



植物边缘种群遗传多样性研究进展

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摘要 边缘种群指地理分布边缘可检测到的一定数量的同种个体集合, 准确评价其遗传多样性对于理解第四纪冰期后气候变化对物种边缘扩展或收缩、遗传资源保护与利用以及物种形成等具有重要意义。该文探讨了维持植物边缘种群遗传多样性的进化机制, 分析交配系统对物种边缘及其遗传多样性的影响, 比较了边缘与中心种群遗传多样性的差异及其形成的生态与进化过程, 并探讨了边缘种群遗传多样性与其所在的群落物种多样性的关系及理论基础。该文提出今后研究的重点是应用全基因组序列或转录组基因序列研究前缘-后缘种群之间或边缘-中心种群之间的适应性差异, 边缘种群与所在群落其他物种之间相互作用的分子机制, 深入解析边缘种群对环境的适应及边缘种群遗传多样性与群落物种多样性关系的生态与进化过程。

关键词 边缘种群; 中心种群; 遗传多样性; 交配系统; 物种多样性;

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Advances in the study of population genetic diversity at plant species' margins

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Abstract

Marginal populations are those at the geographical edge of a species' distribution. Appropriate evaluation of genetic diversity in marginal populations is of crucial significance for understanding the impacts of climate changes on species expansion or contraction in the post Quaternary glaciations, conservation of genetic resources and exploitation, and peripatric speciation. Here, we discuss the evolutionary mechanisms for maintaining genetic diversity in marginal populations, analyze the role of plant mating system in shaping a plant species' range and the genetic diversity in marginal populations, assess the difference or similarity in genetic diversity between central and marginal populations and the underlying ecological and evolutionary processes, and discuss the species genetic diversity correlation (SGDC) and the theory underlying such correlations. We proposed that future research includes the use of genome-wide sequences or transcriptome data to study the adaptive differential between leading- and rear-edge populations or between central and marginal populations and the molecular mechanisms of the interactions between the genetic diversity in marginal populations and the species diversity in the resident community of a focal species. This may help to understand the adaptability of marginal populations to local habitats and the ecological and evolutionary processes for SGDC at species' edges.

Key words marginal population; central population; genetic diversity; mating system; species diversity

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一个物种在地球上的分布总是局限于一定范围内, 其分布范围因物种不同而有所区别。那么, 究竟是什么因素制约物种边界形成呢? 为什么有些物种在看似同质的地域上分布突然中断呢? 为什么在高纬度或高海拔区域存在树线呢? 研究和解析物种边界形成的生态与进化过程是进化生物学领域中的一

个重要内容。一般认为物种边界的形成受生物和非生物因素制约。非生物因素包括河流、山脉、气候条件、生境等自然因素, 当这些自然因素不再满足植物生长条件或阻碍其进一步扩张时, 物种边界便逐渐形成; 生物因素包括受限的扩散、边缘种群的生长动态(如死亡率大于出生率)、种内资源竞争与

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种间竞争(同一营养级之间资源争夺或不同营养级之间的捕食与被捕食)等。达尔文认为物种分布受气候(及其他物理因素)及种间互作影响(Darwin, 1859; Case & Taper, 2000), 其观点部分地与生态位理论一致, 而Haldane (1956)认为物种分布受限于自然选择与基因流的联合作用。至今已有多种模型用于解释物种分布和边界形成(表1), Gaston (2003)列举了许多实例并对物种边界形成进行了较好的概述。然而, 这些理论模型(除Haldane (1956)的观点外; 表1)都只间接地涉及单物种边缘种群对环境的适应, 没有深入分析单个物种边缘种群的遗传多样性及其作用。

此外, 当单个物种边缘种群发生在一个或多个不同的生物群落组成的过渡地带时, 所在群落的物种多样性和生态学特征不同于中心区域的群落(Kimmings, 2004)。已有报道证明单个物种遗传多样性对生态系统功能有直接或间接的影响。例如, Kotowska 等 (2010) 发现当一年生植物拟南芥 (*Arabidopsis thaliana*) 的基因型多样性较高时, 拟南芥及其天敌粉纹夜蛾 (*Trichoplusia ni*) 均会有较高的生物量和存活率。Johnson等(2006)研究发现遗传多样化的植物群落能支持更加多样的动物群落, 且对干扰的耐受性也会更强(Crutsinger *et al.*, 2008)。虽然物种遗传多样性与群落物种多样性的关系已有许多报道(Jump *et al.*, 2003; He *et al.*, 2008; Laikre *et al.*, 2010; Wei *et al.*, 2017), 但边缘种群遗传多样性与所在群落物种多样性的相互作用很少有报道, 因

此, 分析边缘种群遗传多样性有助于深入理解群落过渡带或非过渡带生物多样性的维持机制。

本文主要通过概述物种边缘种群遗传多样性的研究进展, 首先探讨维持边缘种群遗传多样性的进化机制, 从基本进化动力(漂变、迁移、突变和选择)角度入手, 分析维持边缘与中心种群遗传多样性机制的异同, 然后分析与基本进化动力都有相互作用的交配系统的角色, 探讨自交或近交对边缘种群遗传多样性的调控, 之后比较单个物种的边缘与中心种群遗传多样性的差异, 最后讨论单个物种边缘种群与所在群落的物种多样性的关系, 从而系统地阐述边缘种群遗传多样性在种内分布和种间互作中的角色, 为植物遗传资源和生物多样性的保护与利用提供参考依据。

1 边缘种群遗传多样性维持机制

当物种呈离散分布或离散与连续混合分布时, 边缘种群处于相对隔离状态, 如物种分布先扩张后收缩, 容易产生与主要种群完全分离的小种群, 隔离的边缘种群可逐渐形成新物种(Coyne & Orr, 2004)。在无迁移时, 其他基本进化动力都可参与维持隔离种群的遗传多样性。当边缘种群很小时, 如冰期后仍处于隔离状态的原避难所种群, 漂变效应起主导作用, 导致等位基因丢失, 杂合子缺失, 遗传多样性降低。*Corylus avellana*边缘种群比中心种群的遗传多样性低, 这是由冰期后物种边缘扩张时的瓶颈效应或遗传漂变所致(Persson *et al.*, 2004);

表1 物种分布理论模型

Table 1 Theoretical models of a species' distribution

模型 Model	主要观点 Main point	参考文献 Reference
随机生态位模型或断棒模型 Stochastic niche model or broken stick model	每一物种生态位超体积的占有和分布不受其他物种影响。 The niche occupation and its size distribution of each species are random and independent of the niche sizes of other species.	MacArthur, 1957; Whittaker <i>et al.</i> , 2010
对数正态分布模型 Lognormal distribution model	物种占有的生态位是随机分布的并受大量因素综合影响, 并不优待某些种。 The niche size of a species is random and determined by the joint effects of a large number of factors, and no selective advantage is present among species.	Preston, 1948
生态位优先占领模型 Niche pre-emption model	第一位优势种优先占领生态位空间大部, 第二位占领其余下的大部, 以此类推, 末位只占留下 The first dominant species occupies the largest niche space, followed by the species that occupies the second largest niche in the remaining space, and so on. The last species occupies the minimum niche.	Whittaker, 1972
群落中性理论 Neutral community theory	群落内个体总数固定, 某一物种多度的增加必然伴随其他物种的减少; 所有个体出生率、死亡 The community size is fixed, and a decrease of one species' abundance is equally compensated by other species. All individuals in the community have the same birth and death rates.	Hubbell, 2001
自然选择-基因流机制 Mechanism of natural selection-gene flow	基因由中心向边缘种群的迁移与边缘种群的自然选择作用持衡。 Effects of gene flow from the central to marginal population are in balance with the effects of natural selection in the marginal population.	Haldane, 1956

*Stipa pennata*的边缘种群遗传多样性低也是由遗传漂变效应引起的(Wagner *et al.*, 2012)。类似的报道还有对鹅掌楸(*Liriodendron chinense*)(Yang *et al.*, 2016)、欧亚大陆的*Adonis vernalis* (Hirsch *et al.*, 2015)、我国的野生稻(*Oryza rufipogon*)(Gao & Gao, 2016)等的研究, 这些研究揭示了以遗传漂变为主的进化过程对边缘种群遗传多样性的影响。

当隔离的边缘种群较大时, 自然选择可起主导作用, 理论上不同的定向选择或复杂的选择方式可导致不同的遗传多样性水平。当纯合子比杂合子有更高的适合度时(定向选择), 如生境条件从分布区中心到边缘逐渐恶化, 边缘种群遗传多样性随之降低(Chhatre & Rajora, 2014)。随机自然选择可产生类似于漂变的结果, 歧化选择可导致杂合子比例下降, 而纯合子比例升高, 有利于边缘种群趋于生态辐射发展, 形成生态种。负频率依赖性选择有利于维持边缘种群的遗传多样性, 而正频率依赖性选择与定向选择的效应一致(Trotter & Spencer, 2013)。表1提到的生态位理论及达尔文的观点实际上反映了自然选择的作用。Volis等(2016a, 2016b)对地中海及沙漠地区*Avena sterilis*的研究表明, 气候对物种边缘种群遗传变异存在影响; Lázarogal等(2017)对*Cneorum tricocon*的研究揭示了在遗传漂变、定向选择等联合作用下, 边缘与中心区域的种群遗传结构及遗传多样性有所不同。

与即时效应的生态过程不同, 突变对于多数短期隔离的边缘种群遗传多样性的影响有限, 因为边缘种群对环境的适应或消失发生过程相对较快。对于长期存在的边缘种群, 如原避难所种群, 突变生成的等位基因数慢慢积累, 将增加遗传多样性, 从而可增强边缘种群对逆境的适应能力, 有利于物种扩张(Barton, 2001)。例如, 针茅(*Stipa capillata*)边缘和中心种群遗传多样性无显著差异, 这与该物种生活史久(植物生命周期长)或种群足够大有关, 使得边缘种群能避免局域灭绝(Wagner *et al.*, 2011)。因此, 大的边缘种群有利于防止已有的突变等位基因丢失。

多数边缘种群与中心或亚中心种群间存在非对称的迁移关系, 从中心种群流向边缘种群的基因流要比反方向的更频繁, 边缘种群类似于一个库(Kawecki, 2008), 基因流有助于提高边缘种群遗传多样性, 有可能利于边缘种群对逆境的适应。例如,

欧洲赤松(*Pinus sylvestris*)在伊比利亚半岛和苏格兰边缘种群的遗传多样性高于中心种群, 这是由于边缘种群受到来自中心种群迁移的影响, 边缘种群的遗传多样性没有发生衰减(Prus-Glowacki *et al.*, 2012)。中心种群流向边缘种群的基因流也可能降低边缘种群的适合度, Sexton等(2011)采用人工授粉和同质园试验测试基因流对边缘种群遗传变异的影响, 显示当基因(包含适应性差的等位基因)从中心种群流向边缘种群时, 边缘种群的生长发育变得缓慢, 当基因在相似的边缘种群之间流动时, 边缘种群遗传多样性增加, 同时还促进了边缘种群的生长繁殖, 该结论与理论模拟的结果一致(Hu *et al.*, 2003), 同样也支持Haldane (1956)的观点。

迁移与自然选择是影响边缘种群遗传多样性的两个重要过程, 一方面边缘种群对生境的适应有助于其拓展物种分布范围, 另一方面从中心种群迁移过来的基因可限制边缘种群的适应性, 但增加了遗传多样性(Kirkpatrick & Barton, 1997; Barton, 2001)。迁移与漂变联合作用时, 也可能限制边缘种群的扩张, 边缘种群因漂变或随机自然选择导致遗传多样性降低, 这与迁移单独作用时的结果相反(Polechova & Barton, 2015)。而迁移与突变的联合作用有助于物种扩张分布(Barton, 2001)。

边缘种群可同时受多种进化动力影响, 但各动力的相对贡献因物种不同而不同。此外, 植物交配系统与进化动力相互作用, 也会影响边缘种群的遗传多样性(见下节)。生态因子对种群密度的调控也可间接地影响边缘种群遗传多样性, 例如, 应用对数生长和逻辑斯谛生长模型揭示, 当边缘种群密度达到平衡时, 生态与遗传进化调节边缘种群生长率的作用可相互抵消, 这样边缘种群的遗传多样性也就间接地受生态因子调控的影响(Kirkpatrick & Barton, 1997; Barton, 2001)。

2 交配系统影响

植物交配系统描述了遗传物质在世代间的传递方式, 自交使单亲本传递2份基因拷贝到子代, 异交使单亲本传递1份基因拷贝到子代, 混合交配系统则按不同的比例进行自交和异交。在植物交配系统从异交向近交的进化过程中, 物种系统发育分析表明属内的异交种经过多次进化形成不同的自交种

(Busch, 2005; Charlesworth, 2006; Willi & Macaetaen, 2010), 自交种常常在物种进化树的顶端, 因而呈现较短的进化历史(Barrett, 1995, 2014; Veekmans *et al.*, 2014)。混合交配系统常被视为一种过渡状态, 但也被认为具有稳定性(Johnston *et al.*, 2009)。自交确保繁殖成功, 在面临传粉者稀少时, 自交使植物在新的环境下更容易生存和扩张; 异交植物能最大程度地利用外源花粉, 避免近交衰退, 增强植物的适应能力, 因此理论上交配系统可影响物种边缘种群的遗传多样性。

自交降低种群内的遗传多样性, 但增加了种群间的遗传分化(张大勇和姜新华, 2001; Bakker *et al.*, 2006; Onge *et al.*, 2011; Pettengill *et al.*, 2016), 包括增加边缘与中心种群以及边缘种群间的遗传分化(Hampe & Petit, 2005; Griffin & Willi, 2014)。在迁移和漂变联合作用下, 自交率(α)与种群遗传分化系数(F_{st})的理论关系可以从Wright (1969)、Caballero和Hill (1992)及Hu (2011)的研究结果中获得近似表达, 即

$$\frac{1}{F_{st}} = 1 + 4N_e \left(1 - \frac{1}{2}\alpha \right) \left(m_s + \frac{1-\alpha}{2} m_p \right) \quad (1)$$

式中, F_{st} 为种群分化系数, N_e 为有效种群大小, α 为自交率, m_s 为种子迁移率, m_p 为花粉迁移率。图1显示种群遗传分化随着自交率升高而非线性地增加, 当花粉流较大时, 自交的影响更大。图1指出边缘种群自交($\alpha = 1$)或异交($\alpha = 0$)可产生不同的种群间遗传分化。

已有证据表明交配系统可影响物种的地理分布范围。例如, Grossenbacher等(2015)调查15个科20个属数百物种, 结果显示自花授粉种要比异交或双亲遗传后代的物种有更广的地理分布范围, 交配系统差异可解释达20%的物种边界变异。Munoz等(2016)调查了1 996种植物, 指出在群落演替过程中, 演替早期的种类主要为自交种, 演替后期的种类主要为竞争力更强的异交种。Razanajatovo等(2016)研究报道在全球范围内物种自交与其天然分布范围呈正相关关系。这些结果与早期有争论的Baker法则相符。Baker (1955)认为由于新生境花粉源有限或父本数量少, 拓殖新生境的物种主要为自交植物(Baker, 1955, 1967; Stebbins, 1957; Barrett, 1995; Pannell, 2015; Grossenbacher *et al.*, 2016)。Moeller等(2017)的分析揭示出, 物种自交率随地理纬度的变化呈较

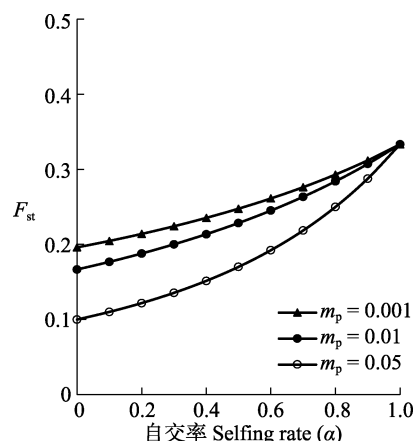


图1 自交对种群遗传结构的影响。种群分化系数(F_{st})是根据公式 $\frac{1}{F_{st}} = 1 + 4N_e \left(1 - \frac{1}{2}\alpha \right) \left(m_s + \frac{1-\alpha}{2} m_p \right)$ 计算出来的, 所用参数为种子迁移率 $m_s = 0.02$, 有效种群大小 $N_e = 50$, 花粉迁移率 m_p 分别为0.001、0.01和0.05。

Fig. 1 Effects of selfing on population genetic structure. The population differentiation coefficient F_{st} was calculated according to the equation $\frac{1}{F_{st}} = 1 + 4N_e \left(1 - \frac{1}{2}\alpha \right) \left(m_s + \frac{1-\alpha}{2} m_p \right)$, and the parameters used were seed flow $m_s = 0.02$, effective population size $N_e = 50$, and pollen flow m_p were 0.001, 0.01 and 0.05.

弱的变化趋势, 表明物种边缘范围大小与纬度的关系不显著。这些例子说明交配系统通过调控传粉或花粉的供应来影响繁殖, 进而影响物种的边界范围。

除上述生态学过程外, 交配系统也可通过调控边缘种群的遗传多样性来影响物种边界范围。通过重组和分配世代间遗传物质来影响子代种群的基因型组成, 改变基因型频率, 进而改变种群适应值的加性方差及遗传与环境的互作, 提高边缘种群的进化潜势和对环境的适应能力(Fisher, 1930), 从而扩大或缩小物种范围。通常交配系统本身不被认为是进化动力之一, 但与基本进化动力(漂变、迁移、突变和选择)互作影响边缘种群的遗传多样性, 表现出复杂的作用模式。与遗传漂变联合作用可通过减小边缘种群的有效种群大小(N_e)来降低遗传多样性(Caballero & Hill, 1992); 与自然选择联合作用时, 减弱了对有害突变基因的选择, 降低了自然选择的功效; 与突变联合作用时, 增加了有害突变等位基因固定的概率, 减小了适应性基因的固定概率, 从而减弱了自然选择功效; 与迁移联合作用时, 调节边缘种群的有效外来花粉流量, 如调节迁移的阈值以降低边缘适应性等位基因的概率(Hu, 2011), 降

低边缘种群的遗传多样性。

交配系统与植物生活史互作可影响配子体与孢子体对物种边界形成的相对贡献。Otto和Marks (1996)从理论上证明自交有利于植物配子体发展(如苔藓类和蕨类植物), 异交有利于孢子体发展(如开花的高等植物)。配子体(单倍体)选择混合交配系统或纯自交系统可产生不同的遗传多样性效应, 同样孢子体(二倍体)选择与交配系统互作可影响边缘种群遗传多样性, 从而改变边缘种群的适应性。交配系统与世代交替互作本质上就是影响边缘种群的适应性基因频率, 从而影响边缘种群进化潜势及物种边界(Hu *et al.*, 2019)。除了调节边缘种群遗传多样性外, 交配系统应该可调节边缘扩展速度, 但这需要进一步的研究。

大多数植物的交配系统类型比较稳定, 中心和边缘种群没有显著的差异, 尤其是进行有性繁殖的树木或多年生植物表现出较稳定的交配系统, 如 *Solanum elaeagnifolium* (Petanidou *et al.*, 2011)和兴安落叶松(*Larix gmelinii*)、长白落叶松(*L. olgensis*)及华北落叶松(*L. principis-rupprechtii*)(Hu & Ennos, 1999)。对于这些植物, 交配系统不应成为引起中心与边缘种群遗传多样性差异的主要原因。但由于交配系统受生物(如种群密度和物种竞争)与非生物因素(如气候变化与种群分布范围破碎化)影响, 少数植物的中心与边缘种群的交配系统存在显著差异。例如, Restoux等(2008)发现冷杉属(*Abies*)、云杉属(*Picea*)、松属(*Pinus*)均为混合交配系统, 但受种群密度影响, 种群间的交配系统可呈现一定程度的变异。Eckert等(2010)分析认为气候变化和生境破碎化

也可影响交配系统。Levin (2012)评述了因环境和传粉因素导致的边缘种群自交率升高现象。表2列出了少数物种在中心/亚中心种群表现为自交不亲和或低自交率, 而在边缘种群为自交亲和或高自交率的现象。边缘种群所处的环境条件一般较差或种群密度低, 有助于自交或自交亲和的交配系统形成。这样就降低了边缘种群的遗传多样性, 从而调节物种边界范围。

3 边缘与中心种群遗传多样性比较

边缘种群遗传多样性与种群密度有关, 但不存在一一对应关系。有性繁殖植物的密度越大, 由遗传漂变引起的遗传多样性衰减越小。生物地理学中一个重要的假设就是“中心-边缘模型”, 即物种分布密度由中心向边缘逐渐减少(Sexton *et al.*, 2009)。基于这一中心-边缘模型, 理论上可预测中心种群遗传多样性要高于边缘种群。至今已有许多研究验证中心-边缘模型。例如, Durka (1999)研究显示 *Corrigiola litoralis*的边缘种群因密度低而呈现出比中心种群的遗传多样性小; Mandak等(2005)调查鞑靼滨藜(*Atriplex tatarica*)的结果同样支持该假设; Hirao等(2017)发现北极高山植物遗传多样性随纬度减小而降低。这些研究都至少部分地支持了中心-边缘模型。

中心-边缘模型在理论和实践上也受到了挑战(Gaston, 2003; Sagarin *et al.*, 2006; Sexton *et al.*, 2009)。理论上, Guo (2012)提出将物种纬度线性变异趋势与中心-边缘模式综合生成偏正态驼峰型分布, 用于评价物种全分布范围内的遗传变异趋势(Hirao

表2 边缘种群交配系统变异

Table 2 Contrasts in mating systems between central and marginal populations of a range of plant species

分类群 Taxonomic group	中心/亚中心种群 Central/subcentral population	边缘种群 Marginal population	参考文献 Reference
<i>Leavenworthia alabamica</i>	自交不亲和 Self-incompatibility	自交亲和/自我受精 Self-compatible/self-fertilization	Busch, 2005
<i>Juncus atratus</i>	低近交率 Low inbreeding rates	高近交率, 异交率为5.6% High inbreeding, outcrossing rate = 5.6%	Michalski & Durka, 2007
<i>Camissoniopsis cheiranthifolia</i>	自交不亲和 Self-incompatibility	自交亲和 Self-compatible	Dart <i>et al.</i> , 2012
<i>Vriesea gigantea</i>	混合交配系统, 低自交率 Mixed mating system, low selfing rates	混合交配系统, 高自交率 Mixed mating system, high selfing rates	Matos <i>et al.</i> , 2015
<i>Echium plantagineum</i> ; <i>Centaurea solstitialis</i>	本地种群自交不亲和 Self-incompatible in native populations	入侵种自交亲和 Self-compatible in invasive populations	Petanidou <i>et al.</i> , 2011
冷杉属, 云杉属, 松属 <i>Abies</i> , <i>Picea</i> and <i>Pinus</i> genera	混合交配系统, 低自交率(高种群密度) Mixed mating system, low selfing rates (high population density)	混合交配系统, 高自交率(低种群密度) Mixed mating system, high selfing rates (low population density)	Restoux <i>et al.</i> , 2008
<i>Arabidopsis lyrata</i>	异交 Outcrossing	自交、混合交配系统 Selfing/mixed-mating	Griffin & Willi, 2014

et al., 2017)。同样, 该模型预测的边缘种群遗传多样性格局也受到挑战, Eckert等(2008)分析了134个研究中115个物种的结果, 发现64.2%研究结果显示边缘种群遗传多样性下降, 70.2%的研究显示边缘种群间遗传分化增强, 但多数研究中中心与边缘种群遗传多样性差异不显著。近期, Pironon等(2017)分析了248个研究, 认为81%的研究显示物种出现在中心区域的频率要比在边缘区域高, 但只有51%的研究显示物种的密度变异模式支持中心-边缘模型, 47%的研究结果显示遗传多样性从中心到边缘逐渐减小。

导致中心-边缘模型预测不准确的原因有多种, 其一是边缘种群受更强的定向选择或环境适应等因素影响, 降低了遗传多样性, 这方面有较多的报道。例如, 大针茅(*Stipa grandis*)种群遗传多样性与经度和年降水量显著相关(水分环境适应性), 边缘种群较低的遗传多样性与生境等因素的影响密切相关(Wu et al., 2010)。Kropf (2012)发现*Anthyllis montana* ssp. *jacquinii*的北部边缘种群遗传多样性要高于中心种群, 认为是远古时期遗传多样性的保存及新突变的积累所致。Callahan等(2013)在大陆尺度上评价了*Populus tremuloides*的遗传多样性, 发现西南分布区边缘种群因气候等因素影响, 其遗传多样性低, 而向北迁移的种群遗传多样性无显著变化。

从中心到边缘种群的基因流也是导致中心-边缘模型预测不准确的原因之一, 基因流有助于维持边缘种群的遗传多样性, 甚至导致边缘种群的遗传多样性高于中心种群(Kirkpatrick & Ravigné, 2002; Hampe & Petit, 2005)。例如, Gugger等(2011)发现北

美花旗松(*Pseudotsuga menziesii*)更新世(Pleistocene, 地质时代第四纪早期)向南迁移的后沿种群(墨西哥北部)保持了较高的遗传多样性。Havrdova等(2015)观测到由于欧洲遗传谱系的混合, *Alnus glutinosa*重建种群的遗传多样性高于避难所种群。Yang等(2016)分析显示, 鹅掌楸边缘与中心种群的不对称基因流使得它们间的遗传多样性无显著差异。

我国在边缘种群遗传多样性方面的一些研究也支持中心-边缘模型。表3简要列出了一些例子, 例如, 陈涛等(2012)对9个野生中国樱桃(*Cerasus pseudocerasus*)种群的研究, 郝蕾等(2017)对于北沙柳(*Salix psammophila*)种群遗传多样性的研究, 吴小培等(2016)对花苜蓿(*Medicago ruthenica*)和青海苜蓿(*M. archiducis-nicolai*)遗传结构及多样性的研究, Feng等(2006)对红松(*Pinus koraiensis*)种群的研究, 均显示出边缘种群遗传多样性低于中心种群, 认为是边缘种群受到奠基者效应或瓶颈效应影响的结果; Wei等(2016)认为冰期后扩张和不对称的基因流导致领春木(*Euptelea pleiospermum*)边缘种群遗传多样性低于中心种群。而刘军等(2013)用SSR标记研究毛红椿(*Toona ciliata* var. *pubescens*)边缘与中心种群的遗传多样性, 显示边缘种群遗传多样性高于中心种群, 不支持中心-边缘模型。

同一物种的边缘种群在不同的生态和进化过程中可产生不一致的遗传多样性格局。在间冰期, 尤其是第四纪冰期后, 气候变化导致避难所保留下来的种群向北扩张或向高海拔生境重建种群, 形成前缘种群, 另一方面, 原避难所种群向南或赤道方向缩小, 种群密度趋于衰减, 形成后缘种群。由于漂变

表3 边缘与中心种群遗传多样性比较及可能的生态或进化过程

Table 3 Comparison of genetic diversity between central and marginal populations of various plant species and the potential ecological or evolutionary processes responsible for the observed differences

植物种 Species	边缘种群与中心种群遗传多样性 Genetic diversity in marginal vs. central populations	生态或进化机制 Ecological or evolutionary mechanisms	参考文献 Reference
樱桃 <i>Cerasus pseudocerasus</i>	边缘种群低于中心种群 marginal populations < central populations	奠基者效应、瓶颈效应 Founder effect, bottleneck effect	Chen et al., 2012
北沙柳 <i>Salix psammophila</i>	边缘种群低于中心种群 marginal populations < central populations	奠基者效应 Founder effect	Hao et al., 2017
花苜蓿、青海苜蓿 <i>Medicago ruthenica</i> , <i>M. archiducis-nicolai</i>	边缘种群低于中心种群 marginal populations < central populations	奠基者效应 Founder effect	Wu et al., 2016
毛红椿 <i>Toona ciliata</i> var. <i>pubescens</i>	边缘种群高于中心种群 marginal populations > central populations	生境破碎化 Habitat fragmentation	Liu et al., 2013
红松 <i>Pinus koraiensis</i>	边缘种群低于中心种群 marginal populations < central populations	奠基者效应、瓶颈效应 Founder effect, bottleneck effect	Feng et al., 2006
领春木 <i>Euptelea pleiospermum</i>	边缘种群低于中心种群 marginal populations < central populations	冰期后扩张、不对称基因流 Postglacial expansion and asymmetric gene flow	Wei et al., 2016

和隔离, 后缘种群的遗传多样性趋减。理论上两类边缘种群的遗传多样性趋于不同, 前缘边缘种群受自然选择, 如环境温度、土壤水分梯度变化或奠基者效应的影响, 导致遗传多样性下降, 已有许多研究证实了这一点。例如, 气候变化驱动北极圈的植物分布范围向北扩展时, 11个物种的遗传多样性随着离避难所的距离变远而显著降低(Pellissier *et al.*, 2016)。

后缘种群有以下特点: (i) 早期避难所, 由于种群小, 经历长期隔离(第四纪冰期后)及遗传漂变, 但仍保留较高的遗传多样性, 可能是时间还不够长, 冰期时保存的等位基因仍然没有完全丢失。例如, 欧洲赤松(*Pinus sylvestris*)的后缘种群保留着较高的遗传多样性(Scalfi *et al.*, 2009; Prus-Glowacki *et al.*, 2012)。(ii) 后缘种群长期隔离, 种群间遗传分化大(de Lafontaine *et al.*, 2013)。(iii) 含有独特适应性的遗传变异, 有利于应对全球气候变化带来的影响(Hampe & Petit, 2005), 但同时后缘种群的遗传变异也处于全球气候变化的危险下(Provan & Maggs, 2012), 表现为退缩到高山或高海拔地带。正因为这些特点, 后缘种群在遗传资源保护中有着十分重要的作用。

由于前缘、后缘种群以及中心种群的形成或维持机制不同, 在基因组遗传结构变异上也会表现出不同的遗传多样性分布模式, 例如杂合子频率和 F_{st} 异常值在位点间的分布或二者的相关性, 以及在染色体上的分布(Hu & He, 2005; Hu *et al.*, 2011), 中性与适应性位点在染色体上的分布等。今后的一个重要研究方向就是利用高通量基因组测序分析边缘与中心种群在适应性位点上的差异, 或者利用转录组数据筛选出种群间的差异表达基因, 寻找与种群边缘适应性相关的基因分布, 揭示导致边缘种群遗传多样性差异的生态和进化过程(Provan, 2013)。

4 边缘种群遗传多样性与群落物种多样性

单个物种边缘种群遗传多样性与所在的群落物种多样性关系复杂。在非过渡植被区域分布范围内, 种间分布因生态位差异往往表现不一致, 当单个物种边缘种群与其他物种共存而组成群落时, 若该物种边缘种群遗传多样性低, 且种群密度小, 该种竞争适应能力低, 在群落中的相对频率小(如小于1%), 成为稀有种, 在群落漂变作用下容易消失, 对群落

(尤其是演替后期)物种多样性的贡献小。但群落物种多样性仍可维持在较高的水平, 或不受少数物种边缘种群遗传多样性的影响。Xu等(2016)对桐栲(*Beilschmiedia roxburghiana*)的研究表明, 群落内物种多样性的增加会使该种群的密度下降, 竞争减少了有效种群大小, 从而降低了遗传多样性; Chu等(2008)对垂穗披碱草(*Elymus nutans*)的研究表明, 群落内的资源竞争使得遗传多样性与物种多样性间的关系复杂, 不同密度种群间存在促进和竞争关系, 对遗传多样性的影响也有所不同。

当单个物种边缘种群的遗传多样性高时, 如边缘种群存在高突变率, 杂合子频率高与等位基因数多等, 种群密度较大, 在群落中的相对频率较高, 其对群落物种多样性的贡献不可忽略。例如, 在恶劣环境下, 许多物种分布的变化趋于一致, 如植被分布的高纬度北界或高海拔极限, 边缘种群遗传多样性与群落物种多样性均下降(Wei *et al.*, 2017)。

理论上群落物种多样性与种群遗传多样性是两个不同层次但又相互关联的概念(Hu *et al.*, 2006)。在群落中性理论假设下(Hubbell, 2001), 若有效群落数量相对稳定, 群落漂变会导致群落内种群遗传漂变, 群落内物种之间的多度应呈负相关关系, 也可导致所谓的单个物种遗传多样性与群落物种多样性相关(species-gene diversity correlation (SGDC); Vellend, 2005)。Laroche等(2015)证明当突变率低时, 群落间个体迁移变异可产生正的SGDC; 当突变率高时, 突变、迁移及竞争联合作用可产生负的SGDC, 因此, 中性过程并不总是产生负的SGDC。实际研究发现单个物种遗传多样性与群落物种多样性既有正相关关系(Blum *et al.*, 2012; Lamy *et al.*, 2013), 又有负相关关系(Puşcaş *et al.*, 2008), 或不相关(Taberlet *et al.*, 2012; Avolio & Smith, 2013), 反映了不同的生态和进化过程作用于两个不同层次系统的结果。

上述中性理论预测同样适合于分析单个物种边缘种群所在的群落(Hu *et al.*, 2006), 只不过用群落在时间上的演替过程中单个物种遗传多样性与群落物种多样性的关系, 来代替在空间上的两者关系来进行分析。当单个物种边缘种群在群落中多度很小时, 群落漂变会加速该物种的消失, 除非该物种从中心种群或其他群落不时地迁移一定数量的个体到边缘种群, 使得边缘种群遗传多样性得以保持。当单个物种边缘种群在群落中多度较大时或为优势种,

群落漂变会加速该物种的固定, 除非新物种形成速率高, 否则该物种边缘种群遗传多样性高但群落物种多样性低。因分析涉及同一群落演替记录, 这些推测尚待实际研究数据验证。

群落交错区物种多样性高, 往往是生物多样性热点地区(Kimmins, 2004)。陈冬梅等(2011)认为我国华中(温带属和古老植物)、南岭(热带和亚热带的过渡区)及横断山脉(具备热带、亚热带、高山寒带植被)三大生物多样性热点地区是许多植物冰期时的避难所, 也是许多物种的分布边缘, 增加了这些区域的物种多样性。由于物种边缘种群遗传多样性与其维持历史有关, 对于在冰期避难所保存下来的种群, 冰期后向北或向南单向扩张, 在过渡群落范围内的种群本身就是边缘种群, 因而保持着较高的遗传多样性(Hampe & Petit, 2005; Gugger *et al.*, 2011; Lepais *et al.*, 2013), 与单向扩张的边缘种群遗传多样性不同(非对称), 其所在的群落物种多样性较高; 对于冰期后, 从北部或南部单向迁移到过渡群落的种群, 有可能成为该物种分布范围边缘的一端, 通常遗传多样性低, 对气候和生境变化的适应性差, 容易消失, 所在的群落物种多样性也低。

总之, 边缘种群遗传多样性与群落物种多样性的关系在过渡群落或非过渡群落都可表现出复杂的关系, 当不同的生态与进化过程作用于种内遗传多样性和物种多样性两个层次时, 二者可表现为不相关。纯中性群落下, 新物种形成、突变、迁移及群落漂变过程也可形成不同的SGDC关系。

5 结论和展望

研究边缘种群遗传多样性维持机制在进化生物学中具有重要的理论意义, 在遗传资源保护和利用方面也有重要的实际意义。与普通种群一样, 理论上边缘种群遗传多样性维持机制涉及基本进化动力(漂变、迁移、突变和选择)的作用, 但实际研究显示各进化过程的相对贡献因物种而异。多个进化过程的联合作用(如迁移-选择和迁移-突变-选择过程)或复杂的自然选择过程(如随机生态位与物种竞争)可用于解释物种边界形成及与其相关的边缘种群遗传多样性的维持机制。

交配系统的角色是通过与基本进化动力相互作用来实现的, 且表现出相对稳定性, 但在一些物种中, 边缘种群的交配系统趋于近交。近交或自交减

小有效种群大小和遗传多样性。近交也可与配子或合子选择作用, 影响边缘种群遗传多样性, 从而影响边缘种群的适应性及物种边界的扩张, 这一过程与Baker法则不同。

比较中心与边缘种群遗传多样性差异时, 一些物种的边缘种群保持着更高的遗传多样性水平, 与中心丰富模型预测的结论不一致。气候变化可导致前缘和后缘种群遗传多样性差异, 后缘种群常保留原避难所遗留的遗传多样性但处于缩减过程中, 边缘种群间的遗传分化要大于中心种群间的遗传分化; 前缘种群常源于第四纪冰期后期, 遗传多样性比中心种群低。

在与群落物种多样性关系上, 边缘种群遗传多样性与该物种在群落中的相对多度有关。多度小的物种有可能因群落漂变而趋于消失, 多度大的物种可能因群落漂变趋于多度增加或固定, 群落进化动力(漂变、迁移、突变和选择)可导致不同的SGDC关系。理论上在中性群落及分子钟假设下, 群落漂变导致正的SGDC, 迁移或突变有助于形成负的SGDC。自然选择可修饰该预期结果, 实际研究表明SGDC可呈正、负或不相关关系。

今后边缘种群遗传多样性研究的重点是: (i)应用核基因组序列或种群间转录组基因表达差异来检测前缘-后缘种群之间或边缘-中心种群之间差异的适应性基因位点和中性位点在基因组上的分布, 分析中心-边缘种群适应性差异的分子基础。(ii)应用共同的核基因组序列或胞质基因组序列检测边缘种群与所在群落其他物种之间相互作用的分子机制, 如测定物种竞争的分子基础。其结果有助于深入理解物种边缘种群对环境的适应性, 以及边缘种群遗传多样性与群落生物多样性关系的生态与进化分子机制。

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