



•研究报告• 繁殖生物学专题

# 雌雄异株物种一把伞南星雌雄株空间分布及性别二态性

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**摘要:** 雌雄异株是有花植物雌雄性别功能在个体水平上由结合到分离的重要进化转变之一, 发生于被子植物的多个科属。雌雄异株物种的雌雄个体通常在分布、形态等方面存在差异。研究其雌雄个体的空间分布及性别二态性, 是理解雌雄异株物种繁殖策略及其适应与进化的重要前提。天南星属(*Arisaema*)是天南星科内已报道唯一存在雌雄异株且较为进化的类群, 一把伞南星(*A. erubescens*)是该属中不同性别个体存在差异的多年生草本植物。本文以湖南省八大公山国家级自然保护区内分布的一把伞南星为研究对象, 通过研究其雌雄个体的空间分布、花期物候、形态结构及访花者类群, 以期明确该物种雌雄植株的空间关联性以及花期物候、形态结构的性别二态性。结果表明: 一把伞南星群体内性比均呈极显著雄性偏倚, 雌雄个体在小尺度范围呈聚集分布, 但在较大尺度上呈随机分布; 雄性个体比雌性个体更早进入花期, 置换多元方差分析显示雌雄植株间形态特征存在显著差异, 其中假茎基径、佛焰苞管部直径、花序基径、花序柄直径等特征对性别二态性有重要贡献; 主要传粉者为白天活动的菌蚊科菌蚊属(*Mycetophila*)的蕈蚊, 其对雄株的访问频率极显著高于雌株。这些结果表明: 雌雄异株物种一把伞南星不同性别植株的空间关联与其传粉者蕈蚊的活动习性相匹配, 其开花物候、形态特征及传粉者访问等方面的性别二态性是对繁殖成功的保障。

**关键词:** 一把伞南星; 雌雄异株; 性别二态性; 性比; 空间分布; 有性繁殖特征; 蕈蚊传粉

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## Spatial distribution and sexual dimorphism of dioecious *Arisaema erubescens*

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### ABSTRACT

**Aims:** The transition to dioecy constitutes a pivotal milestone in the evolution of sexual functions in flowering plants, marking a shift from the integration of male and female reproductive organs within the same individual to their separation. This sexual system occurs across numerous angiosperm families and genera. Both female and male individuals of dioecious species display variations in distribution, morphology, and life history traits. Therefore, it is essential to examine the spatial distribution and sexual dimorphism of dioecious species in order to comprehend their reproductive strategies, adaptability, and evolutionary patterns. The genus *Arisaema* is the only reported taxon within the Araceae family known to possess a dioecious sexual system. In this study, we explored the differences between the dioecious members of *Arisaema erubescens* in the Badagongshan National Nature Reserve, Hunan Province, China, with a specific focus on the spatial distribution and sexual dimorphisms.

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**Methods:** We surveyed the coordinate positions of male and female individuals across four plots, analyzed both the sex ratio and spatial distribution patterns of these individuals. Sexual dimorphism was assessed based on phenological and morphological traits of *A. erubescens*. Additionally, a quantitative comparison of the floral visitor assemblages between female and male individuals was conducted.

**Results:** From our observations, the *A. erubescens* population was significantly dominated by staminate flora. Male and female individuals were found to clusters on small scales and disperse randomly on a large scale. The male individuals flowered 4 days earlier than the females. The permutational multivariate analysis of variance identified significant disparities in morphological traits between male and female individuals, which are pivotal to sexual dimorphism. These traits include the pseudostem basal diameter, the diameter of spathe tube, the inflorescence basal diameter, and the peduncle diameter. The primary pollinators of *A. erubescens* were the diurnal fungus gnats of the *Mycetophila* species, with an extremely higher visitation frequency observed on male individuals compared to those on female individuals.

**Conclusions:** Our study suggests that the spatial association of different genders in *A. erubescens* corresponds to the pollinators' activity habits. The sex dimorphism of *A. erubescens* in flowering phenology, morphological traits, and pollination activity collectively guaranteed the reproductive success of the species.

**Key words:** *Arisaema erubescens*; dioecy; sex dimorphism; sex ratio; spatial distribution; sexual reproduction traits; pollination by fungus gnats

有花植物从两性结合经不同途径多次独立进化形成雌雄性别功能在个体水平上分离的雌雄异株(Charlesworth, 1999; 张大勇, 2004)。与动物不同,植物的两性分离是一种相对罕见的有性繁殖策略,被子植物中仅5%–6%的物种存在雌雄异株性系统,但这些物种却分布于43%的科中(Renner, 2014)。因此,雌雄异株是有花植物由两性结合到分离的重要进化转变之一(Barrett, 2008)。此过程通常伴随着雌雄性别个体间形态、生理和生活史等特征的二态性进化(Barrett & Hough, 2013),既可表现为花期物候(Abe, 2001)、花序特征(Barrett, 1992)、花数量(Avila Jr & Freitas, 2011; Matsuhisa & Ushimaru, 2015)、花大小(Delph et al, 1996; Moquet et al, 2020)和花部报酬(Ashman, 2000; Ushimaru et al, 2023)等有性繁殖性状的差异,也可表现为植株大小(Pickup & Barrett, 2012; Yu et al, 2022)、茎干(Dawson & Geber, 1999)和叶特征(Steven et al, 2007; Midgley, 2010)等植株形态性状的差异。这些差异可能与雌雄两性所面临的选择压力(如生存力选择、传粉媒介选择和性选择等)有关,且这些选择压力还可导致二者生态位的分离(Delph & Ashman, 2006; Barrett & Hough, 2013)。

被子植物雌雄两性功能的分化使其对资源类型及其数量的需求也出现差异,从而导致雌雄植株的出现频率及其空间分布的差异(Dawson & Geber, 1999; Dudley, 2006)。雌雄异株植物自然种群的性比通常偏离1 : 1的理论值,且雄性偏倚是雌性偏倚的

两倍(Barrett et al, 2010),这可能与雌性较高的繁殖成本及死亡率有关(Obeso, 2002; Sinclair et al, 2012)。此外,雌雄植株对资源竞争的潜在冲突还会导致雌雄性别空间分离(Bedhomme & Chippindale, 2007; Mercer & Eppley, 2010)。

天南星属(*Arisaema*)是天南星科内已报道唯一存在雌雄异株且较为进化的类群(Barriault et al, 2010),包含约200个落叶或常绿多年生草本物种(Ohi-Toma et al, 2016),喜马拉雅-横断山脉是该属的分布和分化中心(李恒, 1980)。天南星属物种具天南星科中结构最为特化的直立狭佛焰苞花序(刘德鑫等, 2022),主要由双翅目菌蚊科和眼蕈蚊科的蕈蚊传粉(Matsumoto et al, 2021; Suetsugu et al, 2021)。在每个生长季中,天南星属雌雄异株物种植株均可表现出雌性、雄性和无性3种性别状态,偶见雌雄同株(Doust & Cavers, 1982)。有关天南星属植物的性别转换及其影响因素(Richardson & Clay, 2001; 胡光万, 2008)、种间生殖隔离(Matsumoto et al, 2019, 2021; Zeng L et al, 2023)和传粉者气味吸引(Kakishima et al, 2019; Suetsugu et al, 2021)等已有一些报道。Matsumoto等(2020)报道了克隆繁殖的芦生天南星(*A. ovale*)和无克隆繁殖的细齿南星(*A. peninsulae*)在放牧干扰下的种群结构和空间格局,但对该属雌雄异株物种自然条件下的空间分布及性别二态性还缺乏全面了解。

一把伞南星(*A. erubescens*)是天南星属雌雄异株多年生草本植物。该物种同一植株的性别在年际

间可发生变化,且性别表现由地下球茎在上一个生长周期中所积累的营养决定,其性别分化和转换符合“植株大小优势模型”(胡光万,2008)。我们的野外观察发现:自然种群中其雌雄植株分布与形态存在差异。因此,本研究拟通过观测该物种自然种群性比及空间分布,量化对比雌雄个体开花物候、繁殖特征与营养特征及其访花者类群的差异,旨在回答以下问题:(1)自然种群中一把伞南星的性比和空间分布是怎样的?雌雄个体间存在何种空间关联?(2)其性别二态性主要体现在哪些方面?对繁殖过程有何影响?

## 1 材料与方 法

### 1.1 研究区域及材料

研究地点位于湖南省张家界市桑植县八大公山国家级自然保护区天平山林区(110°03' E、29°46' N,海拔1,400 m)。该区域属于典型的山地常绿落叶阔叶混交林,为北亚热带山地湿润季风气候,年均降水量2,105.4 mm,全年相对湿度90%(卢志军等,2015)。

一把伞南星喜湿润阴凉环境,在研究区域内常沿道路两侧呈带状分布,块茎扁球形,叶柄具鞘部分褐色或绿色,上部浅绿色;佛焰苞绿色,檐部三角状卵圆形或长卵圆形,具线形尾尖;附属器先端膨大且底部常具浅绿色中性花,肉穗花序单性,雄花具短柄,乳白或浅紫色,雌花绿色(吴征镒和李恒,1979)(附录1),花期5月,果期9月。

### 1.2 数据采集

#### 1.2.1 植株性比及其空间分布

为了调查自然种群中一把伞南星雌雄植株分布情况、性比及空间关联,2022年在花期到来前,在研究区域内随机设置4个100 m × 50 m的样方,在无新佛焰苞花序开放时对样方内每个有性植株的坐标进行标定并统计其性别,计算植株雄:雌性比。同时,于该物种分布较集中的地点建立50 m × 20 m的固定样方,每天记录样方内处于开花期植株的性别及数量,计算性比随种群花期的变化情况。

#### 1.2.2 雌雄植株的开花特性

为了探究雌雄植株的开花特性是否存在差异,于2022年和2023年的4-5月对上述固定样方中的所有开花植株进行跟踪记录:当样方内第1株植株开

花时,依次对所有开花植株进行编号并记录性别,每天观察开花情况,直至无新开花植株出现,以此记为种群花期。将佛焰苞檐部打开记为植株始花,佛焰苞萎蔫记为花期结束,以此计算植株花期。

为了检测雄花花粉活力和雌花柱头活性,在自然种群中随机标记未开放的雄株花序并套网袋,开花后及时收集新鲜的花粉,用MTT(3-(4,5-二甲基噻唑-2)-2,5-二苯基四氮唑溴盐)染色法检测花粉活力(Rodriguez-Riano & Dafni, 2000),剩余的花粉置于干燥阴凉处保存,每24 h检测一次;另标记10株生长阶段相近且佛焰苞未打开的雌株,开花当天及之后每24 h在各花序上取5朵小花带回实验室,将柱头置于滴有3%过氧化氢溶液的载玻片上检测柱头活性(胡德美等,2021)。

#### 1.2.3 植株形态与花部结构的性别二态性

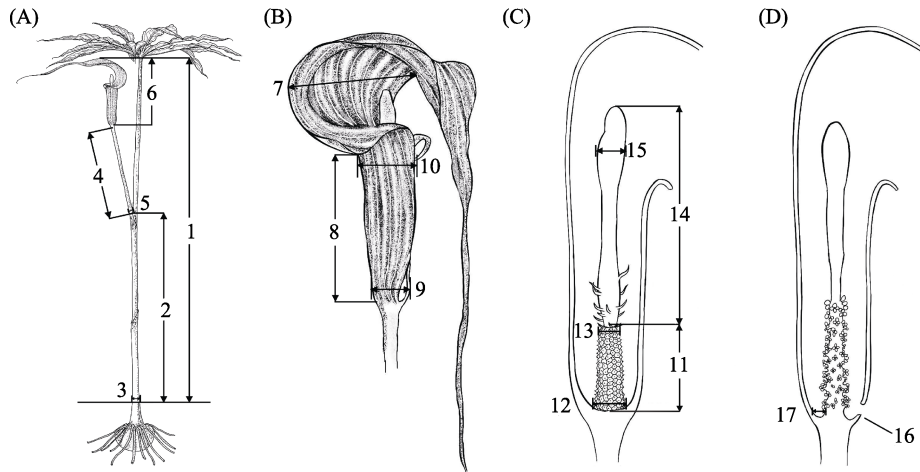
为了比较一把伞南星雌雄个体繁殖期形态特征的差异,于2023年盛花期在自然种群中随机选取雌雄植株各30株,记录叶数,并用卷尺和精度为0.01 mm的数显游标卡尺测量花序高度、假茎长/基径、花序柄长/直径、佛焰苞长、佛焰苞檐宽、佛焰苞管长/基径、喉部直径、花序长、花序基径、花序顶径、附属器长/直径、小花数、小花直径(每花序上、中、下各测一朵;雄花测量未开裂散粉的小花)、佛焰苞基部小孔长/宽、雄花序底部通道直径(图1)。由于雌花序上小花排列较紧密,故用花序表面积/小花表面积来估算雌花序小花数。

#### 1.2.4 访花昆虫及访花规律

为了明确一把伞南星雌雄植株访花者类群及活动概况,于2023年盛花期在该物种分布较集中的区域开展以下实验:

(1)访花者种类。选取佛焰苞即将打开的雌雄植株各20株进行标记,雄株佛焰苞基部小孔(图1D)用脱脂棉堵住,以防进入佛焰苞的访花者逃出;每天用自制捕虫装置(附录2)在不损伤花序的情况下收集每个佛焰苞内被困访花者,记录植株编号及对应虫数,在实验室内用体视显微镜(Leica M205C, Cambridge, UK)观察,并利用分类资料(Mcalpine et al, 1981)将访花者鉴定至属,同时记录访花者虫体携带花粉情况。虫体带粉且在雌雄植株佛焰苞内均捕捉到的访花者视为传粉者。

(2)访花者日活动规律及访花频率。选取佛焰苞



**图1** 一把伞南星植株及花部形态示意图。(A)植株;(B)佛焰苞外部形态;(C)雌株佛焰苞纵切面观;(D)雄株佛焰苞纵切面观。1: 花序高度; 2: 假茎长; 3: 假茎基径; 4: 花序柄长; 5: 花序柄直径; 6: 佛焰苞长; 7: 佛焰苞檐宽; 8: 佛焰苞管长; 9: 管部直径; 10: 喉部直径; 11: 花序长; 12: 花序基径; 13: 花序顶径; 14: 附属器长; 15: 附属器直径; 16: 雄株佛焰苞基部小孔; 17: 通道直径。

Fig. 1 Schematic of individual and floral morphology of *Arisaema erubescens*. (A) Individual; (B) External morphology of spathe; (C) Female spathe vertical-section; (D) Male spathe vertical-section. 1, Inflorescence height; 2, Pseudostem length; 3, Pseudostem basal diameter; 4, Peduncle length; 5, Peduncle diameter; 6, Spathe length; 7, Limb width of spathe; 8, Tube length of spathe; 9, Tube diameter; 10, Throat diameter; 11, Inflorescence length; 12, Inflorescence basal diameter; 13, Inflorescence apical diameter; 14, Appendix length; 15, Appendix diameter; 16, Exit hole at the base of spathe in male individual; 17, Channel diameter.

即将打开的雌雄植株各20株编号标记, 用脱脂棉封堵雄株佛焰苞基部小孔。选择天气晴朗的白天, 早上8:00将佛焰苞中所有宿存昆虫取出, 之后每2 h收集一次佛焰苞内昆虫, 直至18:00, 记录每时段收集到的昆虫数量, 本实验重复4天, 绘出不同时段访花昆虫数量变化曲线。于实验室对每只访花昆虫进行鉴定并记数, 各昆虫相对访花频率 = 每花序收集虫数/总花序数/2 h。

### 1.3 数据分析

采用拟合优度(G-test of goodness-of-fit)来检验自然种群中植株性比是否偏离1 : 1; 空间点格局分析使用R软件中的spatstat包完成, 采用双变量成对相关函数与完全空间随机模型(complete spatial randomness, CSR)分析4个样方雌雄植株间的关联性, 每种分析均采用Monte Carlo方法模拟199次, 产生置信度为99%的置信区间, 函数值 $g(r)$ 位于置信区间以上则代表正相关关系, 在置信区间以下则表示负相关关系, 若函数值位于置信区间内, 则表示两者无相关关系(Baddeley et al, 2015)。

利用广义线性模型(generalized linear model, GLM)中的正态分布恒等相关函数比较雌雄植株花期及其形态特征以及不同访花者访花频率是否存

在差异; 利用主成分分析和基于Bray-Curtis距离的置换多元方差分析(PERMANOVA, 使用R软件中的vegan包完成)来检验雌雄植株形态特征是否存在差异(Oksanen et al, 2022)。

数据分析均在SPSS 23.0 (IBM Inc., New York, USA) 软件和R 4.2.2中完成, 利用Origin 2022 (Origin Lab Inc., Northampton, Massachusetts, USA) 完成绘图。

## 2 结果

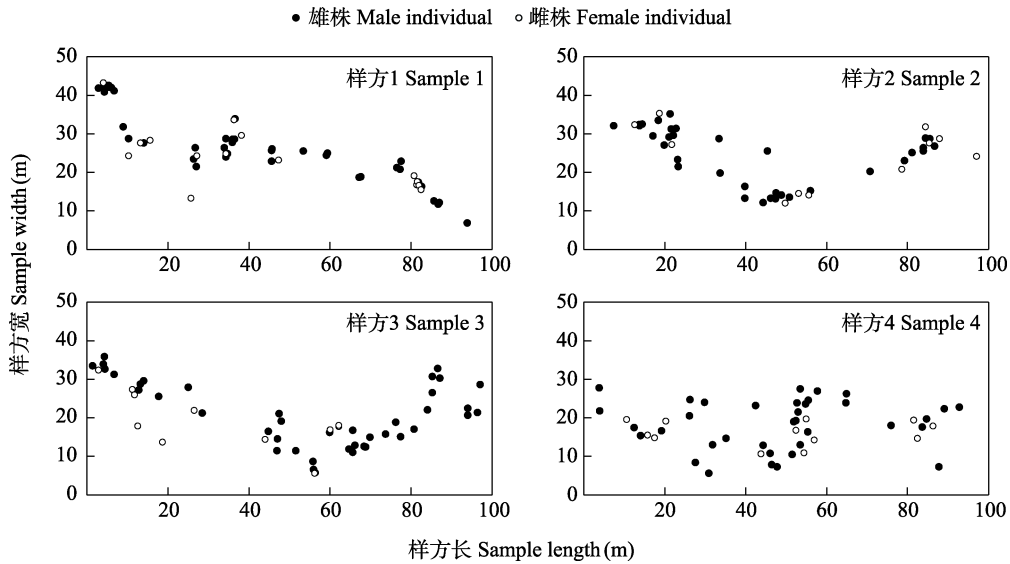
### 2.1 植株性比及空间分布

在2022年的花期结束后, 固定样方内共有有性植株78株(雄57株, 雌21株)。植株动态性比(雄 : 雌)随花期呈先小幅上升后下降的趋势, 种群进入花期后第10天性比最大(雄 : 雌 = 7.67), 后随雌株开放逐渐下降至最低0.33 (附录3)。4个样方(100 m × 50 m)中一把伞南星的最终性比均极显著偏离1 : 1, 平均性比(雄 : 雌)为 $3.01 \pm 0.18$ , 表现出极显著的雄性性别偏倚(表1, 图2)。

空间点格局分析表明: 4个样方内雌雄植株间的分布虽存在一定差别, 但均在较小尺度上偏向于聚集分布而在较大尺度上相互独立呈随机分布的

**表1** 2022年八大公山国家级自然保护区一把伞南星在4个样方中的性比。 $P < 0.01$ 表示性比极显著偏离1:1。  
**Table 1** Sex ratio of *Arisaema erubescens* in four samples in the Badagongshan National Nature Reserve in 2022.  $P < 0.01$  indicates an extremely significant deviation from a 1:1 sex ratio.

| 样方 Sample | 雄株 Male | 雌株 Female | 性比(雄:雌) Sex ratio (Male:Female) | G-检验 G-test | P       |
|-----------|---------|-----------|---------------------------------|-------------|---------|
| 1         | 38      | 15        | 2.53                            | 10.321      | 0.001   |
| 2         | 34      | 11        | 3.09                            | 12.330      | < 0.001 |
| 3         | 41      | 12        | 3.42                            | 16.773      | < 0.001 |
| 4         | 36      | 12        | 3.00                            | 12.558      | < 0.001 |



**图2** 2022年八大公山国家级自然保护区一把伞南星在4个样方中的空间分布  
**Fig. 2** Spatial distribution of *Arisaema erubescens* in four samples in the Badagongshan National Nature Reserve in 2022

特性。其中样方1、3、4整体尺度变化趋势大致为雌雄植株分布随尺度增大由正相关到无相关的特点。样方1雌雄植株在2–5 m尺度上正相关, 其余尺度上无相关或稍显正相关; 样方3雌雄植株在1–4 m和10–11 m尺度上为正相关, 其余尺度上为无相关或轻微负相关; 样方4雌雄植株在1–7 m尺度上为正相关, 7–25 m尺度上则表现为相互独立(图3)。样方2雌雄植株在1–5 m尺度表现为正相关, 5–16 m尺度上相互独立, 16–25 m尺度上略微负相关(图3), 整体尺度变化趋势呈现出随尺度增加由正相关到无关联再到负相关的特点。

### 2.2 雌雄植株开花特性

对样地连续两年的观测表明, 一把伞南星花期为4月末至5月末, 呈现出明显的开花峰值期(图4), 雄株平均始花时间(儒略日期, 2022年:  $126.12 \pm 0.52$  d; 2023年:  $125.54 \pm 0.40$  d)极显著早于雌株(儒略日期, 2022年:  $130.48 \pm 0.90$  d; 2023年:

$128.50 \pm 1.22$  d) (2022年: Wald  $\chi^2 = 18.040$ ,  $P < 0.01$ ; 2023年: Wald  $\chi^2 = 7.825$ ,  $P < 0.01$ )。2022年雄株花期( $13.74 \pm 0.29$  d)极显著长于雌株花期( $11.90 \pm 0.49$  d) (Wald  $\chi^2 = 11.686$ ,  $P < 0.01$ ), 而2023年雄株花期( $14.17 \pm 0.29$  d)与雌株花期( $14.88 \pm 0.74$  d)无显著差异(Wald  $\chi^2 = 0.870$ ,  $P = 0.336$ )。一把伞南星散粉5 d后花粉活性仍可保持在85%以上, 随后逐渐降低, 直至第9 d降至11.7% (附录4A); 柱头可授性持续约11 d, 佛焰苞刚打开时可授性最强, 随后逐渐降低(附录4B)。

### 2.3 植株形态与花部结构的性别二态性

在本研究所测一把伞南星的20个形态性状中, 除佛焰苞檐宽、附属器直径和花序柄长外, 其余性状均表现出显著的性别二态性(表2)。尤其是雄株佛焰苞席卷边缘重叠处形成一个截面积约  $4.26 \pm 0.36$  mm<sup>2</sup>的水滴形小孔(exit hole), 且肉穗花序基部存在一个直径约2 mm的环形通道连接该孔, 而雌

株佛焰苞花序基部无此结构(图1C)。除29%的雌株具2片叶外, 其余雌株为1片叶, 而雄株均为1片叶; 表现出二态性的特征中, 除花序长和小花直径外, 雌株的特征值均显著大于雄株( $P < 0.05$ ) (表2), 表明雌株较雄株高, 且具相对较大的茎干直径和佛焰苞花序。

对一把伞南星雌雄植株共有的18个形态特征进行主成分分析, 提取了累积贡献率为76.2%的前4个主成分(附录5), 主成分1 (PC1)的贡献率为46.7%,

起主要作用的性状是假茎基径、管部直径、花序基径、花序柄直径、小花数、花序顶径; 主成分2 (PC2)的贡献率为15.2%, 起主要作用的性状是花序长和小花直径。雌株和雄株特征性状分别聚为两个类群, 两者间几乎无交叉和重叠(图5), 置换多元方差分析结果表明雌雄植株形态特征存在极显著差异( $F = 76.127, R^2 = 0.563, P < 0.001$ )。

#### 2.4 一把伞南星访花昆虫及访花规律

在一把伞南星佛焰苞花序内共收集到201只访

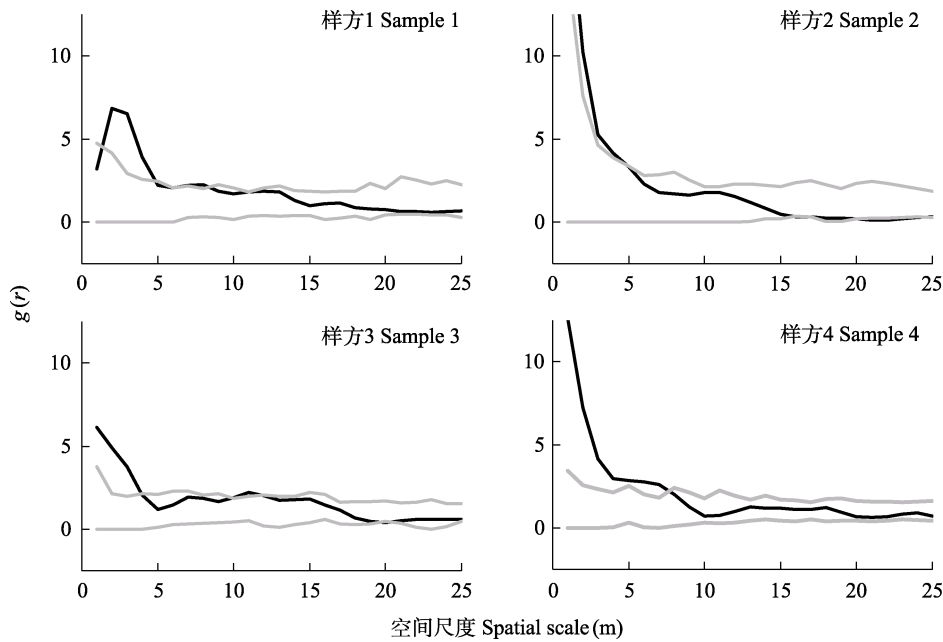


图3 八大公山国家级自然保护区4个样方中一把伞南星雌雄植株间的空间关联。深色线为 $g(r)$ 值, 浅色线为99%置信区间。  
Fig. 3 Spatial associations between male and female individuals of *Arisaema erubescens* in four samples in the Badagongshan National Nature Reserve. The dark lines and light lines are  $g(r)$  values and 99% confidence envelopes, respectively.

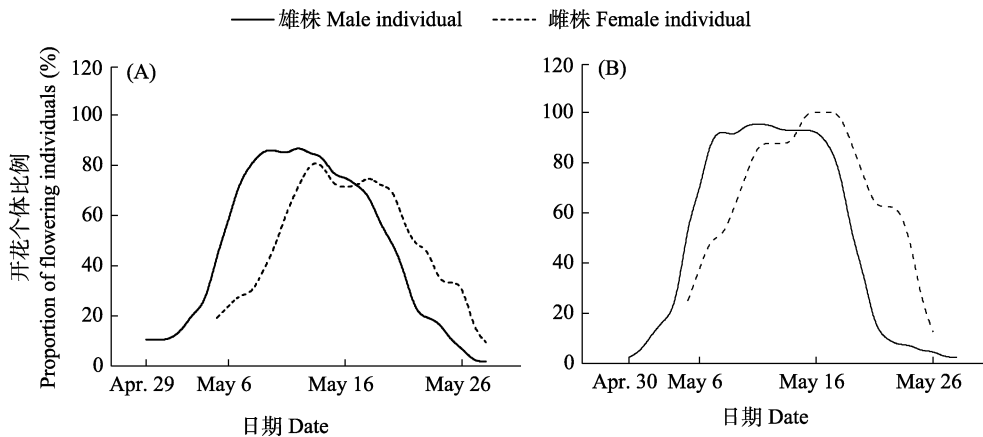
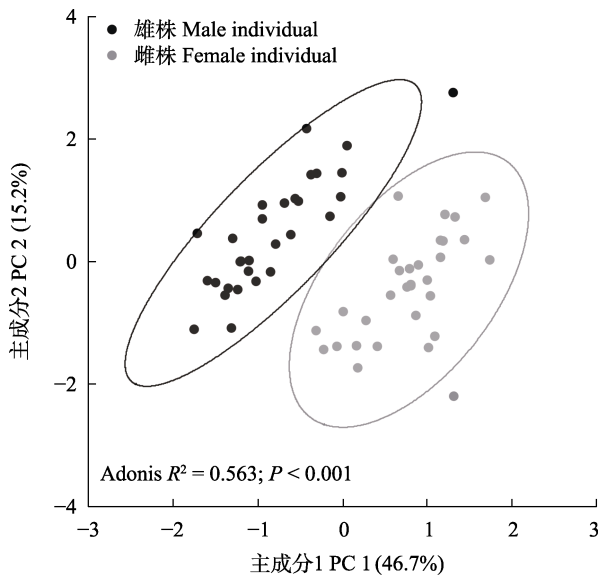


图4 2022年(A)与2023年(B)八大公山国家级自然保护区一把伞南星种群花期动态  
Fig. 4 Flowering phenology of *Arisaema erubescens* in the Badagongshan National Nature Reserve in 2022 (A) and 2023 (B)

**表2** 一把伞南星雌雄特征的比较(广义线性模型)(平均值 ± 标准误)。粗体表示具显著性差异( $P < 0.05$ )特征中的较大值。  
**Table 2** Comparisons of traits between male and female individuals of *Arisaema erubescens* (generalized linear model, GLM) (mean ± SE). The larger value of significant differences ( $P < 0.05$ ) is indicated in bold.

| 特征 Traits                                  | 雌株 Female individual  | 雄株 Male individual  | Wald $\chi^2$ | P       |
|--|-----------------------|---------------------|---------------|---------|
| 叶数 Leaf number                             | <b>1.29 ± 0.08</b>    | 1.00 ± 0.00         | 14.543        | < 0.001 |
| 花序高度 Inflorescence height (cm)             | <b>57.40 ± 1.42</b>   | 44.26 ± 1.35        | 44.899        | < 0.001 |
| 假茎长 Pseudostem length (cm)                 | <b>39.78 ± 2.05</b>   | 26.65 ± 1.18        | 30.352        | < 0.001 |
| 假茎基径 Pseudostem basal diameter (mm)        | <b>12.39 ± 0.44</b>   | 7.85 ± 0.43         | 54.421        | < 0.001 |
| 花序柄长 Peduncle length (cm)                  | 9.76 ± 0.73           | 11.51 ± 0.57        | 3.530         | 0.06    |
| 花序柄直径 Peduncle diameter (mm)               | <b>4.91 ± 0.21</b>    | 3.14 ± 0.15         | 48.564        | < 0.001 |
| 佛焰苞长 Spathe length (mm)                    | <b>76.26 ± 1.60</b>   | 65.69 ± 2.60        | 12.219        | < 0.001 |
| 佛焰苞檐宽 Limb width of spathe (mm)            | 45.96 ± 1.28          | 39.24 ± 1.19        | 1.044         | 0.307   |
| 佛焰苞管长 Tube length of spathe (mm)           | <b>48.04 ± 1.69</b>   | 42.14 ± 1.72        | 5.969         | 0.015   |
| 管部直径 Tube diameter (mm)                    | <b>12.92 ± 0.26</b>   | 8.89 ± 0.28         | 112.205       | < 0.001 |
| 喉部直径 Throat diameter (mm)                  | <b>15.46 ± 0.67</b>   | 12.31 ± 0.50        | 14.079        | < 0.001 |
| 花序长 Inflorescence length (mm)              | 21.71 ± 0.60          | <b>25.79 ± 0.85</b> | 15.551        | < 0.001 |
| 花序基径 Inflorescence basal diameter (mm)     | <b>10.07 ± 0.29</b>   | 5.35 ± 0.21         | 175.015       | < 0.001 |
| 花序顶径 Inflorescence apical diameter (mm)    | <b>6.02 ± 0.15</b>    | 3.70 ± 0.13         | 135.609       | < 0.001 |
| 小花数 Number of floret                       | <b>515.79 ± 22.48</b> | 263.04 ± 12.24      | 95.747        | < 0.001 |
| 附属器长 Appendix length (mm)                  | <b>38.76 ± 1.92</b>   | 27.20 ± 1.62        | 21.014        | < 0.001 |
| 附属器直径 Appendix diameter (mm)               | 4.95 ± 0.26           | 4.71 ± 0.26         | 0.430         | 0.512   |
| 小花直径 Floret diameter (mm)                  | 1.17 ± 0.02           | <b>1.34 ± 0.03</b>  | 32.098        | < 0.001 |
| 出口孔截面积 Exit hole cross-sectional area (mm) | –                     | 4.26 ± 0.36         | –             | –       |
| 通道直径 Channel diameter (mm)                 | –                     | 2.00 ± 0.09         | –             | –       |



**图5** 八大公山国家级自然保护区一把伞南星两种性别表型植株特征的主成分分析  
**Fig. 5** Principal component (PC) analysis of traits in two sex phenotypes of *Arisaema erubescens* in the Badagongshan National Nature Reserve

花者, 主要为双翅目昆虫, 占总访花者的94.5%, 包括菌蚊科菌蚊属(*Mycetophila*, 占总访花者87.1%)、

眼蕈蚊科眼蕈蚊属(*Sciara*, 占总访花者2.0%)和迟眼蕈蚊属(*Bradysia*, 占1.5%)等昆虫(附录6); 偶见蜘蛛目、革翅目等其他访花者(共占5.5%)。由于雌雄花序内均发现虫体携粉的菌蚊属蕈蚊访花(附录1, 附录7), 且访花频率极显著高于其他访花者(Wald  $\chi^2 = 43.603, P < 0.001$ ) (图6A), 故认为菌蚊属蕈蚊是一把伞南星最主要的传粉者; 但其在雄花序的访问频率( $0.53 \pm 0.07$ 次/花序/2 h)极显著高于雌花序( $0.25 \pm 0.06$ 次/花序/2 h) (Wald  $\chi^2 = 9.551, P = 0.002$ ) (图6A)。

通过对样方内雌雄植株累计40 h的访花观测, 发现访花者主要活动时间为白天(即8:00–18:00), 夜间(18:00至次日8:00)活动极少(整个夜间每花序内平均收集虫数分别为: 雄花序 $0.08 \pm 0.03$ 只; 雌花序 $0.08 \pm 0.05$ 只)。白天, 由早至晚访问雌、雄花序的虫数呈下降趋势, 上午8:00–10:00访花昆虫数量最多(平均每花序内虫数: 雄 $1.03 \pm 0.10$ 只, 雌 $0.70 \pm 0.20$ 只), 极显著多于其他时段( $P < 0.01$ ) (图6B)。此外, 除10:00–12:00、16:00–18:00雄花序的访花者数极显著高于雌花序外(分别为: Wald  $\chi^2 =$

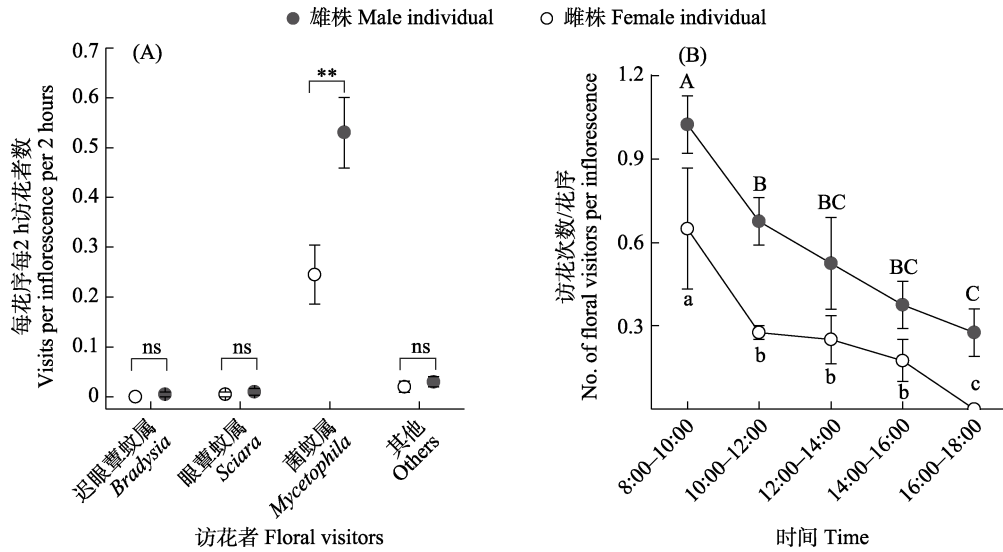


图6 不同访花者对一把伞南星雌雄花序的访花频率(A)及访花者数量日动态(B) (平均值 ± 标准误)。\*\*表示雌雄个体间传粉者访花频率在 $P < 0.01$ 水平下存在极显著差异; ns表示雌雄个体间传粉者访花频率不存在显著差异( $P \geq 0.05$ ); (B)图中不同大、小写字母分别表示雄、雌花序在一天内不同时间段的访花次数在 $P < 0.05$ 水平下差异显著。

Fig. 6 Visit frequency by different visitors between male and female inflorescences (A) and temporal dynamics of the visitors number (B) of *Arisaema erubescens* (mean ± SE). \*\* indicates significant difference of visit frequency between male and female individuals at  $P < 0.01$ , while ns indicates no significant difference. Different capital and lowercase letters in (B) indicate significantly different visitor number in male and female inflorescences between different time of the day at  $P < 0.05$ , respectively.

21.469,  $P < 0.001$ ; Wald  $\chi^2 = 20.603$ ,  $P < 0.001$ ), 其余时段雌雄花序内访花者数量无显著差异。

### 3 讨论

天南星科物种具有独特的佛焰苞花序结构, 该科较原始的类群其花序为暴露的两性花花序(花烛属(*Anthurium*)、白鹤芋属(*Spathiphyllum*)等), 且多雌先熟(Jiménez, 2019)。在演化过程中, 由两性花花序向单性花雌雄同花序(喜林芋属(*Philodendron*)、落檐属(*Schismatoglottis*)等)转变, 此后雌雄性别进一步空间分离, 出现单性花雌雄异花序(天南星属)(伊廷双等, 2002)。随着花部结构的演变, 天南星科物种由异交为主向完全异交转变(刘德鑫等, 2022)。因此具雌雄异株物种的天南星属是该科内较为进化的类群, 以天南星属雌雄异株物种一把伞南星为研究对象开展空间分布及性别二态性研究, 可为理解天南星科雌雄异株物种繁殖策略及其适应与进化积累理论资料。

雌雄异株物种种群的性比通常偏离1:1的平衡预期(Sinclair et al, 2012)。本研究中一把伞南星2022年不同样方最终平均性比为 $3.01 \pm 0.18$ , 均表现出极显著的雄性性别偏倚(表1, 图2), 这与天南星属

其他物种一致(Richardson & Clay, 2001)。由于雌性的繁殖投入较高, 需通过减缓植株生长、推迟繁殖时间或降低开花频率等策略来权衡, 因此经过多次繁殖后性比呈现出雄性偏倚(Lloyd & Webb, 1977)。但存在放牧干扰的天南星属种群, 其性比则会受到严重影响。如在梅花鹿(*Cervus nippon*)密集食草的面积为0.36 ha的样地中, 尽管克隆繁殖的产生天南星和无克隆繁殖的细齿南星并不可口, 但均未观察到两物种的雌性植株, 这可能与梅花鹿偏好啃食较大植株有关(Matsumoto et al, 2020)。此外, 上述两物种在放牧干扰下的空间聚集程度基本一致, 均呈现出小尺度内聚集分布(Matsumoto et al, 2020)。然而, 造成性比变化的同时也会导致雌雄异株植物种群中存在雌雄空间分隔(spatial segregation of the sexes), 据统计约20个科的30多个雌雄异株物种存在该现象(Barrett & Hough, 2013)。而干扰条件下样地内产生天南星与细齿南星无雌株分布, 无法探讨雌雄植株间的空间关联性。一把伞南星具有与产生天南星类似的无性繁殖能力(胡光万, 2008), 本研究4个样方中一把伞南星的雌雄植株空间关联虽有微小差别但总体趋势一致: 均在小尺度(5 m左右)呈聚集分布而在较大尺度(15 m以上)无相关, 呈随机



分布(图3)。这可能与其传粉者为蕈蚊类群相适应, 虽然关于蕈蚊传粉距离没有明确的数据, 但Matsumoto等(2021)介绍: 细齿南星雌株和花粉供体间距离通常不超过44.3 m, 由此可见蕈蚊类传粉者携粉飞行距离较短, 因此一把伞南星较小尺度上的雌雄正相关有利于完成花粉传递促进繁殖成功。

雌雄异株常与攀援型木本植物相关, 且多为非生物传粉(Renner & Ricklefs, 1995)。对于生物传粉的雌雄异株物种, 雌雄繁殖特征的差异程度往往会受到一定限制: 如果传粉者偏好访问一种性别的植株, 或者两种性别的植株吸引不同的传粉者, 那么两性性状的差异将可能影响传粉成功(Delph & Ashman, 2006; Barrett & Hough, 2013)。因此它们的花通常不如两性花艳丽, 花朵较小, 常为白色、淡黄色或绿色(Vamosi et al, 2003)。对原产日本的6种天南星调查发现, 性别二态性主要体现在开花时间和繁殖结构上(Kinoshita, 1986), 本研究结果与之一致: 首先, 连续两年的观测发现一把伞南星雄株平均始花时间均极显著早于雌株, 雄株开花较早具有一定适应意义: 能够保证雌株开花时有花粉供其受精结实, 同时与其他雄性个体相比, 花期较早的雄性个体可能有更多机会使同种胚珠受精, 从而获得更高的繁殖适合度(Bullock & Bawa, 1981)。其次, 一把伞南星雌雄花序均为浅绿色佛焰苞包裹着肉穗花序, 但两种性别植株形态大小存在显著差异(表2, 图5), 主要体现在假茎基径、佛焰苞管部直径、花序基径、花序柄直径等方面(附录5), 总体来说雌株较雄株高, 且具相对较大的茎干直径和佛焰苞花序。由于雄性的繁殖阶段不需要结实及产生种子, 因此雌性将产生更高的资源消耗, 故需要更大的体型进行资源生产和积累(胡光万, 2008)。最后, 值得注意的是虽然一把伞南星雌雄个体的主要访花者均为菌蚊属蕈蚊, 但其对雄性个体的访问频率约是对雌性个体访问频率的2倍(图6A)。天南星属物种几乎不产花蜜(Vogel & Martens, 2000), 对蕈蚊的吸引主要依靠其附属器散发的挥发性化学气味(Suetsugu et al, 2022), 包括拟态蘑菇的形态、颜色和气味来吸引以蘑菇为食或作为交配地、产卵地的蕈蚊(Vogel & Martens, 2000); 亦或是释放类似雌性昆虫性信息素(如正十七烷)气味吸引雄性昆虫前来交配(Kostelc et al, 1980; Andreadis et al, 2015)。然而,

一把伞南星雌雄个体间传粉者访问频率的差异是否与其挥发性气味的性别二态性有关还有待于进一步探究。此外, 蕈蚊会食用花粉作为补充能量和繁殖的营养物质(Song et al, 2014), 一把伞南星的花部报酬仅为花粉, 这也可能是佛焰苞花序内含有花粉的雄性个体被访问更多的原因。

雌雄性状的二态性可通过影响繁殖器官的相对资源分配和繁殖过程, 从而以不同的方式影响雄性和雌性的繁殖成功率(Vitale & Freeman, 1986)。性别二态性研究对于理解选择如何通过雌雄繁殖功能作用于植物性状具有重要意义。例如花粉和种子都依靠风媒散布的一年生心翼酸模(*Rumex hastatulus*), 其高度二态性在生命周期中会发生可预测的变化, 开花时雄株比雌株高, 而在种子成熟期则相反(Pickup & Barrett, 2012), 高大雄性的授粉成功率显著高于与开花雌性等高的雄性, 而高大的雌性比矮小的雌性散播果实的距离更远(Zeng ZH et al, 2023)。对于虫媒传粉雌雄异株物种, 性别二态性和传粉者活动与其繁殖成功密切相关, 因此雌雄特征间的相互匹配至关重要。天南星属物种具有独特的佛焰苞花序结构, 依靠肉穗花序上方的附属器散发气味吸引蕈蚊传粉(Suetsugu et al, 2022)。一把伞南星的佛焰苞结构具有显著的性别二态性: 雌株佛焰苞基部苞片交汇处形成圆形或水滴形小孔, 而雌株佛焰苞基部苞片紧密闭合(图1)。有研究者认为该小孔的存在使传粉者蕈蚊能够携带花粉离开, 有利于雄性个体的花粉散布; 若其再被吸引进入雌株而雌花序佛焰苞基部紧闭, 在反复寻找出口的过程中, 可将身体上的花粉落置在柱头上, 促进传粉成功(Vogel & Martens, 2000; 刘德鑫等, 2022)。因此, 对于虫媒传粉的雌雄异株物种一把伞南星来说, 佛焰苞结构的性别二态性可能是确保花粉输出和充分落置的必要结构。

综上所述, 八大公山国家级自然保护区内一把伞南星种群性比均呈现极显著雄性性别偏倚, 雌雄个体在较小尺度上呈聚集分布而在较大尺度上呈随机分布; 雄性个体比雌性个体更早进入花期, 置换多元方差分析显示雌雄植株间形态特征存在显著差异: 雌株较雄株高, 且具相对较大的茎干直径和佛焰苞花序; 主要传粉者为白天活动的菌蚊科菌蚊属蕈蚊, 传粉者对雄株的访问频率极显著高于雌

株。这些结果表明: 雌雄异株物种一把伞南星不同性别植株的空间关联与其传粉者蕈蚊的活动习性相匹配, 其开花物候、形态特征及传粉者访问等方面的性别二态性是对繁殖成功的保障。

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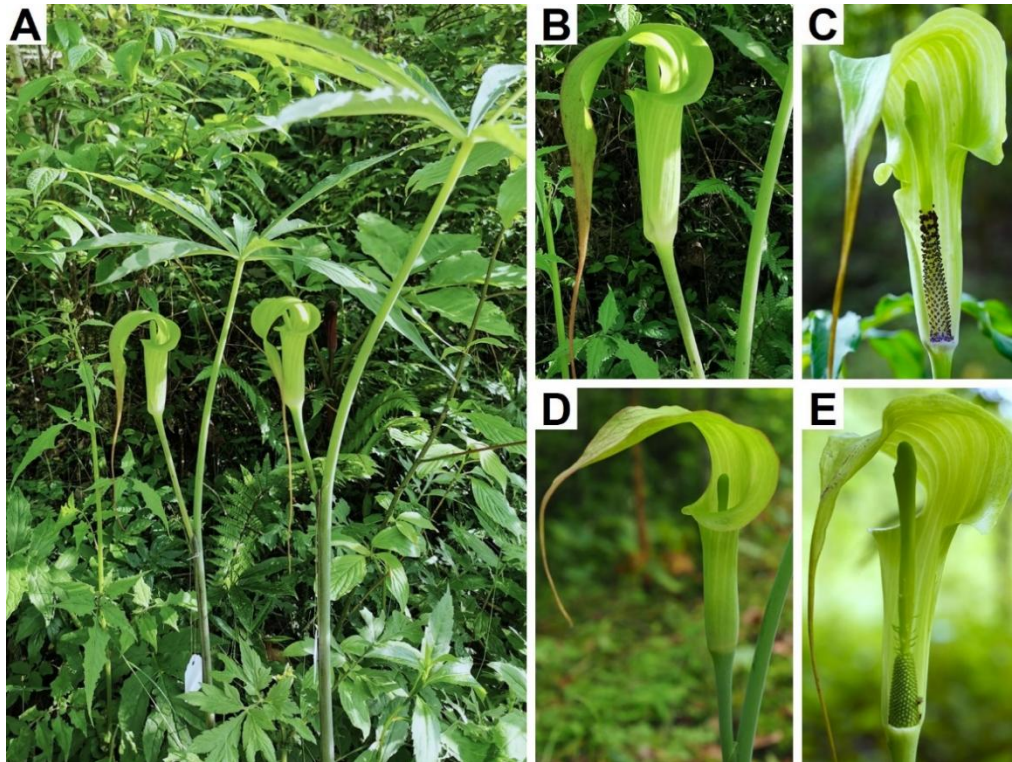
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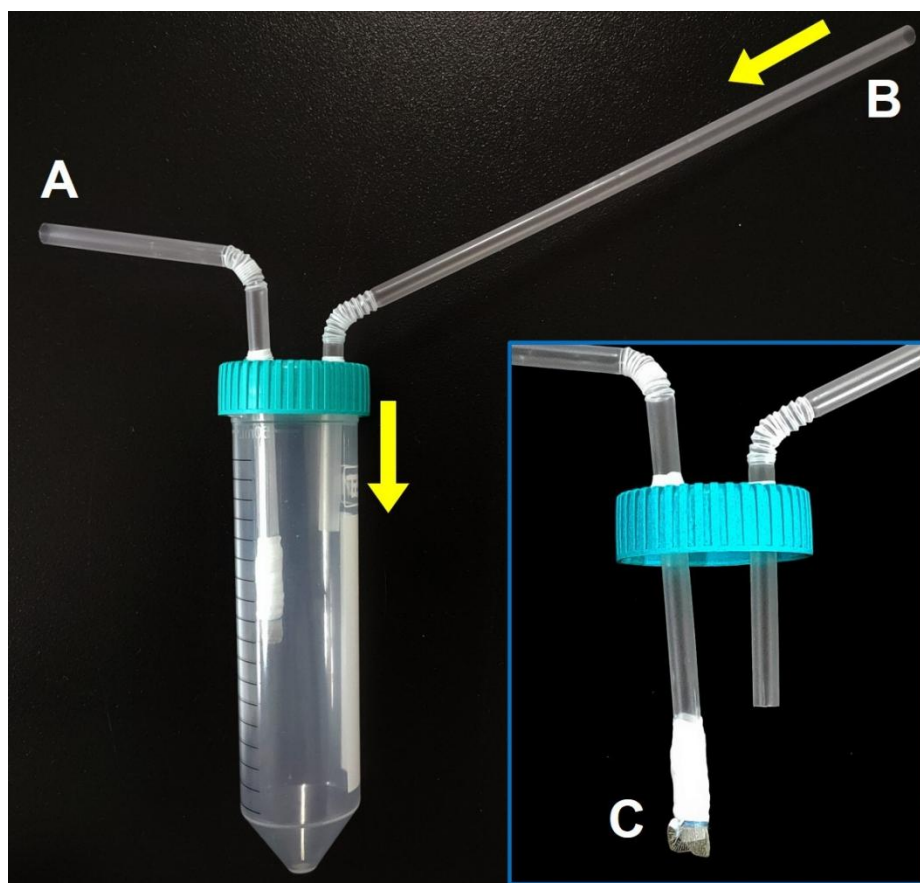
## 附录 Supplementary Material

<https://www.biodiversity-science.net/CN/10.17520/biods.2024084>



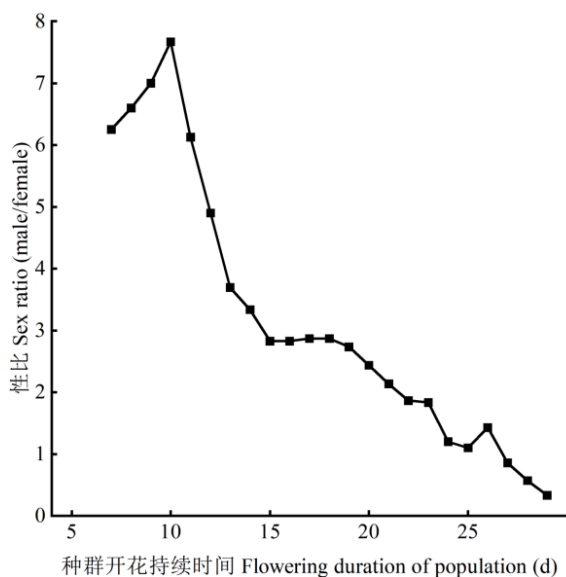
附录1 一把伞南星植株及雌雄花序形态。(A)一把伞南星雌(右)雄(左)植株;(B-C)一把伞南星雄株佛焰苞及花序;(D-E)一把伞南星雌株佛焰苞及花序。

Appendix 1 Female and male individual and floral morphology of *Arisaema erubescens*. (A) Female individual (right) and male individual (left) of *Arisaema erubescens*; (B-C) Male spathe and inflorescence; (D-E) Female spathe and inflorescence.



附录2 自制传粉者收集装置示意图, 右下图为局部放大。A管为吸气口; B管深入佛焰苞管部内, 蕈蚊沿黄色箭头所示方向进入收集瓶; C处用纱网封堵A管末端, 防止蕈蚊进入管中。

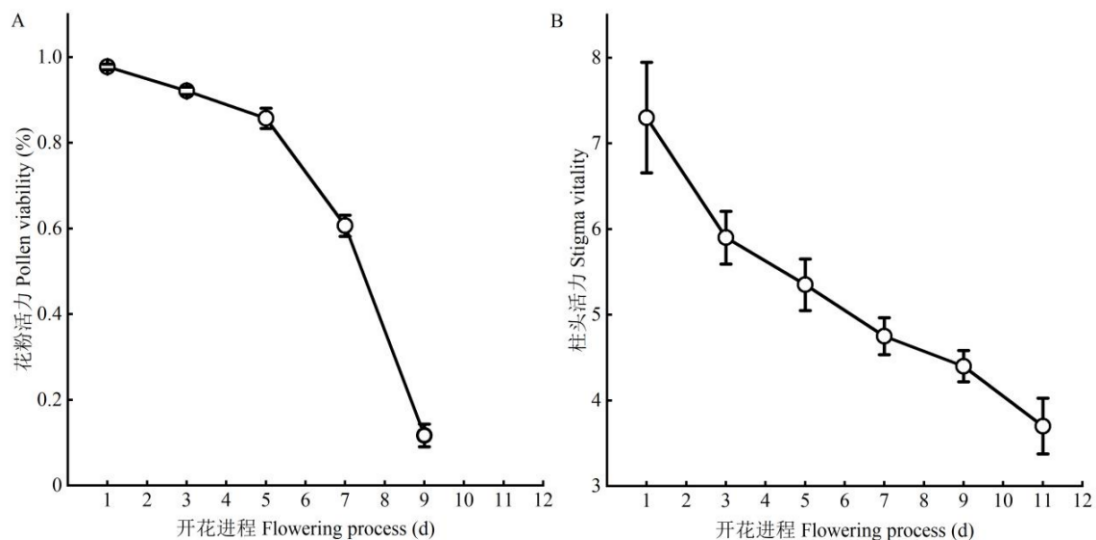
Appendix 2 Schematic of a homemade pollinator collection device, with partial enlargement in the bottom right. Tube A is the suction port; Tube B is deep inside the tube of spathe, and the fungus gnats enter the collection vial in the direction shown by the yellow arrow; The end of tube A is blocked with a gauze at C to prevent the fungus gnats from entering the tube.



附录3 2022年湖南省八大公山国家级自然保护区一把伞南星花期种群开花植株性别比动态

Appendix 3 Sex ratio dynamics of *Arisaema erubescens* during flowering period in the Badagongshan National Nature Reserve in 2022

舒为杰, 何花, 曾罗, 谷志容, 谭敦炎, 杨晓琛 (2024) 雌雄异株物种一把伞南星雌雄株空间分布及性别二态性. 生物多样性, 32, 24084. <https://www.biodiversity-science.net/CN/10.17520/biods.2024084>.

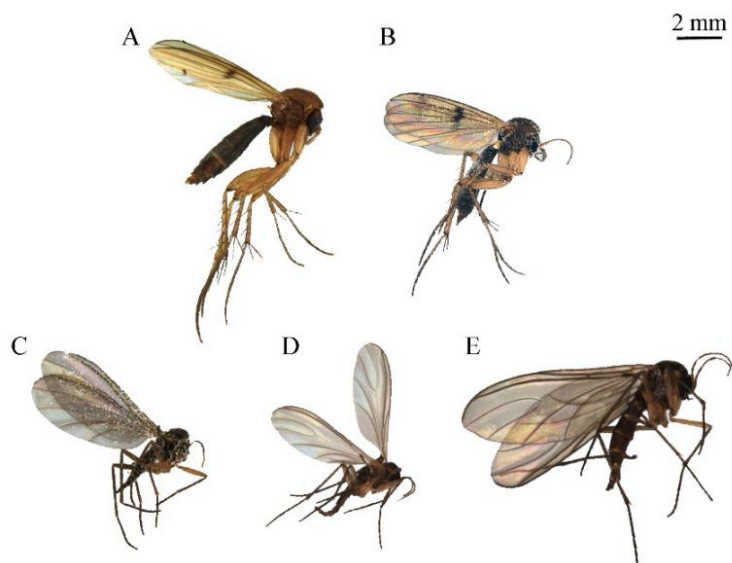


附录4 一把伞南星花粉活力(A)和柱头活性(B)  
Appendix 4 Pollen viability (A) and stigma vitality (B) of *Arisaema erubescens*

附录5 一把伞南星雌雄植株特征前4个主成分的负荷量、特征值、贡献率和累积贡献率  
Appendix 5 Factors loading value, eigenvalue, contribution, and the cumulative contribution of the first four principal components in principal component analysis in two sex phenotypes of *Arisaema erubescens*

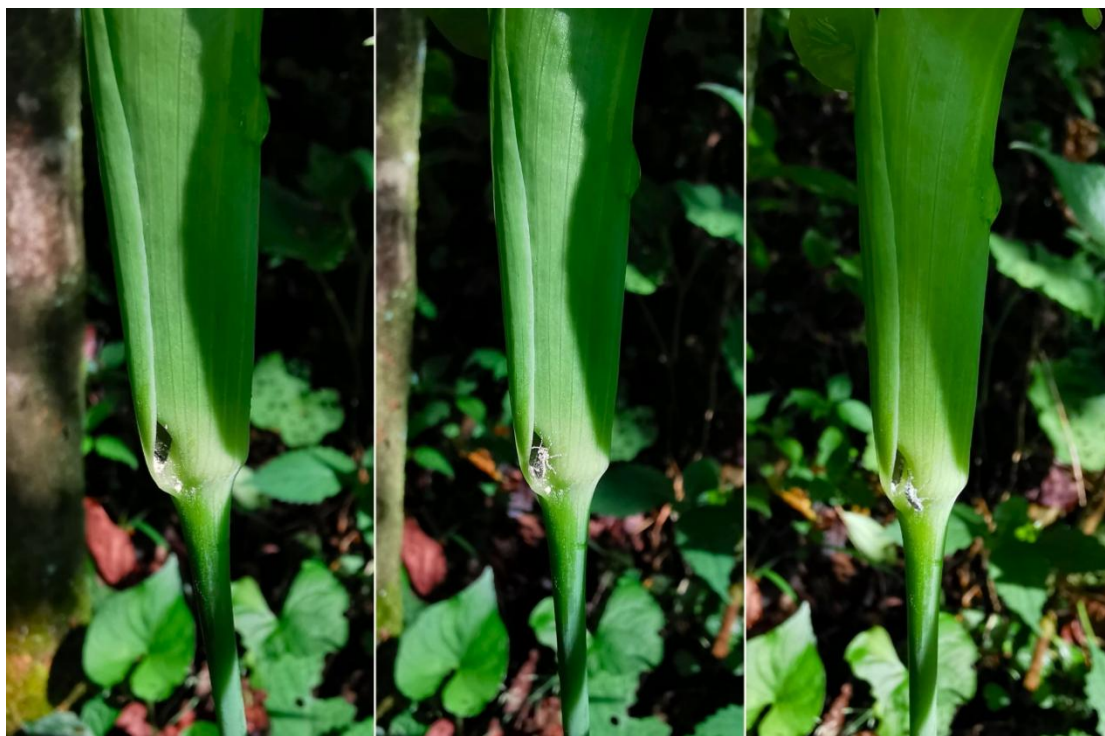
| 表型性状 Phenotypic character              | 成分 Component |        |        |        |
|--|--------------|--------|--------|--------|
|  | 1            | 2      | 3      | 4      |
| 叶数 Leaf number                         | 0.443        | -0.119 | 0.346  | -0.057 |
| 花序高度 Inflorescence height (cm)         | 0.714        | -0.307 | 0.275  | 0.494  |
| 假茎长 Pseudostem length (cm)             | 0.574        | -0.485 | 0.455  | 0.369  |
| 假茎基径 Pseudostem basal diameter (mm)    | 0.882        | -0.074 | 0.113  | 0.122  |
| 花序柄长 Peduncle length (cm)              | -0.135       | 0.419  | -0.586 | 0.504  |
| 花序柄直径 Peduncle diameter (mm)           | 0.855        | -0.085 | 0.095  | 0.018  |
| 佛焰苞长 Spathe length (mm)                | 0.758        | 0.319  | 0.001  | -0.146 |
| 佛焰苞檐宽 Limb width of spathe (mm)        | 0.675        | 0.171  | -0.322 | 0.021  |
| 佛焰苞管长 Tube length of spathe (mm)       | 0.730        | 0.576  | 0.186  | -0.075 |
| 管部直径 Tube diameter (mm)                | 0.882        | -0.041 | -0.243 | -0.003 |
| 喉部直径 Throat diameter (mm)              | 0.667        | 0.241  | 0.020  | -0.411 |
| 花序长 Inflorescence length (mm)          | -0.004       | 0.873  | 0.002  | 0.142  |
| 花序基径 Inflorescence basal diameter (mm) | 0.868        | -0.189 | -0.332 | 0.067  |
| 花序顶径 Inflorescence top diameter (mm)   | 0.827        | -0.173 | -0.310 | 0.107  |
| 小花数 Number of floret                   | 0.845        | -0.096 | -0.378 | -0.115 |
| 附属器长 Appendix length (mm)              | 0.788        | 0.273  | 0.216  | -0.142 |
| 附属器直径 Appendix diameter (mm)           | 0.422        | 0.566  | 0.380  | 0.023  |
| 小花直径 Floret diameter (mm)              | -0.328       | 0.667  | 0.169  | 0.345  |
| 特征值 Eigenvalues                        | 8.404        | 2.731  | 1.533  | 1.038  |
| 贡献率 Contribution (%)                   | 46.690       | 15.174 | 8.517  | 5.766  |
| 累积贡献率 Cumulative contribution (%)      | 46.690       | 61.864 | 70.381 | 76.147 |

舒为杰, 何花, 曾罗, 谷志容, 谭敦炎, 杨晓琛 (2024) 雌雄异株物种一把伞南星雌雄株空间分布及性别二态性. 生物多样性, 32, 24084. <https://www.biodiversity-science.net/CN/10.17520/biods.2024084>.



附录6 湖南省八大公山国家级自然保护区一把伞南星主要传粉蕈蚊。A和B为菌蚊属蕈蚊；C和D为迟眼蕈蚊属蕈蚊；E为眼蕈蚊属蕈蚊。

Appendix 6 Main fungus gnat pollinators of *Arisaema erubescens* in the Badagongshan National Nature Reserve. A and B, *Mycetophila*; C and D, *Bradysia*; E, *Sciara*.



附录7 一把伞南星的主要访花者蕈蚊虫体携带花粉从雄株佛焰苞基部小孔爬出

Appendix 7 The fungus gnat escaping with pollen grains through a hole located at the base of the male spathe of *Arisaema erubescens*