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草地物种多样性对群落可入侵性影响的研究进展

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摘要: 综述草地群落入侵实验中物种多样性和群落可入侵性关系的研究进展。目前, 物种多样性与群落可入侵性主要出现了对立的关系模式, 被普遍接受的解释机制为尺度依赖。但是, 其它研究中出现了更为复杂的关系, 提出物种特性、植物更新、种间关系变化和群落构建机制等其它因素可能是导致物种多样性与群落可入侵性出现复杂关系的原因。建议未来研究中应注意的几个问题, 即物种多样性与群落可入侵性关系在不同营养级适用性, 与群落构建机制变化间的联系和时间尺度对物种多样性与群落可入侵性关系的影响。

关键词: 物种多样性; 群落可入侵性; 尺度依赖; 物种特性; 植物更新; 种间关系; 群落构建

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Research advances in the relationships between species diversity and invasibility in grassland communities

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Abstract: This paper reviewed the progress in the relationship between species diversity and invasibility in the grassland communities. At present, the mechanism of scale dependence was mainly used to explain the opposite results of the relationship between species diversity and invasibility. Basing on the analysis of other complex relationships, we speculated that species character, plant regeneration, interspecific interaction and the mechanism of community assembly may be the reason that led to the complex relationships. Several other issues should be integrated into the study to explain the complex relationship, i.e., the application of species diversity-invasibility relationship in different trophics, the link of the change of community assembly and the species diversity-invasibility relationship, and the effect of time scale on the species diversity-invasibility relationship.

Key words: Species diversity; Community invisibility; Scale dependence; Species character; Plant regeneration; Interspecific interaction; Community assembly

从上世纪 90 年代开始至今, 群落的可入侵性研究已成为生态学家关注的重要领域 (Mata *et al.* 2013), 已有研究结果表明定居群落的物种多样性和物种组成可能是影响群落可入侵性的重要因素

(Crawley *et al.* 1999, Levine and D'Antonio 1999, Mata *et al.* 2013)。在物种多样性与群落可入侵性关系的研究中, 很多学者以 Elton (1958) 提出的物种丰富度假说为理论基础, 认为物种越丰富的群落

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越能够充分利用资源,因此,比物种贫乏的群落具有更强的抗入侵能力。但是,大量的人工和自然草地入侵研究得到了不同甚至对立的结果,本文对这些结果进行归纳,并分析研究中可能影响物种多样性与群落可入侵性关系的因素,对这一领域的研究进行总结。

1 物种多样性与群落可入侵性的关系

目前,关于物种多样性与群落可入侵性关系的研究主要集中在草地群落,但是,这些研究并没有取得一致的研究结果。多数小尺度的草地入侵实验表明草地群落物种多样性与群落可入侵性之间呈现明显的负相关关系(许凯扬等 2004, Dimitrakopoulos *et al.* 2005, Mwangi *et al.* 2007, Selmants *et al.* 2012, Byun *et al.* 2013),而多数大尺度的草地入侵实验表明草地群落物种多样性与群落可入侵性之间呈现明显的正相关关系(Knight and Riech 2005, Ohlemüller *et al.* 2006, Knight *et al.* 2008, Kellner and Hastings 2009, Souza *et al.* 2011)。对于两者间出现相反的关系模式,生态学家提出了一些合理的解释,其中尺度依赖是最为普遍接受的解释机制(Fridley *et al.* 2007)。在小尺度草地实验中,种间作用是主要的影响因素,物种多样性高的草地群落通过种间互补效应能够更充分地利用资源,导致外来物种可利用资源减少,外来物种成功入侵的几率也随之减少(Naem *et al.* 2000, Kennedy *et al.* 2002, Mwangi *et al.* 2007),同时,物种多样性高的群落,含有资源竞争能力强的优势物种的几率可能越高,这些优势物种通过种间竞争作用排斥外来物种入侵,也会导致外来物种成功入侵的几率减少(Huston 1997, Loreau and Hector 2001, Dimitrakopoulos *et al.* 2005)。而在大尺度草地实验中,影响群落物种多样性的环境因素则可能成为主要的影响因素,这些研究中主要有两种解释:一种解释认为环境异质性越高,可以为更多的乡土物种提供生存空间,但同时也为外来物种提供了较多的生存空间,因此,生长在越复杂的环境,自然草地群落物种多样性越高,同时,越容易被外来物种入侵(McKinney 2002, Kellner and Hastings 2009)。另一种解释认为,可利用资源在时间和空间上的变化越不稳

定,可以有越多的乡土物种共存,同时,也越容易被外来物种入侵(Cleland *et al.* 2004, Walker *et al.* 2005, Kreyling *et al.* 2008, Stohlgren *et al.* 2008)。

尽管尺度依赖合理的解释了物种多样性与群落可入侵性间对立的关系模式。但是,小尺度的草地入侵实验中,物种多样性与群落可入侵性间也存在着无相关或正相关关系(Pfisterer *et al.* 2004, Zeiter and Stampfli 2012)。Fridley 等(2007)对这些小尺度草地实验进行归纳,发现小尺度草地实验中物种多样性与群落可入侵性的关系将会随着草地群落类型和地域不同产生明显的差异。在已有大尺度草地入侵实验中,物种多样性与群落可入侵性之间也存在着无相关或负相关关系(Eduardo *et al.* 2002, Herben *et al.* 2005, Richardson and Pyšek 2006)。因此,我们认为除了普遍接受的尺度依赖解释机制,物种多样性与群落可入侵性的关系可能还受到其它因素的影响,导致两者间出现了复杂的关系模式。

2 影响物种多样性与群落可入侵性关系的其它因素

2.1 物种特性

物种多样性抵抗入侵主要通过两种机制:互补效应和选择效应(Naem *et al.* 2000, Loreau and Hector 2001)。互补效应机制认为物种间主要通过生态位互补和互利关系,使群落使群落能够更充分的利用资源(Loreau 1998, Tilman 1999),而选择效应机制主要指物种多样性越高的群落含有竞争能力强物种的几率越高,对外来物种的竞争排除作用也越强(Engelhardt and Ritchie 2001, Roscher *et al.* 2005)。在均匀度较高时,群落中每个物种均发挥一定作用,物种间互补效应将会得到充分体现(Losure *et al.* 2007)。而在许多人工和自然草地群落中,物种均匀度经常较低,群落功能主要由一个或几个优势物种决定,其它物种在群落中发挥相对较小的作用,因此选择效应在抵抗外来物种入侵中起到了重要的作用,因此群落抵抗外来物种入侵主要由优势物种的特性决定(Liancourt *et al.* 2009)。一些研究发现物种多样性高的群落常常被竞争能力弱的物种统治,导致群落具有较低的抵抗入侵能力,并称为负选择效应(Polley *et al.* 2003, Fargione *et al.* 2007,

Isbell *et al.* 2009)。因此,优势物种抵抗入侵能力的强或弱,将决定物种多样性与群落可入侵性的关系。

互补效应机制主要是物种多样性通过种间资源互补利用达到充分利用资源的目的,进而减少外来物种利用资源的可能性(Tilman *et al.* 1997)。因此,只有物种间功能特性存在差异才能减少生态位重叠,使得物种越丰富的群落资源互补利用越充分(Petchey and Gaston 2002, 2006)。但是,当物种具有相似的功能特性时,物种多样性的增加并不一定导致功能多样性的增加(Hooper *et al.* 2005, Balvanera *et al.* 2006)。因此,物种多样性与群落可入侵性的复杂关系可能是由于物种间特性差异不同,导致物种多样性抵抗入侵能力发生变化造成的。

2.2 植物更新

群落的植物更新主要指由于群落自然演替、人类活动或者环境因素等造成的植物破坏后的再生(李小双等 2007)。上述不同尺度的草地入侵实验中物种多样性均是群落建成或群落调查时间点上的群落特征,而不论人工控制或自然草地群落,植物更新则是群落一直存在的动态特征。D'Antonio 等(2001)在对美国阿巴拉契亚山麓的栎树森林群落进行研究发现,五种不同的干扰后,森林群落在植物更新过程中,外来物种数量均明显增加。Belote (2008)预测群落的植物更新可能为外来物种提供定居“窗口”,从而增加群落受到外来物种入侵的可能性。这些研究结果表明植物更新可能会减弱群落抵抗入侵的能力。因此,我们推测物种多样性和可入侵性之间的复杂关系,可能是草地群落植物更新对入侵的影响造成的。

与本地物种更新再生过程相似,外来物种进入被入侵群落也是从种子萌发、幼苗建成到成功定居的过程(Kruse *et al.* 2004)。已有研究表明群落自然更新过程中,外来物种和本地物种间发芽和形成幼苗的相对速度,是决定外来物种能否成功定居的关键(Bottollier-Curtet *et al.* 2013, Walck *et al.* 2011),同时,外来物种幼苗定居后,幼苗对资源的竞争能力可能也是外来物种在植物更新过程中能否成功定居的关键因素(Addo-Fordjour *et al.* 2009, Belote *et al.* 2012)。物种多样性越高的群落,由于选择效应(Loreau and Hector 2001),含有快速发芽和形成幼苗的本地物种的几率应该越高,同时,由于互补和选择效应(Fargione and Tilman 2005),对资源

的竞争利用应该越强,所以在自然更新过程中受到外来物种入侵的几率应该越小。但是,物种多样性丰富的区域往往具有高的物种迁入迁出频率和适合更新定居的环境条件(Souza *et al.* 2011),那么,通过植物更新引入外来物种几率可能会增加。因此,植物更新的影响可能导致物种多样性与可入侵性之间呈现复杂的关系模式。

2.3 种间关系变化

已有的草地入侵研究普遍认为种间竞争是决定群落组成和结构的主要因素,定居物种与外来入侵物种间主要存在生态位竞争(Bulleri *et al.* 2008)。但是,群落的组成和结构应该同时受到种间竞争和互利作用的影响(Bruno *et al.* 2003, Bulleri *et al.* 2008)。而且,已有研究发现定居物种和外来入侵物种间同样存在着互利作用,从而促进了外来物种入侵(Altieri *et al.* 2010, Von Holle 2013)。Von Holle (2013)在对英国东北部的沿海荒地的研究发现,在环境胁迫低和高的两个区域,定居物种间分别主要存在竞争和互利关系,而且,更重要的发现是定居物种与外来入侵物种间同样分别主要存在竞争和互利关系。因此,种间关系不同将对定居群落抵抗外来物种入侵产生不同的影响,而且,定居物种间关系和定居物种与外来入侵物种间关系对环境变化很可能存在相似的反应,这可能是环境等因素对物种多样性与群落可入侵性关系影响的一个重要的潜在机制。

关于竞争和互利种间关系转化的研究,目前主要集中在环境胁迫梯度假说上,该学说认为随着环境胁迫程度的增加,种间关系将由竞争转向互利(Maestre *et al.* 2009; Zarnetske *et al.* 2013)。Bulleri(2008)认为种间互利作用可能会改变以前以资源竞争为基础的入侵预测理论,使目前已有的物种多样性与入侵关系的解释机制更完全和丰富。已有大量的研究表明,在极端环境下,定居物种与外来物种间主要存在互利作用而不是竞争作用,导致物种多样性-入侵之间呈现正相关关系(Bertness and Callaway 1994, Thrush 1992),而一些研究还发现植物、动物和微生物间的互利作用,也使得物种丰富地区受到较多外来物种的入侵(Simberloff and Von Holle 1999, Richardson 2000)。

除了对定居群落抗入侵能力产生影响,种间关系变化对定居群落物种多样性同样可产生重要的影响(Gross 2008, Palmer *et al.* 2013)。以资源竞争

为主要种间关系的群落,其物种共存主要建立在生态位分化等机制上,定居群落的物种多样性受到资源的限制(Bruno *et al.* 2003)。但是,随着种间互利作用的增多,在有限的资源条件下,定居群落可以容纳更多的物种,这可能是物种丰富的自然群落的一个重要形成机制(Bruno *et al.* 2003, Gross 2008)。因此,种间关系变化对定居群落物种多样性的影响也可能对物种多样性与群落可入侵性的关系产生影响。

2.4 群落构建机制

理论生态学研究表明群落构建机制不同将会导致物种多样性-入侵关系的变化(Fridley *et al.* 2007)。关于群落构建目前主要有生态位理论和中性理论两种截然不同的解释机制(牛克昌等, 2009)。生态位理论认为,种间生态位分化等确定性因素在群落构建中占主导地位,物种多样性高的群落,占有生态位越多,受到入侵的可能性越小(Daleo *et al.* 2009),而中性理论认为,扩散和随机作用等非确定性因素是群落构建的主要决定因素,物种入侵决定于群落中繁殖体的迁入迁出速率。基于中性理论的模型预测群落物种多样性与群落可入侵性将呈现正相关关系(Fridley *et al.* 2004, Stark *et al.* 2006)。目前,生态学家开始预测生态位理论和中性理论在群落构建中可能同时发挥作用(牛克昌等, 2009)。已有研究发现在干扰较少,物种组成较稳定的群落环境中,生态位分化等确定性因素在群落构建中可能起主导作用,而在干扰频繁,物种更新变化较快的群落环境中,扩散和随机作用等非确定性因素在群落构建中可能起主导作用(Gravel *et al.* 2006, Daleo *et al.* 2009)。因此,在不同的群落环境中,由于构建机制的不同,也可能导致物种多样性与群落可入侵性关系发生变化。

3 未来仍需解决的问题

目前,我们认为关于物种多样性-入侵关系研究有如下需要解决的问题:

(1)物种多样性-入侵关系的研究结果,在其它营养级(动物或微生物)上是否适用,还需进一步检验。Wilsey 和 Polley(2002)研究表明高的草地物种多样性可以减少寄生昆虫(“沫蝉”)对植物的侵染。其它研究发现本地鸟类和动物可以帮助外来物种进行种子扩散,从而促进外来物种的入侵(Sim-

berloff and Von Holle 1999),一些土壤真菌也被发现可以促进外来物种的入侵(Richardson 2000)。这些研究表明物种多样性对入侵的影响可能发生在营养级之间,但是,在动物群落或微生物群落内,关于物种多样性-入侵关系的研究却鲜有报道。

(2)虽然,基于中性理论预测,在扩散和迁移为主要构建机制的草地群落,物种多样性与群落可入侵性关系应该呈现正相关关系(Brown and Peet 2003),而基于生态位理论预测,在竞争为主要构建机制的草地群落,物种多样性与群落可入侵性关系应该呈现负相关关系(Tilman 2004),但是,只有少数大尺度的草地实验发现入侵的实验数据与中性理论预测相吻合(Davis, 2003, Herben *et al.* 2004),而且,对于中性理论是否适用于入侵生态学研究目前仍存在争论(Daleo, 2009)。因此,验证中性理论在外来物种入侵过程中是否存在,以及中性理论和生态位理论的相对重要性对物种多样性-入侵关系的影响将是入侵生态学未来需要解决重要理论问题。

(3)时间尺度也是未来物种多样性与群落可入侵性关系研究中需要进一步探讨的问题。Clark 和 Johnston(2011)研究发现干扰对物种多样性-入侵关系的影响具有时间效应,干扰在入侵初期导致两者间产生了负相关关系,随着入侵时间延续,干扰则导致两者间产生了正相关关系。而且,随着入侵物种从幼苗到成株,从定居到扩散的不同阶段,入侵物种的特性将会发生演化(Hooper and Dukes 2010),这也会导致物种多样性与群落可入侵性关系在时间尺度上发生变化。但是,关于时间效应对物种多样性-入侵关系影响的研究仍然缺乏,对该领域深入研究将对了解物种多样性在抵抗入侵作用的动态变化具有重要的意义。

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