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滨海湿地植物种群 Allee 效应驱动机制研究进展

焦　乐,孙　涛*,杨　薇,邵冬冬
北京师范大学环境学院,水环境模拟国家重点实验室, 北京　100875

摘要:Allee 效应是指生物个体适应度与种群规模或密度之间呈正向关联的现象,因与植物种群动态和种群灭绝密切相关而受到生态学家的普遍重视。阐释多重胁迫下滨海湿地植物种群响应机制,从保护生物多样性和维持生态系统稳定性层面发展系统性生态修复措施成为相关研究关注的重点。本研究分别从遗传过程、花粉扩散过程和生物互作关系不同层面,总结分析了植物种群 Allee 效应驱动机制的研究进展。一方面,植物因遗传过程中近交衰退、遗传变异丧失、有害突变累积等遗传结构改变造成繁殖失败而引发 Allee 效应;另一方面,植物花粉扩散过程和动植物互作关系影响下的花粉限制也通过影响植物种群繁殖力成为驱动 Allee 效应的关键因素。滨海湿地水盐梯度变异及格局破碎化影响下,植物种群遭受 Allee 效应的风险需引起关注,维持滨海湿地植物种群适宜分布格局和生物连通过程成为缓解 Allee 效应的重要手段。结合生理学与化学生态学研究手段和长时间尺度动态监测技术,有助于进一步阐释环境及生物等多重胁迫下 Allee 效应的非线性驱动机制。

关键词:Allee 效应;滨海湿地;传粉效率;花粉限制;环境胁迫;植物种群

New advances in driving mechanisms of Allee effect in plant population in coastal wetland

JIAO Le, SUN Tao*, YANG Wei, SHAO Dongdong
State Key Laboratory of Water Environment Simulation, School of Environment, Beijing Normal University, Beijing 100875, *China*

Abstract: Allee effect, the positive association between individual fitness and population size or density, has attracted more attentions from ecologists because of its closely relationship with plant population dynamics and population extinction. By explaining Allee effect of plant population under multiple stresses, developing systematic ecological restoration measures based on the biodiversity protection and ecosystem stability has become the focus of relevant research. This study systematically summarized the research results of different driving mechanisms of Allee effect in plant population in coastal wetlands based on genetic process, pollen dispersal process and plant-pollinator interaction. On the one hand, Allee effect was driven by reproductive failure due to genetic structure changes, such as inbreeding depression, genetic variation loss, and harmful mutations accumulation in the genetic process. On the other hand, Allee effect was caused by changes in plant population fecundity due to pollen limitation, which was affected by pollen dispersal process and plant-pollinator interaction. In the context of water and salt gradient variation and pattern fragmentation in coastal wetlands, it is conspicuous for the risk of Allee effect on plant population. It is important for alleviating Allee effect of plant population in coastal wetlands through providing suitable habitat, ensuring biological connectivity, and constructing population patches. Combination of physiological and chemical ecological research methods as well as long-term dynamic monitoring will help to further explain the nonlinear driving mechanism of Allee effect under multiple environmental and biological stresses.

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*通讯作者 Corresponding author.E-mail: suntao@bnu.edu.cn

Key Words: Allee effect; coastal wetland; pollination efficiency; pollen limitation; environmental stress; plant population

作为生态学和进化学诸多领域中的热点议题之一,Allee效应(Allee effect)被认为与种群动态、种群灭绝密切相关[1],是指一种生物个体适应度(individual fitness)或每员增长率(per capita growth rate)与种群密度之间呈正相关关系的现象。从本质上来说,Allee效应是一种低密度下的负密度制约关系,受Allee效应影响的生物种群在低密度下种群增长率降低,造成种群衰退甚至灭绝。其产生机制包括:①遗传过程中近亲繁殖和杂合性丢失造成的适应度下降;②生态过程中对小种群有较大影响的统计学随机性变化(如性比随机波动引起的觅偶限制);③行为过程中社会互动的破坏、反捕食策略有效性的下降等[2—4]。变化环境条件影响下,驱动过程的差异可能产生不同的Allee效应结果。例如,温度的升高可能加剧觅偶过程驱动的Allee效应,而捕食作用驱动的Allee效应却能得以缓解[5]。明确Allee效应的驱动过程和机制,对研究气候变化和人类扰动造成的变化环境下生物种群发展动态,尤其是在濒危生物保育、入侵生物和有害生物防控、经济资源种群开发利用等方面至关重要[5—6]。

滨海湿地是陆海交互作用下变化环境的敏感区域,在气候变暖、海平面上升、海水入侵等气候变化和围填海、环境污染等人类扰动的共同影响下,生物种群的生存和繁殖受到严重威胁,特别是在承载滨海地区物质循环和能量流动、维持滨海湿地生态系统服务功能方面有重要作用的湿地植被[7—10]。近些年来,滨海湿地海草(*Zostera noltei*)种群[11]、互花米草(*Spartina alterniflora*)[12]和芦苇(*Phragmites australis*)[13]种群中先后发现了Allee效应的存在。在不断加剧的气候变化和人为扰动背景下,保障湿地植物种群繁殖成功,避免遭受Allee效应而发生种群进一步退化甚至灭绝,成为滨海湿地植被保护与管理的核心,对加强区域生态系统保护及实现可持续发展具有重要意义。为此,本文从驱动植物种群发生Allee效应的遗传过程、花粉扩散过程和生物互作三方面,分析总结了滨海湿地植物种群中Allee效应的产生机制,探讨了环境胁迫下植物种群遭受Allee效应的潜在风险,提出了变化环境下滨海湿地植物种群中Allee效应的研究重点。

1 植物种群Allee效应的遗传过程驱动机制

驱动Allee效应发生的遗传学机制主要是指由于近交衰退、遗传变异和杂合性的丧失、有害突变的累积等因素造成的种群增长率随种群规模或密度的下降而降低的一种正相关关系[14—15],这种遗传机制往往在几个世代的时间尺度内对种群动态产生明显影响[16]。Luque等将这种遗传学因素驱动下的Allee效应发生过程分成两个阶段,即种群规模的减少导致种群遗传结构的改变,进而导致个体适应度的降低。阶段1中,种群规模的减少增加了近交比例,影响了杂合度、等位基因丰富度以及有害和有益等位基因频率等种群遗传结构变量,这些遗传结构变异通过近交衰退、漂移负荷和迁移负荷造成阶段2中个体适应度的降低[17]。遗传变异在外来生物适应新生境的过程中起到重要作用[18—19]。例如,植物个体在新生境中定殖时往往伴随着传粉者的缺失和原有传粉过程的阻断,造成植物个体产种量的下降,植物种群密度较低或规模较小可能导致交配系统向自交方向转移[20]。当植物可以通过自交产生繁殖保障、提高植物种群的雌性适应度时[21—22],传粉者访问率不足和孤立种群中配偶可利用性降低而产生的花粉限制问题则能够得到一定弥补,植物繁殖成功和定植能力得以增强[23]。但与自交伴随而至的种子活力和生育力下降问题也相应凸显。这是因为,即使植物能够通过自交育种在短时间内抵抗环境胁迫,最终也会由于基因多样性和遗传变异性的大量丢失而无法长期维持种群生长和存活[24]。倘若外来植物能够与本地同类植物杂交,那么外来种建群所需要的定殖个体相对较少,传粉者对定殖者和类定殖者基因型的偏好将进一步降低Allee阈值,使得杂交有助于克服入侵初期植物种群Allee效应,最终加速外来物种的入侵和定殖[25—27]。

遗传学层面上Allee效应驱动机制研究多关注于近交衰退、遗传漂变、远交衰退等遗传学特性引起的后代育性不良和适应度下降,导致植物个体结实产种率衰减的问题。已有研究表明,外界环境条件对植物种群的近交衰退等遗传结构因素有显著影响,但影响结果却并不相同。Fox等研究表明由于近交后代对环境胁迫

的敏感性高于远交后代,环境胁迫条件下近交后代和远交后代的适应度差异增大,相应环境胁迫会放大近交衰退[28]。但 Herry 等认为远交后代能更好的利用最适环境条件,处于最适环境条件时近交后代与远交后代的适应度差异最大,随着环境胁迫的增强两者适应度的差异会逐渐缩小,环境胁迫下近交衰退会降低[29—30]。

环境胁迫条件下,植物种群往往发生繁育系统转变、遗传多样性降低[31—33]。这种遗传结构因素改变之所以造成植物适应度的变化,主要原因在于生物个体对环境胁迫敏感性、适应性的不同,但是这种适应度的变化是否与种群规模或密度呈现出一定的相关关系,或者说种群规模或密度的增加能否改善环境胁迫下生物个体适应度尚不可知。目前关于 Allee 效应驱动机制的研究中,遗传学过程常因为难以观测、被其他过程机制掩盖而被忽略。环境胁迫引起的遗传结构因素改变,以及当两种因素协同发生时,如何驱动植物种群发生 Allee 效应仍有待进一步研究。

2　植物种群 Allee 效应的花粉扩散过程驱动机制

相对于植物种群规模或密度的变化通过影响生物遗传结构变量间接造成植物个体适应度衰减的遗传过程驱动机制,引发 Allee 效应的生态过程则是由于种群规模或密度的减小直接造成了个体适应度下降和种群增长率降低[17]。生态过程层面上产生 Allee 效应的最直观因素就是觅偶(mate finding)[1]。对于营固着生长的植物种群来说,“觅偶”需要雌雄配子相遇从而完成受精过程。这种被动“觅偶”方式需要借助于载体(包括风力、水力、生物等)来完成雌雄配子体扩散,这意味着产生雌雄配子的植物个体相距越远,扩散载体所承载的配子数量稀释越严重[3]。当种群规模小、密度较低或者种群斑块相距较远时,雌雄配子相遇机会减少造成受精效率下降。由于植物种群低密度下花粉数量不足(如访花者较少或所携带的花粉较少)或质量不佳(如异种花粉干扰导致同类植物低密度时传粉成功率的下降)造成的花粉限制(pollen limitation),使得植物繁殖成功与花粉密度之间表现为正相关关系,从而引发 Allee 效应[34—35]。例如,对雌雄异株的海草(*Phyllospadix* spp 和 *Thalassia testudinum*)种群来说,性比是影响繁殖成功的决定因素,个体数量少、种群规模小造成的性比失衡是海草产生 Allee 效应的直接原因[36]。Reusch 利用分子标记研究大叶藻(*Z. marina*)的基因型多样性和异交结实率的结果表明,相比于遗传组成,花枝密度降低是造成大叶藻花粉限制的重要原因[37]。

复杂多变的自然环境中,传粉媒介的丧失或中断,传粉过程受阻则是在更大空间尺度上驱动植物种群 Allee 效应的发生。当植物种群面临生境丧失和破碎化时,更易遭受花粉限制而引起 Allee 效应。生境丧失和破碎化一方面引起植物种群种子/胚珠比下降,造成个体适应度随着种群密度降低而减少[38];另一方面植物种群隔离造成性比失衡、传粉效率低和访花者减少,使得植物种群繁殖成功率下降[39—40]。小规模或低密度的植物种群除了面对传粉限制外,还受到环境条件和物种特异性特征的共同影响,制约着植物种群定植的成败[41—42]。环境胁迫下生物耐受能力的降低会放大繁殖体压力的影响。繁殖体压力与局部环境变量共同作用下,生物种群发生觅偶限制引起的 Allee 效应,使得处于环境胁迫下的种群需要更多的个体数量才能产生与非胁迫下小种群相同的建群可能性[43]。

花粉扩散过程层面中 Allee 效应驱动机制主要由于低密度、小规模、弱聚集造成花粉限制,引起传粉效率下降和种群增长率降低。陆海交互作用影响下,滨海湿地植被面临着高温、干旱、污染及土壤水盐梯度改变等威胁,环境胁迫条件下种群繁殖力的下降,协同花粉限制引起的 Allee 效应,增加滨海湿地植物种群的灭绝风险。

3　植物种群 Allee 效应的生物互作驱动机制

自然界中,植物固着生长的习性使得花粉传递过程有赖于一定的传播媒介,在已知的 25 万余种开花植物中,90% 以上是通过动物传播花粉,尤其是昆虫传粉[44]。植物-传粉者交互作用关系(plant-pollinator interaction)构成了陆地生态系统绝大多数开花植物有性生殖的基础,也成为动物介导的植物种群 Allee 效应最重要驱动因素[45]。

对植物-传粉者这种共生关系而言,传粉者访花和授粉产出之间往往是受密度制约的[46],包括同种植物种群密度与传粉者访问率的正/负相关关系[47],共同吸引传粉者的异种植物之间存在的种间促进[48],以及异种植物的存在降低传粉者访问率的种间竞争[49—50]。通常来说,开花植物密度的增加有助于吸引更多数量的传粉者访花[51]。一种开花植物的存在增加了传粉者对另一种植物的访问,形成传粉促进作用(pollination facilitation)[52]。由于大型开花展示(floral displays)促进了传粉者访花,同期开花的异种植物之间花朵形态的趋同现象被认为是一种相互受益的传粉者吸引策略[53]。在花朵展示相似的植物(通常是同一类群)[48]、欺骗性传粉植物[54—55],以及花朵形态不同但共享传粉者的同期开花植物中均发现了这种间接的正相互作用[56]。这种正向作用有利于群落中不同植物种群之间共享泛化传粉者提供的传粉服务[57—58],缓解植物种群 Allee 效应[59]。当传粉者稀少时,联合吸引的重要性更高,种间促进作用的发生可能更加普遍[60]。另一方面,种群密度过高时植物对资源和传粉者的竞争也相应增加[61—63],这种针对传粉者的竞争在植物-传粉者互作系统中普遍存在[64—65]。竞争作用的强弱会直接影响植物的繁殖产出,包括大种群(*Eritrichium nanum*)对小种群的竞争[66]、外地种(*Euphorbia esula*)对本地种(*Clarkia pulchella*)的竞争[67—68]。这种针对传粉者竞争作用的结果将造成小种群或者本地种等竞争力相对较弱的种群由于无法吸引足够的传粉者而遭受 Allee 效应。

生物互作层面上 Allee 效应的驱动机制主要是由于植物种内/种间促进与竞争作用引起的传粉者响应机制的改变,进而造成传粉效率下降和植物种群繁殖失败。滨海湿地环境要素梯度变化下植物种群种间竞争与促进关系转化现象突出,植被分布格局的变化叠加气候变化、环境污染和生物入侵造成的传粉者种类、数量下降及其响应过程改变[69—70],可能诱导甚至加剧滨海湿地虫媒植物种群发生 Allee 效应。

4 变化环境下的滨海湿地植物 Allee 效应驱动机制

滨海湿地处于陆地、海洋生态系统的过渡地带,受咸水-淡水交互和地下水-地表水交互作用的共同影响,气候、土壤、水文等环境要素在不同尺度上呈现显著时空异质性[71]。在土壤水盐条件梯度分布的影响下,由海向陆方向上典型湿地植被往往呈现条带状分布格局[72]。然而,气候变化和人类扰动耦合作用下,土壤和水文等环境要素的不断变化,水系中断、生境破碎化、局部工程扰动等引起的生物连通过程受阻[73],使得植物种群遭受 Allee 效应的风险突增。

4.1 环境理化要素改变影响下滨海湿地植物 Allee 效应驱动机制

气候变化影响下,海平面上升、风暴潮加剧、海水入侵等因素引起的水文情势改变,使得滨海湿地退化严重,次生盐渍化加剧[74—75]。淡水流量减少、闸坝建设引起的土壤盐度梯度压缩[76—77],以及营养盐、石油烃及重金属产生的环境污染和恶化[78],严重威胁着滨海湿地植物及其传粉者的个体生长发育和生物互作过程。一般来说,环境胁迫通过两种作用方式来影响植物-传粉者交互作用,一种方式是改变植物与传粉者的物候、生理和时空分布[79—81];另一种方式是改变对传粉者有重要吸引作用的物理化学要素,尤其是花蜜和花朵挥发物[82—83]。其中,植物对传粉昆虫吸引过程中,挥发性有机物以不同成分、不同比例的组合赋予每种植物的独特气味,从而建立起更为可靠的植物-传粉者共生关系,尤其对吸引远距离传粉者或面临环境剧烈变化的植物来说[84—85]。

盐胁迫下植物因遭受渗透胁迫、离子毒害和营养缺乏而产生植株生长受抑制,造成植物生物量、花序重量显著下降[86],同时作用于植物生理代谢过程,对植物花朵挥发物中各物质组成比例和释放量产生显著影响,如萜烯类物质含量增加而醛类、醇类物质含量降低[87],使得传粉者传粉效率降低。大气污染物引起花朵挥发物在扩散过程中发生氧化降解和组成成分改变,造成传粉者定位植物资源的成功率和搜寻效率下降[70]。干旱胁迫显著改变了花朵挥发物的组成和含量,降低了传粉者访问率和种子产量[88—89]。同时,干旱、高盐等极端环境下植物往往通过提前开花来规避不良环境条件,造成植物-传粉者之间发生物候错位[90—91]。随着全球气候变暖和植物、传粉者种群数量的下降,由生物多样性和传粉服务维持的群落结构也随之改变[92],植物-传粉者共生关系的崩溃有可能扩大和加速全球变化对生物多样性丧失和生态系统破坏的影响[93]。但另一方

面,生物对环境理化要素改变的适应能力也是值得关注的。例如,对于传粉昆虫这种变温动物来说,气候变暖背景下,温度变异增强、昆虫热驯化以及体型的变化,可通过生物新陈代谢速率、能效特性和生物互作关系强度的改变,缓解环境条件变化的影响,进而提高种群和群落的稳定性和持续性[94—96]。

因此,环境理化要素改变对滨海湿地植物种群和传粉者种群的影响存在非线性的驱动过程,植物种群通过提高自交率、传粉者种群通过改变生理代谢过程提高适应性和觅食效率[97],使得短期内滨海湿地植物种群能够抵御或缓解环境胁迫造成的影响,个体适应度和种群增长率短暂提高,但从长时间尺度来说,植物与传粉者互作系统中生物遗传变异的丧失和表型可塑性的降低,仍有可能对植物种群增长率产生不可逆转的影响,导致滨海湿地植物种群仍面临着 Allee 效应的潜在威胁[98]。

关于环境理化要素改变影响下滨海湿地植物种群 Allee 效应的研究,需要生物学、生理学、生态学等多学科交叉,从植物生理学、化学生态学、昆虫行为学角度,分析环境胁迫下滨海湿地植物花朵挥发物释放规律和传粉者觅食响应规律,以及生理生化层面上植物与传粉者种群对环境胁迫的适应规律,有助于明确物理环境变化下滨海湿地植物种群 Allee 效应驱动机制,更好地预测气候变化对滨海湿地生物多样性和生态系统稳定性的影响。

4.2　格局破碎及过程阻断影响下滨海湿地植物 Allee 效应驱动机制

近几十年来,由于港口建设、水产养殖等围填海活动造成的自然滨海湿地丧失,上游来水量减少引发的河流水系中断,堤坝建设引起的土壤盐度梯度趋缓和梯度压缩,以及外来生物对本地生物栖息地的侵占和隔离,深刻改变了滨海湿地植物种群互作关系和分布格局[99],加速了滨海湿地生态系统的生境破碎化和斑块化,导致水文连通和生物连通过程阻断[100—101],对拥有不同传粉媒介的滨海湿地植物花粉流动过程产生了不同影响。岸线蚀退、潮沟河流水系的中断主要影响水媒植物花粉传递过程,而生境破碎化对虫媒植物及其传粉者的生存和繁殖影响更大[102—103],尤其是传粉效率极高但对生境变化极敏感的蜜蜂[104—105]。植物进行有性繁殖时,花粉扩散过程和距离在很大程度上限定了植物个体间的基因流和交配方式,从而影响后代的遗传组成和繁育系统[106]。长期来看,生境破碎化背景下,传粉过程受阻、传粉距离缩短使得湿地植物种群遭受甚至进一步加剧花粉限制,繁殖成功率下降,对滨海湿地植被组成与动态、滨海湿地生态系统结构与功能产生了深远影响[107]。

传粉昆虫仅能局部传粉,超出昆虫传粉范围后,虫媒植物果实则因花粉限制而败育[108—109]。在有限的空间迁移能力下,生境破碎化使得传粉者的传粉效率显著降低,花粉限制加剧,影响破碎化生境中植物种群繁殖力[110],此时密度较低、访花者较少的植物更易遭受生境破碎化的威胁[111—112]。因为对于小面积的、稀疏的、孤立的植物斑块来说,这样的植物斑块被传粉者发现的概率较小,即使被发现,较少的访花酬物也难以吸引足够的传粉者。而且即使每株植物受到的传粉者访问频率保持不变,但在低植株密度下传粉者很可能携带的花粉较少甚至没有花粉[113]。更严重的是,当生境破碎化和生境丧失相互作用时,植物种群将分裂成规模更小、孤立程度更高的亚种群,使之更易遭受 Allee 效应,灭绝风险会急剧增加[92]。与此同时,由于不同规模的植物斑块中传粉动物的组成往往不同[114—115],生境破碎化和外来物种入侵对不同传粉者的访花行为有不同级别的影响,生境改变对脊椎动物传粉者的影响较大,而物种入侵则对蜂类以外的其他昆虫传粉者影响较大[116]。研究表明,生境破碎化的加剧可能会诱导植物种群发生强 Allee 效应,此时植物种群密度或规模低于维持种群增长所需的临界阈值,种群平均增长率降为负值,植物种群逐渐灭绝[117—118]。

作为一种尺度依赖的过程,生境破碎化导致滨海湿地植物种群在不同时空尺度上呈现不同分布格局,影响生物扩散、迁移和建群,以及群落组成、结构和生态过程[119]。目前对于生境破碎化驱动 Allee 效应的研究大多局限于小范围植物种群分布格局的调查监测,缺乏长时间的定位观测数据,极少考虑尺度效应在这一驱动过程的作用和影响。而处于陆海交互作用下的滨海湿地植物分布格局在长时间序列上不断演变,对植物种群 Allee 效应的驱动规律影响如何,植物遭受 Allee 效应后又将发生怎样适应性变化,解答这些问题需要具备更长时间序列、更广泛范围的观测资料。因此,以生境破碎化为代表的生物连通过程阻断对 Allee 效应驱动

机制影响的研究,需考虑不同时空尺度下生境破碎化对植物种群分布、植物-传粉者交互作用的影响,将局部野外监测试验与航测、遥感和地理信息系统等技术结合,从不同尺度对植物时空分布进行长期监测和评估,长时间、多尺度、多层次的分析空间格局演变下滨海湿地植物种群 Allee 效应驱动机制。

5 结语

植物种群发生 Allee 效应是种群密度或规模影响下遗传结构改变、花粉限制和生物互作关系变化等多种过程作用的结果,最终造成植物种群中个体适应度的降低。驱动 Allee 效应的遗传过程、花粉扩散过程和生物互作过程往往受到外界环境因素的影响,加剧了植物种群中 Allee 效应。由于陆海交互作用下滨海湿地水文情势复杂,环境理化要素时空分布的剧烈变化,水文连通和生物连通过程的阻断,加剧了湿地植物种群斑块化、破碎化,使得变化环境下滨海湿地植物种群生长与繁殖受到严重影响。Allee 效应的驱动过程多体现为非线性变化特征,虽然植物及其传粉者种群在繁殖方式、生理代谢过程上的适应性变化,能够在短期内实现传粉过程不受中断、保障植物种群繁殖成功,但长时间尺度上受到遗传结构变化、传粉过程受阻、传粉效率降低的影响,滨海湿地植物种群仍面临着 Allee 效应的潜在威胁。针对退化滨海湿地的恢复工作中,一方面需要考虑通过水文调节创造适合湿地植物种群生长的物理环境,构建花粉和种子扩散通道保障生物连通过程,避免植物种群由于花粉限制而产生 Allee 效应;另一方面,利用 Allee 效应产生的负密度制约特点,在移栽植物个体时构建合适密度和规模的、聚集的植物种群斑块,将有利于提高植物种群增长率,促进植物种群恢复。

未来关于滨海湿地植物种群 Allee 效应的研究,特别是虫媒植物种群 Allee 效应的研究,需要考虑环境理化要素变化和生物连通过程阻断的影响,利用植物生理学、化学生态学手段,结合不同时空尺度监测技术,从环境胁迫造成的花朵挥发物变异以及生境破碎化导致的生物连通过程阻断两个方面开展滨海湿地植物种群 Allee 效应驱动机制的研究。面对持续变化的气候条件和不断加剧的人类扰动,植物种群 Allee 效应驱动机制的深入研究将对滨海湿地生物多样性保护、濒危生物保育以及入侵生物防控具有重要意义。

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