壤微生物群落组成、丰富度、物种分布和功能对不同全球变化因子变化的敏感性可能不同[10,14]。

1.1 大气 CO_2 浓度升高

国内外关于大气 CO_2 浓度对土壤微生物群落结构和功能的影响研究中，CO_2 浓度的人工控制通常通过开顶箱(open top chamber, OTC)或自由空气 CO_2 富集试验系统(free air CO_2 enrichment, FACE)进行，以比较长期暴露于升高的 CO_2 和环境 CO_2 水平的情景下不同陆地生态系统的响应(表 1)。CO_2 不仅是动植物和微生物呼吸的产物，也是植物、光合微生物光合作用和无机自养型微生物的底物[22]。大气 CO_2 浓度较大幅度升高，短期内会直接影响土壤微生物群落结构和生态功能。例如，碳循环功能微生物类群丰度增加，通过促进代谢活性提升微生物量碳(microbial biomass carbon, MBC)含量等[23]；也可通过增强植物光合作用，增加根际沉积和凋落物的碳输入为微生物提供碳源和养分[24-26]，同时促进有机碳的分解和利用[22]。不同的植物物种对大气 CO_2 浓度升高的反应不同，从而也影响根际碳输入的数量和类型。例如，C4 植物在光合作用方面比 C3 植物更有效[27]，所以 C4 植物可能将更多的碳分配给根际相关的微生物，从而导致群落组成发生变化[20]。植物凋落物和根系分泌物的增加向土壤输入“复合营养物”，通过“激发效应”刺激微生物分解土壤

表 1 大气 CO_2 浓度升高对土壤微生物群落和功能的影响

Table 1 Study on the effect of elevated CO_2 concentration on soil microbial community and function

Soil type	Sample sites	Experimental setup	Conclusions	References
Farmland soil	Changshu Agricultural Ecology Experiment Station	OTC	Elevated CO_2 concentration affected soil nutrient availability and C input by increasing plant root exudates, thus affecting soil microbial metabolic activity	[15]
Farmland soil	Changshu Agricultural Ecology Experiment Station	OTC	Elevated CO_2 concentration affected bacterial: Fungal biomass ratio by promoting the production of root exudates including heterocyclic nitrogen compounds, phenolic acids and phenols, and the biomass of active bacteria in soil increased significantly	[16]
Forest soil	Sky Oaks Field Station in California	FACE	With the increase of CO_2 concentration, the diversity of fungi increased, and the community change was closely related to the fine root yield	[17]
Forest soil	Changbai Mountain Forest Ecosystem Research Station	OTC	The activities of soil urease, amylase, invertase, catalase, polyphenol oxidase and dehydrogenase increased, while soil protease and phosphatase activities decreased significantly under high CO_2 concentration	[18]
Grassland soil	Alpine steppes of Nagqu	OTC	Elevated CO_2 concentration increased soil dissolved organic carbon content and enzyme activity, which increased soil respiration; however, there was no significant effect on microbial biomass and carbon use efficiency (CUE)	[19]
Grassland soil	Temperate grassland of south-eastern Tasmania	FACE	Elevated CO_2 concentration for 5 years significantly reduced the abundance of archaea and increased the abundance of fungi in temperate grasslands; The abundance of *Firmicutes* and *Bacteroidetes* increased significantly, meanwhile, the community structure of microbial carbon functional groups was changed	[20]
Grassland soil	Cedar Creek Ecosystem Science Reserve in Minnesota	FACE	Elevated CO_2 concentration for long-term (>12 years) had different effects on functional genes related to soil nitrogen cycling, which stimulated the increase of gene abundance of organic nitrogen metabolism and nitrogen fixation, and reduced the abundance of genes related to glutamine synthesis and anammox	[21]

有机碳[28-29]，导致更多的 CO_2 释放，最终影响土壤有机碳封存，这一过程被称为温室气体的正反馈效应[30]。大部分研究发现，CO_2 浓度升高会增加土壤呼吸[19,31]；Nie 等[32]发现 CO_2 浓度升高条件下，自养呼吸显著增加，达到 58.9%。由于大气 CO_2 长期处于较高浓度，由此引起的正反馈导致全球变暖“加速度”提升，对生态系统的碳平衡和温室效应造成显著影响。此外，CO_2 浓度升高也可能刺激增加土壤胞外酶活性[18,33]；Xiao 等[34]进行了全球范围的 META 分析发现，大气 CO_2 浓度升高对土壤 β-1,4-葡萄糖苷酶、纤维二糖水解酶、β-1,4-N-乙酰葡糖氨糖苷酶、脲酶的活性有积极影响，而不利于酚氧化酶和酸性磷酸酶的活性。

不同生态系统中微生物对大气 CO_2 浓度升高的响应存在差异。Li 等[14]对草地、农田和森

林生态系统中微生物群落的比较发现，农田生态系统对 CO_2 浓度升高响应最敏感，丰富度和多样性分别增加了32.6%和8.7%。Dunbar等[35]在对美国6种生态系统进行6期10年的升高大气 CO_2 的研究发现，这些生态系统中土壤细菌组成差异很大，但 CO_2 浓度升高对6个生态系统的细菌生物量、丰富度和群落组成无一致的显著影响；随着大气 CO_2 浓度升高，土壤酸杆菌(*Acidobacteria*)丰度普遍增加。Deltedesco等[36]发现大气中的 CO_2 浓度升高不会引起土壤真菌或细菌群落结构的剧烈变化，但升温会造成共生白腐真菌的相对丰度增加。在澳大利亚的草原上，CO_2 浓度升高导致古细菌和真菌以及特定细菌群的迁移，CO_2 浓度升高增加了厚壁菌门(*Firmicutes*)和拟杆菌门(*Bacteroidetes*)的丰度[20]。森林作为陆地生态系统重要的碳汇，研究表明长期升高大气 CO_2 浓度使表层土壤有机碳量增加 5.6%[37]；但不同土壤深度的微生物群落组成出现差异，与其他土层相比，CO_2 浓度升高显著增加0−5 cm土层中泉古菌门(*Crenarchaeota*)、绿弯菌门(*Chloroflexi*)和变形杆菌门(*Proteobacteria*)的丰度[38]。土壤微生物功能和结构基因对土壤养分循环过程的研究非常重要。研究者们通过筛选微生物后代基因组中的基因丰度，发现了在大气 CO_2 浓度升高下土壤微生物组所发挥的潜在功能的变化。例如，在草原生态系统进行的模拟气候变化试验显示，升高的 CO_2 浓度刺激了与分解、固氮、异化硝酸盐还原相关基因的丰度增加，而谷氨酰胺合成和厌氧氨氧化相关的基因丰度降低[21]。在干旱草原上，大气 CO_2 浓度升高导致涉及分解、固氮、固碳、CH_4 代谢、氮矿化和反硝化的微生物基因丰度均增加[39]。

1.2 增温

温度决定了微生物的生长速率和微生物量。研究表明，土壤温度升高促进土壤微生物生长、繁殖，但也有研究表明气候变暖导致土壤微生物生物量显著下降(表 2)。产生以上现象的原因可能是温度升高促进微生物代谢过程和酶活性，加快有机质分解；同时，温度升高使得自养微生物量总体大于非自养微生物量，增加了对有效碳的吸收，加剧养分限制[15]。Donhauser 等[44]通过对 8 种高寒土壤进行增温处理发现，包括伯克霍尔德菌属(*Burkholderia*)和苯基杆菌属(*Phenylobacterium*)在内的具有热适应、较高生长速率和抗逆性共性特征的菌属相对丰度显著增加。土壤呼吸对温度的变化十分敏感，一些较大范围的数据统计发现增温条件下土壤呼吸显著增加了 9%−12%[45-46]。哈佛森林生态研究站进行了 26 年的升温试验，发现微生物呼吸对增温的响应具有适应性，分4个阶段[47]：(1) 呼吸作用加快碳损失；(2) 微生物群落重组；(3) 土壤微生物向一个呼吸作用速率更快、多样性程度更高、贫营养微生物群落转变；(4) 惰性碳库减少并有望进一步改变微生物群落结构。短期内，土壤呼吸的明显适应性可能归因于微生物生物量的减少和土壤呼吸的热适应[48]。对于土壤胞外酶活性，土壤增温会增加植物底物的输入量，进而增加酶的产量，也可以刺激酶的稳定和周转，这些正面和负面影响由对各种植物和土壤变量的直接和间接影响驱动，因此导致升温对土壤酶活性的影响方向并不确定[49]。一般认为，胞外酶的活性随温度升高而升高，但增温造成的水分限制不利于酶和底物扩散及酶活性[50]；同时，微生物为了补偿这一水限制，可能增加胞外酶的分泌，维持自身生存[42]。Sofi 等[51]对比不同陆地生态系统中的田间试验结果发现，增温处理对参与碳元素循环过程的土壤胞外酶(水解酶和氧化酶)活性均无显著影响。

表 2　增温对土壤微生物群落和功能的影响

Table 2　Study on the effect of warming on soil microbial community and function

Soil type	Sample sites	Conclusions	References
Grassland soil	High Plains Grasslands Research Station in Cheyenne, Wyoming	The effects of warming on the soil carbon dynamics of topsoil were relatively weak, while those genes involved in denitrification and ammonification were inhibited	[39]
	Alpine Scrub Ecosystem Research Station of Aba	Warming alleviated the low temperature limiting effect of soil microbial activity, promoted fine root turnover and decomposition, increased soil available nutrient content, and increased soil microbial biomass carbon and nitrogen	[40]
	Garraf Natural Park, south of Barcelona	The seasonal variation of soil moisture in Mediterranean climate region caused obvious change of soil microbial community structure, and when a sufficient amount of soil water was available, soil enzyme activity was increased by warming	[41]
Forest soil	Wuyishan National Park	Warming accelerated water evapotranspiration, reduced soil moisture and increased soil porosity, and accelerated gas exchange between atmosphere and soil, which accelerated the process of soil organic carbon mineralization and reduced the substrate availability, resulting in the reduction of soil microbial biomass carbon	[42]
	Harvard Forest Ecological Research site, Massachusetts	Warming affected the process of litter decomposition, resulting in a 23% increase of lignin content, which promoted the activity of lignin-decomposing enzymes while cellulose-decomposing enzymes were suppressed; and shifts in fungal community composition were significantly correlated with the changes in extracellular enzyme activities, in particular, ectomycorrhizal fungi were more abundant in the heated treatment than the control	[43]

由于真菌和细菌在土壤环境中占据不同的生态位，Jansson 等[29]认为增温可能会利于细菌生长而抑制真菌生长，并且对土壤微生物功能类群有一定的选择性。细菌在土壤氮循环过程中起着重要作用，高思齐等[52]研究表明增温使土壤中氨氧化细菌群落结构发生转移，其丰富度下降；而含 *nirK* 和 *nirS* 基因的反硝化细菌的丰度分别增加 33.97%和 28.75%。然而，一些研究发现升温对森林生态系统真菌生物量和活性可能呈现促进或抑制相反的情况[43,53]，这些差异可能是由于不同地点土壤水分或植被等环境差异所致[54]。然而，森林和草原的升温研究发现了微生物群落组成的共性变化，包括真菌与细菌的比率下降[39]、革兰氏阳性细菌丰度增多，细菌比真菌更具备生长速度和养分的竞争优势[20,39]。草地土壤的长期增温试验后生态响应可能是[55]：(1) 微生物群落结构的变化，主要是由植物群落结构的变化驱动的(C4 植物比 C3 植物更倾向于在升温环境生长)；(2) 对细菌有不同的影响；(3) 增强养分循环，反馈以促进植物生长。此外，温度升高导致功能基因丰度和表达的变化[56]，如升温地块中的微生物胁迫生物标志物显著升高[57]；升温改变细胞膜的脂质组成以减少膜的流动性并抑制热休克蛋白的表达等[24]。土壤升温也对土壤含水量具有明显影响，促使土壤水分加快蒸发损失，从而间接地影响土壤微生物的生存环境[39]。

1.3　降水变化

降水变化通过改变土壤水分含量不仅直接影响土壤养分的扩散，也极大地影响了土壤微

生物群落结构和活性，进而对微生物介导的碳、氮循环过程与土壤生态系统功能造成深刻的影响(表 3)。未来几十年中，半干旱或干旱地区的荒漠化可能加剧[63]。土壤干燥将限制植物和微生物对水分和养分的吸收，不利于呼吸底物的扩散，导致呼吸作用和有机质的分解速率减弱，从而减少土壤碳损失，但微生物功能也随之下降，影响生态系统的可持续性[64]。降水增加和洪水增加导致土壤湿度增加，营造有利于产甲烷和反硝化作用的厌氧环境，从而更多地释放 CH_4 和 N_2O[65]。李博文等[66]研究发现，土壤呼吸对降水变化的响应特征呈现非线性反应，随着降水量的增加，土壤呼吸会达到一个峰值，之后会随着降水量的增多而下降。此外，土壤呼吸模式受降水变化的影响与生态系统类型、土壤微生物群落结构、干旱强度、时长和干湿交替频率等因素密切相关[67]。降水变化对土壤酶活性也会产生影响。一般情况下，土壤湿度的增加会提高土壤胞外酶活性；而土壤水分过高由于厌氧环境、底物扩散和氧含量的限制，会对酶活性产生抑制作用[68]。由于水分变化通过改变土壤 pH、养分有效性及扩散运输能力和植被类型等多方面影响土壤微生物活性及群落结构，进而改变土壤酶活性，因此，探明这些因素的综合作用有助于进一步理解水分变化条件下微生物相关的代谢过程及胞外酶活性的变化特征[67]。

干旱的长期效应可能间接地改变土壤细菌群落结构，在干旱环境下植被将逐渐转移到耐受力强的植物物种上，并随之发生根系相关微生物的变化，这比干旱对土壤细菌群落的直接影响更大[69]。相较细菌而言，真菌对水分胁迫

表 3　降水变化对土壤微生物群落和功能的影响

Table 3　Study on the effect of altered precipitation on soil microbial community and function

Soil type	Sample sites	Conclusions	References
Grassland soil	Semiarid temperate steppe of Inner Mongolia	The metabolic characteristics of soil microbial community were different in response to precipitation. The increase of precipitation changed the mineralization rate of soil nutrients, and then affected the metabolic activity of soil microorganisms	[58]
	Desert steppe of Yanchi County, Ningxia	In water-deficient environment, precipitation increased soil moisture, accelerated the leaching of litter, and promoted the soluble matter in the surface litter and humus to enter the soil, which increased the available substrate for microorganisms and the activities of sucrase, urease and phosphatase	[59]
	Hulunbuir Grassland Ecosystem Research Station	Increasing precipitation did not affect soil respiration, and drought significantly reduced soil moisture; when the soil water content was too low, the diffusion of soluble organic carbon was hindered, bacteria and other microorganisms could not grow and metabolize normally, thus inhibiting soil respiration	[60]
Forest soil	Tiantong National Forest Park	Drought significantly altered fatty acid content that characterized bacteria biomass, but had no significant effect on the ratio of soil fungi to bacteria, as well as the ratio of gram-positive bacteria to gram-negative bacteria	[61]
	Seasonal dry forest of Oaxaca	Changes in precipitation could affect arbuscular mycorrhizal fungi (AMF), and the AMF infectivity and spore density were higher in rainy season than that in dry season, but there were no significant differences in AMF diversity	[62]

的耐受性更强，真菌的菌丝有助于桥连分散的微生物和养分资源，以减缓干旱胁迫带来的生理压力[70-71]；除具有生理结构上的优势外，真菌可以在缺水环境下合成海藻糖、甘油等溶质，使细胞膜处于正常形态，提升其适应干旱的能力[72]。Preece 等[73]利用扩增子测序和磷脂脂肪酸分析研究了长期干旱对森林土壤微生物群落的影响，结果表明，细菌群落 α 多样性和生物量显著降低，真菌则不受影响。另外，一些研究发现，与植物根系形成共生体的丛枝菌根(arbuscular mycorrhiza, AM)真菌在侵染率、孢子密度和多样性等方面也呈现季节性(干湿)差异[62]。土壤微生物已经进化出各种生理策略来应对干旱胁迫。例如，渗透压调节、休眠和再活化、胞外酶合成等[74-75]，具体表现为：为了在较低的土壤基质水势中生存，微生物会积聚溶质(渗透质)以保持细胞充盈[71]；土壤微生物可能在脱水或低水状态(芽孢、孢子等)持续生存，无水分胁迫时恢复生长[76]。某些细菌类群的成员，如放线菌属和芽孢杆菌，由于能够保持活性并在干燥条件下休眠，产生胞外聚合物含有羧基、羟基、氨基等多种亲水活性官能基团，使其对水分具有更强的持留能力[77]，因此它们可以在受干旱影响的土壤中持续存在[78]。此外，土壤微生物群落的功能冗余也被证明是一种有效应对水分胁迫的细胞生理策略。例如，经历长期干旱的高山森林土壤，与灌区土壤相比，虽然细菌和真菌群落结构均出现显著变化，但却具有相似的根系分解速率，确保了土壤碳周转过程的正常进行[79]。微生物群落结构具有弹性，但近些年来研究发现，干旱对土壤生态系统产生的“遗留效应”不可忽视[80]，即干旱胁迫对土壤微生物群落组成的影响具有不可逆性，即便水分恢复到适宜条件，微生物群落结构发生不同程度的改变。Anderud 等[80]利用 ^{18}O 标记的 H_2O 研究发现，不同生态系统土壤经历干旱事件再恢复到适宜水分条件时，69%–74%的原有低丰度稀有物种能够快速响应水分变化，恢复代谢活性，增强了环境干扰下自然生态中的微生物生态网络的抵抗力和恢复力，这对于维持土壤生态系统功能和稳定性至关重要。

1.4 氮沉降

氮沉降的施肥作用增加植被净生产力，地上植被及凋落物等增加土壤碳输入，可能导致微生物生物量和活性升高；也可能导致土壤养分失衡，造成养分限制，限制胞外酶的合成(表 4)。研究表明，土壤微生物群落和功能对氮添加的响应具有生态系统依赖性，在高寒草原生态系统中，氮沉降增加降低碳相关水解酶活性和氧化酶活性[81]，而显著提高了马尾松混交林中 β-1-4 葡萄糖苷酶、纤维二糖水解酶和过氧化物酶的活性[85]。此外，氮沉降增加显著降低微生物呼吸和微生物量[86-87]。李素新等[88]模拟氮沉降增加对土壤呼吸的影响，结果表明低水平的氮沉降可以促进土壤呼吸，而高水平的氮沉降对土壤呼吸产生了抑制作用。除在试验室培养和实地调查研究外，研究人员还通过全球范围内的 META 分析研究其对氮添加的响应特征，结果表明，氮的增加导致土壤呼吸显著增加约 2.0%[89-90]。

对于土壤微生物群落对外源氮输入的敏感响应，学者使用营养生存策略理论解释加氮条件下细菌相对丰度的变化：土壤养分(N)的增加有利于富营养型细菌(copiotrophic)的生长，而不利于寡营养型细菌(oligotrophic)的生长[13]。因此，加氮可以改变真菌和细菌群落结构。Sha 等[91]发现，加氮增加真菌肉座菌目和细菌放线菌门、绿弯菌门的相对丰度，减少细菌变形菌门、酸杆菌门、厚壁菌门的相对丰度。一般认为，AM 真菌对氮添加的响应相对敏感，其主

表 4 氮沉降对土壤微生物群落和功能的影响

Table 4 Study on the effect of nitrogen deposition on soil microbial community and function

Soil type	Sample sites	Conclusions	References
Grassland soil	Naqu Alpine Grassland and Wetland Ecosystem Research Station	Soil microorganisms prefer low molecular weight organic nitrogen and carbon compounds after 5 years of nitrogen addition, which would depress the carbon hydrolase and oxidase, and activate the urase. Nitrogen addition activated plants and increased the absorption of phosphorus, which would improve the activity of phosphatase. The changes in the plant property under nitrogen addition were the most important factors for the soil enzyme at alpine steppe	[81]
Forest soil	Tropical camphor plantation of Jiu Jiang	The increase of nitrogen deposition promoted the decomposition of soil surface organic matter, resulting in the accumulation of organic carbon, and the activities of sucrase, acid phosphatase and amylase decreased with the increase of soil depth	[82]
	Temperate forest in central Massachusetts	The chronic nitrogen (N) enrichment decreased the active fungi biomass, the diversity of ectomycorrhizal fungal community and the fungal: bacterial biomass ratios. This shift in microbial community composition was accompanied by a significant reduction in the activity of lignin-degrading enzyme and catabolic evenness	[83]
Wetland soil	Sanjiang Plain Wetland Ecological Research Station	There were significant differences in functional diversity of microbial communities at different nitrogen deposition treatments. The increase of nitrogen deposition would change soil physiochemical properties and the pattern of microbial substrate use, thus resulting in the change of microbial community structure	[84]

要作用机制可能是氮沉降导致土壤可利用 N 含量增加，通过改变植物群落特征间接影响 AM 真菌的生物量、群落组成与多样性[92]。氮沉降增加给微生物带来的影响也与土壤碳供应有关，当生态系统长期处于氮增加状态时，植物倾向于将更多的碳用于自身生长，进而供应给土壤微生物的碳减少，抑制微生物生长[93]。Ramirez 等[94]对分布于北美洲多组土壤样品进行无机氮添加试验，发现加氮可以改变微生物的新陈代谢能力，抑制微生物分泌胞外酶，导致稳定碳的分解减少，增加固碳潜势。Eisenlord 等[95]利用 GeoChip 4.0 技术研究了氮增加条件下森林生态系统碳循环过程中微生物的介导机制，结果发现氮沉降显著减少了淀粉等碳化合物解聚基因的多样性和丰度，微生物对氮沉降的响应对生态系统碳循环造成反作用。氮沉降增加对氮循环相关功能物种和功能基因的影响也是研究的重点，如氮沉降增加导致氨氧化细菌(ammonia oxidizing bacteria, AOB)、硝化菌属(*Nitrobacter*)丰度的增加，以及硝化螺旋菌属(*Nitrospira*)丰度的减少，说明土壤氮循环过程显著受到土壤可利用氮的影响，且土壤氨氧化菌和亚硝酸盐氧化菌存在耦合[13,96-97]。Nie 等[98]也发现 N 添加显著降低了氨氧化细菌和含 *nos*Z 基因的反硝化细菌的丰度，而增加了含 *nirK* 基因的反硝化细菌的丰度。氮沉降增加影响土壤的过程是一个比已有认知更为复杂的过程，氮沉降增加对微生物群落和功能的影响在不同的生态系统和氮沉降增加时间、强度不同的条件下可能有较大差异。

2 全球变化因子对土壤微生物群落和功能的交互作用

多因子交互作用分为拮抗作用(多因子效应小于单因子效应之和)、协同作用(多因子效应大于单因子效应之和)和加和作用(多因子效应和单因子效应和差异不显著)[13]。当多因子交互作用的效应明显时，单因子试验对于生态系统的预

测不能代表多因子的影响。从前文关于全球变化因子对土壤微生物影响的讨论中可以看出，单个全球变化因子与多因子组合的复合效应难以解耦。因此，了解全球变化因子之间的交互作用对预测土壤生态系统的响应至关重要[24]。

以往的研究发现，升高的 CO_2 浓度和增温对土壤 N_2O 排放以及氨氧化菌和反硝化菌的丰度具有不同程度的拮抗作用，从而影响土壤 N 循环过程[16,99]。在美国怀俄明州草原上进行 12 年的大气 CO_2 浓度升高结合增温试验研究表明，半干旱草原生态系统中，氮循环中涉及的基因对升高 CO_2 浓度和增温共同作用的响应与单独升高 CO_2 浓度处理更为相似，均发生富集；但仅升温的情景下，氮循环相关基因被抑制[35]。此外，温度对土壤微生物活动的影响通常受到水分调节[100]，有研究认为，在降水充足的情况下，增温可以促进土壤微生物活动，但在干旱的情况下，增温却对土壤微生物活动具有抑制作用[101]。另有研究发现，增温和降水的增加会影响土壤微生物群落结构和群落间的潜在相互作用关系[102-103]。例如，降水的增加缓解了由增温引起的青藏高原高寒草原土壤微生物多样性的减少，为微生物物种共存提供更多的生态位；但与单独增加降水相比，两者的共同作用降低了微生物之间的相互作用强度[104]，同时显著改变了土壤有机碳含量[105]。土壤微生物在调控土壤养分循环及释放的过程中发挥重要作用，水和氮作为生态系统中常发生耦合的两个因子，土壤微生物群落对其变化的响应较为复杂[106]。吴文超等[107]研究温带沙漠不同季节的土壤微生物碳氮(MBC, MBN)对环境因子的响应时发现，水氮交互作用在各个季节均显著降低 MBC、MBN 和 MBC/MBN 比值，且土壤微生物群落中细菌较真菌占据优势，可能是因为降水变化改变了土壤的通透性，减少了微生物对氮源和碳源的利用；同时高氮降低了土壤 pH 值，进而影响土壤微生物群落结构[108]。然而 Yan 等[109]发现干旱与氮添加的共同处理对温带森林生态系统土壤微生物群落具有拮抗作用，显著影响了细菌和真菌的群落组成，增加 CO_2 释放量，但增幅小于单因子处理。也有研究认为，微生物对水氮交互作用的响应取决于当前生态系统中氮含量，当处于氮饱和状态且降水充足的情况下，施加少量氮对系统影响不大，细菌的多样性和碳源利用率均无显著变化[110]。许多陆地生态系统的相关研究表明，氮沉降和增温对土壤呼吸和微生物群落组成有显著的交互作用，所产生的协同和拮抗效应主要取决于现有土壤 C、N 含量，加氮量和温度升高的范围及研究区域自然概况[111-113]。

草地生态系统作为陆地生态系统的主体类型之一，全球变化多因子交互作用对其影响的研究受到众多学者的关注[114]。Reich 等[115]对美国明尼苏达州草地生态系统进行了为期 8 年的 4 种全球变化因子(CO_2 浓度升高、增温、降水减少、N 增加)控制试验，发现 4 个因素任意组合之间均存在两两交互作用。Thakur 等[116]通过在北美温带地区草地进行田间试验，研究了 4 个全球变化因子(CO_2 浓度升高、增温、N 增加、夏季干旱)对土壤微生物和酶的影响，发现土壤酶活性及其化学计量受到全球变化因子之间高阶相互作用的强烈影响，表现在：CO_2 浓度升高、降水量降低、升温之间的同时作用降低了土壤中碳磷吸收酶和氮磷吸收酶的比例，土壤中有机磷分解相对增加；也改变了土壤中的主要分解途径，向细菌主导的能量通道发展；大气氮沉降量增加、降水量减少、升温之间的共同作用增强了酸性磷酸酶活性；微生物生物量的变化主要由 CO_2 浓度和温度升高驱动。有研究认为，多因子相互作用之间的关系

主要由水的变化驱动[117]，在干旱的荒漠草原，季节性降水强烈地调节了土壤微生物对增温和 N 增加的响应，显著提高了土壤微生物生物量[118]。另有研究发现，CO_2 浓度升高、增温、N 增加和降水增加及其相互作用对半干旱草地 AM 真菌群落存在不同程度的影响[119]，在各处理组合中，特别是增温和 CO_2 浓度升高的共同作用下，随着 N 的添加，*Paraglomus* 的相对丰度增加，而 *Glomus* 的相对丰度降低；同时，三者的共同作用显著影响了微生物 α 多样性，但对 AM 真菌生物量无明显影响。全球变化因子的高阶相互作用也可能互相抵消影响。例如，升温和干旱对土壤生物的有害影响在 CO_2 浓度升高时减弱或消失[120]；干旱会减缓升温引起的氮矿化和土壤呼吸速率的增加[121-122]，随之增加土壤的氮限制[123]，因此氮沉降增加可以解除干旱带来的氮限制，但在升温和增加湿度的土壤条件下，氮沉降增加也可能会对土壤微生物的生长产生抑制作用[124]。因此，与单一因子的影响相比，多种全球变化因子的综合作用可能引起土壤微生物群落及功能较小的变化，多重因子相互作用的结果通常是非加性的，不能基于单一作用预测联合效应[125]。

3 已有研究的不足及未来研究方向

3.1 全球变化多因子交互作用研究

全球气候变化对土壤微生物群落组成和功能的影响是多种全球变化因子综合作用的结果，且多个全球变化因子之间存在交互作用，不同因子的影响可能相互促进或抵消，增加了研究结果的不确定性[126]。目前已有研究大多为单因子或两因子组合的模拟试验，Rillig 等[10]通过对已发表的关于全球变化如何影响土壤微生物群落和过程的试验研究文献整理，发现约 80%的研究为单因子试验，19%的研究考察了 2 个环境因素的交互作用，仅有不足 2%的研究考虑 3 个或更多环境因素的影响，尤其是对多因子的高阶交互作用(higher-order interaction)研究不足，难以准确分析全球变化整体对土壤生态系统的影响[116]。因此，需要设计完善的多种全球变化因子试验来探究高阶交互作用，以便准确量化土壤变量对未来全球气候变化情景的反馈，其结果将有助于预测未来生态系统的变化，并为完善地球系统模型提供证据和建议。

3.2 长时间、大尺度、多生态系统的监测

陆地生态系统具有复杂的植物、微生物、土壤的交互作用和代偿作用，在受到全球变化因子的影响时，陆地生态系统的反馈可能随着时间的推移产生意想不到的效果[127]。例如，Zhou 等[31]发现土壤呼吸对氮增加的响应随着试验时间的延长而逐渐减弱，而土壤呼吸对干旱单因子，以及干旱和升温联合作用的响应与试验时间呈正相关。因此，土壤微生物群落随时间的变化可能存在一定的滞后性，导致响应需要较长时间才能显现[128]。因此，长期定位观测有助于准确理解微生物在生态系统中介导的关键过程。此外，由于全球变化对土壤微生物群落多样性的直接影响可能有限，植物-微生物的相互作用在调控陆地生态系统对环境变化的响应方面具有重要影响。气候变化引起的植物群落特征变化通过改变土壤的碳输入量和方式间接影响微生物群落组成和代谢功能。已有研究表明，增雨影响植物-微生物之间的正向反馈关系[129]；通过增加植被的多样性可缓解干旱对微生物群落造成的长期影响，提高微生物群落对干旱胁迫的耐受性[130]。然而，目前关于全球变化对土壤微生物与地上植被相互作用的

影响研究较少，涉及不同陆地生态系统中地上-地下的关联性研究更为匮乏，且生态系统的异质性限制了对不同生态系统对全球变化的响应的比较分析。另外，现有相关研究的尺度一般较小且单一，地理分布不均匀，主要集中在北半球[126]。因此，全球变化背景下长期多点位、多生态系统监测网络建立，以研究陆地生态系统随气候变化的时间演变，有利于更准确地预测土壤微生物群落对未来全球变化的响应[131]。

3.3 土壤微生物群落的响应机制和模型模拟

近年来，微生物群落对全球变化的响应和反馈是微生物生态学研究的热点问题之一。目前，大多数相关研究集中在土壤呼吸、微生物量、多样性指数等指标，仅提供了有限数据的理论推断，难以阐明土壤微生物群落对全球气候变化的潜在响应机制。随着现代分子技术的出现，宏基因组学技术如稳定性同位素探测、qPCR、基因芯片和高通量测序等新技术手段将有助于深入理解全球变化对土壤微生物群落及生态功能的影响。基因芯片可用于检测微生物参与物质循环等生态活动的功能基因，为理解微生物功能多样性以及相关土壤碳氮生物地球化学过程如氨氧化、甲烷氧化和固氮作用提供新的见解[132]。宏基因组学在揭示微生物群落结构和功能及其与环境因子之间的相互关系提供了有力途径，为深入探究气候变化下不同类型微生物群落的演化特点和代谢能力奠定了基础[133]。全球气候变化对土壤微生物的影响应充分认识，另一方面，适当调控微生物群落以减缓气候变化，在未来应该受到更多的关注。Peng 等[134]研究发现，由真菌分泌的球囊霉素具有很大的固碳潜能，它可以帮助土壤微粒形成团聚体从而减缓土壤有机质的分解。Meena 等[135]认为将基因工程菌作为微生物接种剂加入土壤中，通过诱导碳酸酐酶基因的表达以增强土壤碳封存能力，是减缓温室气体排放、缓解气候变化风险的有效途径。此外，数据-模型的融合在全球气候变化的研究中至关重要。根据多种全球变化因子及其交互作用，以及土壤微生物群落响应机制，建立综合响应的生态系统模型，将有助于准确预测未来气候变化情景下生态系统的响应动态，为制定相关管理措施，充分发挥微生物减缓全球气候变化的作用，以及维持生态系统的可持续发展提供技术支持。

4 结论

土壤微生物群落结构对全球气候变化的响应至关重要。大气 CO_2 浓度升高、升温、降水变化、氮沉降增加对土壤微生物群落组成和功能产生直接或间接的影响，影响的大小、方向不同且呈现不同的敏感性。多个全球变化因子对土壤微生物群落结构的交互效应可能存在加性、协同、拮抗的交互作用，产生加和的、相互促进或抵消的整体效果。多全球变化因子的长时间、多生态系统、大空间尺度试验设计，以探究多因子的高阶交互作用，建立综合响应的生态系统模型，有助于准确预测未来气候变化情景下生态系统的响应。

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