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·研究论文·

短穗竹居群遗传结构及气候适应性分析

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摘要 短穗竹(*Brachystachyum densiflorum*)是中国特有种。近年来, 由于气候变化和人类活动加剧, 短穗竹栖息地遭到破坏, 破碎化加剧, 居群数量呈减少趋势。该研究对短穗竹6个居群36个个体开展简化基因组测序(RAD-seq), 获得了16 583个单核苷酸多态性(SNPs)位点, 据此评估短穗竹居群遗传结构, 并整合景观遗传学和物种分布模型, 探讨短穗竹对气候变化的适应机制。结果表明, 短穗竹具有中等水平的遗传多样性(*PIC*=0.722 5, *Ho*=0.087, *He*=0.284 3, π=0.317 5), 将不同居群划分为2组, 各居群间存在中度分化(F_{ST}=0.102)和较高的基因流(*Nm*=2.442)。基因型-环境关联分析表明, 短穗竹对气候的局部适应推动2个组的分化, 温差、低温和降水共同驱动遗传变异, 筛选出544个与温差、低温(Bio2、Bio6、Bio11和Bio7)和降水量(Bio19)显著相关的适应性位点。物种分布模型显示, 从末次盛冰期到当前, 短穗竹明显向北迁移, 且其分布面积增加了89.5%。预计在2021–2040年和2041–2060年2个时段适生区波动较小, 2061–2080年适生区范围缩小, 安徽境内高适生区部分衰退和破碎化。研究结果为短穗竹的保护利用提供了理论依据。

关键词 短穗竹, 简化基因组测序, 遗传多样性, 遗传结构, 物种分布模型

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全球气候变化导致生态系统物种多样性和功能多样性下降, 如何应对气候变化直接关系到生态系统的稳定性及其服务功能(Yuan et al., 2023; Jing et al., 2024)。植物如何应对气候变化是其持久生存的基础, 可通过局部适应或迁移到新的合适地点, 亦或通过表型可塑性适应气候变化(AIsos et al., 2012; Keenan, 2015; Poupon et al., 2021; Yang et al., 2022c)。然而, 这些应对策略效果有限, 气候的快速变化打破了基因与环境之间原有的联系, 导致迁徙、局部适应或新突变速率等无法与持续的气候变化保持平衡(Jia et al., 2020; Sang et al., 2022)。遗传多样性决定了物种适应新环境的能力, 也是生物进化的基础, 高杂合性可以抵消有害突变的影响, 增强物种的适应性和抗逆性(Pauls et al., 2013; Exposito-Alonso et al., 2022)。然而, 剧烈的气候变化导致物种遗传多样性大幅降低, 同时降低物种的持久性和进化潜力, 以及改变居群的遗传结构(Guan et al., 2021; Beridze et al., 2023; Liu et al., 2024)。景观遗传学(landscape genetics)为理解物种适应性进化和影响遗传变异的潜在环境因素提供了新见解(Alvarado et al., 2022; Feng and Du, 2022)。景观遗传学研究无需进行大量的胁迫实验, 仅通过遗传变异信息与环境信息或地理信息相结合就能揭示景观特征对遗传变异的影响(Aguirre-Liguori et al., 2021; Haupt and Schmid, 2022)。基因-环境关联(genotype-environment association, GEA)分析和异常位点检验(outlier tests)是了解遗传变异对整个景观适应模式的2种重要方法, 通过上述分析可以确定来自不同环境的物种遗传变异信息中参与环境适应的候选基因和基因组区域(Filipe et al., 2022; Haupt and Schmid, 2022)。利用景观遗传学方法揭示物种在全球环境变化条件下的适应机制, 已在动植物中广泛运用, 如三色黑鹂(*Agelaius tricolor*)、小黄鱼(*Larimichthys polyactis*)、星叶草(*Circaeaster agrestis*)、茴芹叶茄(*Solanum pimpinellifolium*)

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和筒瓣花(*Embothrium coccineum*) (Gibson and Moyle, 2020; Zhang et al., 2020; Barr et al., 2021; Sepúlveda-Espinoza et al., 2022; Wang et al., 2022b)。

竹类遗传多样性研究已取得诸多成果，但多数研究仅采用传统的分子标记，如扩增片段长度多态性(amplified fragment length polymorphism, AFLP)、相关序列扩增多态性(sequence-related amplified polymorphism, SRAP)、表达序列标签-微卫星标记(expressed sequence tags-simple sequence repeat, EST-SSR)、简单重复序列间扩增(inter-simple sequence repeat, ISSR)、简单重复序列(simple sequence repeat, SSR)、随机扩增多态性DNA (random amplified polymorphic DNA, RAPD)和序列标记微卫星(sequence-tagged microsatellite, STMS) (李潞滨等, 2008; Tian et al., 2012; Zhu et al., 2014; Bhandawat et al., 2019; Ely et al., 2019; Silva et al., 2020; Meena et al., 2023a)。随着测序技术的发展，利用高通量测序可在居群水平上对全基因组范围内的变异信息进行筛选并提供大量的变异信息，如单核苷酸多态性(single nucleotide polymorphism, SNP) (Shafer et al., 2015; Wu et al., 2023)。简化基因组测序(reduced-representation genome sequencing, RRGS)技术作为一种高效标记逐渐发展起来(Davey et al., 2011)，其中限制性酶切位点测序(restrictionsite associated DNA sequencing, RAD-seq)作为简化基因组测序，可获得全基因组范围内的大量SNP位点，且所产生的SNP位点在覆盖率、数据质量、稳定性和准确率方面比传统分子标记高，适用于群体遗传学和景观基因组学研究(Morin et al., 2004; Baird et al., 2008; Ouborg et al., 2010; Lin et al., 2021)。RAD-seq技术在评估遗传多样性方面应用广泛，特别是应用于珍稀濒危植物，如荷叶铁线蕨(*Adiantum nelumboides*)、显脉木兰(*Magnolia fistulosa*)、海南风吹楠(*Horsfieldia hainanensis*)和云南蓝果树(*Nyssa yunnanensis*) (张珊珊等, 2019; 蔡超男等, 2021; 孙维悦等, 2022; Yang et al., 2022a)。目前，RAD-seq技术已应用于澜沧梨藤竹(*Melocalamus arrectus*)和云南省极小种群独龙江空竹(*Cephalostachyum mannii*)等竹类的遗传多样性评估(赵虎刚等, 2023; 张如礼等, 2024)。

短穗竹(*Brachystachyum densiflorum*)为竹亚科(Bambusoideae)短穗竹属(*Brachystachyum*)植物，是我国特有种，其地下茎为细型，亦称真鞭，每节有3–5个分枝，箨耳发达，箨片开展易落，假花序，花枝极短缩，呈短穗状或头状，主要分布于华东地区(Li et al., 2006)。研究表明，短穗竹可能由苦竹属(*Pleioblastus*)和刚竹属(*Phyllostachys*)杂交形成，其分枝样式与苦竹属相似，箨耳、花序和假小穗与刚竹属类似(Zhang et al., 2012)。近年来，随着经济的快速发展，城市化进程加快，污染物排放量逐年增加(董芳淑等, 2023)，短穗竹的栖息地遭到破坏，破碎化加剧，种群数量呈减少趋势。目前，短穗竹已被列入安徽省重点保护野生植物名录(https://www.ah.gov.cn/public/1681/554202981.html)。同时，气候变化也加剧了竹类栖息地退化和破碎化的风险，特有或稀有的竹类极易受到栖息地变化的影响(Isik, 2011; Phair et al., 2021; Boban et al., 2022)。遗传多样性是开展珍稀濒危种群保护时需要考虑的重要部分，而上述环境风险使植物种群发生基因漂移和近亲繁殖，从而导致遗传多样性水平降低(Bonin et al., 2007; Salvado et al., 2022)。因此，开展短穗竹遗传多样性研究，评估气候变化对其遗传变异的影响，对于制定短穗竹的保护措施具有重要意义。

本研究针对中国特有种短穗竹，利用RAD-seq技术获得了短穗竹6个居群的SNP数据集，进而评估短穗竹居群遗传结构和遗传多样性水平，同时基于景观遗传学方法，分析气候变化对短穗竹现有遗传结构分布格局的影响和驱动因素，利用物种分布模型(species distribution model, SDM)预测短穗竹当前潜在适生区以及未来气候变化下的分布区变化，以期为短穗竹的保护提供理论依据。

1 材料与方法

1.1 植物材料采集

2012年6月在安徽、江苏和浙江采集到短穗竹(*Brachystachyum densiflorum* (Reudle) Keng) 6个居群的36个个体(表1)，每个个体间隔1 km以上，以避免采集到来自同一个克隆的植株。每个居群采集3–10个个体，每个个体采集3–5片幼嫩无病虫害的叶片，置于分子采集袋中并迅速用硅胶干燥，用于后续DNA提取。

表1 短穗竹居群采集信息

Table 1 Sampling information of *Brachystachyum densiflorum* populations

Population	Locality	Sample individuals	Longitude	Latitude
AHYX	Yuexi, Anhui	7	116°14′49″ E	30°55′27″ N
AHHS	Huoshan, Anhui	4	116°26′38″ E	31°24′01″ N
AHGD	Guangde, Anhui	9	119°14′10″ E	30°48′56″ N
JSLY	Liyang, Jiangsu	3	119°28′30″ E	31°14′39″ N
JSYX	Yixing, Jiangsu	10	119°47′54″ E	31°16′49″ N
ZJCX	Changxing, Zhejiang	3	119°52′31″ E	31°07′24″ N

1.2 DNA提取、文库构建及测序

采用CTAB法(Doyle and Doyle, 1987)提取短穗竹全基因组DNA, 用1%琼脂糖凝胶电泳检测DNA提取质量, 确保符合后续建库要求。RAD建库采用单酶切法, 全基因组DNA用*Eco*RI (5'-GAATTC-3')限制性内切酶进行酶切, 在DNA片段的两端添加P1接头, 用超声波将其打断, 然后选择含有P1接头的片段添加P2接头, 并进行PCR扩增。将检测合格的PCR产物送至北京诺禾致源生物信息科技有限公司Illumina Novaseq 6000平台进行双端测序(PE=150 bp)。测序之后用Fastp v0.23.4 (https://github.com/OpenGene/fastp)软件过滤掉低质量的reads, 保留795.5 Mb reads, 平均GC含量为42.84%, Q30≥91.58%。使用Stacks v2.62 (http://catchenlab.life.illinois.edu/stacks/)软件中的process-radtag模块将Clean reads截短至140 bp。

1.3 SNP筛选和过滤

以毛竹(*Phyllostachys edulis*)基因组(Zhao et al., 2018)为参考基因组。首先, 使用BWA v0.7.17软件(https://github.com/lh3/bwa)的mem模块将reads比对到参考基因组, 平均对比率为98.89%, 用SAMtools v1.6软件(https://github.com/samtools/samtools)的view和sort模块转化格式并进行排序和去除重复。然后, 利用Stacks软件的gstacks模块合并比对成功的reads并构建位点, populations模块用于输出SNP。最后, 利用VCFtools v0.1.16软件(https://vcftools.github.io/documentation.html)过滤SNP, 仅保留平均深度≥5的SNP (–minDP=5), 剔除次数等位基因频率低于0.05的SNP (–maf=0.05)。

1.4 遗传多样性和居群遗传结构分析

利用Stacks软件populations模块计算遗传多样性指标, 包括多态性信息含量(*PIC*)、观测杂合度(*Ho*)、期望杂合度(*He*)、核苷酸多样性(π)和近交系数(*Fis*)。使用NeEstimator v2.0软件(https://help.rc.ufl.edu/doc/NeEstimator)评估6个居群的当前有效群体大小。基于最大似然法(maximum likelihood, ML)利用IQ-TREE v2.2.0.3软件(http://www.iqtree.org/)构建系统发育树, 靴带值(bootstrap)重复1 000次并进行ASC矫正, 以减小长枝影响。建树最适模型为GTR+F+I+G, 该模型基于贝叶斯信息准则(Bayesian Information Criterion, BIC), 利用IQ-TREE软件自带的ModelFinder模块筛选得出。随后用R v4.3.1语言LEA包(https://www.r-project.org/)进行遗传结构分析, 假定分群数*K*值为2–15, 且每个*K*值重复运行10次, 交叉检验错误率(cross-validation error, CV error)最小时即为最优分群。使用adegenet包进行主成分分析(principal component analysis, PCA)和主成分判别分析(discriminant analysis of principal components, DAPC)。遗传分化指数(F_{ST})反映居群间的遗传差异, 使用hierfstat包评估居群间的遗传分化指数。利用BayesAss v3.0.4软件(https://rannala.org)评估当前短穗竹群体间的基因流动率。

1.5 遗传变异与气候关联分析

从WorldClim v.2.1数据库(Fick and Hijmans, 2017; https://www.worldclim.org/data/worldclim21.html)下载1970–2000年19个生物气候因子数据, 空间分辨率为30″ (1 km × 1 km)。使用raster包根据每个短穗竹采样地点的经纬度提取气候数据(附表1), 然后用皮尔逊(Pearson)相关系数进行相关性检验(附表2), 保留相关系数小于0.75 (r<|0.75|)的气候因子。最终保留8个气候因子, 分别为平均气温日较差(Bio2)、最冷月份最低温度(Bio6)、气温年较差(Bio7)、最湿季度

平均温度(Bio8)、最冷季度平均温度(Bio11)、降水量季节性变化(Bio15)、最湿季度降水量(Bio17)和最冷季度降水量(Bio19)。用基因-环境关联分析确定遗传结构与地理或气候变量之间的关联性。使用vegan包进行冗余分析(redundancy analysis, RDA)。为了确定影响遗传变异的关键气候因子，需进行冗余分析和梯度森林(gradient forest, GF)分析，其中梯度森林分析用gradientForest包完成。为了识别与遗传局部适应和气候密切相关的SNP位点，使用3种方法筛选异常SNP (outlier SNP)。一是使用BayeScan v2.1软件(https://github.com/mfoll/BayeScan)进行筛选，该软件采用贝叶斯法搜索处于自然选择下的高分化SNP，将错误发现率(false discovery rate, FDR)低于0.01的SNP视为异常SNP，这些SNP可能与局部适应有关(Jia et al., 2020)。另2种方法均基于基因-环境关联分析进行筛选，分别用vegan包和lfmm包完成。首先进行冗余分析，从前3个约束轴中筛选出异常SNP；然后设置标准差为3作为分界(two-tailed *p*-value=0.002 7) (DeSaix et al., 2022)；最后用lfmm包中潜在因素混合模型(latent factor mixed modeling, LFMM)筛选出异常SNP，潜在因子数量为遗传结构分析中交叉检验错误率(CV error)最小时的*K*值(Yang et al., 2022b)，使用*q*-value包在错误发现率(FDR)为0.01的条件下识别异常SNP (Jia et al., 2020)。

1.6 潜在地理分布预测

物种分布模型广泛用于预测当前和未来气候变化背景下物种的潜在分布(Yang et al., 2022b)。为明确过去和当前气候条件下短穗竹的潜在分布区以及预测未来全球气候变化下其空间分布趋势，我们根据短穗竹已知位置进行物种分布建模。通过野外调查和检索全球生物多样性信息组织(https://www.gbif.org/)、中国国家标本资源平台(http://www.nsii.org.cn/2017/home.php)、中国数字植物标本馆(https://www.cvh.ac.cn/)和相关文献，共获得175个短穗竹分布地点(附表3)。为消除采样偏差的影响，使用spThin包删除距离小于10 km的分布地点，最终保留103个分布地点。末次盛冰期(Last Glacial Maximum)、全新世中期(Mid Holocene)、当前和未来的19个生物气候因子均从WorldClim数据库中下载，空间分辨率为2.5′ (2.5 km × 2.5 km)。未来时段(2021–2040年、2041–2060年以及2061–2080年)选择BCC-CSM2-MR模型下2种共享社会经济路径(shared socioeconomic pathways, SSPs)，分别为SSP 1–2.6和SSP 5–8.5 (He et al., 2022)。基于筛选的8个气候因子，使用ENMeval包筛选要素类型与正则化乘数，要素类型为LQ，正则化乘数为1 (附表4)。随后，使用MaxEnt v3.4.4软件(https://biodiversityinformatics.amnh.org)预测短穗竹在不同气候情景下的潜在分布格局，设置25%的分布点为测试集，75%的分布点为训练集，设置5 000作为最大迭代次数，重复训练10次。最后，将MaxEnt预测结果导入ArcGIS v10.8.1软件(https://www.esri.com)中，根据自然间断点分级法将分布区域分为非适生区、低适生区、中适生区和高适生区。

2 结果与分析

2.1 SNP位点统计和遗传多样性评估

研究显示，经VCFtools软件过滤后保留了16 583个高质量SNPs (附图1)，其中9 196个SNPs发生了转换，转换率为55.5%，7 387个SNPs发生了颠换，颠换率为44.5%，转换与颠换的比值为1.24。基于16 583个SNPs评估6个短穗竹居群的遗传多样性(表2)，表明短穗竹居群具有中等水平遗传多样性(*PIC*=0.722 5, *Ho*=0.087, *He*=0.284 3, *π*=0.317 5)，各居群遗传多样性水平差异不大，安徽广德(AHGD)和江苏宜兴(JSYX)两居群的遗传多样性较高，而浙江长兴(ZJCX)居群的遗传多样性最低。各居群近交系数(*Fis*)均为正值，平均为0.566 5，居群存在杂合子缺失且以近交或自交为主。6个居群当前有效群体大小分析显示，江苏溧阳(JSLY)居群无法获得*Ne*值，可能其*Ne*值为无限大，也可能由于个体数量较少导致，其余5个居群的当前有效群体大小在3.8 (3.6, 4.0)– 9.4 (8.4, 10.4)之间。当前有效群体大小均值(5.6)极低，可能在过去经历了瓶颈效应，导致短穗竹分布区发生严重的居群收缩。

2.2 居群遗传结构

通过系统发育和遗传结构分析、主成分分析(PCA)和主成分判别分析(DAPC)明确了短穗竹现有居群遗传结构分布格局。系统发育树包括2个主要分支(图1A),

表2 6个居群遗传多样性指标

Table 2 Genetic diversity indices of six populations

Population	*PIC*	*Ho*	*He*	*π*	*Fis*	*Ne* (95% CI)
AHYX	0.8102	0.0880	0.3051	0.3295	0.6466	5.4 (5.2, 5.7)
AHHS	0.6412	0.0863	0.2712	0.3099	0.4899	9.4 (8.4, 10.4)
AHGD	0.8802	0.0885	0.3148	0.3339	0.7123	3.8 (3.6, 4.0)
JSLY	0.5502	0.0841	0.2492	0.2990	0.4098	Inf (inf, inf)
JSYX	0.9069	0.0884	0.3183	0.3358	0.7385	4.0 (3.9, 4.2)
ZJCX	0.5462	0.0865	0.2474	0.2969	0.4017	4.8 (4.5, 5.1)
Mean	0.7225	0.0870	0.2843	0.3175	0.5665	5.6 (5.1, 5.9)

AHYX、AHHS、AHGD、JSLY、JSYX和ZJCX同表1。*PIC*: 多态性信息含量; *Ho*: 观测杂合度; *He*: 期望杂合度; *π*: 核苷酸多样性; *Fis*: 近交系数; *Ne*: 当前有效群体大小; Inf: 无限大

AHYX, AHHS, AHGD, JSLY, JSYX, and ZJCX are the same as shown in Table 1. *PIC*: Polymorphism information content; *Ho*: Observed heterozygosity; *He*: Expected heterozygosity; *π*: Nucleotide diversity; *Fis*: Inbreeding coefficient; *N*e: Contemporary effective population size; Inf: Infinity

安徽霍山(AHHS)和安徽岳西(AHYX)两居群地理位置相对较近，最先分离，表明两居群之间亲缘关系较近。安徽广德(AHGD)、江苏溧阳(JSLY)、江苏宜兴(JSYX)和浙江长兴(ZJCX) 4个居群聚为一支，它们可能拥有共同的祖先，但个体间存在交叉混合。

遗传结构分析表明，遗传聚类值*K*=2时交叉检验错误率(CV error)最低(图2)，说明遗传物质来源于2个祖先并表现出稳定的遗传结构(图1A)。随着*K*值(3–4)的增加，有不同的遗传信息加入，并在安徽广德(AHGD)、江苏溧阳(JSLY)、江苏宜兴(JSYX)和浙江长兴(ZJCX) 4个居群中表现最明显，安徽霍山(AHHS)和安徽岳西(AHYX)两居群遗传结构较稳定(图1A)。主成分分析(PCA)显示，前2个轴分别解释3.3%和3.2%的遗传变异，安徽霍山(AHHS)和安徽岳西(AHYX) 2个居群与其余4个居群分别形成独立的聚类且二者之间存在明显的遗传分化(图1B)。利用上述3种分析方法所得结果一致，主成分判别分析(DAPC)进一步验证了短穗竹当前遗传结构的稳定性，并确定短穗竹2个组的划分(图1C)。

短穗竹居群存在中度遗传分化(F_{ST}=0.102，0.05< F_{ST}<0.15)，遗传分化值(F_{ST})介于0.048–0.151之间(表3)。江苏溧阳(JSLY)和浙江长兴(ZJCX)两居群虽然地理位置相近，但居群间的遗传分化值(F_{ST}=0.151)是所有群体中最大的。分子方差分析(AMOVA)显示(附表5)，遗传变异主要发生在居群内(*Va*=79.71%)，居群间变异很小(*Va*=0.45%)。尽管各居群存在中度的遗传分化(F_{ST}=0.102)，但是基因流水平很高(*Nm*=2.442，*Nm*>1)，说明居群间存在一定的遗传交换，从而抵消了基因漂变造成的强烈遗传分化(表3)。但是，短穗竹各居群间近期(1–3代)基因流动率较低(附表5)，其范围在0.020 7–0.037 4之间，平均值为0.029 4。

2.3 遗传变异与气候关联分析

为明确气候与地理是否影响短穗竹现有遗传结构分布格局，对地理、气候以及两者混合的影响进行分析。独立的气候因素占总解释量的35.48%，独立的地理因素占22.22%，气候和地理混合因素占42.30%，说明气候因素更能解释短穗竹的遗传变异(附表6)。分别对地理和气候(图3C)、地理(图3E)、气候(图3A)进行冗余分析对比，显示8个气候因子将6个居群划分为2个类群(图3A)，与遗传结构分析结果一致(图1)，气候因素比地理因素更能解释遗传变异(附表6；图3)，局部适应在推动2个类群的形成和分化过程中发挥重要作用。

基于冗余分析和梯度森林分析，将8个气候因子与短穗竹的遗传信息联系起来，进一步确定影响其居群间遗传变异的因子(图3A，B)。冗余分析表明，RDA1和RDA2轴分别解释14.00%和12.88%的遗传变异(图3A)。RDA1轴中Bio6和Bio2的载荷最高(图3A)，RDA2轴主要受到Bio11和Bio7的影响(附表6)，表明遗传变异与温差和低温之间密切相关。利用ordistep函数逐步排除法筛选可解释遗传变异的独立因子(附表6)，表明Bio19也是显著的预测因子(P< 0.05，R_{adj}^2=0.004 4)，这有助于解释遗传结构的差异。梯度森林分析表明，Bio2是最重要的预测因子，其次是Bio6 (图3B)。Bio2在8.2–9.0°C时发生变化，

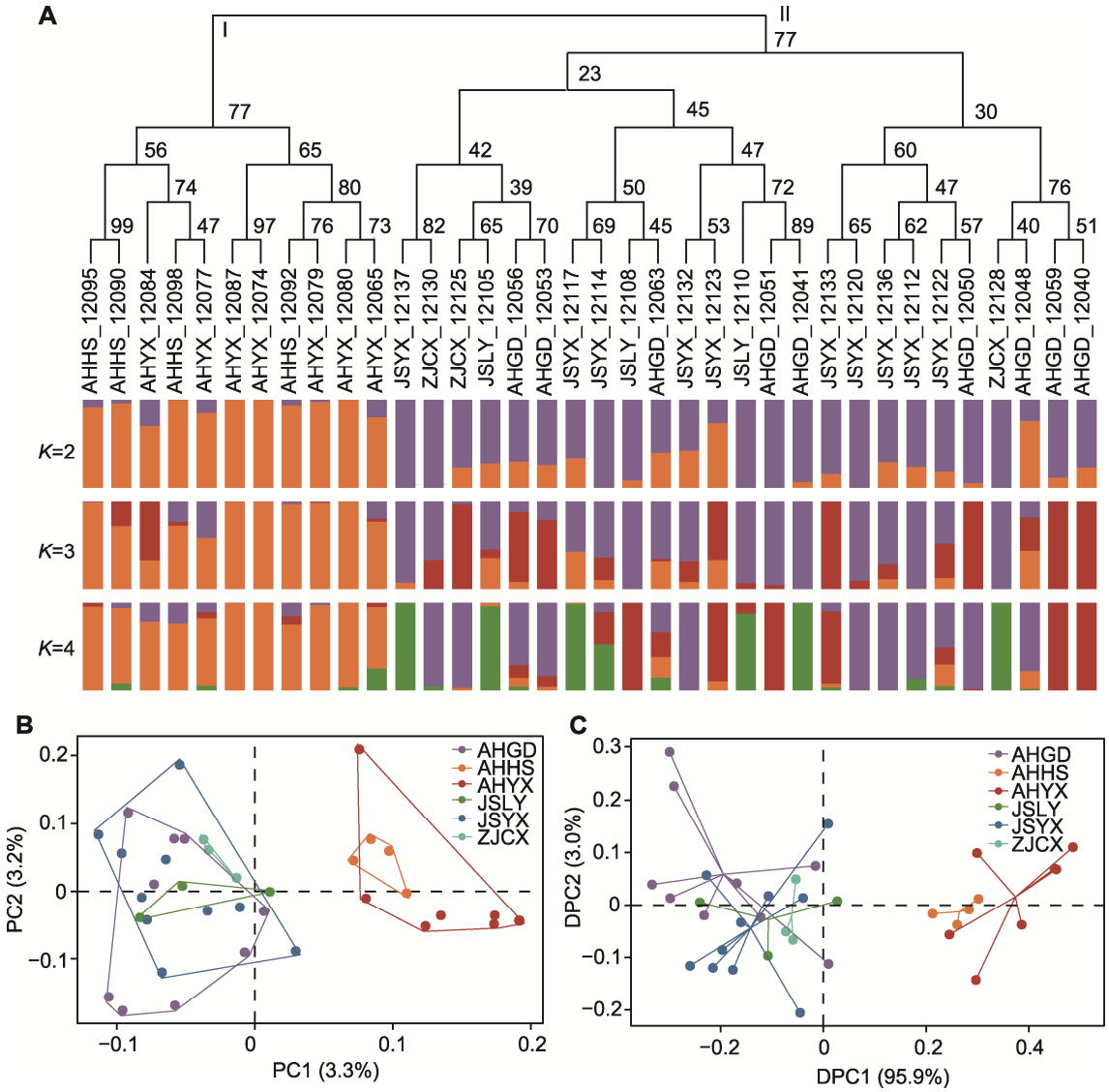


图1 短穗竹居群遗传结构分析

(A) 系统进化树和*K*=2, 3, 4时每个个体的遗传成分, 分支上方的数字表示靴带值; **(B)** 主成分分析(PCA); **(C)** 主成分判别分析(DAPC)。AHYX、AHHS、AHGD、JSLY、JSYX和ZJCX同表1。

Figure 1 Population genetic structure analysis of *Brachystachyum densiflorum*

(A) Phylogenetic tree and individual genetic components at *K*=2, 3, 4, the numbers above the branch are the bootstrap values; **(B)** Principal component analysis (PCA); **(C)** Discriminant analysis of principal components (DAPC). AHYX, AHHS, AHGD, JSLY, JSYX, and ZJCX are the same as shown in Table 1.

在8.9°C时突然变化(图3D); Bio6在–2.1– –0.7°C时发生变化, –2.1– –1.4°C变化较为平缓, –1.2– –0.7°C变化幅度较大(图3F)。此外, 排在前5位的气候因子中还有最冷季度降水量(Bio19), 说明降水和低温影响短穗竹的遗传变异。

综合冗余分析和梯度森林分析, 表明遗传变异与5个气候因子(Bio2、Bio6、Bio19、Bio11和Bio7)之间存在显著关联, 共同驱动短穗竹的遗传变异。本研究筛选出短穗竹居群适应性位点(异常SNPs) 617个, 去除重复后剩余544个。利用BayeScan软件基于贝叶斯概率法检测出98个潜在的候选位点(图4A)。通过冗余分析识别出170个异常SNPs (图4B), 其中57个适应Bio19, 37个适应Bio2, 26个适应Bio6, 26个适应Bio7, 24个适应Bio11。基于潜在因素混合模型(LFMM)

筛选出349个异常SNPs (图4C), 其中217个与Bio19相关, 99个与Bio7相关, 23个与Bio11相关, 6个与Bio2相关, 4个与Bio6相关。冗余分析和偏冗余分析(pRDA)进一步验证了适应性位点与5个气候因子之间的关联性(附表7), 结果显示适应性位点与温差、低温(Bio2、Bio6、Bio11和Bio7)和最冷季度降水量呈(Bio19)极显著相关(R_{adj}^2=0.034, P<0.01)。

2.4 潜在地理分布预测

MaxEnt模型能够准确预测短穗竹不同时期的适生区域(AUC值>0.9), 其ROC曲线下方面积AUC值为0.976, 平均标准偏差为0.006 (附图2)。基于综合贡献率、置换重要值(附表8)和刀切法检验(附图3), 结果表明短穗竹的分布和生长主要受Bio6、Bio11、Bio17和Bio19四个因子的影响。

通过MaxEnt模型预测短穗竹在末次盛冰期、全新世中期、当前和未来的潜在分布区, 发现从末次盛冰期(图5C)、全新世中期(图5B)到当前(图5A)短穗竹栖息地随着时间的推移发生了巨大变化, 适生区波动明显, 其分布范围不断扩大, 由1.06×10^5 km^{2}增大到1.02×10^6 km^2, 分布面积增加了89.5%且明显向北迁移(附表9; 图5A–C), 说明短穗竹在末次盛冰期和全新世中期不同气候条件下通过迁移持续进行适应性生长并延续至今。当前气候条件下, 短穗竹实际分布点被适生区覆盖, 且集中分布于高适生区内(图5A); 适生区分布范围在108°–120°E、23°–34°N之间, 其中高适生区面积为1.9×10^5 km^2 (附表9), 主要位于浙江、安徽中部至南部和江苏南部, 江西和湖南交界处也有分布(图5A)。未来气候条件下, 在2021–2040年(图5D, G)和2041–2060年(图5E, H) 2个时段, 相比当前适生区面积和分布区波动将较小。在SSP 1–2.6路径下高适生区有向北迁移的趋势(图5D, E), 在2021–2040年高适生区面积将略有增加, 但在2041–2060年将减小。预计2061–2080年(图5F, I), 高适生区范围将缩小, 特别是在SSP 5–8.5路径下, 短穗竹在湖南的适生区将明显收缩, 在安徽高适生区将出现部分衰退和破碎化(图5I)。

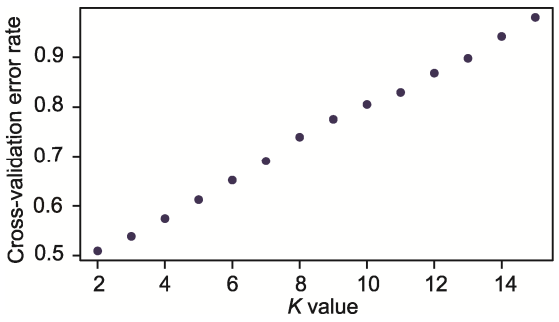


图2 *K*值对应的交叉检验错误率

Figure 2 The cross-validation error rate of *K* value

3 讨论

3.1 短穗竹遗传多样性

遗传多样性水平反映了物种短期生态适应和长期进化所需遗传资源的可用性(Meena et al., 2019)。竹类的遗传多样性表现在广泛的变异(Perez-Alquicira et al., 2021)。本研究中, 短穗竹具有中等水平的遗传多样性(*PIC*=0.722 5, *Ho*=0.087, *He*=0.284 3, π=0.317 5), 遗传多样性水平高于RAD测序的2种热带木本竹类澜沧梨藤竹(*Ho*=0.160, *He*=0.162, π=0.174)和独龙江空竹(*Ho*=0.217, *He*=0.252, π=0.257) (赵虎刚

表3 6个居群间遗传分化值(F_{ST}, 左下三角)和基因流(*Nm*, 右上三角)

Table 3 Genetic differentiation (F_{ST}, lower left triangle) and gene flow (*Nm*, upper right triangle) among six populations

Population	AHGD	AHYX	AHHS	JSLY	JSYX	ZJCX
AHGD	0.000	3.596	2.497	2.065	4.958	2.108
AHYX	0.065	0.000	2.382	1.869	3.848	1.887
AHHS	0.091	0.095	0.000	1.523	2.591	1.562
JSLY	0.108	0.118	0.141	0.000	2.154	1.406
JSYX	0.048	0.061	0.088	0.104	0.000	2.177
ZJCX	0.106	0.117	0.138	0.151	0.103	0.000

AHYX、AHHS、AHGD、JSLY、JSYX和ZJCX同表1。

AHYX, AHHS, AHGD, JSLY, JSYX, and ZJCX are the same as shown in Table 1.

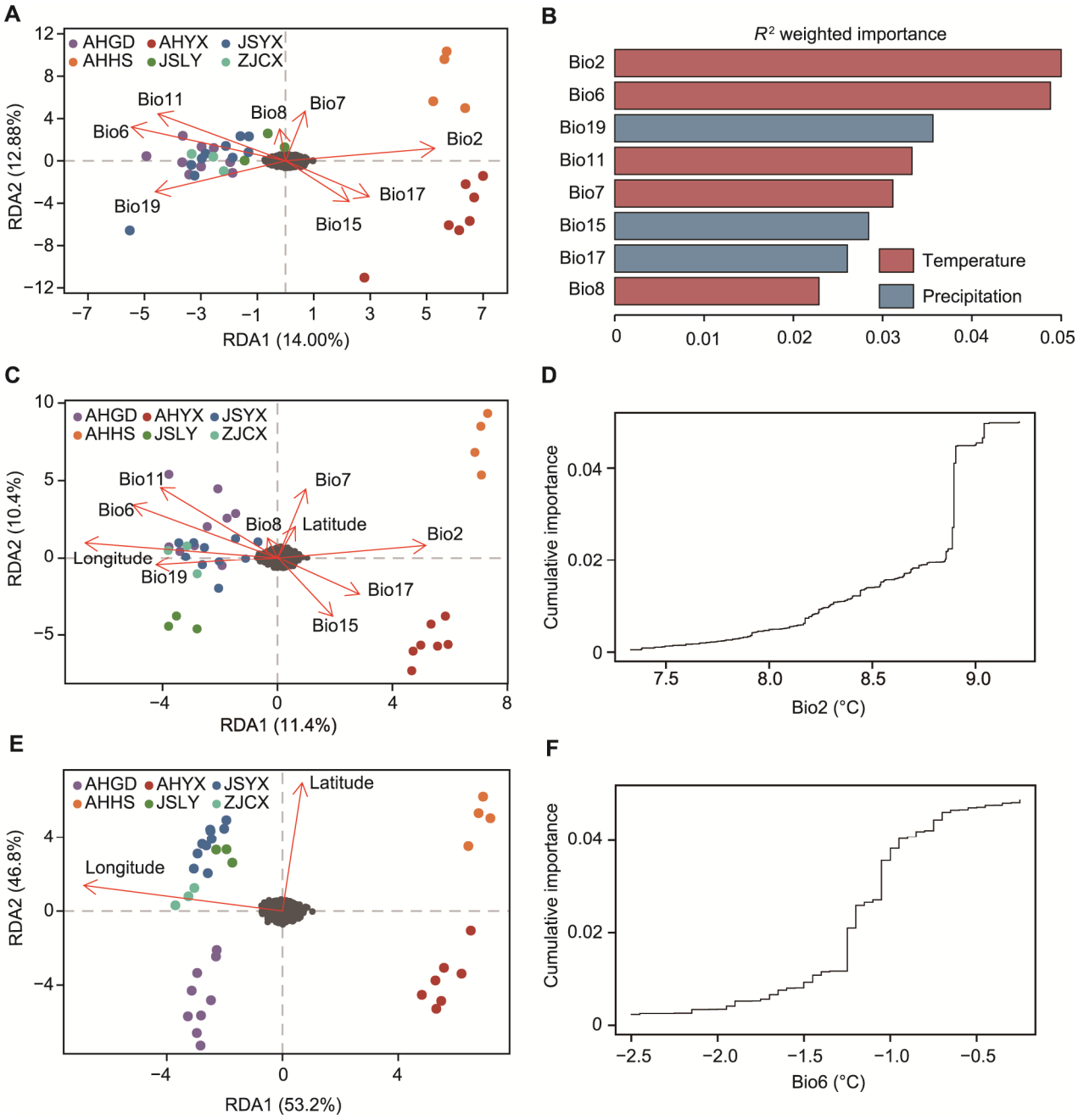


图3 冗余分析(RDA)和梯度森林(GF)分析

(A), (C), (E) 气候和地理与遗传结构之间的关联分析; **(B)** 梯度森林分析; **(D), (F)** Bio2和Bio6响应曲线。Bio2: 平均气温日较差; Bio6: 最冷月份最低温度; Bio7: 气温年较差; Bio8: 最湿季度平均温度; Bio11: 最冷季度平均温度; Bio15: 降水量季节性变化; Bio17: 最湿季度降水量; Bio19: 最冷季度降水量。AHYX、AHHS、AHGD、JSLY、JSYX和ZJCX同表1。

Figure 3 Redundancy analysis (RDA) and gradient forest (GF) analysis

(A), (C), (E) Association analysis between climate, geography and genetic structure; **(B)** Gradient forest analysis; **(D), (F)** Bio2 and Bio6 response curves. Bio2: Average daily temperature range; Bio6: The lowest temperature in the coldest month; Bio7: Annual temperature range; Bio8: The average temperature of the wettest quarter; Bio11: The average temperature of the coldest quarter; Bio15: Seasonal variation of precipitation; Bio17: The wettest season precipitation; Bio19: The coldest season precipitation. AHYX, AHHS, AHGD, JSLY, JSYX, and ZJCX are the same as shown in Table 1.

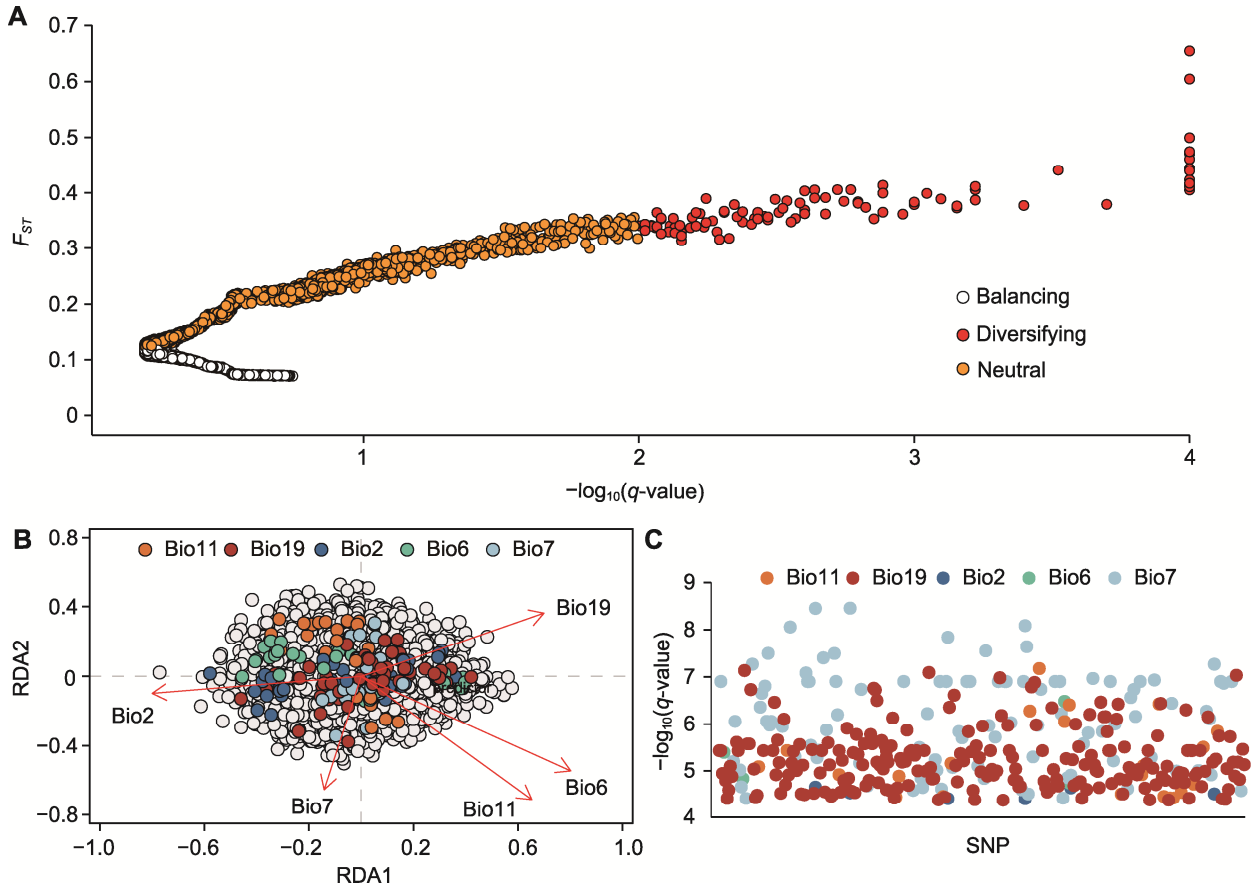


图4 利用3种方法筛选的异常单核苷酸多态性(SNP)位点
(A) BayeScan软件筛选; **(B)** 冗余分析(RDA)筛选; **(C)** 潜在因素混合模型(LFMM)筛选。F_{ST}: 遗传分化指数。Bio2、Bio6、Bio7、Bio11和Bio19同图3。

Figure 4 Screening of outlier single nucleotide polymorphism (SNP) sites by three methods
(A) Screening by BayeScan software; **(B)** Screening by redundancy analysis (RDA); **(C)** Screening by latent factor mixed modeling (LFMM). F_{ST}: Fixation index of subdivision. Bio2, Bio6, Bio7, Bio11, and Bio19 are the same as shown in Figure 3.

等, 2023; 张如礼等, 2024)。多种因素决定了物种的遗传多样性, 多倍体是使竹类保持高水平遗传多样性的因素之一, 原因是每个基因座的等位基因数量较多(Perez-Alquicira et al., 2021)。目前, 已在基因组水平证实木本竹类是不均匀的多倍体, 短穗竹隶属青篱竹族(Arundinarieae), 是四倍体温带木本竹类(2*n*=46–48)的一员(Guo et al., 2019; Clark, 2023)。地理分布范围广或多年生的物种保持较高的遗传多样性, 短穗竹在江苏、浙江、安徽、福建、湖北和江西均有分布(附表3)。木本竹类也是禾本科乃至单子叶植物中寿命最长的物种, 其寿命长达15–150年, 广泛而连续的分布和较长的寿命使得短穗竹具有丰富的遗传多样性(Meena et al., 2019; Oumer et al., 2020; Poupon et al., 2021; Clark, 2023)。此外, 克隆植物居群可能具有多个多源基因型, 并保持较高的遗传多样性。竹类繁殖多以克隆为主且进化速率较慢, 基因组变异较小, 现有居群可能保留了其祖先的高遗传多样性, 尽管最近的气候变化和人为压力导致居群数量减少, 但居群仍表现出较高的遗传多样性(Yang et al., 2012; Das et al., 2017; Jiang et al., 2017; Li et al., 2020; Clark, 2023)。取样不足或取样范围较小也会影响对遗传多样性的评估。本研究中短穗竹个体主要采集于当前的分布中心区域(表1), 且每个居群个体较少(3–10个)。地理代表性取样不够全面可能会影响等位基因的获取, 导致评价结果无法反映出居群整体的遗传多样性水平(Wang et al., 2017; 张如礼等, 2024)。

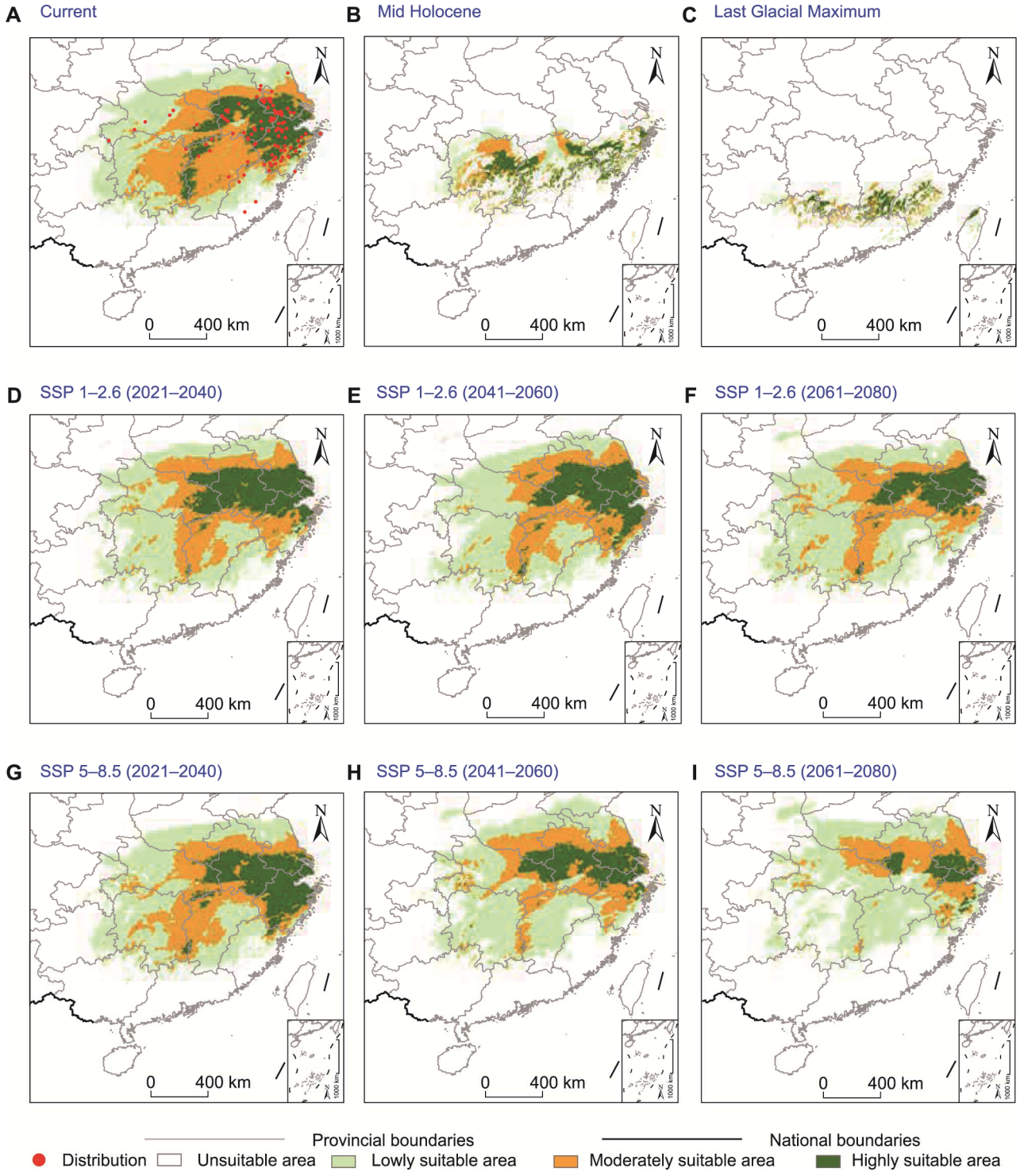


图5 不同时期短穗竹适宜性生境分布

(A) 当前(1970–2000年)气候条件下; **(B)** 全新世中期气候条件下; **(C)** 末次盛冰期气候条件下; **(D), (G)** 2021–2040年间气候; **(E), (H)** 2041–2060年间气候; **(F), (I)** 2061–2080年间气候

Figure 5 Distribution of suitable habitats for *Brachystachyum densiflorum* in different periods

(A) Current (1970–2000) climate scenarios; **(B)** Mid Holocene climate scenarios; **(C)** Last Glacial Maximum climate scenarios; **(D), (G)** 2021–2040 climate scenarios; **(E), (H)** 2041–2060 climate scenarios; **(F), (I)** 2061–2080 climate scenarios

3.2 居群遗传结构和遗传分化

本研究中, 通过遗传结构分析将6个居群划分为2组, 安徽霍山(AHHS)和安徽岳西(AHYX) 2个居群与其余4个居群之间有很强的遗传结构分化(图1)。基因流受限是居群遗传结构形成的主要原因, 而地理距离较远阻碍了2个组之间的连通性, 如安徽霍山(AHHS)和安徽岳西(AHYX) 2个居群与其余4个居群地理距离较远(274.4–346.42 km), 阻碍了2个组之间的基因交流(Hardy et al., 2006; Perez-Alquicira et al., 2021; Wang et al., 2022a)。此外, 居群的历史事件、自然选择和人为压力也会促进居群遗传结构的形成(Cheng et al., 2020)。研究还发现地理分布区域邻近的居群遗传背景具有较高的相似性, 大多数竹类居群可通过无性繁殖建立并扩展到附近区域, 共享相同的基因库, 因此居群间的亲缘关系较近, 同源性较高(Meena et al., 2019; Oumer et al., 2020; Silva et al., 2020)。本研究中短穗竹取样个体并未完全覆盖分布区域内的所有居群(附表3), 除当前的分布中心(表1)区域外, 尚缺乏对福建、江西、湖北、江苏北部及浙江南部等地的取样(图5A), 可能会造成对居群遗传结构评价的偏差, 从而无法准确判断居群间的遗传关系。因此, 增加地理代表性分布区域内居群取样并确保每个居群有足够的个体数量, 从而增加遗传信息数量, 提高物种居群遗传结构预测的准确性(Perez-Alquicira et al., 2021)。

短穗竹居群较大的遗传变异比例局限在居群内(79.71%), 但依然存在中度遗传分化(F_{ST}=0.102), 在一些竹类中也存在中度遗传分化, 如须弥箨竹(*Himalayacalamus falconeri*) (F_{ST}=0.121)、瓜多竹(F_{ST}=0.098)和*Kuruna debilis* (F_{ST}=0.113) (Attigala et al., 2017; Perez-Alquicira et al., 2021; Meena et al., 2023b)。居群间的遗传分化与基因流动呈负相关, 尽管短穗竹居群之间基因流水平很高(*Nm*=2.442), 但地理分布较近的江苏溧阳(JSLY)与浙江长兴(ZJCX)的居群存在较大分化(F_{ST}=0.151>0.15)。即使地理位置接近的居群, 由于开花时间不同步、开花不频繁及花的数量少等原因造成花粉传播率低, 可能会阻碍基因流动, 促进居群间的分化(Nilkanta et al., 2017; Perez-Alquicira et al., 2021)。人为压力增大及全球气候变化等原因导致栖息地退化和破碎化可能加剧江苏溧阳(JSLY)和浙江长兴(ZJCX)两居群的遗传漂变, 从而导致基因交流减弱(近期基因流动率为0.029 4), 因而表现出更强的遗传分化(Nilkanta et al., 2017; Meena et al., 2019)。

3.3 遗传变异与气候关联分析

气候和地理是影响居群遗传变异的重要驱动力。冗余分析表明, 与地理因素(22.22%)相比, 气候因素对遗传变异的解释率(35.48%)更高, 在推动居群分化的过程中气候因素比地理因素更重要。虽然地理隔离可能会引起最初的分化, 但气候因素的分化选择会进一步提高居群的遗传分化(Wang et al., 2017; Bolte et al., 2022)。气候推动短穗竹居群分化为2个组(图2A)。局部适应被认为是导致分化的重要原因, 许多物种存在对气候变化条件下的局部适应(Harrisson et al., 2017; Wang et al., 2022b)。

冗余分析和梯度森林分析表明, 短穗竹适应性遗传变异很大程度上与Bio2、Bio6、Bio7、Bio11和Bio19这5个气候因子紧密关联, 温差和低温是影响短穗竹遗传变异的关键因子, 此外也与最冷季度降水量(Bio19)有关。温度是许多物种存在适应性变化的驱动因素, 其通过影响光合作用、呼吸作用和蒸腾作用影响植物的生长(Jia et al., 2020; Butler et al., 2022)。温度和降水是影响植物生长发育、生存和繁殖的重要因素, 但还需综合考虑其它相关因素, 如土壤特性和光照辐射, 这可能会改变对适应性遗传变异的认识和理解(Perez-Alquicira et al., 2021; Filipe et al., 2022)。本研究基于16 583个SNPs筛选适应性位点(异常SNP), 但由于大多数SNP是中性的, 仅发现98个高分化的SNP位点(图4A)。 Wang等(2017)认为利用简化基因组测序技术在基因组水平上筛选适应性位点有一定的局限性, 可能无法发现与适应性有关的低频等位基因。通过冗余分析和潜在因素混合模型筛选, 发现与降水量(Bio19)有关的异常SNP比各温度因子多(图4B, C)。气候因子可能不是某些假定的适应性SNP变异的主要驱动因素, 相关SNP可能具有多效性并受到其它生物或非生物因素的选择(Filipe et al., 2022)。

3.4 潜在地理分布预测

第四纪气候在冰期和间冰期之间振荡对当今物种的分布格局产生重要影响。许多植物无法适应寒冷干燥的气候而被迫向南迁移避难, 众多物种被隔离在不同

的避难所(胡菀等, 2020; Polic et al., 2022)。在末次冰期许多植物并未完全迁移到24°N以南区域，在末次盛冰期大降温背景下短穗竹的分布范围在23°–27°N之间，说明该分布区(图5C)可能是短穗竹在冰期的避难所(胡菀等, 2020)。全新世中期气候开始变暖，一些物种向北迁移并且分布面积增大(胡菀等, 2020; He et al., 2022)。短穗竹在全新世中期明显向北扩张且分布范围扩大59.12% (图5B; 附表9)。全新世中期到当前短穗竹同样向北迁移和扩张(图5A, B)，此期间温度降低可能是影响短穗竹扩张的原因，已证实全新世中期(约6 000年前)到当前发生了5次冷事件，分别发生在5.9、4.2、2.8、1.4和0.4 kyr (Wang et al., 2013)。在进行短穗竹分布预测时也发现最冷月份最低温度(Bio6)、最冷季度平均温度(Bio11)和最冷季度降水量(Bio19)影响短穗竹的分布和生长。未来气候条件下，物种的承受能力将受降水和温度等因素的影响，物种的分布范围可能会缩小或转移(Yebeyen et al., 2022)。2021–2040年和2041–2060年2个时段，在SSP 1–2.6路径下短穗竹高适生区有向北迁移的趋势。此外，预测江西和湖南交界处的高适生区面积将减小甚至消失，以及在2061–2080年间SSP 5–8.5路径下高适生区会出现部分衰退和破碎化，短穗竹可能将受到全球变暖的严重威胁。

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Population Genetic Structure and Climate Adaptation Analysis of *Brachystachyum densiflorum*

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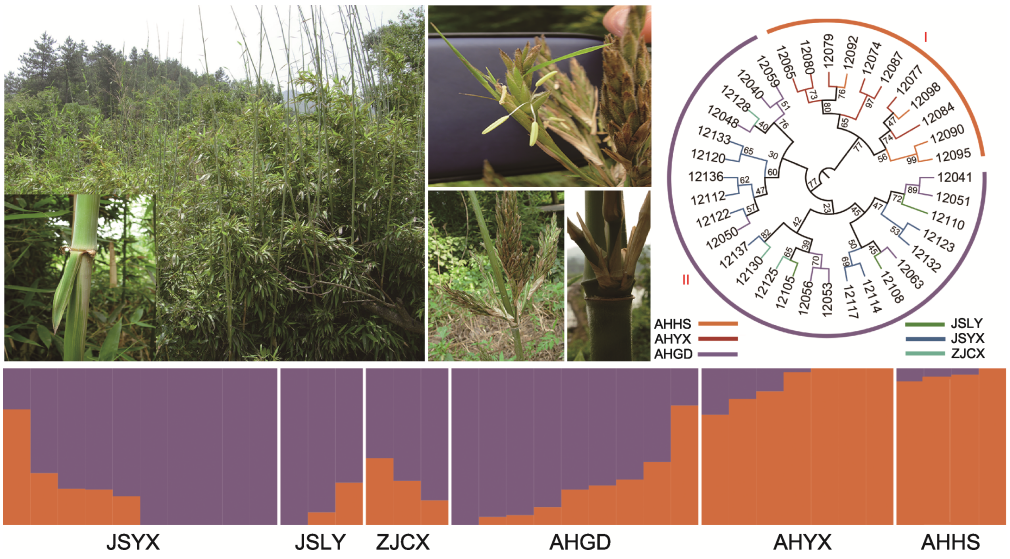
INTRODUCTION: Genetic diversity is considered as a crucial aspect in assessment and conservation of rare and endangered species. *Brachystachyum densiflorum* is a species endemic to eastern China. In recent years, with rapid economic development, accelerated urbanization, and escalating pollutant emissions, the habitat of *B. densiflorum* has been continuously degraded, habitat fragmentation has intensified, and its populations have shown a tendency to decline.

RATIONALE: Genetic diversity endows species with abundant genetic resources and plays a pivotal role in shaping their capacity to adapt to new environments. To elucidate the genetic diversity of *B. densiflorum* and evaluate the influence of climate change on its genetic variation, reduced-representation genome sequencing technology was employed to obtain single nucleotide polymorphisms (SNPs), and subsequently population genetics and landscape genetics together with species distribution modelling were analyzed.

RESULTS: *B. densiflorum* had a moderate level of genetic diversity. Six populations were divided into two groups, and there was moderate differentiation (F_{ST}=0.102) and high gene flow (Nm=2.442) between them. Genotype-environment association analysis indicated that the two groups were diverged attributable to local adaptation to the climate. Temperature differences and low-temperature regimes interacting together with precipitation gave rise to genetic variation of this species. In total, 544 adaptive loci were identified, which displayed significant correlations with temperature difference, low-temperature factors (Bio2, Bio6, Bio11, and Bio7), and precipitation factors (Bio19). *B. densiflorum* migrated evidently

northward from the Last Glacial Maximum to the current, with its distribution area increased by 89.5%. However, during the period from 2061 to 2080, the extent of the suitable area for this species will be contracted, and there will be partial degradation and fragmentation occurring in highly suitable areas within Anhui Province.

CONCLUSION: *B. densiflorum* showed a moderate level of genetic diversity and a moderate degree of genetic differentiation. Local adaptation drove the formation of the current genetic pattern of *B. densiflorum*, and temperature differences, low-temperature, and precipitation led to genetic variation. *B. densiflorum* has evidently migrated northward from the Last Glacial Maximum to the current with increase of distribution area. However, niche modelling indicated that during the period from 2061 to 2080, the suitable habitat area of *B. densiflorum* would be contracted, with partial degradation and fragmentation occurring in highly suitable areas within Anhui Province. These results provide the basis for conservation and utilization of *B. densiflorum.*



Population genetic structure analysis of *Brachystachyum densiflorum*

Key words *Brachystachyum densiflorum*, reduced-representation genome sequencing, genetic diversity, genetic structure, species distribution model

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附表1 从短穗竹采样地点经纬度提取的气候数据
Appendix table 1 Climate data extracted from latitude and longitude of the sampled sites of *Brachystachyum densiflorum*

附表2 19个气候因子相关性分析
Appendix table 2 Correlation analysis of 19 climate factors

附表3 短穗竹分布位置筛选
Appendix table 3 Screening of the distribution of *Brachystachyum densiflorum*

附表4 要素类型与正则化乘数
Appendix table 4 The feature combinations and the regularization multipliers

附表5 分子方差分析
Appendix table 5 Analysis of molecular variance (AMOVA)

附表6 地理和气候、气候、地理3组数据对短穗竹遗传结构影响对比
Appendix table 6 Comparison of the effects on the genetic structure of *Brachystachyum densiflorum* of three data sets: climate and geography, climate, geography

附表7 适应性位点冗余分析和偏冗余分析
Appendix table 7 Redundancy analysis and partial redundancy analysis of adaptive loci

附表8 8个气候因子及其重要性参数
Appendix table 8 Eight climate factors and their importance parameters

附表9 不同时期短穗竹的潜在分布面积
Appendix table 9 The potential distribution area of *Brachystachyum densiflorum* under different periods

附图1 SNP转换与颠换统计
Appendix figure 1 Transition and transversion statistics of SNP

附图2 MaxEnt模型中的ROC预测
Appendix figure 2 Prediction of the ROC in the MaxEnt model

附图3 气候变量对短穗竹潜在分布模型的Jackknife检验得分
Appendix figure 3 Jackknife test scores of climate variables on potential distribution model of *Brachystachyum densiflorum*

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