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基于分子生物学方法的外来入侵物种入侵历史重构

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摘要:生物入侵是一个世界性的问题。全球每年因生物入侵造成的损失超过 1 万亿美元。探究入侵物种在入侵地的入侵历史对了解生物入侵的生物生态学机制、制定阻截及防除措施有重要意义。分子标记方法的兴起和大规模应用打开了入侵生物入侵历史研究的新天地。采用分子标记的方法可鉴定入侵物种的种类、追溯其来源地、回溯其扩散路径、分析扩散模式及探究物种入侵过程中对入侵种群本身的变化及其对生态系统所造成的各种影响。分子标记的应用使得多个入侵物种的入侵历史得以重现。由于分子标记方法重构的入侵历史受采样范围、采用的分子标记的种类及数量等因素的影响,该方法呈现入侵历史是否是真实发生的入侵过程还存在争议。

关键词:生物入侵;外来物种;入侵历史;分子标记

Inference on the invasion history of invasive alien species based on molecular methods

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Abstract: Biological invasions are a worldwide challenge, inducing losses of up to more than one trillion dollars (US) per annum. Having a detailed knowledge about the invasion process by following the invasive species from their source to their incursion areas i.e., their invasion history, may reveal the biological and ecological mechanisms that result in successful invasions. This information may assist researchers in finding effective controls. Applying molecular markers to the population genetics of an invasive species provides a new approach to investigate invasion history. Molecular methods have been applied to infer the invasion history, for example identifying the invasive species, the origin and pathway of the invader, reconstructing the colonization routes, analyzing the dispersal models, inferring the changes in the invasive alien species and the ecosystem effect on the regions invaded. Although the invasion processes of many species have been reconstructed using molecular makers, the reliability of these invasion history is debatable, because the inferred invasion scenarios may be affected by factors such as sampling range, type and the number of molecular markers used.

Key Words: biological invasion; invasive species; invasion history; molecular markers

生物入侵是指原本不属于某一生态区域或地理区域的物种,通过不同的途径被传播到一新的区域,并在

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新的栖息地定殖、建群、扩展和蔓延,同时对传入地的经济和生态带来一些负面影响的过程[1-2]。引起该现象的物种称为外来入侵物种[1]。在过去的几百年中,多种植物、动物或其他物种被传入到世界各地[3]。随着经济全球化的深入发展,频繁的国际贸易、旅游加速了物种向新的地域扩散的速度[3]。根据我国近 100 年来从境外传入的外来有害生物的不完全统计,目前入侵我国的外来入侵生物有 520 余种;而在世界自然保护联盟公布的全球 100 中最具威胁的外来生物中,我国就有 50 种[4]。

生物入侵的过程分为引入、定殖、潜伏、扩散及暴发等几个阶段[5]。据统计外来入侵物种能够成功从上一阶段进入下一阶段个体的比例为 10%左右[6]。但是,人为有目引入的外来种其成功的比例要高得多[6]。外来物种在入侵的最初阶段可能由于个体数量较少且分布较分散而不易被察觉[7-8]。经过一段潜伏期后,入侵种的种群数量可能已具有相当大的规模,当外来入侵物种的种群数量及分布范围达到一定的阈值后,就可能发生爆发性的扩展[9]。一种是通过种群数量增长向周边地域的短距离扩展[10],另一种是通过人或动物的活动而实现的长距离扩展[11-12]。短距离扩展是连续的,而长距离扩展则往往呈现跳跃式。

复现外来入侵物种的入侵过程,亦即重构其入侵历史对解析入侵物种成功入侵的生物、生态学机制及制定有针对性的防控措施具有重要作用。本文就近年来外来入侵物种入侵历史的研究进行了总结,以期为我国相关领域的研究提供参考。

1　重构外来入侵物种入侵历史的意义

1.1　理论意义

生物入侵改变物种的分布及入侵地的群落结构[13-14]、威胁生物多样性、影响生态系统功能过程[15-18],是生态系统及进化过程产生快速变化的推手[19-21]。生态学家及进化生物学家提出了诸多关于外来入侵物种入侵机制的假说,如“物种多样性阻抗假说”[22]、“生态系统干扰假说”[14]、“入侵进化假说”[23]、“新武器假说”[24],“天敌逃避假说”[25]、“繁殖体压力假说”[26]及“环境发生化学变化假说”[27]等。这些假说的论证有利于入侵物种入侵历史的完善,同时完善入侵历史又推动了新假说的产生[28]。

外来入侵物种在新生境中通常由于选择压力的作用而产生以表型变化为标志的适应性进化。这种适应性进化表现为由表型可塑性所决定的“前适应性”或遗传分化所形成的“后适应性”。直接比较来源地种群与入侵种群间表型上的差异是分析选择压力在适应性进化上所起作用的重要方法,因此准确鉴定入侵种群的来源地至为关键。大陆果蝇 *Drosophila subobscura* 原产地为欧洲,在传入美国不到 20 年的时间就产生了形态上的变化以适应入侵地的气候条件[29];生活在高盐环境的桡足类动物 *Eurytemora affinis* 扩散到低盐环境中后,很快就产生了适应性变化[30]。选择压力是上述两入侵物种适应性进化（表型变化）的主要推动力。随着越来越多的入侵物种入侵历史的重构,发现新生境中的选择压力推动的适应性进化不是导致表型变化的唯一因素。入侵物种在引入、建立种群及暴发扩散过程中所表现出的表型上的变化有可能是中性的。在引入过程中入侵物种种群数量的突然减少及种群建立过程中入侵地低密度的种群数量都有可能造成来源地种群与入侵地种群间与选择压力无关的表型变化[31]。

1.2　实践意义

1.2.1　预测生态影响

预测外来入侵物种可能产生的生态影响是生物入侵研究中最薄弱的环节,有效预测方法相当缺乏[32-34]。分析入侵物种在已入侵地区的生态影响是预测入侵物种在可能入侵地区生态影响的重要手段[34]。数种入侵物种的入侵历史表明,这些入侵种在大多数入侵地区的生态影响都大致相似[35-41]。在既有入侵地域生态影响的信息已成功用于预测一些广泛分布的入侵种扩散到新的地域后的生态影响。基于入侵历史采用 meta-analysis,以生物量及入侵时间为预测变量的预测模型可预测锦鲤 *Cyprinus carpio* 在新生境中达 91%的生态影响[34]。

以入侵历史作为预测外来入侵物种生态影响的手段还面临许多挑战。首先,由生物入侵导致的生态影响

的信息还相当缺乏,且不能确定有多少信息与特定入侵物种造成的生态影响相关,这些信息是否可用于定量分析[42-43]。其次,入侵物种引起的生态影响是多种多样的,这些影响的大小甚至方向会随着时空的改变而变化[44-46]。考虑到由入侵物种所引起的生态影响的不确定性及不同入侵物种间生态影响信息量的差异,入侵历史还不可能广泛用于预测入侵物种在潜在入侵区域的生态影响的方式、方向及强度[34]。

1.2.2 防控

外来入侵物种入侵历史的重构有助于制定合理的检疫措施、阻截及防控方案。外来入侵物种在其起源地是完整的生物链中的一环,明确其起源地是引入捕食性或寄生性天敌控制入侵种群的基础。确定入侵种的来源地可有针对性的实施产地检疫,从源头上切断入侵种的传播。复现扩散路径可对入侵种的扩散采取分段阻截的措施,防止入侵种向新的区域蔓延。入侵种群遗传信息的获得可为制定合理的防控方案提供遗传学上的指导[47-50]。

根据入侵历史美国地中海实蝇 *Ceratitis capitata* 的防控是入侵历史应用于防控策略制定的典型范例之一。地中海实蝇于20世纪下半叶侵入美国加利福尼亚州、田纳西州及佛罗里达州。采用分子标记技术对美国地中海实蝇的来源及迁移路径进行分析后制定了包括对来源地果蔬实施严格检验、设置阻截带防止分散的分布区间个体的迁移及释放不育昆虫等防控措施[51]。原产于新热带植物区(Neotropics)的猫爪藤 *Macfadyena unguis-cati* 及红叶麻风树 *Jatropha gossypiifolia* 近年来侵入澳大利亚。但这两种入侵植物呈现出截然不同的入侵历史,猫爪藤入侵种群可能形成于单次入侵事件或最初入侵的种群数量很小,而红叶麻风树入侵种群是由不同来源地的多重入侵或由遗传多样性丰富的来源地种群反复入侵形成的。根据两种植物的入侵历史,制定了有针对性的防控策略:对于遗传多样性低的猫爪藤入侵种群,单一的采用天敌控制就可能取得较好防控效果,而对于遗传多样性高的红叶麻风树入侵种群则应采取多种措施相结合的防控策略[52]。在我国,立足于对入侵历史的研究,开展了对紫茎泽兰 *Ageratina adenophora*[53-57]、红火蚁 *Solenopsis invicta*[58-59]、松材线虫 *Bursaphelenchus xylophilus*[60] 及苹果蠹蛾 *Cydia pomonella*[61] 等外来入侵物种的阻击和灭除行动。

2 重构入侵历史的方法

外来入侵物种入侵历史的重构根据手段不同可分为基于历史发生记录的直接方法[62]和基于遗传信息的间接方法[63-71]。

2.1 直接方法

重构入侵历史的直接方法以入侵物种的有无及发现的先后时间等记录为基础[72]。机场及港口对入侵物种的截获记录反映了入侵物种的直接来源地。结合生态学及生物气候学信息,这些记录还可用于回溯入侵物种的扩散路径。例如,白纹伊蚊 *Aedes albopictus* 扩散路径及扩散范围的回溯就结合了国际航运、空运数据库及气候条件[73]。机场和港口的截获记录虽然反映了入侵种的直接来源地,但不能从这些记录获得入侵后续过程的信息。加之入侵物种扩散记录的缺乏,采用直接方法重构入侵生物的入侵历史特别是回溯扩散路径不能获得较为精确的结果[74]。

2.2 间接方法

入侵物种的鉴定是重构入侵历史的前提。采用传统的形态学的方法辅以分子生物学手段可有效地确定入侵物种的分类单元。对于一些在形态上难以和其近缘种相区分的入侵物种,分子生物学鉴定更是重要手段。入侵物种种群间遗传信息的差异有助于推断入侵种群的来源地。通过构建入侵种群与来源地种群间的系统发育树计算各种群间的遗传距离,外来入侵物种扩散过程中的各种情形得以呈现[75]。如果多个入侵种群来自同一来源地,这几个入侵种群可能由于入侵初期的瓶颈效应导致彼此间较大的遗传距离,种群系统发育树将会呈现出来源地种群位于树的根部而各入侵种群相对独立的位于系统发育树末端的状态。种群系统发育树的枝长反映了入侵种群进化历史的长短,根据入侵种群的枝长可描述外来入侵物种的扩散方向[76]。玉米根萤叶甲 *Diabrotica virgifera* 北美1个种群及欧洲5个种群的邻接系统发育树 显示,该虫从北美分别扩

散到欧洲各地,巴黎可能是玉米根萤叶甲在欧洲的最初登陆地[63]。近年来,以 Structure[77]及 Geneland[78]为代表的聚类方法也越来越多的应用到外来入侵物种入侵历史的重构中。与入侵种群清晰地聚类在一起的种群有可能是其来源种群。如果入侵种群与多个来源地种群共祖,说明入侵种群可能是由不同来源地的多重入侵形成[64,78-81]。进一步分析每个个体的祖先来源,若个体的祖先亦为多个种群,则来自不同来源地的入侵个体进入到新的地域后可能发生了种内杂交[64,81]。

3　外来入侵物种的进化遗传学

3.1　选择压力

由于入侵种广泛的生态适应性及表型可塑性,在新生境中遭遇的选择压力可使其潜在的生态适应性得以显现,从而推动成功入侵[82-86]。桡足类动物 *E. affinis* 复合种的生态适应性很广,从高盐的沼泽地到低盐的淡水湖泊均有该类生物的存在。尽管该复合种中的类群产生了适应性上的分化,但当选择压力存在的时候,高盐环境中生存的桡足类动物很快就可以适应低盐的环境[30]。

3.2　遗传变异

足够的加性遗传变异可推动入侵种对新生境的进化适应[87]。越来越多的研究表明,来源地种群高水平的加性遗传变异是推动入侵种成功入侵的重要因素之一[88-91]。成功入侵前的潜伏阶段正是为了积累足够的加性遗传,而不是个体数量[92]。阿根廷蚂蚁 *Linepithema humile* 在北美的入侵属于例外,由于瓶颈效应的作用使得入侵种群同质性的增加,减少了入侵种群不同巢穴间的争斗,从而形成了有利于其入侵的行为特性[93]。

研究表明,上位遗传变异在入侵物种的适应性进化过程中也有重要作用。在没有突变发生的前提下,上位遗传变异可在入侵种群内及种群间产生新的遗传特征。这些遗传特征可通过遗传漂变或自然选择固定下来[94]。对扩散到不同寄主植物上的无患子虫种群的研究发现,与适应性进化相关的遗传变异中大约 40%—80%为上位遗传变异[88]。

3.3　特殊基因

一些基因可能决定的外来入侵物种的扩散能力[23]。通过克隆从南美侵入美国的红火蚁 *S. invicta* 工蚁的基因发现,*Gp*-9 这个编码信息素合成的基因影响工蚁识别同巢蚁后的能力[95]。缺乏自我识别的能力使分属不同巢穴的红火蚁形成一个高密度的超级入侵种群,促进其向新的区域入侵[92,96]。通过数量性状基因座位作图发现,一些基因与假高粱 *Sorghum halepense* 的生长、扩散及蔓延密切相关[97]。

3.4　对环境梯度的适应性进化

外来入侵物种在扩散过程中通过表型可塑性的“前适应性”及入侵后产生遗传变异的“后适应性”对分布地域内的环境梯度产生响应,从而在地理尺度上表型出地理尺度上的渐变群[98-100]。从欧洲传入北美的大陆果实蝇 *D. subobscura*,随着海拔高度的增加,翅的长度也增加,形成了随海拔梯度变化的渐变群[27]。入侵植物对环境梯度的适应性进化表现得尤为明显。入侵我国的紫茎泽兰 *A. adenophora* 的种子的大小、重量、发芽速率及发芽率分枝数及叶片的高温耐受力呈现出明显的海拔渐变群格局,高海拔种群的紫茎泽兰种子大、发芽速率快且发芽率高[101]。分枝数与海拔高度呈正相关,而叶片的高温耐受力与海拔高度呈负相关[102]。入侵植物对纬度梯度的适应性进化也常常观察到。千屈菜 *Lythrum salicaria*[103]、具腺凤仙花 *Impatiens glandulifera*[104]、巨大一枝黄花 *Solidago gigantean*[105]、北美一枝黄花 *S. altissima*[105]及窄叶黄菀 *Senecio inaequidens*[106]等入侵植物在不同的纬度上呈现出明显不同的生物生态学特征,形成纬度梯度渐变群。这种格局可能是不同纬度上不同的生长季节长度对基因型自然选择的结果。另外,入侵植物对不同生境中降雨、温度、水分环境梯度等的适应进化而表现出的局域适应特征也会导致地理渐变群的产生[103,105,107-111]。

3.5　物种形成事件

生物入侵可能会导致新物种的形成。当入侵物种侵入与来源地截然不同的生境中后,选择压力的作用可导致表型的改变[112-113]。入侵种生理生化上的改变可能会阻碍来源地与入侵地种群间的基因交流,甚至产生

生殖隔离,最终导致新物种的产生或物种复合种的形成[112-113]。植食性的昆虫在迁移到新的寄主上后形成彼此间生殖隔离的寄主专化型这一现象反映了生物入侵导致新物种形成的可能性[114]。另外,红鲑 *Oncorhynchus nerka* 在海滩仅饲养 13 代后就与其野生种群产生了显著的遗传分化,生殖隔离现象也开始显现[115]。

4 基于遗传信息的外来物种入侵历史的研究

4.1 鉴定入侵物种

明确是何种物种引起的生物入侵是研究其入侵历史的前提。一些外来入侵物种存在多个隐种,如烟粉虱 *Bemisia tabaci*[116-117],或属于复合种的一员,如桔小实蝇 *Bactrocera dorsalis*[118-119]。采用形态分类的方法很难将入侵种与其近缘种区分开。

随着分子生物学技术的发展,分子标记越来越多的运用入侵物种的鉴定。烟粉虱生物型的鉴定是采用分子标记技术鉴定入侵种的范例。采用随机扩增多态性 DNA 标记确定了入侵突尼斯、委内瑞拉、哥伦比亚、法国及西班牙等国的烟粉虱为 B 型烟粉虱[120]。通过对比线粒体 DNA *cox*1 基因片段发现,入侵我国的烟粉虱为 B 型和 Q 型[121]。分子生物学技术的应用还使原来从形态上不能分辨的近缘种与桔小实蝇区分开来[122-126]。

4.2 确定入侵种群来源地

分子标记的方法是确定缺乏发生历史记录的入侵种群的来源地的重要手段。地中海实蝇 *Ceratitis capitata* 在美国多个地区对农业生产造成了严重的威胁,但是长期以来不能确定这些地区入侵种群的来源。通过对入侵美国加利福尼亚州和夏威夷群岛的地中海实蝇种群及南美洲的秘鲁、巴西、危地马拉、厄瓜多尔、阿根廷和萨尔瓦多等地区地中海实蝇遗传信息的分析发现,美国加州的入侵种群可能来源于厄瓜多尔[51]。

采用分子标记的方法确定入侵种群的来源地还可与入侵种发生历史记录相互印证。遗传信息显示,美国加利福尼亚州的虎纹钝口螈 *Ambystoma mavortium* 来自美国中部的平原地区及美国西南部;发生历史记录也表明,虎纹钝口螈从德克萨斯州、新墨西哥州及科罗拉多州向其他地方扩散[127]。基于遗传信息的推断的入侵种群的来源地有时与发生历史记录相矛盾。历史记录显示,美国加利福尼亚州塔玛莉海湾的蛤蜊 *Gemma gemma* 种群来自于大西洋中部,而分子生物学证据则表明该地区的种群由不同来源地的蛤蜊独立入侵形成[67]。在确定入侵种群的来源时,联合发生记录及分子数据可获得更加可信的结果。根据红火蚁 *S. invicta* 的发生记录及分布区内种群的遗传信息,南美洲被认为是该物种的起源地。红火蚁从南美进入美国后,再通过美国这个桥头堡扩散到世界上其他地方[128]。

通过分子数据推断入侵种群的来源地受到许多因素的影响,如样本采集的覆盖度、分子标记的灵敏性及入侵地种群与来源地种群间遗传变异的程度等[129]。由于在印度及中东地区采样不足,印度红颊獴 *Herpestes auropunctatus* 的来源仅划定为斯里兰卡或巴基斯坦这一大致的范围[130]。

4.3 回溯扩散路径

入侵物种在不同地域的发生记录在一定程度上反映了入侵种的扩散路径。但是,单一的以发生历史记录为依据来描述入侵种的扩散路径往往会导致偏差。玉米根萤叶甲 *D. virgifera* 原产于墨西哥及北美洲东海岸,1992 年在南斯拉夫的贝尔格莱德首次发现该虫入侵到欧洲地区,此后该虫以每年 100km 左右的速度迅速向欧洲东部及中部扩散。理论上,入侵物种的扩散是一个连续的过程,但在玉米根萤叶甲扩散的前沿地带发现了数个孤立的入侵点。这一现象被认为是位于扩散前沿的种群跳跃式入侵所形成的[63]。但是,采用分子标记对起源地种群及入侵地种群遗传信息分析后却表明,这几个孤立的入侵种群是玉米根萤叶甲直接从起源地跨越大西洋形成的[63,131]。分子标记的方法基于种群间内在的遗传联系,以独特的视角重现了入侵物种的扩散路径。

全球范围内,采用分子标记的方法重现了多个入侵物种的入侵路径[63-71,79-82,132-135]。尽管我国是遭受生物入侵最严重的地区之一,但在侵入我国的 500 多种外来入侵生物中,仅有极少数几个入侵物种的扩散路径通

过分子标记的方法得以复现。利用扩增长度多态性标记发现,紫茎泽兰 *A. adenophora* 可能从缅甸、老挝及越南等地侵入我国云南南部,然后再向北部的四川、东北部的贵州及东部的广西等地区扩散,风及水流是其在我国传播扩散的主要载体[136]。

4.4　检测入侵过程中的瓶颈效应或奠基者效应

非本土种被远距离传入到新的区域中时,可能会经历种群发展的瓶颈时期,来源地与入侵地间剧烈的环境变化会导致种群数量急剧减少,甚至使种群面临灭绝[137-138]。种群的瓶颈效应导致等位基因的缺失速度快于遗传多样性降低的速度,从而表现出杂合度过量[139]。通过检测多态性位点上等位基因的频率及比较哈迪-温伯格平衡 假设下期望杂合度与实际观测杂合度之间的差异可以发现种群近期是否发生过瓶颈效应[139-140]。对入侵物种大量的遗传信息的分析表明,大多数入侵种在扩散的过程中都会经历明显的瓶颈效应[129]。外来入侵物种在新入侵地区中所经历的瓶颈效应可能会导致入侵种群间产生显著的遗传分化。德国黄胡蜂 *Vespula germanica* 起源于欧洲,在入侵大洋洲的过程中由于种群瓶颈效应的作用导致塔斯马尼亚岛种群与其余入侵种群间产生了显著的遗传分化[141]。入侵过程中不断发生的瓶颈效应形成了入侵种群间的遗传距离与地理距离呈正相关的遗传格局[141]。

进入新生境的外来入侵物种的个体数量可能很少,这些奠基者只携带了来源地种群少部分的遗传特征,导致新建立的种群遗传多样性降低[142]。由人为传播所引起的生物入侵事件中,几乎在每一个外来入侵物种上都存在奠基者效应[129]。由于缺乏基因交流,奠基者效应在入侵物种扩散到一个相对封闭的环境中后表现得尤为明显[129]。

4.5　分析扩散模式

4.5.1　扩散过程中的桥头堡效应

在回溯外来入侵物种的扩散路径时发现,某一特定的成功入侵的种群扮演了作为其余地区入侵种群来源的角色,这种现象被称为入侵过程中的“桥头堡”效应[143]。尽管在一些入侵物种的扩散过程中观察到了“桥头堡”效应[68,131,144-146],但要获取令人信服的结果还存在一些困难——回溯入侵物种扩散路径的方法相对缺乏;回溯扩散路径时种群数量有限,不能获得入侵物种在全球范围内的完整的扩散过程[76,143]。

原产于亚洲的异色瓢虫 *Harmonia axyridis* 在全球范围内的扩散呈现出显著的“桥头堡”效应[143]。该虫是1916 年作为防治蚜虫的天敌引入北美洲的[147-148],直到 1988 年才在美国东部发现其野生种群[149],其后又于1991 年在美国西北部发现入侵种群[150]。2001—2004 年相继在欧洲、南美洲及非洲发现异色瓢虫的入侵种群[151-153]。采用近似贝叶斯估算,结合微卫星分子标记数据及发生历史记录发现,欧洲、南美洲及非洲地区的异色瓢虫不是直接来源于亚洲,上述地区的入侵种群是美国东北部的异色瓢虫入侵形成的,该地区的种群在异色瓢虫向其余地区扩散的过程中扮演了桥头堡的作用[143]。

4.5.2　多重入侵及种内杂交

外来入侵物种不同来源地的多重入侵是生物入侵过程中的普遍现象[154-170]。多重入侵被认为是入侵种群克服种群建立阶段的瓶颈效应或奠基者效应的重要机制[137]。不同来源地的遗传背景不同入侵个体在侵入同一区域后,增加了入侵种群的遗传多样性,种内杂交导致的基因重组进一步增加了种群的遗传多样性。在由多重入侵形成的入侵种群中检测不到瓶颈效应或奠基者效应[129]。

同一入侵区域内的种内杂交产生的后代由于杂种优势,往往表现出比母代更强的适应性,因此多重入侵被认为是推动成功入侵的重要因素[86]。尽管由多重入侵后的种内杂交推动的成功入侵在一些文献中已有描述,但这一假说还需要进一步检验。综合采用遗传信息、室内实验及野外数据分析,证实多重入侵后的种内杂交推动了瘤拟黑螺 *Melanoides tuberculata* 的成功入侵。来自于日本、马来西亚及印西马来群岛等地区瘤拟黑螺无性繁殖系在入侵到南美的提尼克岛后,产生了两个有性繁殖系。与无性繁殖的母种群相比,有性繁殖的瘤拟黑螺产生的后代的数量较少但个体变大,这一生活史策略使有性繁殖系在自然环境中具有更强的竞争力[171-172]。

Wolfe 等[173]提出,多重入侵后的种内杂交推动成功入侵需满足 3 个条件:1) 不同来源地种群间的遗传分化显著,2) 来自于不同母种群的个体间可交配,3) 杂交后代与入侵性相关的特征与母种群不同。异色瓢虫 *H. axyridi* 在欧洲的成功入侵符合上述假设[179]。入侵法国的种群与用于生物防治的种群间有显著的遗传分化;无飞行能力的用于生物防治的种群与野外种群交配后,产生了可以飞行的后代;与入侵种群相比,杂交后代世代时间更短、个体更大、遗传多样性更丰富[174]。

4.6 探究种间杂交及基因渗透

当外来入侵物种与入侵地的本土物种存在杂交时,外来物种更易成功入侵。一方面,种间杂交抑制本土物种种内的交配,降低本土种群的遗传多样性,导致本土种加速消失,甚至灭绝[175]。另一方面,种间杂交可使本土物种的基因渗透到外来入侵物种,增强其在新生境中的适合度[176]。另外,种间杂交还可减缓外来入侵物种种群建立过程中加性遗传消失的速度,使入侵种群保持较高遗传多样性[176]。

利用微卫星分子标记对大西洋北部地区的条纹平鲉 *Sebastes fasciatus* 及尖吻平鲉 *S. mentella* 种群遗传多样性的分析发现,在两者的混合分布区,条纹平鲉的种群遗传多样性显著高于其单独分布区的种群,而该区域尖吻平鲉的遗传多样性则显著低于单独分布区[177]。外来入侵物种与本土物种的杂交还可能导致新物种的产生。采用 RAPD 证实了互花米草 *Spartina alterniflora* 从北美传入英国后,与当地的海岸米草 *S. maritima* 杂交产生了入侵性更强的大米草 *S. aglica*[178]。

5 存在的问题

采用分子标记的方法对许多入侵生物的入侵历史有了全新的认识,但是该方法的局限性也显而易见。采用分子标记方法描述的入侵历史只是入侵物种复杂的入侵历史中的一小部分,具有很高的随机性。造成该现象的主要原因为,用于遗传信息分析的个体数量对整个入侵种群的个体数量来说相当有限,这些个体不能代表整个入侵种群的真实情况[76]。不同的采样范围、不同的采样方法或不同的个体数量都可能得出不同的入侵历史[76,83]。另外,在分析入侵历史时,不管采用多少分子标记都不可能全面反映入侵种遗传变异及进化的过程,分子标记的数量,不同类型分子标记的组合都可能影响入侵历史重构的结果[84-85]。尽管通过入侵物种遗传信息来重构入侵历史有诸多局限,但该方法仍是最为行之有效的手段[86]。

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