

小蠹虫伴生真菌功能特征及病虫复合危害防控展望

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摘 要: 昆虫作为媒介传播的林木病害在全球范围广泛分布, 并造成毁灭性的危害。害虫和病原物对林木形成复合危害, 因其发生机理复杂和危害症状隐蔽, 以及二者间通过跨界互惠共生提高单个物种的适生度、增强对环境变化的缓冲适应能力和维持特定的生态功能等特点, 使得对这类病虫复合危害的控制难度极大。小蠹虫(象甲科 Curculionidae 小蠹亚科 Scolytinae)与真菌在长期协同进化过程中, 形成了稳定的体外共生关系, 这些真菌被称为小蠹虫的伴生真菌(associated fungi), 其中许多种类能引起严重的森林病害, 并与小蠹虫表现出密切的互惠共生关系。本文主要围绕小蠹虫和伴生真菌中了解最深入的长喙壳类真菌形成的伴生体系, 从伴生真菌多样性、长喙壳类真菌生态功能和病虫复合危害防控展望3个方面, 介绍相关领域的最新研究进展, 为认识这类危害的作用机理积累科学基础, 并为森林病虫害的有效控制提供新思路。

关键词: 森林病害; 长喙壳类真菌; 虫菌伴生; 复合危害; 防控

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Functional features of the associated fungi of bark beetles and the prospect of management of the synergetic infection of insect pests and pathogens

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Abstract: Insect-borne diseases are a class of major forest diseases that occur globally in epidemic proportions. Both insect pests and pathogens form synergetic infection to forest trees, which are extremely difficult to control due to the complexity of their mechanisms of occurrence, the insidious nature of damage symptoms, and mutualistic symbioses between insect pests and pathogens, which increase the fitness of each individual species, enhancing the buffering and adaptive capacity of species to environmental change, and maintaining specific ecological functions. Bark beetles (Curculionidae Scolytinae) and fungi have formed stable ectosymbiosis during the long-term co-evolution process. These fungi are called associated fungi of bark beetles, many of which can cause serious forest diseases and show close mutualistic symbioses with beetles. The present paper focuses primarily on the bark beetle-ophiostomatoid fungi companion system, which is the most well understood associated fungi, and provides an overview of the latest research progress in related fields from three perspectives, namely, the diversity of associated fungi, ecological functions of ophiostomatoid fungi, and prospect of strategies for prevention and control of the synergetic infection of insect pests and pathogens. It is hoped that the findings summarized in this review can aid in building a scientific basis for understanding the mechanisms of action of such damage and offer novel ideas for effective control of forest insect pests and pathogens.

Key words: forest diseases; ophiostomatoid fungi; insect-fungal association; synergetic infection; pest management

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小蠹虫在长期进化中与真菌形成稳定的体外共生关系,二者在森林生态系统中生态位重叠,发展出相互依存的互惠共生关系,这些真菌被称为小蠹虫的伴生真菌(associated fungi)。寄主树木-小蠹虫-伴生真菌之间的互作关系十分复杂,包括互惠共生、寄生和拮抗等(图1)。从寄主角度而言,其会利用抗性物质、物理屏障等防御机制应对小蠹虫的取食和伴生真菌的致病性;从小蠹虫角度而言,蛀干害虫利用其成虫钻蛀入树体内的习性可携带传播伴生真菌,并且协助其侵入寄主组织;伴生真菌则可通过提供营养、解毒(或克服寄主防御)和调控小蠹虫种群聚集等方式使小蠹虫获益。同时,伴生真菌又可作为病虫复合危害防控的资源库。本文以小蠹虫伴生真菌多样性为切入点,梳理长喙壳类真菌生态功能,展望虫菌复合危害防控前景。

1 小蠹虫伴生真菌多样性

随着多种小蠹虫类群造成的危害周期性暴发成灾,其伴生真菌区系也受到研究者的关注,并逐步得到解析,呈现出丰富的物种和区系多样性特征。越来越多的证据表明,小蠹虫与伴生真菌间存在着协同进化,“特异性伴生”以及伴随的“协同成种”是其中的一个重要特征。

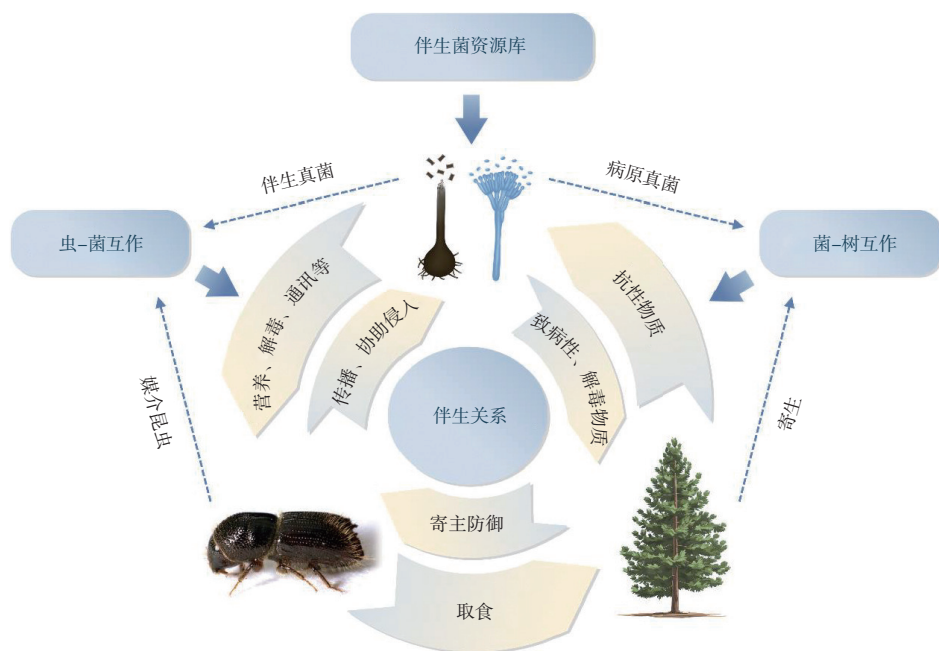


Fig. 1 Interaction model of host trees-bark beetles-associated fungi

1.1 物种多样性

与小蠹虫伴生的真菌种类主要分布在子囊菌门 Ascomycota 和担子菌门 Basidiomycota, 其中子囊菌门的长喙壳类真菌(ophiostomatoid fungi)是小蠹虫伴生真菌中最主要的类群,得到了系统和广泛的研究。长喙壳类真菌是形态和生态特征相似,系统发育相距较远的一类真菌的总称(Kirisits, 2004; de Beer et al., 2013)。在长期进化过程中,该类真菌发育形成了包括具有长喙状的子囊壳、延长柄的分生孢子梗或孢子梗束,以及各自顶端的黏性子囊孢子团和分生孢子团等的特殊形态构造。这类构造十分利于昆虫的携带和传播(Wingfield et al., 1993)。长喙壳类真菌统指子囊菌门的2个系统分支:肉座菌亚纲 Hypocreomycetidae 的微囊目 Microascales 的部分类群和粪壳菌亚纲 Sordariomycetidae 的长喙壳目 Ophiostomatales 的所有类群,包括微囊目的3科12属和长喙壳目的1科20属,合计500余种(de Beer et al., 2013, 2014, 2022)。在中国,自与切梢小蠹伴生的云南细帚霉 *Leptographium yunnanense* X.D. Zhou, K. Jacobs, M.J. Wingf. & M. Morelet(Zhou et al., 2000)被发现以来,已有10属(包括长喙壳目的 *Ceratocystiopsis*、*Esteya*、*Graphilbum*、*Grosmannia*、*Leptographium*、*Masuyamycus*、*Ophiostoma*、*Sporothrix* 和微囊目的 *Endoconidiophora*、*Graphium*)167种小蠹虫伴生长喙壳类真菌陆续被报道(Wang et al., 2024b, c)。其中大多数物种属于长喙壳目的长喙壳属 *Ophiostoma* spp.和细帚霉属 *Leptographium* spp., 分别为67种和44种(Wang et al., 2024b, c)。

隶属子囊菌门肉座菌目 Hypocreales 的 *Geosmithia* 属也是一类广泛分布但长期被忽视的小蠹虫伴生真菌(Pepori et al., 2018; Kolařík and Hulcr, 2023)。该属具有相对较高的系统发育多样性,超过68个系统发育种,其中33个物种已被正式描述(Kolařík and Hulcr, 2023; 梁玲瑜等, 2024)。目前,中国报道了13个物种,远低于欧洲及地中海周边的36种和北美洲的47种。此外,子囊菌类和担子菌类的酵母菌也是小蠹虫伴生真菌中的优势类群(Lim et al., 2005; Giordano et al., 2013; Davis, 2015),但有关其系统发育和分类的资料十分有限和零散,本文不对其多样性进行讨论。

自然界可培养微生物种类仅占全部微生物区系的极小一部分,绝大多数为不可培养微生物。与昆虫伴生的微生物种类绝大多数也属于不可培养类型,在伴生关系中同样起着重要作用。宏基因组学等新一代测序技术的应用极大推动了环境微生物群落的挖掘。利用高通量测序分析小蠹虫体表伴生真菌,

在验证了可培养区系物种组成的多样性和丰度的基础上,极大地拓展了对群落组成多样性的认识(Kostovcik et al., 2015),包括子囊菌、担子菌、球囊菌、芽枝霉、壶菌和接合菌等6个门142个科的416个种和948个OTUs与切梢小蠹伴生(Wang et al., 2019)。

1.2 区系多样性

解析长喙壳类真菌的区系组成对于揭示小蠹虫伴生真菌多样性的形成机制及虫菌伴生关系具有重要意义,体现在不同地区、不同小蠹和不同寄主3个方面中真菌类群的发生规律。由于大多数不同种类小蠹虫的地理分布与寄主范围并不重叠,导致难以控制单一变量进行比较(Wang et al., 2024b)。因此,具体哪个因素对长喙壳类真菌的区系组成起主要作用仍不明确。

目前,中国已知3种大小蠹的伴生长喙壳类真菌种类,分别为红脂大小蠹 *Dendroctonus valens* LeConte 的15种(Lu et al., 2009a, b; Marincowitz et al., 2020)、云杉大小蠹 *Dendroctonus micans* Kugelann 的14种(Yin et al., 2016; Chang et al., 2020; Wang et al., 2021)和华山松大小蠹 *Dendroctonus armandii* Tsai et Li 的7种(Wang et al., 2022)。尽管三者都以松科植物为寄主,但是它们的伴生真菌区系完全不同,没有共享物种。从地理因素分析,国内的红脂大小蠹和云杉大小蠹与美国、欧洲的同种小蠹虫伴生长喙壳类真菌区系也几乎不重叠(Lieutier et al., 1992; Marincowitz et al., 2020)。对分布于中国东北、西北、青藏高原及其周边地区针叶林中10种齿小蠹伴生真菌的系统研究(Wang et al., 2024b),为区系多样性比较提供了理想模式。不同虫种、寄主和地理分布均影响了齿小蠹伴生真菌区系丰度和多样性的组成,且同一影响因素下,小蠹虫伴生真菌区系重叠种类均小于5种(Wang et al., 2024b)。利用宏基因组的高通量测序方法分析云南切梢小蠹 *Tomicus yunnanensis* Kirkendall & Faccoli、横坑切梢小蠹 *Tomicus minor* Hartig 和短毛切梢小蠹 *Tomicus brevipilosus* (Eggers)体表伴生真菌区系组成,结果表明,地理分布和寄主对小蠹虫体表真菌区系组成影响较大,而切梢小蠹种类对其影响并不显著(Wang et al., 2019)。

1.3 种特异性伴生关系

近年来通过分子序列的系统发育分析等方法,不断揭示出小蠹虫伴生真菌隐存种和种下分化的存在。越来越多的研究表明,小蠹虫与伴生真菌间存在着协同进化,一个重要特征便是“特异性伴生”(Six, 2012),以及往往同时存在着的“协同成种”。这种特异性伴生的现象在大小蠹属内得到了反复印

证(Six and Paine, 1997; Alamouti et al., 2011; Roe et al., 2011)。西松大小蠹 *Dendroctonus brevicomis* Le Conte 和其他小蠹常混生在一起,但仍然在大范围内不同季节的变换中,与特定种类的真菌存在着稳定的种间特异性伴生。进一步研究发现双方种下协同趋异分化的现象:优势伴生真菌 *Entomocorticium* sp. B 有不同单体型的分化,形成了 2 个不同的地理变异种群,其宿主小蠹也存在 2 个地理亚种(Tracewell and Six, 2014)。然而,只有与小蠹虫宿主来源同一个地区的伴生真菌,在实验室控制条件下与小蠹虫形成伴生关系(在小蠹虫储菌器内发现),而非同一来源的伴生真菌个体无法与小蠹虫宿主形成伴生关系,表明小蠹虫对特定种类伴生真菌的选择性,即种或基因型的特异性伴生(Tracewell and Six, 2015)。对山松大小蠹 *Dendroctonus ponderosae* Hopkins 伴生真菌 *Leptographium clavigerum*(H.P. Upadhyay) T. C. Harr., Six & McNew 的 67 个基因组区域的碱基差异进行筛选,开发出 15 个蛋白质编码基因片段进行系统发育分析,发现 *L. clavigerum* 种下分化出 2 个明显的种群(Lee et al., 2007; Alamouti et al., 2011; Roe et al., 2011),验证了种间特异性伴生的关系。

在欧亚大陆广泛分布并造成严重危害的齿小蠹中,也发现与先锋长喙壳类真菌存在种间特异性伴生现象,包括欧洲云杉 *Picea abies*(L.) H. Karst.-云杉八齿小蠹 *Ips typographus* Linaeus-*Endoconidiophora polonica*(Siemaszko) Z. W. de Beer, T. A. Duong & M. J. Wingf、欧洲落叶松 *Larix deciduas* Mill-欧洲落叶松八齿小蠹 *Ips cembrae*(Heer)-*Endoconidiophora laricicola*(Redfern & Minter) Z. W. de Beer, T. A. Duong & M. J. Wingf 和日本落叶松 *Larix kaempferi*(Lamb.) Carr-亚洲落叶松八齿小蠹 *Ips subelongatus* Matschulsky-*Endoconidiophora fujiensis* M. J. Wingf, Yamaoka & M. Marín) Z. W. de Beer, T. A. Duong & M. J. Wingf 的“寄主-害虫-病原菌”的特异性伴生(Harrington et al., 2002; Marín et al., 2005; 孟贤静等, 2015)。这 3 种齿小蠹形态和遗传距离都极为接近,与此类似的是,各自稳定伴生的真菌 *E. polonica*、*E. laricicola* 和 *E. fujiensis* 在形态上也几乎无法区分,借助多基因序列的系统发育分析才将它们分为不同种。这种特异性伴生关系也延展到了种下分化。亚洲的云杉八齿小蠹种群发生分化,形成有别于欧洲种群的一个亚种(Stauffer and Lakatos, 2000; Sallé et al., 2007),平行地,二者的主要伴生真菌 *E. polonica* 的遗传分析也表明两个地区的种群存在显著的遗传差异(Marín et al., 2009),即欧洲云杉-云

杉八齿小蠹-*E. polonica* 欧洲种群和日本云杉 *P. jezoensis*-云杉八齿小蠹日本亚种 *I. typographus* f. *japonicus* Nijima-*E. polonica* 日本种群协同分化现象的发生。在中国落叶松八齿小蠹的伴生真菌 *E. fujiensis* 在宿主小蠹发生种下分化(Song et al., 2011)的同时,也存在丰富的种下分化特征(孟贤静等, 2015)。最近的研究发现 2 组新的伴生组合,即西伯利亚落叶松 *Larix sibirica* Ldb.-亚洲落叶松八齿小蠹-*E. laricicola* 和青海云杉 *Picea crassifolia* Kom.-云杉大小蠹-*E. laricicola*, 表明 *E. laricicola* 可能发生了媒介昆虫的跨物种传播及对非落叶松寄主的危害(Wang et al., 2021, 2024b)。

伴生真菌区系发生规律也与其媒介齿小蠹的遗传分化和种群形成有明显关系。通过对欧洲、日本、中国东北和新疆地区的云杉八齿小蠹伴生真菌区系比较发现,4 个地区呈现极少数共有、绝大多数特有的特点(Paciura et al., 2010; Chang et al., 2019; Wang et al., 2024b),恰好与云杉八齿小蠹的 4 个遗传群体匹配(Mayer et al., 2015; 王正等, 2021)。在中国,已报道的 118 种齿小蠹伴生长喙壳类真菌中的 96 种是与它们各自的齿小蠹媒介特异性伴生的(Wang et al., 2024b)。有趣的是,姊妹种东喜马拉雅云杉齿小蠹 *Ips schmutzenhoferi* Holzschuh 和西藏重齿小蠹 *Ips stebbingi* Strohmeier 的伴生真菌同样是姊妹种。在欧洲,齿小蠹属昆虫的 2 种主要伴生真菌 *E. polonica* 和 *E. laricicola* 都是强致病菌,具有明显的寄主分化特征,接种试验证明只能在各自的寄主(欧洲云杉或欧洲落叶松)上造成显著的病斑(Harrington et al., 2002)。野外观种试验也表明, *E. fujiensis* 的致病性在不同落叶松上存在着显著的寄主分化特征(Wang et al., 2020)。这些遗传和致病力差异的发现为进一步揭示种间特异性伴生规律提供了有力的证据。

2 长喙壳类真菌生态功能

小蠹虫与伴生真菌间存在着密切的共生关系,这种共生因昆虫宿主的种类繁多、危害严重和共生真菌的严重致病性,以及受气候变化等因素影响显著,多年来一直是共生关系中的研究热点(Guerrero et al., 2013)。小蠹虫可以从伴生长喙壳类真菌受益的方式,包括利用真菌病原物的致病性,直接引起寄主病害,甚至死亡,以协同克服寄主抗性;另外,长喙壳类真菌还会通过为小蠹虫生长发育供给营养、解毒林木寄主防御性化合物、产生信息素增强小蠹虫种群聚集以成功侵入寄主,以及拮抗有害微生物等多种方

式,为二者的共生发挥作用。

2.1 引起植物病害

长期以来,伴生真菌的致病性被认为是小蠹虫-真菌共生关系中的一个重要元素,是小蠹虫从共生关系中获利的主要特征。伴生真菌的强致病性或群体致病性能够协同小蠹虫克服、消耗寄主抗性,使小蠹虫以更低的种群密度成功侵入寄主并实现定殖(Lieutier et al., 2009)。长喙壳类真菌作为病原菌造成多种毁灭性的森林病害,最著名的是榆树枯萎病(Dutch elm disease, DED),病原菌榆长喙壳 *Ophiostoma ulmi* (Buisman) Nannf 和新榆长喙壳 *O. novo-ulmi* Brasier 在榆小蠹 *Scolytus* spp. 取食健康榆树枝条时,被携带至新的寄主,引起榆树输导组织堵塞,整个枝条或者树干在短时间内迅速枯萎死亡。该病害于20世纪初和20世纪40年代在欧美连续2次大流行,给当地榆树造成灭顶之灾(Brasier et al., 2021)。近几年,这2种病原菌相继在日本和韩国被发现(Masuya et al., 2010; Miyamoto et al., 2019; Lee et al., 2022),榆树枯萎病病原菌传入中国的风险陡增。除此之外,还有多种长喙壳类真菌引起的林木病害,症状包括蓝变、枯萎、溃疡、腐烂、黑根等(表1)。观察发现,与致病性真菌伴生很可能是某些侵入能力强的小蠹虫的一个重要特征,甚至是小蠹虫侵入寄主的一个先决条件(Christiansen et al., 1987)。

与小蠹虫伴生的长喙壳类真菌具有多样化的致病力水平,除能直接致死健康寄主外(Yamaoka et al., 1998),还能够消耗寄主抗性物质,协助小蠹虫以较低水平入侵、定殖健康寄主。红脂大小蠹成功入侵中国,与其伴生真菌长梗细帚霉 *Leptographium procerum* (W.B. Kendr.) M.J. Wingf 具有独特的基因型、表现出更高的寄主致病性、能够降低寄主油松抗性和诱导寄主产生红脂大小蠹聚集信息素3-萜烯等有关,而3-萜烯是红脂大小蠹最有效的引诱剂,因而促进了红脂大小蠹向寄主聚集,提高了红脂大小蠹入侵过程中的适应性(Lu et al., 2010)。基于上述结论,研究者提出了返入侵假说:在原产地的次期性害虫-伴生菌组合,在新的入侵地发生变异后,如再返回到原产地,也有可能造成严重的生物灾害(Lu et al., 2011)。引起榆树枯萎病的新榆长喙壳也能够上调榆树倍半萜释放量,吸引更多的媒介昆虫榆小蠹聚集(McLeod, 2005)。

长喙壳类真菌种类繁多,除危害林木外还是多种农作物病原菌,甚至对人类或动物健康也有相当大的影响。长喙壳类真菌引起多种农作物的腐烂病、溃疡病和枯萎病,如 *Ceratocystis fimbriata* Ellis & Halst. 引

起甘薯黑斑病(Halsted, 1890; Baker et al., 2003), *Thielaviopsis paradoxa* (De Seynes Höhn.) 引起香蕉 *Musa nana* Lour.、杨桃 *Averrhoa carambola* L.、椰子 *Cocos nucifera* L. 和菠萝 *Ananas comosus* (Linn.) Merr. 等热带水果和作物的根腐病及果腐病(Ploetz, 2003; Pinho et al., 2013; de Beer et al., 2014)。而 *Sporothrix* 属的种类引起人类或动物孢子丝菌病(Sporotrichosis), 通常入侵人体或动物的皮肤和黏膜。

2.2 营养供给

木材本身营养贫乏,真菌成为生活在其中的昆虫的重要营养来源(Koski et al., 2024)。小蠹虫完全或部分依赖于共生真菌提供食物以完成其生活史,真菌共生体的这种作用被称作小蠹虫的“根系系统”或“外部胃”(Hulcr and Dunn, 2011)。材小蠹又被称为“食菌小蠹”,幼虫在木质部内发育,木质部由难以消化利用的木质素构成,小蠹虫个体发育完全依靠取食坑道内生长的真菌——“栽培作物”。针叶树韧皮部也是一个营养相对贫乏的环境(Scriber and Slansky, 1981),其N和P含量分别比昆虫所需的低数十倍甚至数千倍(Fagan et al., 2002; Filipiak and Weiner, 2014)。这种情况下,真菌为小蠹虫的生长发育提供了必需的氮素、氨基酸、碳水化合物和甾醇等(Ayres et al., 2000; Bentz and Six, 2006)。真菌的生长也使植物基质更适合小蠹虫取食、消化和吸收(Dowd, 1992)。食菌小蠹以及同时取食木质部或韧皮部和真菌的树皮小蠹能够更有效地获取营养,1a可以完成1个或者数个发育历期,而在同样栖境中没有与真菌共生的吉丁虫 Buprestidae、天牛 Cerambycidae 等鞘翅目昆虫,却往往需要数年才能完成1个发育历期(Harrington, 2005)。

伴生真菌能够改变小蠹虫的取食策略。没有真菌可以取食的小蠹虫为了获取足够的营养用于发育,往往需要比有真菌伴生的小蠹虫构筑更长的坑道,并通过大量取食才能弥补营养不足。室内控制试验下,小蠹虫幼虫主要集中在被真菌定殖的树皮部分,伴生真菌能够将边材内的氮素吸取并转运到韧皮部供小蠹虫幼虫取食。布满伴生真菌的小蠹虫坑道内氮素含量上升40%,能够显著增大小蠹虫个体(Ayres et al., 2000; Bleiker and Six, 2009)。个体尺寸被认为与小蠹虫存活、繁殖、信息素产生和扩散有密切关系。然而,不同真菌在小蠹虫营养供给上也存在差异,山松大小蠹伴生真菌 *L. clavigerum* 比 *Ophiostoma montium* (Rumbold) Arx 能够聚集更多的氮素(Cook et al., 2010),而这种差异可能也解释了为何携带 *L. clavigerum* 的

表 1 长喙壳类真菌引起的主要病害
Tab. 1 Diseases caused by ophiostomatoid fungi

病原 Fungus	分布 Distribution	寄主 Host	病害 Disease	参考文献 Reference
<i>Bretziella fagacearum</i>	北美洲	栎树 <i>Quercus</i> spp.	栎树枯萎病	de Beer et al., 2017
<i>Ceratocystis acaciivora</i>	南非	金合欢 <i>Acacia mearnsii</i>	枯萎	Tarigan et al., 2011
<i>C. albofundus</i>	南非	金合欢 <i>A. mearnsii</i>	枯萎 Wilt	Roux et al., 2007; Nasution et al., 2019
<i>C. fimbriata</i>	热带、亚热带和温带	多种农作物 Variety of agricultural crops	腐烂、溃疡、枯萎	Baker et al., 2003
<i>C. fimbriata</i>	非洲中部、南部、 南美、亚洲	桉树 <i>Eucalaptus</i> spp.	枯萎	Roux et al., 2000; Roux and Wingfield, 2009
<i>C. fimbriata</i> f. <i>platani</i>	欧洲、北美洲	悬铃木 <i>Platanus</i> spp.	溃疡、枯萎	Tsopelas and Angelopoulos, 2018
<i>C. hulioh</i> <i>C. lukuohia</i>	北美洲	铁心木 <i>Metrosideros polymorpha</i>	枯萎	Barnes et al., 2018
<i>C. manginecans</i>	阿曼、巴基斯坦	芒果、金合欢 <i>Mango, A. mearnsii</i>	枯萎	Van Wyk et al., 2007
<i>C. pirilliformis</i>	南非、澳大利亚	桉树 <i>Eucalaptus</i> spp.	枯萎	Roux et al., 2004
<i>C. tsitskammensis</i>	南非	金合欢 <i>A. mearnsii</i>	枯萎	Van der colff et al., 2017
<i>Chalara australis</i>	澳大利亚	假山毛榉 <i>Nothofagus</i> spp.	枯萎	Kile and Walker, 1987
<i>Davidsoniella virescens</i>	北美洲	糖槭 <i>Acer sacharum</i>	枯萎、腐烂	Bal et al., 2013
<i>Endoconidiophora fujensis</i>	欧洲、日本、中国	落叶松 <i>Larix</i> spp.	溃疡	Yamaoka et al., 1998; Liu et al., 2024
<i>E. laricicola</i>	欧洲、日本、中国	落叶松 <i>Larix</i> spp.	溃疡	Yamaoka et al., 1998; 刘亚, 2024
<i>E. polonica</i>	欧洲、日本、中国	云杉 <i>Picea</i> spp.	溃疡	Yamaoka et al., 2000; Hlásny et al., 2021; 刘亚, 2024
<i>E. rufipenni</i>	北美洲	云杉 <i>Picea</i> spp.	溃疡	Solheim and Safranyik, 1997
<i>Leptographium clavigerum</i>	北美洲	美国黑松 <i>Pinus contorta</i>	溃疡	DiGuistini et al., 2011
<i>L. procerum</i>	北美洲、欧洲、 新西兰、中国	松树 <i>Pinus</i> spp.	根病	Lu et al., 2009b
<i>L. qinlingense</i>	中国	华山松 <i>P. armandii</i>	溃疡	Wang et al., 2024a
<i>L. serpens</i>	欧洲、南非	松树 <i>Pinus</i> spp.	根病	Matusick et al., 2012
<i>L. wagneri</i>	北美洲	针叶树 Conifers	黑根病	Cobb, 1988
<i>L. wingfieldii</i>	欧洲	松树 <i>Pinus</i> spp.	溃疡	Hausner et al., 2005
<i>L. yunnanense</i>	中国	云南松 <i>P. yunnanensis</i>	溃疡	Pan et al., 2018; 王慧敏, 2019
<i>Ophiostoma dryocoetidis</i>	北美洲	高山冷杉 <i>Abies lasiocarpa</i>	溃疡	Lalande et al., 2020
<i>O. minus</i>	欧洲、北美洲	松树 <i>Pinus</i> spp.	溃疡	Gorton and Webber, 2000
<i>O. narcissus</i>	北美洲、欧洲、新西兰	水仙花 <i>Narcissus</i> spp.	黑根病	Davies et al., 1998
<i>O. ulmi</i> <i>O. novo-ulmi</i>	北美洲、欧洲、 亚洲、新西兰	榆树 <i>Ulmus</i> spp.	榆树枯萎病	Potter et al., 2011
<i>Raffaelea lauricola</i>	美国东南部	樟科 Lauraceae	枯萎	Harrington et al., 2008; Rodrigues et al., 2020
<i>Sporothrix schenkii</i> <i>S. brasiliensis</i> <i>S. globosa</i>	世界性的	人类 Humans	孢子丝菌病	Rodrigues et al., 2013, 2020
<i>Thielaviopsis paradoxa</i>	热带、亚热带	多种农作物 Variety of agricultural crops	根腐、果腐	Pinho et al., 2013

山松大小蠹比携带 *O. montium* 的山松大小蠹发育的更好且存活率更高(Goodsman et al., 2012; Bleiker and Six, 2014)。

红脂大小蠹与伴生菌的互利共生提高了其入侵过程中的适应性,碳水化合物在多营养级间不同的分配模式起到关键作用,氮是调节分配的关键挥发物(Zhou et al., 2017)。氮气诱导了伴生真菌 *L. procerum*

葡萄糖淀粉酶 *AMYG* 基因调控的淀粉代谢通路,将韧皮部中丰富的淀粉转化为营养价值更高的葡萄糖,补偿了真菌碳水化合物的消耗,维持了“红脂大小蠹-伴生真菌-细菌-寄主油松”跨四界互惠共生体的稳定(Liu et al., 2020)。

2.3 解毒寄主化学成分

小蠹虫侵入寄主的不同阶段受到寄主不同化学

成分乃至浓度变化的显著影响(Wallin and Raffa, 2000)。针叶树通常分泌高浓度的萜烯类与酚类化合物抵御小蠹虫及其伴生真菌的定殖(Franceschi et al., 2005; Keeling and Bohlmann, 2006),而伴生真菌表现出的解毒寄生防御性物质,一定程度上保证了小蠹虫的成功入侵。真菌通过自身丰富的酶库,降解寄主植物富含防御性物质的木质纤维素组织,解除萜烯类、生物碱和酚类等对宿主小蠹虫的毒性(Wadke et al., 2016; Itoh et al., 2018; Zhao et al., 2019)。在消耗寄主抗性、协助小蠹虫成功定殖的同时,将这些物质转化为小蠹虫信息素或可被小蠹虫直接消化吸收的成分。D-松醇对红脂大小蠹具有拒食效应,不利于其生长发育,但对其伴生真菌的生长发育具有促进作用。红脂大小蠹利用伴生真菌 *L. procerum* 作为其体外降解系统帮助其降解寄主油松中的碳源 D-松醇,协助自身入侵寄主与暴发成灾(Liu et al., 2022b)。云杉八齿小蠹和十二齿小蠹 *Ips sexdentatus* Boerner 的伴生真菌 *E. polonica* 和 *Ophiostoma brunneo-ciliatum* Math.-Käarik 均可以降低寄主酚类物质对小蠹虫入侵的抗性(Lieutier et al., 1996; Hammerbacher et al., 2013; Wadke et al., 2016)。山松大小蠹伴生真菌 *L. clavigerum* 和 *O. montium* 能够富集表达解毒代谢寄主抗性物质的功能基因,可将寄主萜烯类化合物用作碳源供自身生长(Diguiastini et al., 2011; Liu et al., 2021)。

青藏高原特有种光臀八齿小蠹 *Ips nitidus* Eggers 偏好选择 *Ophiostoma bicolor* R. W. Davidson & D. E. Wells 定殖了的树皮基质取食和钻蛀。基因组和转录组的联合分析发现,光臀八齿小蠹取食优势伴生真菌 *O. bicolor* 定殖的针叶树树皮基质后,与直接取食没有真菌定殖的树皮基质相比,其解毒相关基因下调表达、高海拔低氧适应相关基因上调表达,显示伴生真菌协助昆虫宿主解毒寄生防御性化合物(Wang et al., 2023),提高了小蠹虫宿主的生态适应性。

2.4 产生小蠹虫信息素

小蠹虫能够产生聚集信息素实现个体之间的高效化学通讯,以达到成功定殖和建立种群的目的。研究表明,长喙壳类真菌在人工培养条件下,可以产生多种挥发性有机化合物,包括醇类、醛类、酯类、酮类、萜类和芳香族化合物等(Morath et al., 2012; Macias-Rodriguez et al., 2015)。这些化合物不仅能够通过促进或抑制真菌的生长和繁殖来影响真菌间的竞争(Cale et al., 2016),还可以作为跨界通信信号(Davis et al., 2013; Davis and Landolt, 2013; Schulz-Bohm et al., 2017)影响小蠹虫行为,吸引小蠹虫定向移动,

帮助小蠹虫寻找食物和栖息地,有助于它们的生殖和群体稳定性(Koski et al., 2024),形成二者化学信息素的跨界趋同进化(Zhao et al., 2019)。与云杉八齿小蠹共生的 *Grossmannia europioides*(E. F. Wright & Cain) Zipfel, Z. W. de Beer & M. J. Wingf 可以利用葡萄糖作为碳源,合成其聚集信息素的主要成分 2-甲基丁烯醇 MB(Zhao et al., 2015)。山松大小蠹伴生真菌 *L. clavigerum* 和 *Ips pini* (Say) 伴生真菌 *Ophiostoma ips*(Rumbold) Nannf 能够将 (-) 反式马鞭草烯醇转化为 (-)-马鞭草酮(Cale et al., 2019),减少树皮小蠹之间的种内和种间竞争,表明长喙壳类真菌在小蠹虫系统的化学生态中发挥重要作用。

2.5 拮抗有害微生物保护小蠹虫

长喙壳类真菌被证明能够产生乙醇、萜烯等次级代谢产物,拮抗环境中的有害微生物,为小蠹虫提供保护(Davis, 2015; Flórez et al., 2015; Kandasamy et al., 2019)。乙醇是许多小蠹虫引诱剂的主要成分,寄主衰弱木和诱饵木产生乙醇,从而引诱小蠹虫的攻击。最新研究表明,小蠹虫还利用乙醇提高食物产量,保证成功定殖:乙醇可以促进光滑足距小蠹 *Xylosandrus germanus*(Blandford) 伴生长喙壳类真菌 *Ambrosiella grossmanniae* C. Mayers, McNew & T. C. Harr、*Ambrosiella roeperi* T. C. Harr. & McNew 和 *Raffaelea canadensis* L. R. Batre 的生长,同时能够抑制坑道内的有害伴生真菌 *Aspergillus* 和 *Penicillium*(Ranger et al., 2018)。红翅大小蠹 *Dendroctonus rufipennis* (Kirby) 伴生真菌 *Leptographium abietinum* (Peck) M.J. Wingf 可以显著抑制白僵菌 *Beauveria bassiana* (Bals.-Cryi) Vuill 的生长(Davis et al., 2019)。南部松大小蠹有益伴生真菌 *Entomocorticium* sp. A 和 *Ophiostoma ranaculosum*(J. R. Bridges & T. J. Perry) Georg Hausner, J. Reid & Klassen 通过竞争抑制了对其不利的伴生真菌 *Ophiostoma minus*(Hedgec.) Syd. & P. Syd 的生长(Hofstetter et al., 2005)。西松大小蠹共生的酵母菌 *Ogataea pini*(Holst) Y. Yamada, M. Matsuda, K. Maeda & Mikata 可以产生乙醇、二硫化碳和 Δ -3-萜烯,这些挥发物可以明显促进伴生真菌虫生伏革菌 *Entomocorticium* sp. 的生长,并抑制昆虫病原真菌白僵菌的生长(Davis et al., 2011)。

3 病虫复合危害防控展望

尽管上述研究表明长喙壳类等小蠹虫伴生真菌在协助小蠹虫和自身对寄主的危害中表现出重要作用,但丰富的长喙壳类真菌资源及其复杂的功能特征,也从另外一个方面展现出作为控制小蠹虫等钻蛀类害虫及其传播病害的一个重要潜在途径(图2)。



图 2 基于长喙壳类真菌的病虫害复合危害防控展望

Fig. 2 Prospect of management of synergistic infection of insect pests and pathogens based on ophiostomatoid fungi

3.1 长喙壳类真菌弱毒菌株、弱毒菌株的利用

小蠹虫坑道栖居和体表携带多种微生物, 这些微生物和昆虫宿主间有着复杂的共生关系, 除了互惠共生外, 也包括拮抗和偏利共生等, 例如南部松大小蠹中的 *O. minus* 与小蠹虫存在着拮抗关系 (Hofstetter et al., 2006), 红脂大小蠹伴生真菌中也存在这样的拮抗关系 (Shi et al., 2012)。这些拮抗伴生真菌具有对小蠹虫的生防潜力。

利用和发挥树木自身抗性, 是实现森林病虫害持续有效控制的一个根本途径 (Jamil et al., 2022)。不同类型长喙壳类真菌致病性具有明显差异, 先锋种具有强致病性, 引起寄主抗性的长期上调表达, 而优势种具有弱致病性, 引起寄主短暂且温和的抗性升高 (Liu et al., 2024)。将先锋种 *E. polonica* 接种到优势种 *O. bicolor* 预处理过的红皮云杉上可减小病斑, 使蓝变颜色变浅并向木质部内延伸缩小, 说明预处理提高了寄主抗性 (Liu et al., 2022a)。利用弱毒菌株诱导寄主产生防御警备的绿色疫苗接种方案, 产生的抗病效果在落叶松和云杉中得到了相互验证 (Wang et al., 2024a)。长喙壳类真菌弱致病菌 *Ophiostoma canum* (Münch) Syd. & P. Syd. 诱导提高苏格兰松抗性, 抵抗 *Leptographium wingfieldii* M. Morelet 的大面积入侵 (Krokene et al., 2000)。这一现象解释了小蠹虫伴生真菌群落的演替规律, 先锋种主要发生在小蠹虫危害盛期, 而优势种则主要发生在小蠹虫种群平稳、有

虫不成灾的时期 (Solheim, 1992, 1993; Lu et al., 2009b)。

欧洲对板栗疫病的防治是利用弱毒菌株防治森林病害的典型例子。弱毒菌株中的 dsRNA 真菌病毒 CHV-1 通过营养亲和传递到强致病力菌株中, 减弱病原菌毒力, 起到良好防治效果 (Rigling and Prospero, 2018)。弱毒菌株 *O. bicolor* 中也发现了独特的单链正义 RNA 病毒 ObEV1 (Zhu et al., 2022), 是否也同板栗疫病弱毒菌株中的真菌病毒一样起到拮抗病原菌的作用, 甚至发挥诱导寄主产生系统抗性的作用, 将是下一步研究的重点。此外, 对于榆树枯萎病, 欧美地区多年以来使用的一种已注册的生防菌剂, 展现出良好的防治效果 (Postma and Geijn, 2016)。维管束病害的病原大丽轮枝菌 (*Verticillium*) 的白化非致病性菌株, 利用其适合在树木导管系统定殖和生存的特点, 通过激发寄主抗性, 起到保护树木的作用。长喙壳类真菌白化菌株也被证明可以有效拮抗小蠹虫伴生的 2 种互惠共生真菌, 起到降低小蠹虫危害和控制木材变色的作用 (Klepzig et al., 1998), 并被开发成商业菌株 (Cartapin-97), 广泛用于造纸用材的前期处理。

3.2 长喙壳类真菌介导的融合 (fusion) dsRNA 作用于小蠹虫、病原菌

作为农药史上的第三次技术革命, RNAi 生物农药正在对森林病虫害防控产生深刻影响 (Singewar and Fladung, 2023)。目前, 多项研究表明, 基于 dsRNA 的森林保护产品因其具有种间特异性、没有非靶

效应以及能够改善整个森林健康等优点,展示出广阔的应用前景(Kyre et al., 2019, 2020; Hollowell and Rieske, 2022; 张苏芳等, 2022)。然而,在树木和森林中使用RNAi技术,不像在农业中易于推广。如何开发新型RNAi介导手段,实现森林病虫害,尤其钻蛀性害虫的防控,是亟待攻克的难题之一。利用微生物介导的RNAi(MIGS, Microbe-induced gene silencing)将是重要突破口(Wen et al., 2023),也更适应于森林病虫害防治。

长喙壳类真菌已被证明易于在韧皮部、木质部、土壤和腐殖层中定殖,并在树木输导组织内传输(Jankowiak et al., 2021; Bilański et al., 2023)。此外,具备伸出基质延长的分生孢子梗和长颈的子囊壳和产囊体顶端聚生大量黏性分生孢子和子囊孢子,浓烈的芳香气味吸引媒介昆虫趋向。而且,其与小蠹虫等栖境相同等特点,使得长喙壳类真菌是一种理想的RNAi介导微生物,尤其具备良好的林间应用条件。

3.3 长喙壳类真菌野外增强小蠹虫引诱作用

长喙壳类真菌与小蠹虫的长期伴生使二者产生了趋同进化,即前者能够跨界产生小蠹虫的信息素(Zhao et al., 2015, 2019; Kandasamy et al., 2019)。室内试验表明, *Grosmannia penicillata* (Grosmann) Goid.、*E. polonica* 和 *Leptographium europioides* (E. F. Wright & Cain) M. Procter & Z. W. de Beer 等产生的挥发性有机化合物能够成功吸引其媒介昆虫云杉八齿小蠹。野外试验发现,利用长喙壳类真菌能够实现林间增效、持效、长效诱捕云杉八齿小蠹(Jirošová et al., 2022)。并且除信息素外,真菌产生的杂醇和乙酸酯等混合物对小蠹虫同样具有吸引能力。这为利用长喙壳类真菌增强小蠹虫的引诱作用,实现对其的监测与防控提供了新思路。

3.4 应用长喙壳类真菌防治松材线虫病

长喙壳类真菌中的 *Esteya vermicola* J. Y. Liou, J. Y. Shih & Tzean (Ev 菌) 已被证明对松材线虫具有杀灭效果,并且在防治实践中已被重点使用(Pires et al., 2022)。韩国利用Ev菌预先接种处理,可保护松树免受松材线虫侵染致死。松树存活率在处理后的5a内(2009—2014年)一直保持在30%~50%,而未经Ev菌处理的对照,第1年即全部死亡。在6a的试验期内,Ev菌都可以从接种的成年赤松中分离到(Wang et al., 2018)。近年来,在中国的云南切梢小蠹和华山松大小蠹伴生真菌中也分离获得了Ev菌(Wang et al., 2019, 2022)。该属的第二个种 *Esteya floridanum* Y. Li, Araújo & Hulcr 也展现出良好的预防松材线虫病效果

(Li et al., 2021)。目前,在松材线虫病伴生真菌区系中,长喙壳类真菌群落也得到了越来越多的重视,其可能起到的拮抗松材线虫作用,是用于松材线虫病防治的良好生防资源(Vicente et al., 2022)。

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