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苏打盐碱地丛枝菌根真菌群落结构与多样性特征

陈晓烨[1,2#]，朱欢欢[1,2#]，孙晨雨[1,3]，李秋实[1,2]，张雅然[1,2]，杨艳[1,2]，曹瑞卿[1,2]，王聪[1]，仰剑霞[1]，董强[1]，李杏春[1]，陈沛霖[1*]，高程[1*]

1 中国科学院微生物研究所，微生物多样性与资源创新利用全国重点实验室，北京
2 中国科学院大学 生命科学学院，北京
3 山东农业大学 生命科学学院，山东 泰安

陈晓烨, 朱欢欢, 孙晨雨, 李秋实, 张雅然, 杨艳, 曹瑞卿, 王聪, 仰剑霞, 董强, 李杏春, 陈沛霖, 高程. 苏打盐碱地丛枝菌根真菌群落结构与多样性特征[J]. 微生物学报, 2025, 65(8): 3413-3431.
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摘　要：盐碱地是全球范围内广泛分布的一类退化土壤，其中苏打盐碱地因其盐碱共存的特征治理难度较大，是制约土壤资源有效利用的重要障碍。丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)通过促进养分吸收和增强抗逆性改善植物的生长与存活能力，为苏打盐碱地的改造利用提供潜在途径。【目的】探究在苏打盐碱胁迫梯度下 AMF 群落结构和多样性随胁迫和其他环境因子的变化。【方法】采集吉林省长岭县和大安市中受到不同程度苏打盐碱胁迫的土壤样品，包括长有碱蓬(*Suaeda glauca*)的荒地(pH 10.0−10.5)、无植被覆盖的裸地(pH 9.5−10.0)和胁迫程度不同的玉米(*Zea mays* L.)农田(pH 8.5−10.0)。利用 18S rRNA 基因高通量测序方法检测 AMF 群落结构与多样性。【结果】检测到的 AMF 在属水平上以内养囊霉属(*Entrophospora*)、斗管囊霉属(*Funneliformis*)、根孢囊霉属(*Rhizoglomus*)和多氏囊霉属(*Dominikia*)为主。AMF 相对多度与土壤总碳、总氮、总磷、有效氮显著正相关，与土壤 pH、电导率和盐度显著负相关。AMF 群落结构与土壤总碳和 pH 显著相关；AMF 香农多样性(α 多样性)与土壤全磷含量和盐度呈显著正相关；AMF 群落结构离散度(β 多样性)与电导率显著负相关；AMF 的 α 多样性和 β 多样性显著负相关。【结论】盐碱胁迫对 AMF 群落施加了同质性选择，使其群落变小、β 多样性降低、α 多样性升高、种类组成发生改变。

关键词：盐碱地；丛枝菌根真菌；微生物群落结构；微生物群落多样性

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#These authors contributed equally to this work.
*Corresponding authors. GAO Cheng, Tel: +86-10-64807024, E-mail: gaoc@im.ac.cn; CHEN Peilin, +86-10-64807020, E-mail: chenpl@im.ac.cn
ORCID: GAO Cheng (0000-0003-2522-7909), CHEN Peilin (0009-0006-1613-3352)
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Structures and diversity of arbuscular mycorrhizal fungal communities in soda saline-alkali land

CHEN Xiaoye[1,2#], ZHU Huanhuan[1,2#], SUN Chenyu[1,3], LI Qiushi[1,2], ZHANG Yaran[1,2], YANG Yan[1,2], CAO Ruiqing[1,2], WANG Cong[1], YANG Jianxia[1], DONG Qiang[1], LI Xingchun[1], CHEN Peilin[1*], GAO Cheng[1*]

1 State Key Laboratory of Microbial Diversity and Innovative Utilization, Chinese Academy of Sciences, Beijing, China
2 College of Life Sciences, University of Chinese Academy of Sciences, Beijing, China
3 College of Life Sciences, Shandong Agricultural University, Tai'an, Shandong, China

Abstract: Saline-alkali land is a common type of degraded soil with wide distribution across the globe. Among all types of saline-alkali land, soda saline-alkali land, characterized by the coexistence of high salinity and alkalinity, is particularly difficult to be managed and represent a major obstacle to the effective utilization of soil resources. Arbuscular mycorrhizal fungi (AMF) enhance plant growth and survival by improving nutrient uptake and increasing stress resistance, offering promising potential for the reclamation and utilization of saline-alkali land. **[Objective]** To explore how the structures and diversity of the AMF community vary along a soda saline-alkaline stress gradient in response to stress and other environmental factors. **[Methods]** We collected soil samples subjected to varying levels of soda saline-alkaline stress from Changling County and Da'an City in Jilin Province. The sampling sites included *Suaeda glauca*-covered wildland (pH 10.0−10.5), unvegetated bare land (pH 9.5−10.0), and maize (*Zea mays* L.) farmlands under varying levels of stress (pH 8.5 − 10.0). The structures and diversity of AMF communities in these soil samples were analyzed by Illumina-based 18S rRNA gene sequencing. **[Results]** AMF communities were predominantly composed of *Entrophospora*, *Funneliformis*, *Rhizoglomus*, and *Dominikia*. The relative abundance of AMF was significantly positively correlated with soil total carbon, total nitrogen, total phosphorus, and available nitrogen, and it was significantly negatively correlated with soil pH, electrical conductivity, and salt content. The AMF community structure was significantly associated with soil total carbon and pH. The Shannon diversity (alpha diversity) of AMF showed significantly positive correlations with total phosphorus and salt content, while the AMF community structure dispersion (beta diversity) was significantly negatively correlated with electrical conductivity. Moreover, the alpha diversity and beta diversity of AMF had a significantly negative correlation. **[Conclusion]** Saline-alkaline stress exerted homogeneous selection on the AMF community, leading to reduced community size, decreased beta diversity, increased alpha diversity, and altered community composition.

Keywords: saline-alkali land; arbuscular mycorrhizal fungi; microbial community structure; microbial community diversity

盐碱地主要是指盐土、碱土和各种不同程度盐化和碱化土壤的总称，盐土主要指以氯化物和硫酸盐阴离子为主的土壤，电导率(electrical conductivity, EC)>4.0 dS/m，pH<8.5；

✉ actamicro@im.ac.cn, ☏ 010-64807516

碱土则主要指以碳酸盐和重碳酸盐阴离子为主的土壤，EC<4.0 dS/m，pH>8.5；当土壤的 EC>4.0 dS/m，pH>8.5 时，即为盐碱土[1-3]。土地盐碱化问题是各国一直以来面临的困难与挑战，长期制约着耕地资源的可持续利用，严重威胁粮食安全和农业可持续发展[4-5]。据联合国粮食及农业组织统计，目前全球有超过 13.81 亿 hm^2 的土地受到盐碱化影响，占全球陆地面积的 10.7%[6]。全球每年因盐碱化导致退化的土地面积约 1 000 万 hm^2，已成为干旱和半干旱地区土地资源利用的主要限制因素之一[7]。

我国盐碱地分布范围广、面积大且类型多样，面积约 1 亿 hm^2，土壤类型主要以黄河滩地和滨海盐土、西北内陆盐碱土和东北苏打盐碱土最为典型[8-9]。其中，苏打盐碱土的盐分以碳酸盐和重碳酸盐为主，具有盐碱并存、治理难度大的特点，以其特有的理化性质区别于其他盐碱土类型，盐碱土的高盐高碱复合胁迫会加剧对生物生长和生存的抑制作用[10-11]。松嫩平原是中国苏打盐碱地的典型分布区域，也是全球苏打盐碱地的主要分布区域之一，盐碱化土地面积达 393.7 hm^2 [12-15]。同时，该区域又是我国重要的粮食主产区，在国家粮食安全战略中具有重要地位。我国耕地资源紧张、粮食安全压力加大，亟需在提升现有耕地产能的同时科学开发盐碱地等后备耕地资源，以夯实粮食安全底线[16]。缓解松嫩平原苏打盐碱化程度、提升苏打盐碱地可利用性，对增加耕地产出效益、保障国家粮食安全和实现农业生产可持续具有重要的现实意义与战略价值。

盐胁迫通过对植物产生渗透和氧化胁迫导致叶片失水和体内盐分增加，破坏植物细胞结构，而碱胁迫的高 pH 值还会进一步对植物造成损害，抑制养分和水分吸收，产生离子毒性[17-18]。面对盐碱胁迫，植物进化出一系列生理生化和分子机制来适应环境，例如积累渗透性物质、调节光合作用途径和增强抗氧化酶和抗氧化分子等[19-21]。然而在更加强烈或长期的盐碱胁迫下，自身机制通常难以有效维持植物的正常生长和生理功能，因而有益微生物的帮助显得尤为重要。丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)作为连接土壤微生物和植物的重要桥梁，能与陆地上大部分维管植物形成互惠共生结构，促进植物对营养物质的吸收，增强植物对生物胁迫(如病原菌)和非生物胁迫(如干旱和盐分胁迫)的耐受性[22-26]。已有研究表明，丛枝菌根真菌可以通过增强养分吸收、维持离子稳态、改善水分状态、提升抗氧化能力和促进光合作用等多个方面增强植物对盐碱胁迫的适应能力[27-30]。AMF 与植物形成紧密的共生关系，植物为 AMF 提供光合作用产物，AMF 反过来为植物提供难以获取的养分，促进植物对氮、磷等无机营养物质的吸收[31-32]。同时，AMF 的菌丝可以连接植物宿主根系形成共同菌丝网络(common mycorrhizal network, CMN)，能够调节植物间的养分分配、信号传递和植物种群变化[32-33]。

微生物作为土壤生态系统的重要组成部分，其群落组成和功能受到环境和植物的塑造，同时也通过调控养分循环、缓解非生物胁迫等过程影响土壤和植物健康[34-36]。目前关于盐碱胁迫对细菌群落组成和功能的研究已较为丰富。研究表明盐碱胁迫会显著降低土壤细菌群落多样性，细菌对碳源的代谢活性和功能多样性也显著下降[37-39]。此外，细菌群落与真菌群落对盐碱胁迫表现出不同的响应，细菌群落对盐碱胁迫比真菌群落更敏感，其群落结构显著改变，嗜盐碱和寡营养类群得到富集[40-41]。与细菌不同，AMF 作为与植物密切联系的专性共生体，具有较复杂的生活史和有限的扩散能力。盐度和 pH 能够直接影响 AMF 的孢子萌发、菌丝生长以及其在植物根部的定殖率[42-43]，从而调控 AMF 群落的空间分布特征。与其他类型盐碱地相比，苏打盐碱地具有更强的碱性，其与盐胁迫共同作用形成更复杂和严峻的胁迫环境。尽管有研究表明 AMF 对盐碱胁迫具有适应能

力[44-46]，但在苏打盐碱地的盐碱复合胁迫下，顺盐碱梯度 AMF 群落组成和多样性如何变化仍不明确。

本研究提出以下假设：沿盐碱梯度 AMF 群落结构趋于简单化，物种多样性降低，群落间相似性增加。本研究选择受不同程度盐碱胁迫的苏打盐碱地土壤：有碱蓬(*Suaeda glauca*)的荒地(pH 10.0−10.5)、无植被覆盖的裸地(pH 9.5−10.0)和种有玉米(*Zea mays* L.)的农田(pH 8.5−10.0)，探究盐碱胁迫梯度下 AMF 群落组成和多样性如何变化。

1 材料与方法

1.1 研究地点与土壤处理方法

本研究采样地点位于吉林省松原市长岭县和大安市白城市，选取了 3 类不同土地利用类型的样地：(1) 有碱蓬(*Suaeda glauca*)生长的荒地，土壤 pH 为 10.0−10.5；(2) 无植被覆盖的裸地，pH 为 9.5−10.0；(3) 种植玉米(*Zea mays* L.)的农田，pH 为 8.5−10.0。在长岭县采集了 5 种类型土壤样品，在大安市采集了 3 种类型的土壤样品，每个样品采集 5 份，共 40 份土壤样品(表 1)。所选玉米农田均经历了不同年限的土壤改良工作，根据土壤改良年限及玉米植株的生长状况划分为高度胁迫、中度胁迫和低度胁迫 3 类。其中，高度胁迫玉米地的土壤改良年限不足 1 年，植被覆盖度低，存活下来的玉米植株生长严重受限。中度胁迫玉米地的改良年限为 1−2 年，玉米植株生长状况优于高度胁迫玉米地，但株高明显低于低度胁迫玉米地，植株分布也较为稀疏。低度胁迫玉米地的改造年限超过 2 年，其中玉米长势良好，无明显的胁迫迹象。

采集过程中避开植物根际，收集表层(0−10 cm)的非根际土壤，用孔径为 2 mm 的土壤筛进行筛分，去除土壤中较大颗粒、碎石和植物残体等。取适量筛分后的土壤于自封袋中，采集得到的土壤一部分使用冰袋运输至实验室后−80 ℃冰箱中储存，另一部分在常温下风干，用于土壤理化性质测试。

1.2 土壤理化性质测试

本研究中测定的土壤理化性质包括总碳(total carbon, TC)、总氮(total nitrogen, TN)、全磷(total phosphorus, TP)、有效磷(available phosphorus, AP)、有效氮(available nitrogen, AN)、pH、电导率(electrical conductivity, EC)和盐度(表 2)，由内蒙古鼎铖检测服务有限公司测定。总碳、总氮使用元素分析仪(Elementar 公司)测定[47-48]，全磷通过碱熔-钼锑抗比色法利用紫外分光光度计(PerkinElmer 公司)测量[49]，有效磷通过碳酸氢钠浸提-钼锑抗比色法利用紫外分光光度计(PerkinElmer 公司)测定[50]，有效氮使用碱解蒸馏法通过凯氏定氮仪(FOSS 公司)测定[51-52]。土壤 pH 通过 pH 计(Sartorius 公司)测

表1 采样点基本信息

Table 1 Basic information of sampling sites

Sampling site	Habitat type	Longitude (E)	Latitude (N)
Changling County	*Suaeda* land	123°27′34″	44°31′16″
	Bare land	123°27′15″	44°31′24″
	Heavily stressed maize land	123°27′34″	44°31′20″
	Moderately stressed maize land	123°27′35″	44°31′21″
	Weakly stressed maize land	123°27′35″	44°31′16″
Da’an City	*Suaeda* land	123°51′09″	45°36′21″
	Heavily stressed maize land	123°38′01″	45°25′59″
	Weakly stressed maize land	123°51′17″	45°36′37″

表2 采样点土壤理化性质

Table 2 Soil physicochemical properties of sampling sites

Sampling site	Habitat type	Soil physicochemical properties							
		TC (g/100 g)	TN (g/100 g)	TP (g/100 g)	AP (mg/kg)	AN (mg/kg)	EC (dS/m)	pH	Salt content (g/100 g)
Changling County	*Suaeda* land	0.736±0.057	0.052±0.005	0.025±0.002	4.920±0.626	34.447±5.663	0.604±0.597	9.884±0.090	0.426±0.141
	Bareland	0.691±0.097	0.054±0.004	0.028±0.006	6.880±2.061	42.691±6.665	1.290±0.429	9.684±0.076	0.560±0.226
	Heavily stressed maize land	1.117±0.506	0.097±0.033	0.026±0.004	14.100±4.953	73.899±18.486	0.761±0.338	8.980±0.203	0.126±0.110
	Moderately stressed maize land	1.086±0.132	0.097±0.018	0.035±0.014	32.500±13.915	70.366±9.676	0.483±0.096	8.700±0.116	0.123±0.064
	Weakly stressed maize land	0.978±0.286	0.089±0.022	0.037±0.005	11.460±5.619	68.600±23.150	0.127±0.073	8.694±0.137	0.045±0.012
Da'an City	*Suaeda* land	1.313±0.086	0.052±0.008	0.031±0.003	45.840±6.437	26.203±3.515	10.202±1.518	10.350±0.096	4.115±1.120
	Heavily stressed maize land	0.873±0.109	0.073±0.019	0.030±0.008	30.160±22.632	56.529±14.816	0.882±0.217	9.898±0.306	0.817±0.277
	Weakly stressed maize land	1.671±0.048	0.132±0.009	0.049±0.007	4.940±1.467	80.377±10.441	0.078±0.007	8.528±0.083	0.107±0.130

定，测定所用土样和水的质量体积比为 1:2.5[53]。土壤电导率使用电导率仪(上海仪电科学仪器股份有限公司)对土样与水质量体积比为 1:5 的土壤浸提液测定得到，盐度通过质量法测定得到[54-55]。

1.3 DNA 提取和 PCR 扩增

1.3.1 DNA 提取

使用 DNeasy PowerSoil DNA Pro Kit，(Qiagen 公司)对土壤微生物 DNA 进行提取，参照说明书并进行适当优化：样品加入 CD1 缓冲液后于 65 ℃水浴加热 10 min，随后使用 FastPrep-24 5G 均质仪(MP 公司)以 6 m/s 的速度处理 10 s。提取的 DNA 经 NanoDrop 2000 分光光度计(ThermoFisher Scientific 公司)测定浓度和纯度，并在−20 ℃保存备用。

1.3.2 PCR 扩增和 DNA 测序

PCR 反应体系(20 μL)：2×Phanta Flash Master Mix 酶 10 μL，上、下游引物(10 μmol/L)各 2.5 μL，DNA 模板(5 ng/μL) 2.5 μL，ddH_2O 0.5 μL，0.3% 牛血清蛋白 2 μL。对真菌 ITS 区域进行 PCR 扩增使用的引物对为 fITS7 (5′-GTGARTCATCGAATCTTTG-3′)和 ITS4-Fun (5′-AGCCTCCGCTTATTGATATGCTTAART-3′)[56-57]。PCR 反应条件：98 ℃预变性 30 s；98 ℃变性 10 s，58 ℃退火 5 s，72 ℃延伸 40 s，35 个循环；72 ℃终延伸 1 min。采用巢式 PCR 对 AMF 的 ITS 区域进行扩增，第 1 轮使用的引物对为 GeoA2 (5′-CCAGTAGTCATATGCTTGTCTC-3′)和 AML2 (5′-GAACCCAAACACTTTGGTTTCC-3′)[58-59]。PCR 反应条件：98 ℃预变性 30 s；98 ℃变性 10 s，58 ℃退火 30 s，72 ℃延伸 40 s，20 个循环；72 ℃终延伸 1 min。第 2 轮使用的引物对为 NS31 (5′-TTGGAGGGCAAGTCTGGTGCC-3′)和 AMDGR (5′-CCCAACTATCCCTATTAATCAT-3′)[60-61]。PCR 反应条件：98 ℃预变性 30 s；98 ℃变性 10 s，58 ℃退火 30 s，72 ℃延伸 40 s，30 个循环；72 ℃终延伸 1 min。

将每个样本的 PCR 产物等体积混合，通过

胶回收试剂盒(Axygen 公司)进行纯化，并用 Qubit 2.0 荧光剂(Life Technologies 公司)测定纯化产物浓度。最终利用 Illumina NovaSeq 6000 平台(上海派森诺生物科技有限公司)进行测序。

1.4 生物信息分析

利用 QIIME 2 (v2023.7)进行测序数据处理和质量控制[62]。利用 demultiplex (去混合)操作，根据条码序列(barcode)将样品的序列数据分配到对应的样品中。使用 USEARCH (v11.0.667)和 cutadapt 合并配对序列，对测序数据进行引物修剪，丢弃长度小于 100 bp 的短序列[63-64]。对测序数据进行质量控制，去除期望错误过多、最大质量评分小于 42 的低质量序列，再将得到的序列进行去重复和去除低频序列。利用 USEARCH 根据 97% 的相似性对序列进行聚类，划分为不同的可操作分类单元(operational taxonomic unit, OTU)[63]。将真菌和丛枝菌根真菌 OTU 代表序列利用 BLAST (v2.16.0+)[65]分别与 EUKARYOME 数据库(v1.9.4)[66]进行比对，并按照比对一致性(percent identity)阈值大于 90% 的标准进行筛选。将筛选后的丛枝菌根真菌 OTU 序列在 Galaxy v22.05 平台(https://galaxy.pasteur.fr/)上构建系统发育树。具体步骤为：使用 MAFFT 工具进行比对，采用 BMGE (block mapping and gathering with entropy)进行序列清理，最后使用 MrBayes 进行系统发育树的构建，生成树文件用于确定比对后的 OTU 是否属于目标分类群，并验证其系统发育关系在发育树中的一致性和可信度。树文件的可视化在 iTOL 平台(https://itol.embl.de/)完成。

1.5 数据分析和可视化

数据分析和可视化均在 R v4.4.1 中完成[67]。对于多组样本之间的差异，使用 agricolae 包(v1.3.7)[68]中的 kruskal 命令进行 Kruskal-Wallis 非参数检验。通过 vegan 包(v2.6.8)中的 adonis2 函数进行置换多元方差分析(permutational multivariate analysis of variance, PERMANOVA)，检验不同样本间群落结构的差异。所有数据可视化均使用 ggplot2 包(v3.5.1)[69]实现。α 多样性计算通过 vegan 包(v2.6.8)[70]中的 diversity 实现，β 多样性计算中的 Bray-Curtis 距离和 Jaccard 距离通过 vegan 包(v2.6.8)中的 vegdist 功能计算。Simpson 成对相异性指数通过 betapart 包(v1.6)[71]中的 beta.pair 命令计算得到。冗余分析(redundancy analysis, RDA)通过 vegan 包(v2.6.8)实现，利用 envfit 函数来检验环境变量与微生物群落分布之间的关系。基于构建的系统发育树和群落组成数据，利用 picante 包(v1.8.2)[72]中的 ses.mpd 函数，通过平均成对系统发育距离(mean pairwise distance, MPD)乘以−1 计算净种间亲缘关系指数(net relatedness index, NRI)。使用“taxa.labels”零模型构建方法，对系统发育树的物种标签进行随机置换，重复 999 次，通过置换检验评估 MPD 是否显著偏离随机期望。NRI 指数为正表明系统发育结构聚集，NRI 指数为负则表明系统发育结构发散。利用 vegan 包(v2.6.8)的 betadisper 函数对 AMF 群落的 Bray-Curtis 距离矩阵进行主坐标分析(principal coordinates analysis, PCoA)。

2 结果与分析

2.1 土壤理化性质

本研究比较了不同土壤样品的盐碱理化特征，包括 pH 值、电导率和盐度(图 1)。各样品在 pH、电导率和盐度这 3 种理化性质表现出显著的梯度变化。其中，大安市碱蓬地的 3 项指标显著高于其他样地，表明其处于最强的盐碱胁迫状态；玉米地中 pH 和电导率呈现出与作物长势相对应的由高至低的梯度分布。土壤样品的盐碱理化因子构成了一个连续的、可用于 AMF 群落分析的自然胁迫梯度。

2.2 AMF 的群落组成

通过 Illumina 高通量测序将处理后的 AMF 序列进行划分和比对，得到 58 个符合条件的

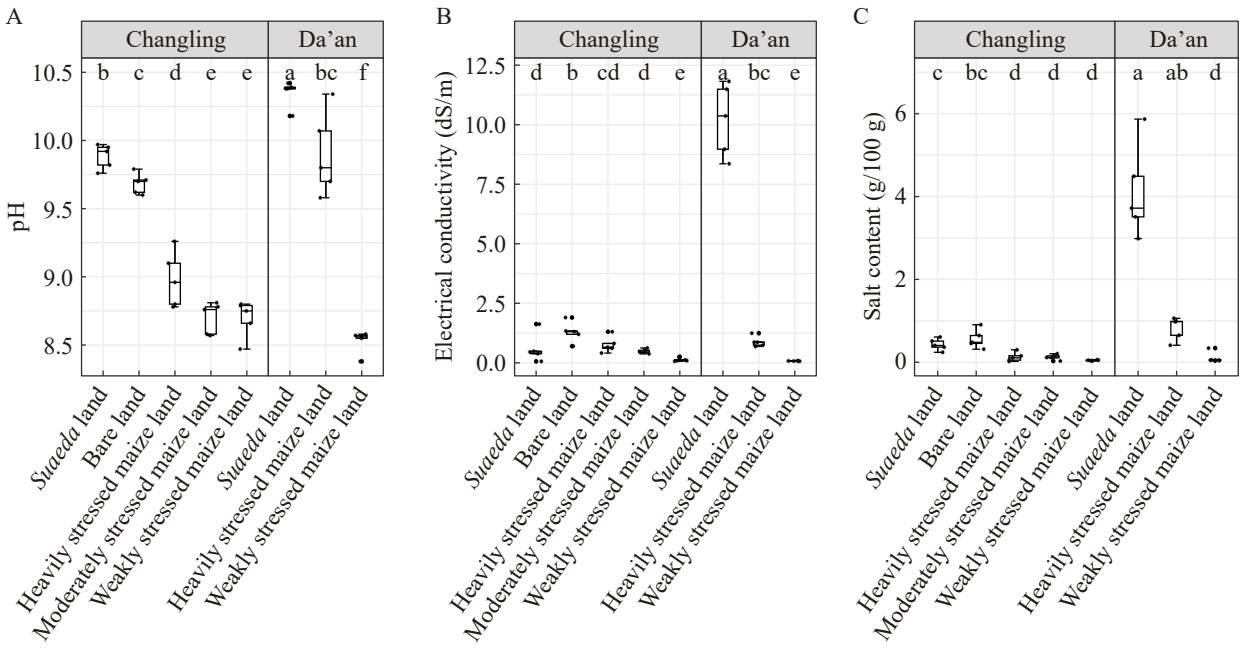

图1 采样点土壤盐碱理化特征。A：pH值；B：电导率；C：盐度。须状线表示大部分数据的分布范围，落在须状线之外的点为异常值。采样点之间的显著差异用小写字母表示，通过Kruskal-Wallis检验在0.05显著性水平下确定。

Figure 1 Saline-alkaline properties of soil in each sampling site. A: pH; B: Electrical conductivity; C: Salt content of each sampling site. Whiskers represent the distribution of most data points, while outliers are those falling outside the whiskers. Lowercase letters indicate significant differences among sampling sites, which are determined by Kruskal-Wallis test at a significance level of 0.05.

OTUs，共 523 919 条 AMF 的相关序列。为减少样本之间因测序深度不同导致的后续分析差异，选取最小序列数 189 对 AMF 的 OTUs 数据进行抽平处理，移除在所有样本中丰度为 0 的 OTUs (OTU488 和 OTU696)，最终得到 56 个 OTUs (图 2A)。

用抽平后的 OTU 表格进行群落组成分析，得到各个土壤样品中 AMF 在不同分类水平的群落组成(图 2C)。检测得到的 AMF 均属于球囊菌门(*Glomeromycota*)，在属水平上主要由内养囊霉属(*Entrophospora*, 22.0%)、斗管囊霉属(*Funneliformis*, 19.0%) 和根孢囊霉属(*Rhizoglomus*, 14.1%)组成，其次是多氏囊霉属(*Dominikia*, 12.4%) (图 2C)。值得注意的是，长岭县高胁迫玉米地内养囊霉属(*Entrophospora*)的占比和中度胁迫玉米地根孢囊霉属(*Rhizoglomus*)显著高于其他生境，分别达到 50.7% 和 45.2%。冗余分析(RDA)进一步探究环境因子对 AMF 群落结构的影响(图 2D)。结果表明，前两轴共解释了 56.59% 的群落结构变异(RDA1 为 44.73%，RDA2 为 11.86%)。其中，总碳和 pH 对 AMF 群落结构具有较强的解释力，可能是驱动 AMF 群落组成差异的重要因子。净种间亲缘关系指数(NRI)与 pH 的回归分析表明，样本 NRI 值与 pH 无显著关系。置换检验显示，每个样本的 NRI 值均不显著，说明群落中物种之间的系统发育距离分布无显著聚集或发散趋势，表现为随机的 AMF 群落系统发育结构(图 2B)。

利用 AMF 序列占全部真菌序列的相对比例来计算 AMF 的总丰度，AMF 序列相对占比在

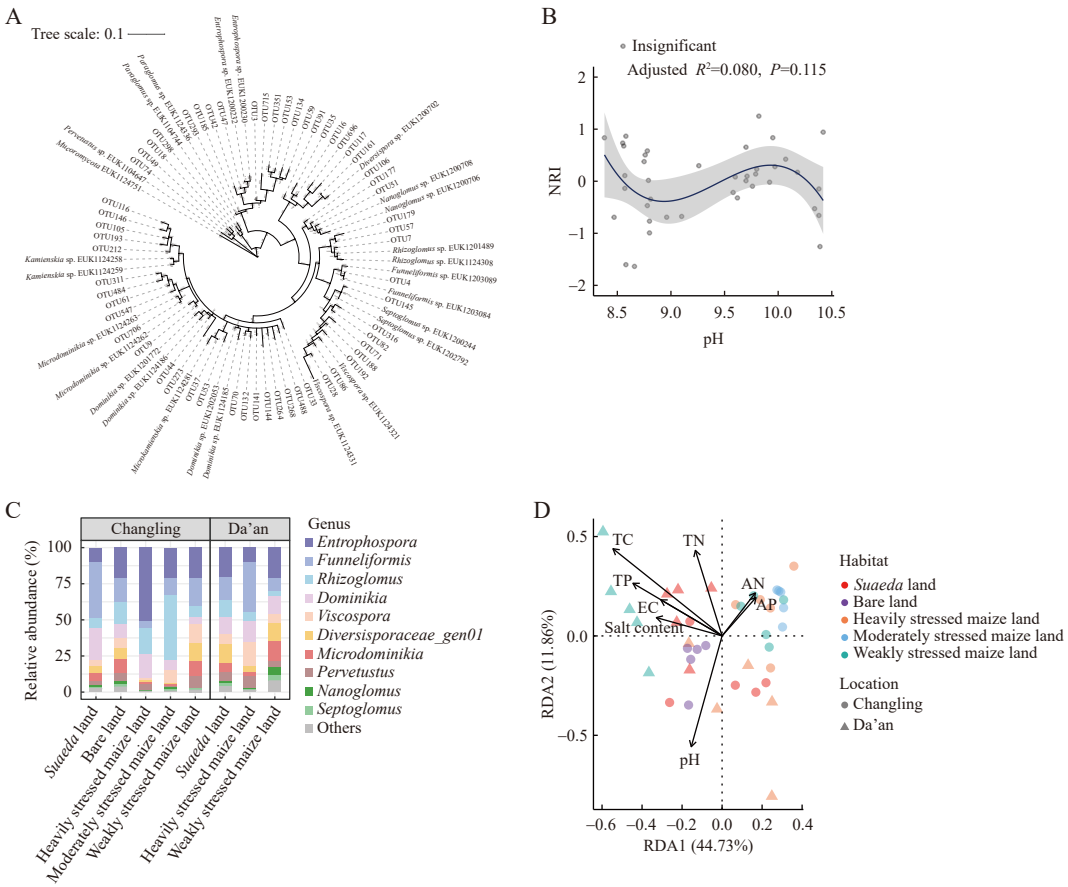

图2　AMF系统发育结构和群落组成及其对土壤理化因子的响应。A：根据OTUs序列和检索自EUKARYOME数据库已知的丛枝菌根真菌分类群和毛霉门(*Mucoromycota*)的代表序列构建得到系统发育树(支长在分支上显示，代表分类单元之间的系统发育距离；bootstrap支持率在节点处标明，反映各分支的置信度)；B：实线表示用3次多项式回归模型[NRI-poly (pH, 3)]进行的拟合，展示了NRI随土壤pH的变化趋势(每个点表示各个独立样本，阴影区域表示95%置信区间)。C：AMF群落在属水平的结构；D：土壤理化性质解释了AMF群落组成的差异性(双轴图展示了前2个RDA轴与其对应的解释度，反映了AMF群落组成与不同环境因子之间的关系；通过envfit分析得到的显著理化性质用星号表示；TC：总碳，TN：总氮，TP：全磷，AN：碱解氮，AP：有效磷，EC：电导率)。

Figure 2　Phylogenetic structure and community composition of AMF and their responses to soil physicochemical factors. A: The tree was constructed based on OTUs sequences and representative reference sequences of known AMF taxa and *Mucoromycota* retrieved from the EUKARYOME database (Branch lengths are shown along the branches, representing the phylogenetic distances between taxa; Bootstrap support values are indicated at the nodes which reflect the confidence of each clade); B: The solid line represents a cubic polynomial regression fit [NRI-poly (pH, 3)], showing the variation trend of NRI along the soil pH (Each point stands for an individual sample and the shaded area represents 95% confidence interval); C: The structure of AMF communities at the genus level; D: Soil physicochemical properties accounted for the differences in AMF community composition (The biplot shows the first two RDA axes with their corresponding degree of explanation, reflecting the relationship between AMF community composition and different properties; Significant physicochemical properties are denoted by asterisk, as determined by the envfit analysis; TC: Total carbon; TN: Total nitrogen; TP: Total phosphorus; AN: Available nitrogen; AP: Available phosphorus; EC: Electrical conductivity).

两地不同生境中的变化趋势相似，并且不同生境类型中 AMF 占比存在显著区别(图 3A)。在低胁迫玉米地中 AMF 的平均相对多度(长岭县 2.48% 和大安市 6.88%)显著高于其他类型生境，而碱蓬地(长岭县 0.27% 和大安市 0.63%)和裸地(0.09%)中 AMF 比例最低。AMF 序列相对占比与土壤理化性质的相关性分析进一步表明，除土壤有效磷(图 3F)外，其他环境因子均与 AMF 占比呈显著线性关系：总碳、总氮、全磷和碱解氮与其呈正相关(图 3B−3E)，而 pH、电导率和盐度与其则呈负相关(图 3G−3I)。这说明土壤养分状况和环境胁迫对 AMF 的分布具有显著影响。

2.3 AMF 群落的 α 多样性

在长岭县玉米地中 α 多样性指数呈现随胁迫强度增加而减小的趋势，低度胁迫玉米地 AMF 群落的香农多样性指数高于其他玉米地，大安市低度胁迫玉米地也表现出相似的趋势(图 4A)。值得注意的是，长岭县的裸地和大安市的碱蓬地显示出较高的 α 多样性水平。AMF 群落香农多样性指数关于不同土壤理化性质的相关性分析表明，AMF 的 α 多样性与全磷(R=0.335，P=0.035)和盐度(R=0.323，P=0.042)呈显著正相关(图 4B、4C)，与其他土壤理化性质无显著相关性。

2.4 AMF 群落的 β 多样性

为了进一步比较不同样地 AMF 群落结构的差异和变化模式，基于 Bray-Curtis 距离进行了主坐标分析(PCoA)和 β 多样性分析(图 5A−5C)。PERMANOVA 检验(F=2.78，P=0.001)和 Kruskal-Wallis 检验(χ^2=25.3，P=6.778×10^{-4})说明不同生境下土壤 AMF 群落结构存在明显差异，且 AMF 群落在各个样点内的离散度差异显著(图 5A)。为进一步评估不同生境中 AMF 群落结构和组内离散度差异，进行了 Bray-Curtis 相异性分析和 β 离散度分析(图 5B、5C)。不同样地 Bray-Curtis 相异性分析结果表明，相比碱蓬地和裸地，玉米地 AMF 群落间组成差异较大(图 5B)。大安市碱蓬地和长岭县裸地中 AMF 群落结构的离散度均低于玉米农田，表明在玉米农田中 AMF 群落的内部变异性更大，群落结构更为分散(图 5C)。

为进一步探究土壤理化性质对 AMF 群落结构的影响，分析了基于 Bray-Curtis 距离计算的群落结构相异性与不同土壤理化性质欧式距离矩阵之间的相关性，结果显示两者之间的相关性并不显著，表明单一土壤理化因子对 AMF 群落结构变异的解释力有限。AMF 群落组成可能受到多个环境因子共同作用，且其响应关系可能较为复杂，难以用单一理化性质的线性关系加以解释。接着对 AMF 群落结构离散度与土壤理化性质的关系进行探究，发现 AMF 群落的结构离散度与 pH (R=−0.224，P=0.165) (图 5I)和盐度(R=−0.312，P=0.050) (图 5K)无显著线性关系，而与电导率呈显著负相关(R=−0.380，P=0.016) (图 5J)。

用不同 β 多样性度量方式，包括 AMF 群落的 Bray-Curtis 相异性、组内离散度、Jaccard 相异性和 Simpson 距离与 AMF 群落 α 多样性进行相关性分析(图 6)，发现 AMF 的 α 多样性与 β 多样性指标均呈负相关关系。这说明随 AMF 群落内部的离散度和群落结构差异增加，群落的 α 多样性减小。

3 讨论与结论

3.1 AMF 群落组成和多样性受到土壤养分和盐碱胁迫共同驱动

本研究中总碳和 pH 是影响 AMF 群落组成最显著的因子(图 2D)。Yang 等[73]研究表明，地上植物生物量变化可能引起土壤总碳含量的变化，进而调控 AMF 群落结构和多样性。虽然本研究未直接测定地上植物的生物量，但在玉米地等人类活动干扰强、生物量高的生境中土壤总碳含量较高，能够在一定程度上反映碳分配

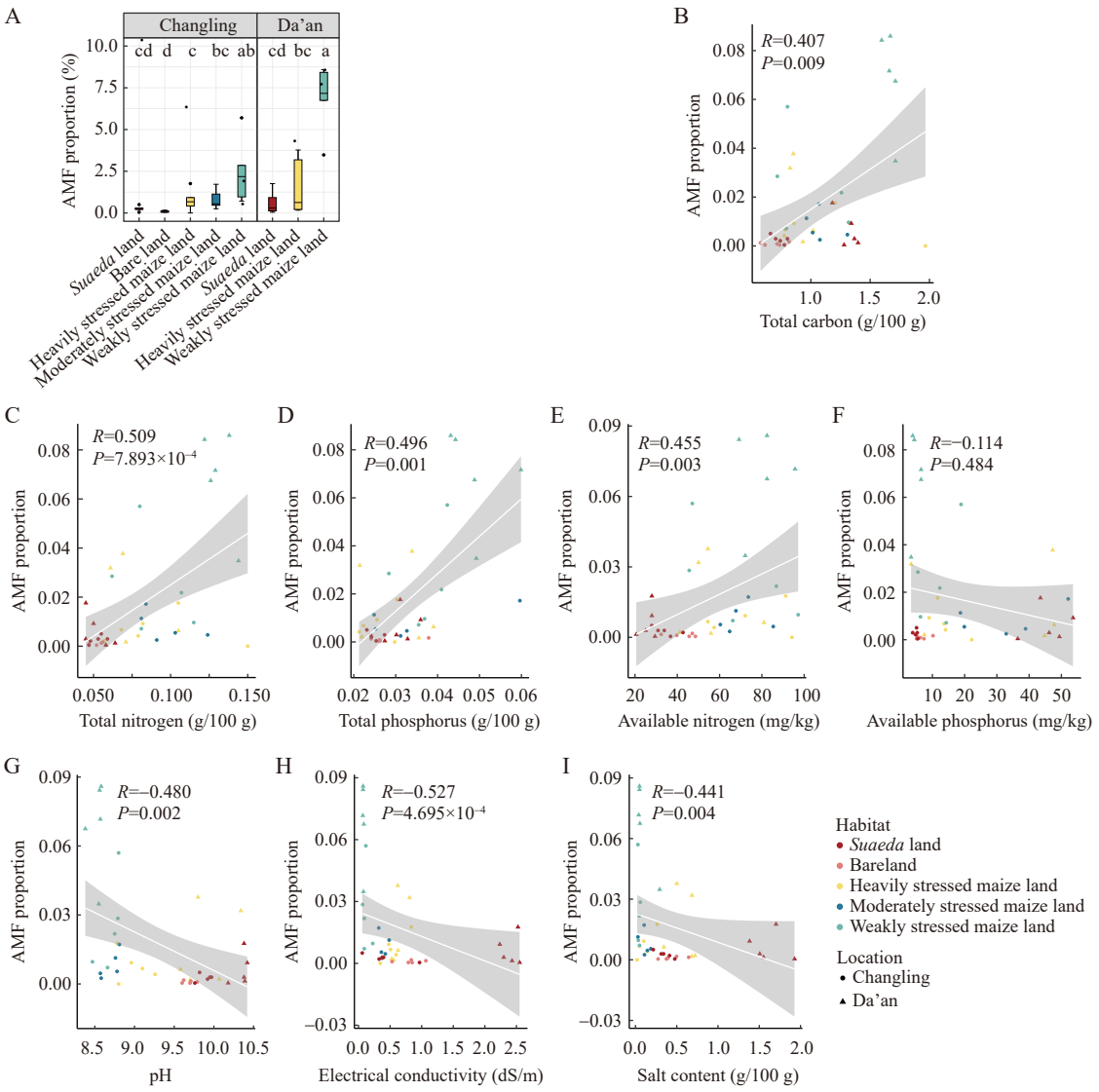

图3　不同样地中AMF序列数占全部真菌序列数的比例及其与土壤理化性质间的相关性分析。A：不同采样点中AMF序列数占真菌总序列数中的相对多度(样品之间的显著差异用小写字母表示)；AMF序列数相对占比和总碳(B)、总氮(C)、全磷(D)、碱解氮(E)、有效磷(F)、pH值(G)、电导率(H)和盐度(I)之间的线性关系。为减小极端值的影响，土壤电导率和盐度值在分析前经过ln (*n*+1)转换。用Spearman相关性分析来检验相关性，*P*值用伪发现率法(FDR)矫正。每个点表示不同的采样点，颜色表示生境，形状表示地点。

Figure 3　Proportion of AMF sequences in relation to the overall sequences of the whole fungal sequences and its correlation with soil physicochemical properties. A: Relative abundance of AMF sequences relative to total fungal sequences across different sampling sites (Lowercase letters indicate significant differences among the samples); Linear relationships between the proportion of AMF sequences and total carbon (B), total nitrogen (C), total phosphorus (D), available nitrogen (E), available phosphorus (F), pH (G), electrical conductivity (H) and salt content (I). Electrical conductivity and salt content were ln (*n*+1) transformed before analysis to reduce the influence of extreme values. Spearman correlation analysis was performed to test the relationships and *P*-values are adjusted by false discovery rate (FDR) method. Each point represents a sampling site. Colors denote different habitat types, while shapes correspond to sampling locations.

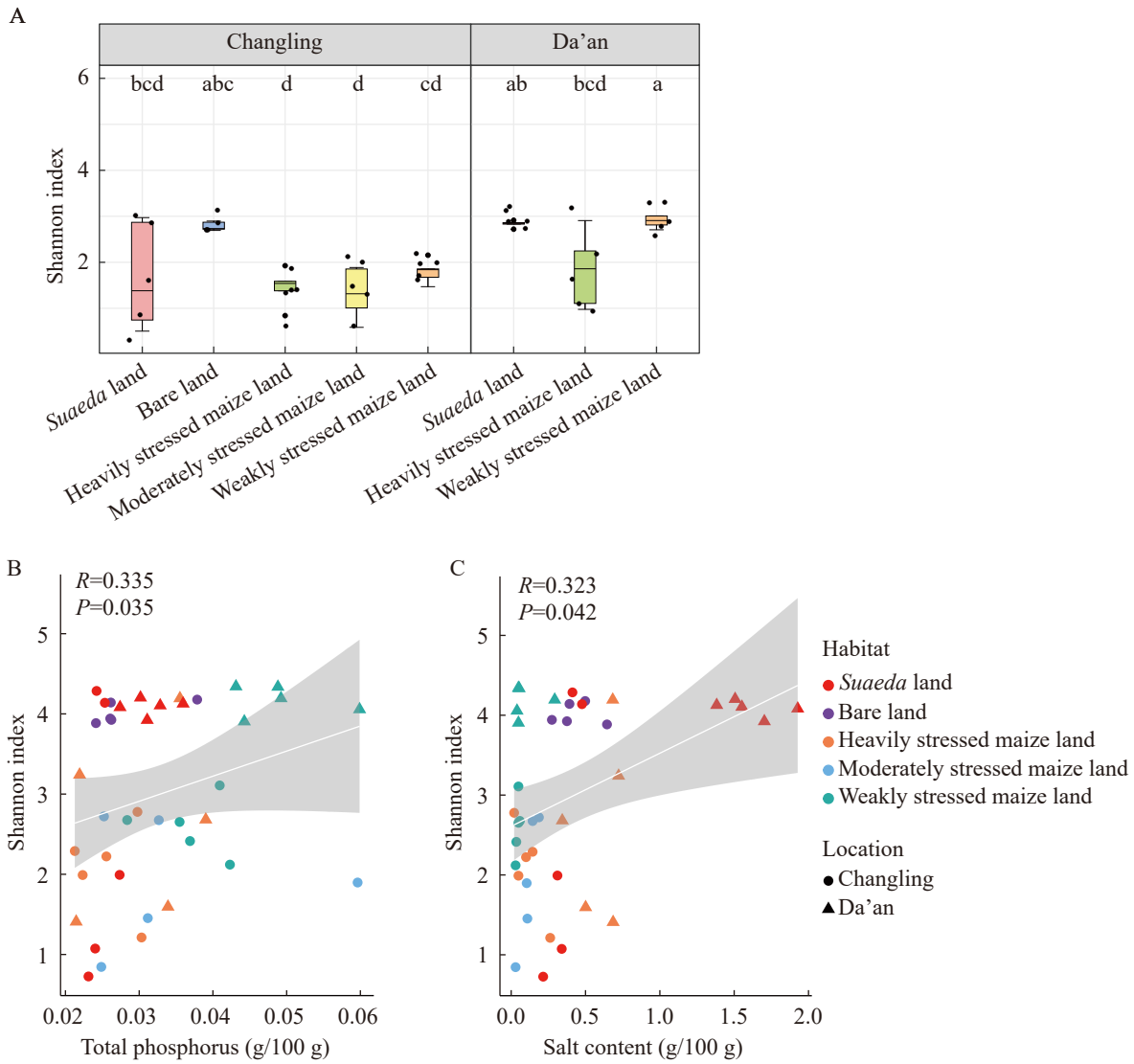

图4 AMF群落的α多样性和相关性分析。A：通过香农多样性指数衡量的每个采样点的AMF真菌群落α多样性[小写字母表示样点间的显著差异，由Kruskal-Wallis检验确认得到，*P*值通过伪发现率法(FDR)校正]；香农多样性指数和全磷(B)与盐度(C)之间的线性关系。为减小极端值的影响，土壤电导率和盐度值在分析前经过ln (*n*+1)转换。用Spearman相关性分析来检验相关性，*P*值用伪发现率法(FDR)矫正。每个点表示不同的采样点，颜色表示生境，形状表示地点。

Figure 4 Alpha diversity and correlation analysis of AMF communities. A: Alpha diversity measured as Shannon index of AMF communities in each sampling site [Lowercase letters denoting significant differences were determined by Kruskal-Wallis test and *P*-values were adjusted by false discovery rate (FDR) method]; Linear relationship between Shannon index and total phosphorus (B) as well as salt content (C). Salt content was ln (*n*+1) transformed before the analysis to reduce the influence of extreme values. Spearman correlation analysis was performed to test the relationships. Each point represents a sampling site and *P*-values are adjusted by false discovery rate (FDR) method. Colors denote different habitat types, while shapes correspond to sampling locations.

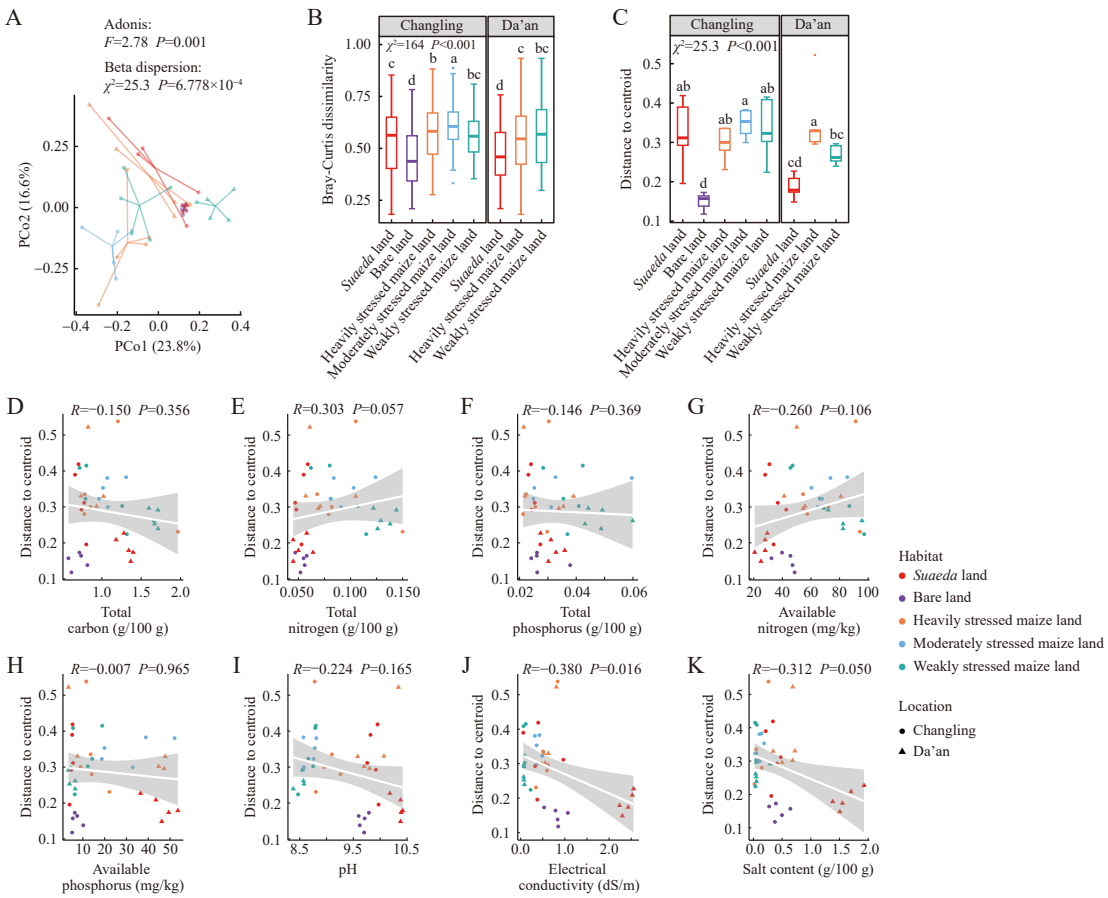

图5　AMF群落主坐标分析(PCoA)和β多样性分析及群落离散度与土壤理化性质之间的相关性分析。A：基于Bray-Curtis距离的主坐标分析结果；B：用Bray-Curtis相异度衡量不同样本的β多样性；C：根据Bray-Curtis距离，用到质心的距离来描述β多样性。样本到各自组内质心的距离反映了组内异质性。统计差异通过置换多元方差分析(PERMANOVA，Adonis2)和Kruskal-Wallis检验进行评估，*P*值经伪发现率法(FDR)校正；AMF群落离散度(以到质点的距离衡量)和总碳(D)、总氮(E)、全磷(F)、碱解氮(G)、有效磷(H)、pH值(I)、电导率(J)和盐度(K)之间的线性关系。为减小极端值的影响，土壤电导率和盐度值在分析前经过ln (*n*+1)转换。用Spearman相关性分析来检验相关性，*P*值用伪发现率法(FDR)矫正。每个点表示不同的采样点，颜色表示生境，形状表示地点。

Figure 5　Principal coordinated analysis (PCoA) and beta diversity analysis of AMF communities and correlations between community dispersion and soil physicochemical properties. A: Results of PCoA based on Bray-Curtis distance; B: Beta diversity measured as Bray-Curtis dissimilarity of different samples; C: Beta diversity is depicted by the distance to centroid, based on Bray-Curtis distance. The distances from the group centroid represent heterogeneity within each group. Statistical differences were tested using permutational multivariate analysis of variance (PERMANOVA, Adonis2) and Kruskal-Wallis test with *P*-value adjusted by false discovery rate (FDR) method; Linear relationships between AMF community dispersion (measured as distance to centroid) and total carbon (D), total nitrogen (E), total phosphorus (F), available nitrogen (G), available phosphorus (H), pH (I), electrical conductivity (J), and salt content (K). Electrical conductivity and salt content were ln (*n*+1) transformed before analysis to reduce the influence of extreme values. Spearman correlation analysis was performed to test the relationships. Each point represents a sampling site and *P*-values are adjusted by false discovery rate (FDR) method. Colors denote different habitat types, while shapes correspond to sampling locations.

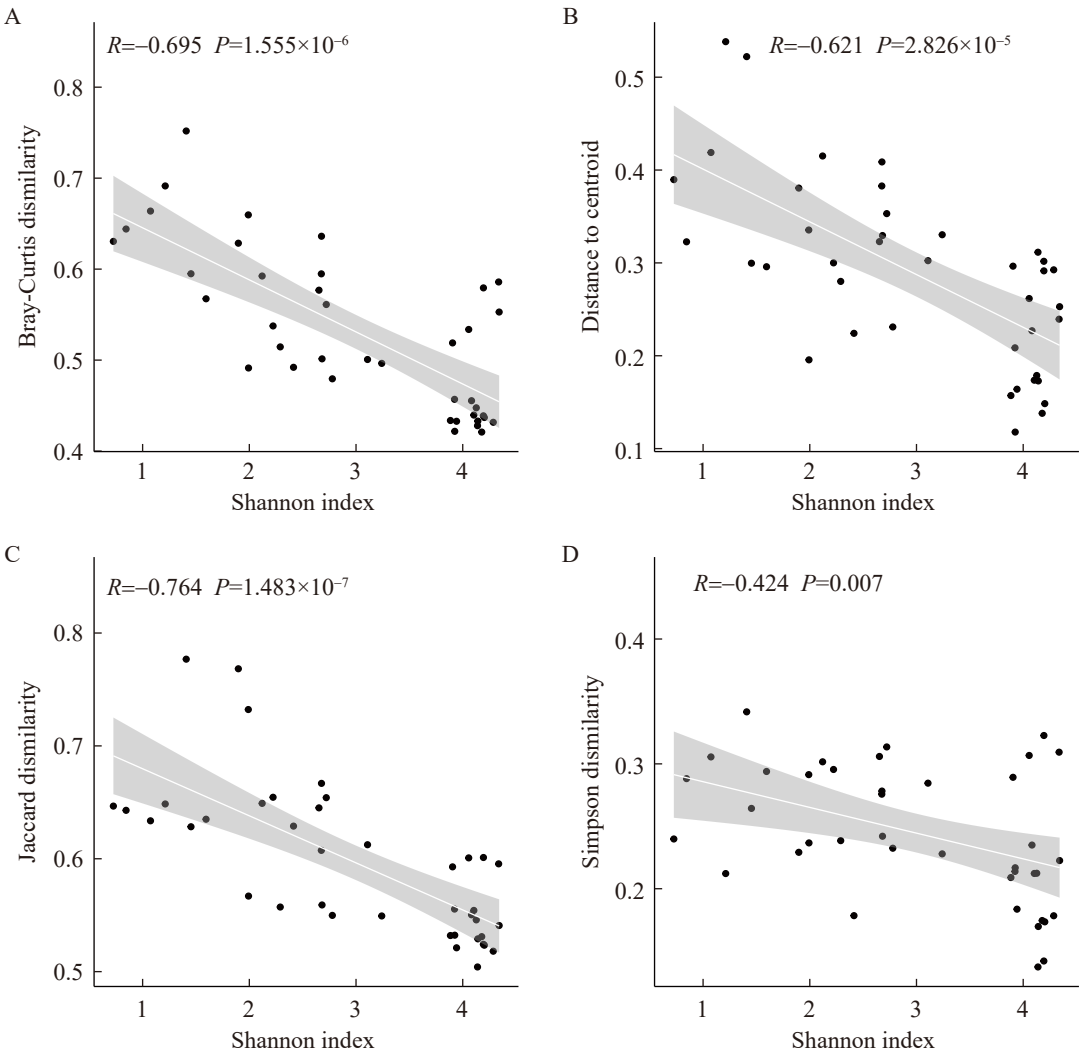

图6 α多样性(香农多样性指数)与β多样性指标之间的相关性分析。香农多样性指数和Bray-Curtis相异度(A)、群落离散度(以到质心的距离表示) (B)、Jaccard相异度(C)、Simpson相异度(D)之间的线性关系。阴影区域表示95%置信区间。

Figure 6 Correlation analysis between the alpha diversity (Shannon index) and beta diversity metrics. Linear relationships between the Shannon index and Bray-Curtis dissimilarity (A), community dispersion (measured as distance to centroid) (B), Jaccard dissimilarity (C), and Simpson dissimilarity (D). Shaded areas represent 95% confidence intervals.

对 AMF 群落的调控。此外，土壤 pH 值对 AMF 群落构建和生存也十分关键。pH 可能直接影响 AMF 孢子萌发、菌丝生长及定殖过程[43,74]，并在不同生态系统中对 AMF 群落组成和多样性产生重要影响[45,75-76]。与前人研究结果一致，在受到盐胁迫的生态系统中，尽管 pH 显著影响 AMF 的群落组成，但对多样性的影响并不显著[77]。

顺盐碱胁迫梯度 AMF 群落物种多样性增加，而群落结构变得更加趋同(图 4C、图 5J)。这说明盐度对 AMF 群落多样性的影响并非简单的抑制作用，高胁迫环境可能筛选出适应高盐

碱环境的 AMF 种类，并且这些物种能够在高盐碱环境下稳定共存。此外，土壤全磷含量也表现出与 AMF 的 α 多样性正相关关系(图 4B)。目前已有许多研究证明土壤养分含量尤其是氮和磷与 AMF 多样性存在密切联系[78-80]。土壤中磷含量会影响 AMF 的 α 多样性，通常有效磷和 AMF 的 α 多样性呈负相关，环境中磷含量充足时植物分配给 AMF 的碳减少，导致 AMF 的多度减小[81-82]。然而，本研究中除全磷外其他养分元素并未与 AMF 多样性呈现直接的线性关系，可能在高度盐碱的局域尺度下 AMF 群落组成和多样性随胁迫梯度的变化并非单一因子驱动，而是受到多种因素的交互作用与微环境异质性的影响。

3.2 植被特征与人类活动共同影响 AMF 群落分布格局

AMF 群落的结构变化不仅能够反映其对土壤理化因子的直接响应，也可能体现其与植物共生网络和遗留效应之间的复杂关系。尽管本研究未直接收集地上植物相关数据，但已有研究表明植物种类也显著影响 AMF 群落。例如，在碱蓬生境中 AMF 的根系定殖率通常低于 10%[46,83]，而玉米中定殖率通常较高[84-85]。裸地 AMF 序列数的相对占比最低，且玉米地 AMF 序列数相对占比随胁迫程度的减小而增加(图 3A、3G−3I)，推测在植被覆盖度较高、生物量较大的地点中，即使植物死亡土壤中残留的 AMF 也可能通过孢子和菌丝网络维持较强的生存能力。

α 多样性分析表明裸地 AMF 群落的多样性水平较高，同时裸地的 β 多样性却显著低于其他生境(图 4A、5B、5C)，表明尽管裸地中 AMF 物种丰富度较高，但样本间群落结构较为一致，空间异质性较低。这可能与植被覆盖缺失导致 AMF 与植物的互作关系缺乏有关。裸地缺少与植物的相互作用，受到的人类活动扰动也较小，可能为多种适应高盐碱环境的 AMF 提供了生存空间，体现为更高的 α 多样性。相比之下，碱蓬作为典型的盐生植物，可能对 AMF 起到特定的招募作用[46]，而玉米农田也可能因为长期的农业活动筛选出特定的 AMF 物种[86-87]。然而，β 多样性显著降低，反映盐碱胁迫施加的同质选择效应。在该选择压力下，AMF 群落结构收敛、空间异质性降低，而物种丰富度可能维持在较高水平。

AMF 群落在各种生境下的 α 多样性和不同 β 多样性度量方式均表现出显著的负相关性(图 6)。这与前人研究结果一致，Zhu 等[88]对盐碱荒地和非盐碱农田中 AMF 群落的研究发现，农田和荒地中 AMF 的 α 多样性和 β 多样性也呈相反的变化趋势，在非盐胁迫的农田中 AMF 的 α 多样性更低、β 多样性更高，而在盐胁迫荒地中 AMF 群落拥有更高的 α 多样性和更低的 β 多样性。耕作活动可能会干扰和破坏 AMF 通过菌丝形成的菌丝网络[89-90]，使得 AMF 群落被分割成多个小而孤立的区域，这些分散的区域内群落的个体数量较少，稀有种易随机灭绝，更容易受到随机漂变的影响，导致 α 多样性减小和 β 多样性增加。群落个体数量少更易受到随机漂变的这种现象已在许多研究中被提出[91-94]，并且有研究显示随机漂变增强与较低的 α 多样性和较高的 β 多样性存在关联[95-97]。这些变化趋势反映了垦殖活动对土壤 AMF 群落的影响，说明在苏打盐碱地土壤改良过程中土壤生态系统中的 AMF 群落向适应农业生产方向改变。该结果有助于更好地了解盐碱地在改良过程中 AMF 群落变化规律，为苏打盐碱地科学开发和改良提供了理论支持，对推动苏打盐碱地的有效利用和保障粮食安全具有积极意义。

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作者声明不存在任何可能会影响本文所报告工作的已知经济利益或个人关系。

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