

# 丛枝菌根真菌多样性对植物群落构建和稀有种维持的研究进展

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**摘要** 丛枝菌根(AM)是植物与微生物联系中最为古老的共生体, 全球范围内约80%的陆生植物与AM真菌共生形成丛枝菌根。这一共生关系在气候稳定和土壤磷贫瘠的热带、亚热带森林中更为普遍。以往的研究表明AM真菌通过提高植物对磷的吸收促进植物生长和定植, 即产生植物-土壤正反馈。植物-土壤正反馈可降低由土壤病原菌引起的植物-土壤负反馈, 进而降低植物-土壤负反馈维持植物多样性的能力, 这与热带、亚热带森林中极高的植物多样性以及占比惊人的稀有种相悖。随着对热带、亚热带森林中AM真菌多样性研究的不断深入, 越来越多的研究发现AM真菌多样性在不同的生境条件下以及不同的宿主植物间存在较大差异, 这些差异可引起植物适合度的不同, 进而影响植物群落构建。该文整合了AM真菌在宿主植物群落构建、宿主植物共存及稀有种维持等方面的研究进展, 以期验证“稀有种优势”假说提出新的研究思路, 进而更有效地保护稀有植物。

**关键词** 丛枝菌根真菌; 生物多样性; 物种多度格局; 稀有种优势; 物种共存

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## Insight into recent studies on the diversity of arbuscular mycorrhizal fungi in shaping plant community assembly and maintaining rare species

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### Abstract

Arbuscular mycorrhiza (AM) is one of the oldest symbionts between plants and soil microorganisms, and about 80% terrestrial plant species can associate with AM fungi on earth. Because of the stable climate and poor soil phosphorus content in tropical and subtropical forests, this mutualistic symbiosis is much more common there. Previous studies have extensively investigated the diversity of AM fungi in tropical and subtropical forests, and have shown that AM fungi can promote plant recruitment and growth. However, this positive effect of AM fungi on plants (i.e., the positive plant-soil feedback) can weaken the contribution of the negative plant-soil feedback (caused by soil-borne pathogens) to maintaining tree species diversity, which appears to contradict with the surprisingly high tree diversity and high proportion of rare tree species in tropical and subtropical forests. Recently, a mounting number of empirical studies have found that the diversity of AM fungi varies significantly in different habitats and AM colonization depends on the identity of host species, thereby affecting the fitness of plants and further shaping the plant community structure. Through synthesizing the current research about the diversity of AM fungi in promoting plant coexistence and maintaining community diversity, we expect to put forward a promising study direction for testing the “rare species advantage” hypothesis, therefore improving the conservation of rare plant species.

**Key words** arbuscular mycorrhizal fungi; biodiversity; species abundance pattern; rare species advantage; species coexistence

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土壤是陆地生物最主要的储存库,孕育了地球上极高的生物多样性(Ahanger *et al.*, 2014; Guerra *et al.*, 2021)。传统上认为生态系统的地上及地下部分相互隔离,随着研究的不断深入,人们逐渐意识到陆地生态系统的地上部分与地下部分虽蕴藏着自身独特的生物多样性,但是彼此间也存在紧密联系,甚至互为驱动力(Hooper *et al.*, 2000; Wardle *et al.*, 2004; van der Heijden *et al.*, 2008)。早在20世纪90年代, Bever (1994)提出了植物-土壤反馈(plant-soil feedback, PSF)的概念(即植物的出现引起了土壤生物因子或非生物因子的改变,转而影响植物更新和生长),将土壤生物(如微生物)的影响整合到地上植物群落动态的研究当中。近年来,越来越多的研究表明土壤微生物(如菌根真菌、病原真菌等)调控着植物的适合度,对地上植物多样性维持产生或正或负的影响,进而调控植物群落物种组成和多度分布(Bever, 1999; Mangan *et al.*, 2010b; Anacker *et al.*, 2014; Teste *et al.*, 2017)。

宿主植物的生长状态受土壤病原菌和菌根真菌的共同影响(Turner *et al.*, 2013; Vandenkoornhuysen *et al.*, 2015; Trivedi *et al.*, 2020)。随着植物的出现,土壤病原菌的积累将抑制植物的生长与存活,即引起植物-土壤负反馈(van der Putten *et al.*, 1993; Kliromanos, 2002; Liu *et al.*, 2012);菌根真菌通过提升植物对养分的吸收能力以及拮抗病原菌对植物的危害,促进植物生长,即产生植物-土壤正反馈(Bever *et al.*, 2012)。自然条件下,由于土壤病原菌对植物生长的有害影响易被观察到(Liu *et al.*, 2012; Parker *et al.*, 2015; Jia *et al.*, 2020),而菌根真菌对植物群落的有益影响通常不明显(Saia *et al.*, 2020),所以在植物多样性的维持中广泛认为土壤病原菌是驱动植物群落动态变化的重要因素(Comita *et al.*, 2010; Mangan *et al.*, 2010b; Bever *et al.*, 2015; Liu & He, 2019)。目前,菌根真菌及其多样性对植物共存的影响以及菌根真菌在宿主植物多度格局塑造中扮演的角色尚待揭示。

依据解剖学形态特征,菌根主要包括4种类型:丛枝菌根(arbuscular mycorrhiza, AM)、外生菌根(ectomycorrhiza, ECM)、杜鹃花科菌根(ericoid mycorrhiza, ErM)及兰科菌根(orchid mycorrhiza, OrM)。

其中,AM在植物与土壤微生物的共生关系中最普遍,如陆地植物中有大约80%的植物会与AM真菌形成共生关系(Smith & Read, 2008),且AM真菌贡献了超过10%的土壤微生物数量(Fitter *et al.*, 2011)。从分布范围来看,AM真菌几乎遍布所有大洲及大多数生物区系(Tedersoo *et al.*, 2014; Davison *et al.*, 2015; Powell & Rillig, 2018)。在热带森林中,与AM真菌共生的植物则更为普遍(Toussaint *et al.*, 2020)。涉及全球365个位点近15 000个土壤样品的微生物测序分析结果显示,包括AM真菌在内的多数真菌类群的多样性峰值出现在热带(Tedersoo *et al.*, 2014)。植物多样性假说认为,热带高的植物多样性增加了土壤有机质的复杂性,产生了更多的生态位空间,因而可容纳更多样的土壤生物类群(Hooper *et al.*, 2000; Waldrop *et al.*, 2006)。此外,在热带地区由于氮限制被磷限制所取代,植物更倾向于选择与对磷元素吸收更有优势的AM真菌共生(Read, 1991)。尽管如此,直至21世纪初,对热带、亚热带森林土壤中AM真菌多样性的研究依旧甚少(Alexander & Selosse, 2009),AM真菌多样性对热带、亚热带森林树种多度格局塑造影响的相关研究则更为匮乏。

关于AM真菌的研究始于19世纪30-40年代,但当时AM真菌的存在并未得到学界广泛的认同。近年来,随着高通量测序技术的出现与发展,植物与微生物间复杂的互作关系被慢慢揭开(Turner *et al.*, 2013),对AM真菌基因组和转录组信息的挖掘成为研究AM真菌与植物共生关系的重要手段。至此,关于AM真菌的许多猜想得以更准确地验证,对AM真菌多样性的相关研究迎来新的发展契机。然而目前有关植物-AM真菌互作效应的研究多集中于农田及草地生态系统(van der Heijden *et al.*, 1998b; Montesinos-Navarro *et al.*, 2012; Liang *et al.*, 2017; 杨文莹等, 2019),热带、亚热带森林生态系统中虽也开展了不少研究,但因森林树种组成与森林环境的复杂性以及技术上的限制(如AM真菌具有基因组数量大、可变性高的特点,大量AM真菌基因无法通过现有的生物信息学技术进行注释),仍有较大的研究空白。本文结合国内外有关AM真菌研究的进

展,整合了AM真菌在宿主植物群落构建、宿主植物共存及维持稀有种等方面的研究现状,以期从AM真菌与植物互作、AM真菌多样性对植物群落物种共存的影响角度出发,为验证“稀有种优势”假说提出新的研究思路(该假说认为植物物种在稀有时具有种群增加的趋势,确保其在群落中与其他物种长期共存;戴冬等, 2021)。

## 1 AM真菌与植物群落构建

### 1.1 生态位理论与物种共存

生物多样性决定了陆地生态系统的功能及稳定性(Hooper & Vitousek, 1997; Mi *et al.*, 2021), 关注生物多样性本质上就是关注多物种间的稳定共存(Chesson, 2000)。Grinnell (1917)首次用生态位的概念来描述物种的生存范围及条件,认为同一地点的两个物种必须存在资源利用上或时间、空间上的生态位分化才能和谐共存,即经典的生态位理论。除了生态位分化,当代物种共存理论还强调了竞争能力上的差异,即平均适合度差异对多样性维持的必要性(Chesson, 2000)。生态位理论的提出为理解控制物种分布的因素及预测种间相互作用(如竞争、捕食、互利共生等)的结果提供了理论基石(Connell, 1971; Chesson, 2000)。植物与菌根真菌共生能拓宽植物及菌根真菌的生态位(Bever *et al.*, 2010), 当存在资源限制时,菌根的存在提高了宿主植物的适合度(Dybzinski & Tilman, 2007; Rúa *et al.*, 2016)。资源竞争理论(resource competition theory)对有限资源最低需求量( $R^*$ )的法则认为,当多个物种的生长同时受到同一资源的限制时,对这一限制资源需求量最低的物种能够在竞争中取胜,而菌根真菌能通过改变土壤中资源的可利用性间接影响植物间的竞争作用(Hodge & Fitter, 2013), 或者通过资源分化扩展生态位空间,从而在宿主植物生态位的形成中发挥着重要作用(Chase & Leibold, 2004)。Peay等(2016)基于Chase和Leibold (2004)的当代生态位理论(contemporary niche theory, CNT)提出了互惠共生的生态位概念,并对此做了进一步阐述,植物与菌根真菌共生能够降低植物对有限资源的最低需求量,且当土壤中存在多种功能互补的菌根真菌时,宿主植物通过菌根吸收多种形式的土壤养分,扩展了植物的需求生态位(requirement niche, 指维持某一特定种群所必需的最低环境条件),降低植物生态位

的重合度,从而促进物种间的稳定共存。

### 1.2 AM真菌与物种共存

近几十年来研究愈加深入的Janzen-Connell假说(即J-C效应:同种成年个体或者同种聚集吸引大量天敌,导致接近母树的种子和幼苗或者高密度地区的种子和幼苗具有相对高的死亡率的现象)(Janzen, 1970; Connell, 1971; Song *et al.*, 2021)以及植物-土壤负反馈理论(Bever *et al.*, 1997; Bennett & Cahill Jr, 2016; Crawford *et al.*, 2019)是植物物种多样性维持的主流观点。与不同类型菌根共生的植物所受到的植物-土壤反馈强度的差异也会影响局域地区多样性的维持(Bennett *et al.*, 2017; Kadowaki *et al.*, 2018)。由于AM真菌无法在植物根系附近形成菌根鞘,对病原菌的防御能力有限,因此相比于ECM树种,AM树种根系周围会积累相对较多的病原菌,抑制了同种幼苗在其母树周围的生长,利于该地区植物多样性的维持(Bennett *et al.*, 2017; Johnson *et al.*, 2018; Kadowaki *et al.*, 2018)。除了菌根类型,植物根系的菌根侵染程度也会影响宿主植物受到的植物-土壤反馈强度,生长快、竞争能力强的植物其根系AM真菌侵染率较低,对病原菌的抵御能力有限,因此会受到更强的植物-土壤负反馈(Moora & Zobel, 2010)。此外,AM植物的菌根及地下菌丝网络能促进弱势竞争对手的生长,降低了弱势植物被竞争排除的风险,从而在局域尺度上调节植物共存和多样性,塑造了植物种群与群落(Tedersoo *et al.*, 2020)。Moora和Zobel (2010)通过一项综合了许多研究的meta分析发现AM真菌能降低植物种间竞争,尤其当成年植株与幼苗间产生相互作用时,AM真菌通过菌丝网络将从成年树上获取的碳转运给幼苗,促进其生长。以上研究表明,AM真菌在促进植物物种共存方面的作用同样不容忽视(Grime *et al.*, 1987; Gange *et al.*, 1993)。

由于AM真菌的广布性,且与植物共生的AM真菌能够减轻宿主植物根系被致病真菌侵染的程度(Newsham *et al.*, 1995),即减轻植物受到的植物-土壤负反馈,以往的研究普遍认为AM真菌会对植物施加泛性的正效应(AM真菌不具有或具有低的宿主专性(Law, 1988; Fitter, 1990)且产生正反馈),从而不利于物种共存(Bever, 2003)。然而,越来越多的研究表明,在不同的生境条件下(Hood *et al.*, 2004)、不同的宿主植物中(Kiers *et al.*, 2000),乃至同一宿主

植物的根内或根际土壤中的AM真菌多样性均有显著差异(Herre *et al.*, 2005)。Bever (2002a)将从美国北卡罗来纳州草原分离出的8个常见AM真菌物种分别接种于4个共存植物根部, 结果显示AM真菌与宿主植物的亲和力及AM真菌的产孢率存在明显的宿主依赖性; 也有研究在温带草原、亚热带森林均发现AM真菌存在一定程度的宿主专性(Montesinos-Navarro *et al.*, 2012; Chen *et al.*, 2017)。在植物的不同生长阶段, 由AM真菌调控的植物-土壤反馈也可能发生由正到负的转变, 植物的获益程度往往取决于与其存在相互作用的AM真菌(Johnson *et al.*, 1997; Kiers *et al.*, 2000; Klironomos, 2003)。需要注意的是, AM真菌与宿主植物间由资源交换的不均衡或环境条件改变所致的寄生关系往往不稳定, 相比于刚建立起合作关系的菌根, 已建立长期关系的植物和菌根真菌间更倾向于进化成互惠合作的关系(Johnson *et al.*, 1997; Rúa *et al.*, 2016)。最新的研究却指出与本地植物相比, 非本地植物从AM真菌处获得的生长益处更显著, 即AM真菌加剧了生物入侵(Sheng *et al.*, 2022), 因此在关注植物与AM真菌互作效应时, 除了探讨植物自身因素的影响外, 综合考虑多方因素的潜在影响也尤为重要。Klironomos (2003)认为不同宿主植物对接种的AM真菌较高的偏好性差异可能是影响当地植物多样性维持的关键因素。具体表现在: 植物的生长状态会随着土壤中AM真菌群落物种组成的改变而改变, 宿主植物与AM真菌间不对称的共生关系促进了两个竞争物种间的共

存(Bever, 1999, 2002b, 2003)。

因此, AM真菌虽与绝大多数植物共生, 但是其功能的发挥存在环境依赖性及宿主依赖性, 且AM真菌对植物受到的植物-土壤反馈的方向及强度有调节作用, 进而影响着树种间的共存(图1)。AM真菌群落内, 不同的AM真菌在植物根系的定植部位不同(Smith *et al.*, 2000)、养分吸收策略不同(Koide, 2000)以及占据的土壤养分分配的生态位的分化差异降低了AM真菌间的竞争, 促进了AM真菌群落内物种共存(Tedersoo *et al.*, 2020), 塑造了AM真菌的多样群落, 进而影响地上植物群落结构。AM真菌对群落动态的影响毋庸置疑, 但是如何影响及其影响程度正是目前需要深入探讨的问题。

## 2 AM真菌多样性与植物群落结构

影响植物群落结构(如: 植物多样性、植物的空间分布及多度差异等)的因素主要包括植物种间和种内(Singh & Baruah, 2021)、植物-食草动物(Huisman & Olf, 1998)以及植物-病原菌间的相互作用等(Liu *et al.*, 2012, 2016; 皮磊等, 2018), 而AM真菌及其多样性也会对植物群落结构、多样性和生产力产生影响(Smith & Read, 2008; Mangan *et al.*, 2010a)。但是, 现有的涉及AM真菌多样性的研究多着眼于不同生态系统中AM真菌多样性的差异(Davison *et al.*, 2015; Shi *et al.*, 2019; Vieira *et al.*, 2019), 而非植物对AM真菌多样性的响应差异上, 这很容易掩盖AM真菌多样性对植物群落构建的重要作用。事

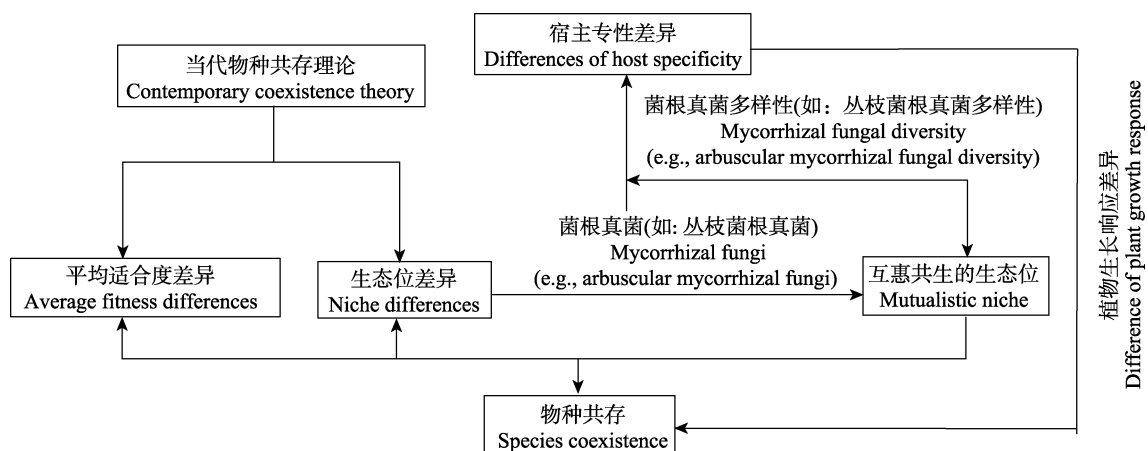


图1 基于当代物种共存理论, 由菌根真菌介导的物种共存理论框架。

Fig. 1 Theoretical framework of species coexistence mediated by mycorrhizal fungi based on contemporary species coexistence theory.

实上, 同一地区的植物对单一接种及混合接种AM真菌的响应存在很大差异, 且相比于单一接种, 混合接种可使植物获取的效益最大化(van der Heijden *et al.*, 1998a; Rowe *et al.*, 2007), 因此, 亟需将AM真菌多样性纳入对植物群落结构影响的考量中。

早在20世纪末, van der Heijden等(1998b)就提出当宿主植物对接种的AM真菌物种或群落存在生长响应差异时, 这些AM真菌物种及其群落组成也能影响到植物的群落结构。群落水平上植物-植物、植物-AM真菌相互作用的分析结果显示, 随着根际AM真菌多样性的增加, 存在专性相互作用的植物(某种植物的成年树能促进另一植物的幼苗生长)能相互促进共存, 进而影响植物群落结构(Montesinos-Navarro *et al.*, 2012)。而在退化生态系统的植被及土壤的恢复与重建过程中, AM真菌更是发挥着群落构建者的作用, 维持了植物多样性及群落稳定性(杨宏宇等, 2005; Rowe *et al.*, 2007; 钟思远等, 2017)。近期对美国8 200个森林样地的分析结果显示, 存在单一类型菌根(AM或ECM)的森林展现出较低的植物多样性, 多种菌根类型形成的菌根优势更利于植物群落多样性的维持(Carteron *et al.*, 2022), 该研究弱化了单一菌根类型对植物多样性影响的同时, 却也强调了菌根多样性对植物多样性维持的重要意义。而由于条件限制, 某些研究较少区域的AM真菌多样性可能被严重低估(Kivlin *et al.*, 2011; Öpik *et al.*, 2013), 这势必会影响植物群落结构对AM真菌多样性响应的评估结果。AM真菌无处不在, 那么在热带、亚热带森林生态系统中到底有多少种类的AM真菌在发挥作用? 这些AM真菌功能的发挥是相互补充还是相互叠加(Edathil *et al.*, 1996; Jansa *et al.*, 2008)? AM真菌多样性在植物多样性的维持中究竟发挥何种作用(Hooper *et al.*, 2000; Toussaint *et al.*, 2020)? 如此多样化的AM真菌在物种多度格局的形成与塑造中扮演何种角色? 这些问题都亟需回答。

## 2.1 AM真菌多样性对森林树种多度的影响

森林中树种多度的差异是由物种间同种负密度制约(conspecific negative density dependence, CNDD)或植物-土壤反馈强度的不对称性引起的(Comita *et al.*, 2010; Mack & Bever, 2014), 这种不对称是不同树种下病原菌积累数量的差异所致(Liu *et al.*, 2015; Kempel *et al.*, 2018)。AM真菌对植物的保护作用能

减轻病原菌的不利影响(Liang *et al.*, 2015), 从而在宿主植物多度格局的塑造过程中发挥作用。

那么AM真菌多样性在森林树种多度格局的塑造中究竟发挥着怎样的作用? 亚热带森林中专性病原真菌导致的同种负密度制约驱动了森林多物种间的共存, 同样具有一定程度宿主专性的AM真菌却能降低甚至抵消病原菌在该过程中的部分不利影响(Liang *et al.*, 2015), 由AM真菌形成的菌根网络更是对植物幼苗密度制约的存活与生长产生促进作用, 从而利于局域地区植物物种多度的增加(Liang *et al.*, 2021), 后者更是突出了AM真菌多样性对森林树种多度维持的积极影响。温带森林中对AM树种及ECM树种在同种树、异种树影响下幼苗及幼树的存活情况的监测结果显示, AM植物幼苗及幼树的多度与CNDD的强度呈正相关关系(Jiang *et al.*, 2020)。这表明植物结合的菌根类型及菌根多样性能够不同程度地影响植物受到的CNDD强度, 进而影响森林树种多度格局形成。

此外, 宿主植物与根际共生真菌间的相容性和共生真菌一定程度的宿主专性可能是影响植物群落结构的先决条件, 且宿主植物的相对多度可能与根际真菌尤其是AM真菌间的宿主专性及彼此间相互作用的强度有密切联系(Schroeder *et al.*, 2018)。然而, 宿主植物多度与根相关真菌(root-associated fungi)多样性的关系, 特别是宿主植物多度与AM真菌多样性间关系的机制其实尚不清楚(Schroeder *et al.*, 2019), 且受限于当前高通量测序新技术平台的缺陷, Illumina MiSeq测序虽然被广泛运用到细菌、真菌多样性的研究中, 但由于其测序长度较短, 除了基于18S rRNA基因片段的AM真菌的检测, 很少有合适片段的AM真菌特异性引物适合于该平台(Jiang *et al.*, 2015; 刘敏等, 2016)。同时由于AM真菌离体培养的难操作性(AM真菌被认为是一种高度依赖宿主植物碳源的共生菌, 无法在脱离寄主根系的情况下实现纯培养), 传统土壤培养条件下难以获得足够纯净的AM真菌菌丝及孢子, 很大程度上限制了对AM真菌的研究(熊天等, 2021)。如果未来能设计出更适配的AM真菌特异性引物, 探寻出实现AM真菌完全离体纯培养的可行性办法(通过脂肪酸的添加在一定程度上实现了纯培养, 但产孢率极低), 关于植物对AM真菌多样性的响应以及AM真菌多样性对植物多度影响的研究都将发生质的飞跃。

## 2.2 AM真菌及其多样性——稀有种维持的潜在驱动力

全球植物多样性的一大特征是稀有种类多而常见种少,目前地球上已知的435 000种陆生植物中约36.5%都是极度稀有的物种,热带、亚热带森林稳定的气候条件更是孕育了丰富的稀有种,塑造了极高的生物多样性(Enquist *et al.*, 2019)。自然界中为什么有些物种丰富而有些物种稀少一直困扰着众多生态学研究( Klironomos, 2002; Chisholm & Muller-Landau, 2011; Chen *et al.*, 2019),而如此多的稀有种能持久存在的原因更是亟待揭示(Yenni *et al.*, 2012),这对于更好地保护生物多样性有极为重要的意义(保护稀有种是生物多样性保护的核心内容)。

尽管土壤病原菌引起的J-C效应(植物-土壤负反馈)被认为是促进森林树种多样性维持最主要的驱动因素之一(Klironomos, 2002; Mangan *et al.*, 2010b; Bachelot *et al.*, 2015; Chen *et al.*, 2019),但是其强度与物种多度的关系目前还存在争议。与此同时,越来越多的研究发现除了土壤病原菌之外,与AM真菌共生的植物通过特殊的菌根结构增强植物对养分的吸收,协助植物产生物理或化学防御,产生的植物-土壤正反馈削弱了由病原菌引起的植物-土壤负反馈(Cameron *et al.*, 2013),影响了植物多样性的维持,并可能对稀有种的维持产生潜在的影响。群落尺度上的研究发现,AM真菌多样性会使稀有种受益(Bachelot *et al.*, 2017)。因此,土壤病原菌与菌根真菌在稀有种维持机制的研究中同样重要。Connell等(1984)在研究热带雨林树种多样性的维持机制时发现,当物种数量较低时其种群维持正的增长率,即稀有物种存在群落补偿趋势(community compensatory trend, CCT)。物种稀有时种群增加的趋势在当代物种共存理论中被称为“可入侵性准则”,Grainger等(2019)将其称为生态学研究上的“通用货币”。AM作为热带森林中最具优势的菌根类型(Newman & Reddell, 1987; Tedersoo *et al.*, 2014),在其宿主植物稀有时是否发挥着关键作用亟待探索。在AM真菌多样性较低的地区,当AM真菌群落物种组成发生变化时会导致地上植物群落发生较大的波动,从而影响了生态系统的稳定性,而多度较低的非优势物种对AM真菌多样性变化的响应则更为强烈(van der Heijden *et al.*, 1998b),因此推测AM真菌多样性对稀有树种的影响可能强于常见树种,且在

物种稀有时种群正增长率的维持中可能发挥着至关重要的作用。例如,以往的研究发现,稀有植物、入侵植物对AM真菌及病原菌的响应存在明显差异。具体表现在当入侵种入侵某一新地点时,专性天敌的不利影响被削弱甚至消失(即天敌逃逸),AM真菌维持了其种群正的增长率(Klironomos, 2002),从而促进了其种群的入侵、建立及长期存在,该研究强调AM真菌对多度较低的植物种群增长的促进作用,也否认了AM真菌一定程度上的宿主专性。相反地,Schroeder等(2018)提出,植物-土壤微生物间专化的相互作用依赖于植物物种的多度(相较于稀有种,与常见种存在专性相互作用的AM真菌会更为普遍),即认为AM真菌与宿主植物间的专化相互作用更有利于常见种,稀有种反而处于劣势地位。然而,对墨西哥热带森林3对同科但多度差异极大的常见种及稀有种根组织真菌的测序结果显示,常见种根组织专化真菌的数量并不优于稀有种,且宿主植物多度与其根组织真菌多样性负相关,与AM真菌的负相关关系更为显著(Schroeder *et al.*, 2018),这表明稀有种在与AM真菌的互作上存在优势,其优势体现在AM真菌多样性上。

尽管如此,不少研究者长期所持有的观点依旧是稀有种会受到更强的植物-土壤负反馈,即稀有种劣势(Klironomos, 2002; Mangan *et al.*, 2010b; Kempe *et al.*, 2018)。若事实如此,稀有种本身由于数量稀少加上受到更强的植物-土壤负反馈作用,稀有种应当走向灭绝。而真实情况却是地球上稀有种数量众多,尤其在热带、亚热带森林更是孕育了丰富的稀有种(Enquist *et al.*, 2019)。为了调和稀有种既受到更强的植物-土壤负反馈作用,而其自身又存在“稀有种优势”二者之间的矛盾,Schroeder等(2020)通过构建空间显式模型追踪了菌根真菌、病原菌的群落动态以及这二者影响下宿主植物的群落动态变化,他们认为常见种受到的负反馈强度弱的原因是:同种土壤下积累的有害生物少,或者更有害的病原菌都积累到了其他常见异种树下,互惠共生真菌则较多地积累在同种土壤下,因此同种土壤下常见种的幼苗存活率要高于稀有种,异种土壤对稀有种幼苗定植的促进作用反而要优于常见种(Schroeder *et al.*, 2020)。该研究强调了兼性病原菌对植物生长的负影响也不可小觑,也进一步强调了微生物群落动态在稀有种维持方面的潜力。

目前,关于AM真菌多样性在稀有种维持方面的实证研究尚且欠缺,且受限于对野生型AM真菌的分离、鉴定和培养技术,宿主与AM真菌的亲合力差异及宿主对AM真菌多样性的响应差异如何影响植物群落物种的多度还缺乏更具体的证据,这也为今后关于“稀有种优势”机制的研究指出了方向。

### 3 结论

AM是陆地生态系统中最广泛存在的植物-微生物共生关系,AM真菌在维持植物生长、促进植物养分吸收及减缓植物受到的生物、非生物胁迫方面发挥着重要作用。热带、亚热带森林作为AM真菌最主要的分布区,蕴藏着极高的AM真菌多样性及超高的植物多样性。高多样性森林最典型的特征就是存在大量的稀有树种,稀有种维持机制一直是诸多研究中的热点问题,除了考虑病原菌在植物多样性维持、物种多度格局塑造过程中的作用外,AM真菌及其多样性对物种多度格局塑造的影响亦不容忽视。而关于宿主多度与AM真菌多样性间的关系以及相关机制的研究更是未来的关注重点,这或许会成为AM真菌与植物互作效应及AM真菌多样性对植物物种多度格局塑造、稀有种机制相关研究新的切入点。

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