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•综述• 创刊30周年纪念专辑

近十年植物入侵生态学重要研究进展

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摘要: 外来植物入侵对本地生物多样性、生态安全、社会经济发展和人类健康造成了严重威胁。因此, 探究植物入侵机制及其生态效应对我国生态可持续发展具有重要意义, 也是植物入侵生态学的主要研究内容。过去10年, 生态学家开展了大量研究, 取得了丰硕成果, 为推动入侵植物防控与生物多样性保护提供了理论指导。为深入解析外来植物入侵机制, 为其防控管理提供依据, 本文从以下3个方面综述了植物入侵生态学重要进展: 首先是外来植物生物学特性、生物和非生物环境对植物入侵的调控作用; 其次是外来植物入侵对本地生态系统的影响; 最后介绍了外来植物入侵的类比研究范式——本地植物入侵, 以及多组学技术在入侵生态学研究中的应用。基于这些研究进展, 本文展望了该领域的未来发展趋势, 包括: (1)研究对象从单一物种扩展到多物种比较; (2)研究地理范围从局域尺度扩大到纬度梯度格局; (3)入侵机制从单一理论验证到综合阐释多个假说。

关键词: 生物互作; 生物入侵; 多样性; 生态学效应; 全球变化; 入侵机制

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Research advances of plant invasion ecology over the past 10 years

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ABSTRACT

Background & Aims: Alien plant invasion has significantly threatened native biodiversity, ecological security, socio-economic development, and human health. Consequently, exploring the mechanisms of alien plant invasion and its ecological impacts are of great importance to the ecologically sustainable development of our country. Both questions are also key topics in the field of invasion ecology. Over the past decade, ecologists have conducted much research and achieved fruitful outcomes, providing theoretical guidance for the prevention and management of invasive alien plants and biodiversity conservation.

Progresses: Based on domestic and international studies in this field over the past decade, the present article reviews the progress of plant invasion ecology, focusing on the following three aspects of the field. First, we present the roles of species characteristics, biotic and abiotic environments on alien plant invasion. Second, we review the impacts of alien plant invasion on native ecosystems. Third, we briefly introduce the term 'native plant invasion' as an analog to alien plant invasion, as well as applications of multi-omics technology in the area.

Prospects: The review looks ahead to further developments in invasion ecology, including that (1) multiple species experiments rather than single species experiments are more suited to obtaining gerneralizable findings; (2) the geographical scale is increasing, such as from local scale to latitudinal gradient pattern; (3) more studies are integrating multiple invasion theories, rather than one hypothesis, into a unified framework.

Key words: biotic interaction; biological invasion; diversity; ecological effects; global change; invasion mechanism

外来植物入侵严重威胁生物多样性、生态安全、社会经济发展和人类健康(类延宝等, 2010; Vilà et al, 2011; Schaffner et al, 2020; Diagne et al, 2021)。随着跨境贸易和旅游的增加, 以及极端气候事件的频发, 入侵植物的数量逐年攀升, 其危害不断加剧(Seebens et al, 2018, 2021)。阐明入侵机制、评估生态危害是入侵生态学的重要内容(刘建等, 2010; Courchamp et al, 2017; Faulkner et al, 2020)。这些研究不仅为防控外来植物入侵和维持生态系统稳定性提供理论基础, 还对我国生态可持续发展与生态文明建设具有重要的现实意义。

外来植物到达新的区域后能否成功定殖、建立种群、传播扩散往往取决于其自身与入侵生境的特性以及外来植物与其他生物和环境要素的互作过程(van Kleunen et al, 2018)。已有诸多假说试图解释外来植物的成功入侵机制(部分相关假说见附录1), 但任何单一假说均不具有普适性, 表明外来植物成功入侵的驱动因素具有多样性和复杂性特点(Jeschke, 2014)。为了揭示其中的奥秘(部分热点科学问题见表1), 生态学家开展了大量研究, 取得了丰硕成果, 为推动入侵植物防控与生物多样性保护提供了理论指导(鞠瑞亭等, 2012)。

基于过去10年的代表性研究成果, 本文综述了植物入侵生态学领域以下3个方面的重要研究进展(部分专业名词释义见Box 1): 首先是外来植物生物学特性以及生物和非生物环境对物种入侵的调控作用; 然后阐述了外来植物入侵对本地生态系统的影响; 最后介绍了外来植物入侵的类比研究范式——本地植物入侵, 以及组学技术在入侵生态学研究中的应用。基于这些研究进展, 本文提出了未来研究的一些潜在热点方向。

1 外来植物的入侵性与本地群落的可入侵性

1.1 外来植物的入侵性

外来植物具备什么样的特性更容易成为入侵物种是入侵生态学的一大基本问题。van Kleunen等(2010)基于1986–2008年间117项个例研究的Meta分析发现, 与非入侵植物(包含196种本地植物和外来植物)相比, 外来入侵植物(125种)具有更大的叶面积、更高的光合速率、氮利用效率、水分利用效率、生长速率以及更高的根生物量占比、株高、生物量和适合度等。之后的诸多研究也多次验证了外来入侵植物的这些性状优势(Dyderski & Jagodziński, 2019; Mathakutha et al, 2019; Liu WW et al, 2020), 尽管某些广域分布的本地优势植物也存在相似的性状特征(Zhang & van Kleunen, 2019)。这些性状优势与外来植物入侵过程中的快速进化密切相关: 即外来植物在其入侵地常常缺失天敌控制(Keane & Crawley, 2002), 长期的选择压力可能驱使其降低防御性状投资而增加生长和繁殖资源投资(Blossey &

表1　近10年植物入侵生态学热点科学问题
Table 1　Top questions of plant invasion ecology over the past decade

编号 Number	近10年植物入侵生态学热点科学问题 Top questions of plant invasions over past decade
1	外来入侵植物拥有强入侵性的决定因素 What determines the strong invasivability of invasive alien plants?
2	多维度本地生物多样性对外来植物入侵的抵御机制 What is the mechanism behind the resistance of multidimensional native biodiversity to alien plant invasion?
3	基于化学诱导反应的地上-地下植食者互作对植物入侵的影响机制 How do chemical-induced interactions between above- and below-ground herbivores affect alien plant invasion?
4	根/叶际有益-有害微生物及其相互作用对外来植物入侵的调控机制 How do rhizosphere/phyllosphere mutualistic and pathogenic microorganisms, as well as their interactions affect alien plant invasion?
5	环境波动及多环境因子耦合对外来植物入侵的直接影响 What are the direct effects of environmental variability and interaction between multiple environmental factors on alien plant invasion?
6	营养级互作对外来植物入侵响应环境变化的调控机制 How do other trophic levels mediate alien plant invasion under environmental changes?
7	外来植物入侵对本地群落动态和演替进程的长期效应 What are the long-term effects of alien plant invasion on local community dynamics and succession?
8	外来植物入侵对生态系统结构与功能的影响方向 What is the impact direction of alien plant invasion on ecosystem structure and function?
9	本地植物生境快速跃迁的机制及其对生态系统的影响 What drives rapid range-expansion of native plants, and how does it affect ecosystems?
10	外来植物快速适应与进化的分子机制 What are the molecular mechanisms of rapid adaptation and evolution of alien plants?

Box 1　部分专业名词释义

生物入侵(biological invasion): 生物由原分布区侵入到另一个新的区域，并对入侵地的生物多样性、农林牧渔业生产以及人类健康造成负面影响的过程。
本地种(native species): 出现在其自然分布范围及其扩散潜力以内区域的物种、亚种或以下分类单元。
外来种(alien species): 出现在其自然分布范围及其扩散潜力以外区域的物种、亚种或以下分类单元，包括其所有可能存活、继续繁殖的部分。
外来归化种(naturalized alien species): 在自然或半自然生境中能正常繁育后代，并大量繁衍成野生状态的外来种。
外来入侵种(invasive alien species): 对生态系统功能、人类健康或经济建设造成负面影响的外来归化种。
外来非入侵种(non-invasive alien species): 并未对生态系统功能、人类健康或经济建设造成负面影响的外来归化种。
入侵性(invasiveness): 一个外来物种能够成为入侵种的潜在能力。
可入侵性(invasibility): 群落易受外来种入侵的程度，用于全面评价某群落或地区易遭受生物入侵的程度。
定殖(colonization): 外来种进入一个地区后在可预见的将来能长期生存。
化感作用(allelopathy): 一种植物通过向体外分泌代谢过程中的化学物质，对其他植物产生直接或间接的影响。

Notzold, 1995; Heckman et al, 2019)。基于此，Feng等(2009)提出“氮分配进化假说” (hypothesis of the evolution of nitrogen allocation)，认为天敌缺失使外来入侵植物降低叶片内氮素向防御系统(如细胞壁)的分配，同时增加氮向光合机构的分配。这种进化方向使外来入侵植物不仅提高了光能利用效率(Wang et al, 2013)，还缩短了叶片建成成本(construction cost)的补偿时间(Feng et al, 2011)。Liu等(2021)提出了内源性激素进化调控假说(endogenous hormone evolutionary regulation hypothesis)，认为天敌的缺失驱动外来植物下调与防御相关的激素水平(如茉莉酸)、上调与生长相关的激素水平(如赤霉素)，实现其快速生长并获得竞争优势。

化感作用也在外来植物入侵过程中发挥着重要作用(Callaway & Ridenour, 2004; Hierro & Callaway, 2021; Kalisz et al, 2021)。但是，Cummings等(2012)提出的“国土安全”假说(homeland-security hypothesis)认为，本地植物也可以通过化感作用抑制外来植物生长，导致外来植物的竞争劣势。因此，

化感作用能否促进外来植物入侵是一个富有争论的话题。Zhang ZJ等(2021)通过对约1.6万条包含286种外来植物与548种本地植物的化感作用数据进行Meta分析, 发现更强的化感作用促进了外来植物的竞争优势, 有助于其在入侵地成功归化。另外, Zheng等(2015)通过对我国典型外来入侵植物飞机草(*Chromolaena odorata*)的研究, 发现其入侵种群的飞机草素含量显著高于原产地种群。并且, 作为飞机草特有化感物质, 飞机草素对中国本地种的抑制作用也显著高于墨西哥本地种(Zheng et al, 2015)。尽管大部分研究都在探讨化感作用对外来植物成功入侵的贡献, 但是通过筛选强化感作用的本地植物来防控外来植物入侵仍然是一个值得探索的方向。

此外, 具有较高的胁迫耐受性和表型可塑性也被认为是外来植物成功入侵的一个重要原因(Davidson et al, 2011; 张紫妍等, 2015)。例如, Li WT等(2022)发现外来入侵植物飞机草到达入侵地后, 耐干旱胁迫的能力增强; Wang Y 等(2021a, b)发现外来入侵植物空心莲子草(*Alternanthera philoxeroides*)比同属的本地植物莲子草(*A. sessilis*)具有更强的耐重金属胁迫能力。Xu等(2022b)发现互花米草(*Spartina alterniflora*)群落中的矮个体可以通过增加比叶面积与光强利用效率来缓解养分富集引起的不对称光竞争压力, 进而提高了其群体的入侵性。但是, 最近有研究表明外来植物小蓬草(*Erigeron canadensis*)的入侵性与其对土壤养分变化的可塑性响应无关(Wang S et al, 2022)。这可能是由于植物性状的可塑性对不同环境变化的响应具有特异性导致的(van Kleunen et al, 2011)。因此, 亟需明确哪些性状的表型可塑性决定了外来植物入侵性及其对环境变化的响应。

1.2　本地群落的可入侵性

外来植物的成功入侵不仅由外来植物自身的入侵性驱动, 还由本地群落的可入侵性决定。本地群落内资源的波动性(详见下文3.1节)与物种多样性是影响其可入侵性的两大关键因子(Elton, 1958; Davis et al, 2000; van Kleunen, 2018)。自1958年Charles Elton提出“多样性–入侵性”假说(diversity–invasibility hypothesis)以来, 生物多样性抵御外来植物入侵的作用与机制一直是入侵生态学研究的核心问题之一(Elton, 1958)。该假说认为本地群落物种多样性越高, 外来植物成功入侵的概率越低。这可能是因为物种多样性高的群落内空余生态位较少, 留给外来植物可利用的资源更少, 因此降低了其入侵机会(Elton, 1958; Levine & D’Antonio, 1999; Zheng et al, 2018)。除物种多样性外, 越来越多的研究暗示外来植物与本地群落物种的系统发育关系(Li et al, 2015; Feng & van Kleunen, 2016; Zheng et al, 2018; Malecore et al, 2019)以及功能特征的相似性(Feng & van Kleunen, 2016; Zheng et al, 2018)同样影响了外来植物的成功入侵。例如, Zheng等(2018)与Feng和van Kleunen (2016)的研究表明外来植物更容易入侵远缘物种组成的本地群落。然而, Li等(2015)发现外来植物更容易在其近缘物种组成的本地群落中定殖并占据优势。这并不意味着以上研究结果是冲突的, 也可能是系统发育距离对外来植物成功入侵的影响本就是非线性的(Malecore et al, 2019)。Zheng等(2018)的研究表明, 本地群落内的物种与外来入侵植物飞机草的功能特征越相似(即功能特征距离越近), 其抵抗飞机草入侵的能力越强。但Feng和van Kleunen (2016)认为, 功能特征的相似性并不影响外来植物与本地植物之间的竞争强度。因此, 从物种多样性、系统发育多样性和功能性状多样性等多维度探讨“多样性–入侵性”关系将有助于推动入侵生态学理论的发展。

“多样性–入侵性”之间的关系并不是一成不变的, 许多研究表明其具有尺度依赖性——小尺度的实验研究多证实两者存在显著的负相关关系(Feng et al, 2019; Zhang et al, 2020a; Wang CY et al, 2021; Li SP et al, 2022), 而大尺度的调查研究却发现两者通常呈现正相关关系(Jauni & Hyvönen, 2012; Zeiter & Stampfli, 2012; Zhu et al, 2015)。然而, 一项基于全球范围204项案例的Meta分析显示本地植物多样性越高越能促进外来植物入侵, 并且这种促进效应随着研究尺度的增加而增强(Peng et al, 2019)。另一项基于161例(来自87项野外研究) “多样性–入侵性”案例的Meta分析指出本地群落对植物入侵的易感性在不同尺度上可能受到不同因素的驱动, 从而导致了“多样性–入侵性”相关关系的尺度依赖性(Tomasetto et al, 2019)。除此之外, 围绕“多样性–入侵性”这一问题, 目前的研究多侧重于植物多样性

对外来植物入侵的影响，对地上地下多营养级生物类群在植物多样性抵御生物入侵中的角色和作用认知有限。然而，德国研究机构最新的研究表明，提高本地植物多样性能增加土壤中外来植物致病真菌的种类，进而抑制了外来植物东北柳叶菜(*Epilobium ciliatum*)、黑麦草(*Lolium multiflorum*)、窄叶黄菀(*Senecio inaequidens*)和长柔毛野豌豆(*Vicia villosa*)的生长(Zhang et al, 2020a)。综上，找到多样性–入侵性关系的一般性规律及其深层机制有望为入侵植物的替代控制和本地群落的生态恢复提供明确的科学指导。

2 外来植物入侵与生物互作

2.1 外来植物入侵与植食性动物互作

外来植物与入侵地植食性天敌互作是影响其定殖与种群扩张的重要因素之一。天敌逃逸假说认为外来植物逃逸了原产地的专食性天敌，因此在与入侵地的植物竞争中获得优势，从而成功入侵(Keane & Crawley, 2002)。的确，许多研究发现入侵地的一些植食性动物偏好取食本地植物，从而抑制了本地植物的生长，间接促进了外来植物入侵(Enge et al, 2013; Kalisz et al, 2014)。然而，越来越多研究发现入侵地一些植食性天敌的采食行为也可能阻抗外来植物入侵(Kempel & Chrobock et al, 2013; Schultz et al, 2017; Zhang et al, 2018; Christianen et al, 2019)。例如，战争导致莫桑比克戈龙戈萨国家公园大型哺乳动物种群急剧下降，与此同时入侵灌木大含羞草(*Mimosa pigra*)的种群密度急剧升高；而随着战后大型哺乳动物的恢复，大含羞草的丰富度又急剧下降(Guyton et al, 2020)。当然，也有研究表明入侵地有些植食动物并不影响外来植物的入侵。例如Allen等(2021)发现与本地植物相比，外来植物虽然经历更强的昆虫采食，但由于其快速增长的特性，外来植物仍然能够成为群落的优势物种。尽管入侵地植食动物是否促进外来植物成功入侵尚无定论，但评判其在植物入侵过程中的具体作用时，应同时考虑植食动物的偏好性以及外来植物对这些采食行为的相对抗性和耐受性(Maron & Vilà, 2001; Huang et al, 2010; Schaffner et al, 2011)。

地下植食性动物与外来入侵植物的相互作用在过去10年中日益受到关注。Huang等(2012)发现，与对地上专食性昆虫的响应类似，乌桕(*Triadica sebifera*)入侵种群对地下专食性昆虫的抵抗力同样下降；其重要原因是入侵种群根部抗虫次生代谢物质单宁含量降低(Huang et al, 2014)。此外，地上和地下生物并不是割裂的，它们往往可以通过植物的系统诱导反应、植物对资源的重新分配、叶片挥发物和根际分泌物的释放等方式(Tian et al, 2021; Yu et al, 2022)形成复杂且多样的互作关系。因此，研究地上和地下植食者的相互作用以及入侵植物对地上地下的响应与化学诱导反应是今后的重要方向(Wan et al, 2022)。

2.2 外来植物入侵与微生物互作

外来植物与多种微生物之间存在紧密的相互作用，这不仅对外来植物生长发育有重要影响，还会调控外来植物与本地植物的种间竞争(闫静等, 2016; 付伟等, 2017; Mariotte et al, 2018; Zhang X et al, 2021)。菌根真菌在外来植物入侵中的作用近年来得到了关注(Suding et al, 2013; Bunn et al, 2015; Dickie et al, 2017; Chen et al, 2020)。“共生促进”假说(enhanced mutualisms hypothesis)认为，外来植物在入侵地与当地一些高效的共生真菌形成新的相互作用，促进其入侵(Reinhart & Callaway, 2006; Baynes et al, 2012; Tian et al, 2021; Sheng et al, 2022; Yu et al, 2022)。例如，与原产地种群相比，乌桕与小飞蓬(*Conyza canadensis*)的入侵地种群的菌根真菌寄生率更高、植物生物量更大(Yang et al, 2015; Sheng et al, 2022)，这种更强的“共生促进”关系主要是由根系分泌物中类黄酮的变化驱动的(Tian et al, 2021)。并且随着入侵植物与菌根真菌共生时间的增加，这种促进效应在入侵性更强的外来植物上体现更为明显(Moyano et al, 2021)。但是，基于假臭草(*Eupatorium catarium*)和三叶鬼针草(*Bidens pilosa*)的研究表明，菌根真菌对外来入侵植物生长的促进作用随土壤磷浓度的升高而减弱(Chen et al, 2020)。除此之外，菌根真菌对外来植物入侵的作用还可能受菌根真菌来源和种间竞争的影响。例如，Vlk等(2020)发现外来松科入侵植物更加依赖于与其同时引入的菌根真菌，而外来桉树(*Eucalyptus* spp.)则与入侵地的菌根真菌建立更多的联系。而Waller等(2016)发现菌根真菌不影响单独种植的入侵植物黄

矢车菊(*Centaurea solstitialis*)的生长，但显著抑制了与本地植物共同种植的黄矢车菊的生长。综上，准确评估菌根真菌在外来植物入侵过程中的作用需要同时考虑其他多种影响因素的作用。

此外，病原微生物也在外来植物入侵过程中发挥着重要作用。例如，外来植物募集(recruit)的病原微生物会随着入侵时间的增长而增加，增加的这部分病原微生物可能会抑制外来植物自身的生长，进而阻碍其入侵(Callaway et al, 2013; Stricker et al, 2016)，也可能通过溢出效应对邻近植物产生抑制，从而促进入侵(Eppinga et al, 2006; Zhang et al, 2020b)。同理，本地植物也会募集一些病原微生物抑制外来植物入侵(Zhang et al, 2020a)。另外，本地植物募集的病原微生物对外来植物的抑制作用通常高于外来植物募集的病原微生物对外来植物的抑制作用(Zhang et al, 2020b)，从而导致已经发生外来植物入侵的本地群落更容易被后来的外来植物入侵。综上，尽管病原微生物对外来植物入侵的作用尚无定论，但是其核心机理是病原微生物不对称抑制外来植物与本地植物生长，进而促进或阻碍外来植物的成功入侵。

为了弥补单一物种研究结论普适性差的短板，将更多的物种纳入到统一的研究体系正成为近年来的新趋势。例如，Wei等(2021)通过对来自26种本地植物与27种外来植物根际微生物的分析发现，两者之间根际微生物的多样性差异不显著，表明外来植物入侵后能够迅速与本地微生物产生新的互作关系。尽管植物–微生物互作在外来植物入侵中的作用得到了越来越多的关注，然而已有研究多关注土壤真菌的作用，对土壤细菌与叶际微生物作用的了解非常有限。但是，两者的作用却同样不可忽视。例如，Du等(2022)发现紫茎泽兰(*Ageratina adenophora*)可在根际募集特定的芽孢杆菌类群来提高自身竞争优势；Fang等(2019)则发现紫茎泽兰在叶际会募集更多的亚隔孢壳属(*Didymella*)及镰刀菌属(*Fusarium*)真菌，这些叶际微生物能够延长其种子萌发时间、降低种子萌发率和抑制幼苗生长。

外来植物入侵与植食性动物互作以及外来植物入侵与微生物互作并不是割裂存在的，常常会同时发生(Waller et al, 2020; Allen et al, 2021)。自Bennett (2013)综述并强调了这种复杂多类群互作对外来植物入侵过程的影响后，该研究方向在近年来也日益受到关注。例如Kempel和Nater等(2013)发现菌根真菌可以影响入侵植物对地上植食性昆虫的组成抗性和诱导抗性，但是这种影响具有物种特异性；Lu等(2018)发现土壤致病真菌多样性以及侵染本地植物莲子草的土壤根结线虫随纬度上升呈下降趋势，而侵染入侵植物空心莲子草的土壤根结线虫则无明显的纬度梯度变化；受不同维度带土壤生物影响，本地和入侵植物的生长表现及其对植食性昆虫莲草直胸跳甲(*Agasicles hygrophila*)的影响沿纬度梯度变化格局也不同；Gao等(2022)发现植食性昆虫莲草直胸跳甲取食能够改变入侵植物空心莲子草的根际微生物组结构，这种改变延长了其对本地植物莲子草的土壤负反馈效应，同时提高了空心莲子草后代的抗虫水平。综上，整合研究不同生物类群在外来植物入侵中的作用是生物入侵生态学研究的一个新的生长点，将为生物入侵机制的解析提供更多视角。

3 外来植物入侵与环境变化

3.1 环境变化的直接影响

全球气候变化，包括气候变暖、大气CO_2浓度上升、大气氮沉降、极端气候事件频发等，将直接影响外来植物入侵的进程。两项Meta分析结果表明增温与CO_2浓度上升会促进外来植物入侵(Liu et al, 2017)，并且这种促进效应在水生系统更加明显(Sorte et al, 2013)。增温(Haeuser et al, 2017, 2019)与大气CO_2浓度上升(Blumenthal et al, 2013; Mozdzer & Caplan, 2018)驱动外来植物入侵的现象也不断被证实。一项基于全球13个国家64片草地的养分添加实验发现，养分增加显著提高了外来植物优势度(Seabloom et al, 2015)。同样，水分和光照等资源的增加也可能加速外来植物的入侵过程(Davidson et al, 2011; Sorte et al, 2013)。最新的研究暗示城市化进程中路灯建设引起的夜间光污染促进了一些外来植物的入侵(Speißer et al, 2021; Liu YJ et al, 2022; Murphy et al, 2022)。另外，与单一的光照或养分增加相比，光照与养分同时增加更能加剧外来入侵植物对本地植物的竞争排斥(Zhang et al, 2022)。因此，Richards等(2006)指出许多外来入侵植物在应对生存条件变优越、资源增加的环境变化时

更具优势，而引起环境胁迫的变化则可能使其处于劣势，即“专家型策略” (master of some)。最新的研究显示干旱(Copeland et al, 2016; Liu et al, 2017; Valliere et al, 2019)与臭氧胁迫(Wang LC et al, 2022)确实对外来植物的成功入侵起到一定的阻碍作用。由于环境变化的复杂性，更多的研究需要聚焦到那些尚未被反复论证的环境变化类型(如夜晚灯光、臭氧浓度上升、微塑料污染等)或多类型资源耦合(如氮水交互、多环境因子叠加等)对外来植物入侵的影响。

除环境变量的稳态变化(即平均值差异)，环境变量的非稳态变化(即环境变异率差异)也会影响外来植物的入侵过程。“资源波动”假说认为：资源波动引起的入侵生境可利用性资源的增加可以促进外来植物成功入侵本地群落(Davis et al, 2000)。尽管该假说在2000年就已被提出，但对资源脉冲效应的关注度仅在最近10年才得到明显提升(Parepa et al, 2013; Liu & van Kleunen, 2017; Tao et al, 2021; Li YJ et al, 2022)。其中最具代表性的是Parepa等(2013)针对欧洲入侵植物日本虎杖(*Fallopia japonica*)进行的研究，他们发现与时间尺度上恒定的养分添加模式相比，时间尺度上的养分波动显著提高了日本虎杖在本地群落中的优势度。此后，国内外诸多学者也分别从不同角度验证了该假说(Koerner et al, 2015; Liu & van Kleunen, 2017; Zheng et al, 2020; Tao et al, 2021)。但是，这些研究大多停留在现象验证阶段，对于资源波动促进外来植物入侵的内在机制与适用条件尚需进一步挖掘。比本地植物更高的资源获取速率或/和资源利用效率可能是外来入侵植物更加受益于资源波动的直接原因(Davis et al, 2000; Parepa et al, 2013; 秦文超等, 2021)，但是到目前为止，这并没有得到明确的实验验证，稳定性碳、氮、氧等同位素标记技术的应用将有助于进一步揭示这些内在机制。

3.2 环境变化的间接影响

除直接影响外，环境变化还会通过其他营养级类群间接影响外来植物的入侵过程。例如，最新的多物种实验表明地上采食昆虫以及土壤微生物均能够调控养分波动对外来植物入侵的促进作用(Zhang et al, 2020a; Li YJ et al, 2022)。这也解释了为什么个别研究发现资源波动不影响(Frevola & Hovick, 2019; Shi et al, 2021)甚至抑制外来植物入侵(Liu et al, 2018)，因为资源波动对植物入侵的影响可能会同时受到其他因素的调控。又如，另一项多物种实验发现中型土壤动物的存在会减弱水分增加对植物入侵的促进效应(Jin et al, 2022)。

不仅如此，其他营养级生物还可以调控气候变暖对外来植物入侵的影响。以恶性入侵植物空心莲子草为例，气候变暖使得其沿纬度的扩散速率高于天敌昆虫莲草直胸跳甲，进而加剧了该植物在高纬度区域的“天敌逃逸” (Lu et al, 2013)；气候变暖也改变了本地同属植物莲子草的生活史，加剧了莲草直胸跳甲对高纬度区域莲子草的取食危害，进而增强了该天敌昆虫的生物防治“非靶标效应” (Lu et al, 2015)；气候变暖还提升了空心莲子草–莲子草混发群落中空心莲子草种群的天敌昆虫发生量，使得当生防天敌存在时，变暖可驱使空心莲子草优势群落向本地莲子草优势群落转变(Lu et al, 2016)。综上，因为其他营养级生物与外来/本地植物之间存在复杂的互作关系(如共生、寄生、取食等)，进一步解析其他营养级生物在外来植物与本地植物资源竞争过程的调控机制正成为该领域新的生长点。

4 外来植物入侵对本地生态系统的影响

4.1 外来植物入侵对本地群落演替的影响

外来植物入侵是一个长期和动态的过程。在一种外来植物入侵过程中，通常伴随着其他外来和本地植物的定殖、替代和丧失过程，进而会对群落结构和演替进程产生深远影响。关于植物入侵如何影响本地群落动态和演替进程，存在着截然相反的两种观点。一种观点认为，外来入侵植物是群落动态变化的“过客” (passengers)，尽管其会在干扰或环境变化中获益，进而抑制本地植物的生长、减缓本地群落的更新和恢复进程，但其危害程度会随着时间逐渐衰减，群落最终还是会向着由本地植物主导的自然群落发展(Bauer, 2012)。另一种观点则认为，外来入侵植物是群落动态变化的“主导者” (drivers)，驱动着群落发展的方向，最终实现外来植物和本地植物的长期稳定共存，并形成与本地群落截然不同的新型群落(novel community)或新型生态系统(novel ecosystem, Richardson & Gaertner, 2013)。这一争论在近些年引起了生态学家的广泛关注，使得

植物入侵的长期影响成为入侵生态学研究的热点问题。2017年，*Journal of Ecology*发表了关于“Long-Term Dynamics and Impacts of Plant Invasions”的专刊，从多个角度揭示了植物入侵的长期和动态影响的复杂性(D’Antonio & Flory, 2017)。

大部分关于植物入侵的研究聚焦于较短的时间尺度，仅有不到8%的研究其时间跨度超过4年(Stricker et al, 2015)，长期实验的缺乏是限制该领域发展的关键瓶颈(D’Antonio & Flory, 2017)。以美国Buel-Small演替实验为代表的长期连续观测研究为解析植物入侵的长期影响提供了契机。通过分析该农业弃耕地近60年演替进程中外来植物入侵和本地植物丧失的动态变化，Li等(2015)发现和本地植物亲缘关系近的外来植物更容易入侵成功并成为优势物种，此外，在这些物种成功入侵之后，会对其近缘的本地物种产生更大的危害，甚至造成其局部灭绝，形成外来植物与其远缘本地植物共存的现象。在演替早期，群落中外来植物占据主导地位；但是随着演替的深入，外来植物的种类及其丰度均逐渐下降；在经历了近60年的次生演替之后，群落中本地乔木逐渐占据主导地位(Meiners et al, 2015; Li et al, 2016)。在物种水平上，外来植物和本地植物在功能性状上差异不明显，但是在群落水平上，本地植物群落相比外来植物群落通常具有更高的叶碳和更低的叶氮含量，这可能是本地植物在演替后期占据优势的重要原因(Duffin et al, 2019)。相比外来物种，本地物种在演替进程中正相互作用的频率和强度都更高，进而抑制群落中已有外来种对其他外来种的促进作用，这可能是外来物种随着演替逐渐衰退的重要原因(Yin et al, 2022)。今后，基于与Buel-Small演替实验类似的长期实验平台，论证不同入侵植物和不同生境中植物入侵长期影响差异的来源，解析外来植物与本地植物长期互作中的进化过程，揭示外来植物入侵后对本地群落长期的遗留效应(legacy effects)，将有利于阐释目前复杂的研究结果，揭示外来植物入侵影响群落演替的驱动机制。

4.2 外来植物入侵对传粉网络的影响

外来植物入侵不仅直接影响群落结构，还会通过打破本地植物及其传粉者之间(尤其是特化的传粉系统)长期进化形成的稳定互作关系而间接影响本地植物群落结构及动态。例如，一些具有更多花报酬、更大花展示的外来入侵植物会竞争本地植物传粉昆虫，从而增强本地植物的花粉限制并降低了其在群落中的适合度(Charlebois & Sargent, 2017; Parra-Tabla et al, 2021)。其中，具有泛化传粉系统的外来植物入侵对本地群落传粉的影响尤为强烈。Parra-Tabla等(2019)在墨西哥尤卡坦(Yucatán)半岛北部滨海沙丘生态系统的研究显示入侵植物三叶鬼针草能够抢占整个群落60%的传粉者。然而，因与本地传粉者的强大的互作能力(即与多种传粉者互作)，外来植物入侵后可能成为植物-传粉者网络的核心物种(hub species role)，对传粉网络的嵌套性(nestedness)、连通度(connectance)和稳健性(robustness)等可能无显著影响(Bartomeus et al, 2008; Stouffer et al, 2014; Parra-Tabla et al, 2019; Corcos et al, 2020)。目前，外来植物入侵对传粉影响的研究主要关注对传粉者的访问频率、传粉网络结构相关参数(如嵌套性、连通度、稳健性等表征)的影响，这些现象描述并不能揭示植物入侵如何跨营养级影响植物群落过程与构建机制。传粉介导的植物入侵在群落结构变化中的长期潜在效应逐渐获得关注，相关研究成果有助于授粉媒介的保护与可持续利用(Parra-Tabla & Arceo-Gómez, 2021)。

4.3 外来植物入侵对生态系统营养结构的影响

外来植物入侵在一定时期内会剧烈改变本地群落组成，尤其是导致本地植物群落(即生态系统生产者)组成发生显著变化。一个稳定的生态系统拥有独特的本地物种组成结构，当系统的本地生产者比例降低之后，整个系统的营养结构和环境特征也将随之改变。有赖于生产者的其他营养级生物的组成及多度都会因此而变化，这些变化通常会形成更强烈的、有利于外来植物成功入侵的“正反馈”效应，从而引起生物多样性及生态系统功能的持续恶化(Zhang P et al, 2019)。一个最典型的案例是，入侵植物互花米草传入我国滨海湿地以来，通过直接的竞争力优势(Liu WW et al, 2020; Qiu et al, 2020; Xu et al, 2022b)，以及植食动物(Xu et al, 2022a)和致病微生物(Li et al, 2014)等介导的间接影响，显著改变了我国南方红树林和中、北部盐沼生态系统的植物群落组成与结构(Wang et al, 2019; Ren et al, 2021)，导致依赖于本地生产者为营养源或栖息生境的昆虫(Sun KK et al, 2020)、土壤生物(Zhang YZ et al,

2019)与鸟类(Ma et al, 2014)等生物类群的多样性或生物学特征发生明显变化；这些变化又通过物理环境变化的叠加影响(Qiu et al, 2020)显著改变了湿地生态系统过程，最终影响了我国滨海湿地生态系统的能量流动和物质循环等功能(Ju et al, 2017; Wang et al, 2019; Ren et al, 2021)。

5 本地植物入侵

全球气候变化正导致许多植物的自然分布区正在向两极和高海拔地区扩张(Alexander et al, 2015)。对于这些快速实现自然分布区扩张而又成功占据新生境的植物(range expander)，在新分布区内往往逃离了原分布区地上以及地下天敌对其的控制(Wilschut et al, 2019)，不仅能够改变其新占据生境的植物群落组成(Alexander et al, 2015)和地上昆虫群落(Bezemer et al, 2014)，还可以改变这些区域的土壤线虫群落(Wilschut et al, 2016)和微生物群落(Ramirez et al, 2019)组成，进而影响植物与土壤群落之间的反馈效应(Koorem et al, 2020; Yang et al, 2022)，改变生态系统功能(Manrubia et al, 2019; Yang et al, 2022)。因为这些物种扩张生境进入新分布区的过程与外来植物入侵本地生态系统过程具有相似性(Alpert et al, 2000; Pauchard et al, 2016)，因此也逐渐被归于广义的植物入侵研究范畴：即本地植物入侵(Alpert et al, 2000)或“新本地植物”(neonative) (Essl et al, 2019)。在全球环境变化不断加剧的情景下，这些本地植物分布幅快速扩张的机理及影响研究也被逐渐重视起来，成为植物入侵生态学研究的一个前沿问题(Alexander et al, 2015)。因此，将外来植物入侵生态学的理论与方法应用到本地植物入侵研究体系形成类比研究，对系统深入解析广义的植物入侵过程及机制具有重要意义。

6 组学技术在入侵生态学中的应用

近10年来，入侵生态学研究正从表观现象描述进入到深层分子机制探究阶段。越来越多的研究者将基因组学、转录组学、蛋白质组、代谢组学、微生物组学等方法运用到外来植物入侵生态学研究中。例如，通过比较基因组学分析原产地种群和入侵地种群的遗传差异，发现入侵植物豚草(*Ambrosia artemisiifolia*)的成功入侵得益于多次引种导致了较高的种群遗传多样性(van Boheemen et al, 2017)。与豚草相似，互花米草的成功入侵也受益于多次引种过程，促进了其在入侵地形成杂交种群和快速进化，进而成功入侵(Qiao et al, 2019; Liu WW et al, 2020)；而表观基因组学分析则显示，互花米草的DNA甲基化与土壤石油污染存在显著的关联，呈现出在强环境扰动中的适应性，加剧入侵(Robertson et al, 2017; Alvarez et al, 2018)。但利用转录组学、蛋白质组学和代谢组学等单一方法，或整合多组学手段进行外来植物入侵机制研究的案例仍较少(Maroli et al, 2018; Li et al, 2020; Mounger et al, 2021)。无疑，借助多组学大数据的多维尺度整合手段，可以更加全面深入地解析外来植物入侵性状的成因，探究不同环境中入侵植物的适应性进化机制，从而理解入侵植物基因型到表型之间的“黑箱”过程。例如，在最新的案例研究中，Liu B等(2020)发现薇甘菊(*Mikania micrantha*)由于一次近期的全基因组二倍化和大量的片段复制事件，其光合作用光反应与暗反应、氮磷钾的代谢和运输等基因家族发生了显著扩张，可在白天和夜晚分别利用不同的光合途径进行CO_2的固定，充足的碳水化物导致了它的快速生长特性；同时，薇甘菊还可以通过自身的化感物质有效地富集固氮菌和氨化细菌，加速了根际土壤的养分循环，为其快速生长提供充足的养分。该研究利用比较基因组学、代谢组学、转录组学和土壤宏基因组学技术，从薇甘菊的光合作用、化感物质、与土壤微生物互作等方面揭示了其快速生长和环境适应的分子机制。Sun Y等(2020, 2022)通过基因组、代谢组和表型组的多组学整合分析，证明在入侵地气候条件下，入侵植物后代在提高天敌防御的同时它们的生长受到抑制，说明其在防御性和入侵性上存在明确的权衡关系；而气候变暖情景下，入侵植物豚草通过遗传变异提高了后代的生长性状，同时其后代的天敌防御能力也得到了显著地提升，阐明了入侵植物豚草建立了新型的天敌防御策略和入侵性状间的同步关系，该研究系统揭示了气候变暖下入侵植物豚草的生物防治效果减弱的潜在分子遗传机制及其代谢可塑性机理。

7 结论与展望

过去10年里，国内外围绕决定外来植物成功入

侵的生物学特性，本地群落可入侵性，外来植物在其入侵地形成的植物–生物互作、植物–环境互作关系，以及外来植物入侵对本地物种、种群、群落与生态系统的影响等方面开展了大量研究，并取得了长足进步。这些发现进一步阐释了植物入侵机制、揭示了植物入侵效应。尽管其中大部分研究聚焦特定物种在局域尺度上(如群落尺度)的单一生物入侵机制理论的验证与发展，但是这些研究正越来越明朗的呈现出以下趋势:

(1)研究对象: 从聚焦单一物种扩展到多物种比较。尽管近10年很多研究仍集中于单一物种的入侵机制探索，但是越来越多的研究将更多的物种纳入其研究体系。由于近缘种的形态与遗传学特性比较相似，这些研究多对外来入侵植物与其本地近缘种的功能性状差异及其对环境变化的响应规律进行比较，这将更有助于归纳分析植物入侵机制(Bunn et al, 2015; Liu & van Kleunen, 2017; Liu MC et al, 2022; Yu et al, 2022)。

(2)研究地理范围: 从局域(local)到纬度梯度变化。局域条件下环境异质性小造成研究结果的解释度有限。因此，拓展地理尺度是植物入侵生态学研究的必然趋势。近年来，众多学者在比较研究外来入侵植物与本地植物功能性状的纬度格局，及其在纬度梯度上对生物与非生物因子的响应和适应——特别是外来入侵植物–天敌互作演化方面——获得了诸多重要进展(Bhattarai et al, 2017; Lu et al, 2018; Gao et al, 2021; Liu et al, 2021)。

(3)入侵机制理论: 从验证单一理论到综合阐释多个假说。外来植物入侵是一个极为复杂的生物与生物、生物与环境相互作用的生物地理变化过程。因此，任何一个从单一的生物(如天敌逃逸假说)或非生物角度(如资源波动假说)提出的植物入侵理论都有其局限性。与以往聚焦单一的植物入侵机制理论研究相比，近年来研究者开始逐渐在同一研究内容中，综合多个假说阐释植物入侵机制(Qin et al, 2013; Zheng et al, 2015; Inderjit et al, 2021; Li YJ et al, 2022)，以期更为系统地解释决定外来植物成功入侵的关键因素。

入侵生态学研究涉及多个学科的基础理论，面临巨大的挑战，在很多方面仍存在争议，充分阐释植物入侵机制、入侵过程与生态学效应，离不开多学科理论和技术的交叉融合。另外，拓展国际合作，在全球尺度上综合多个生物(植物、植食性动物/昆虫、病原微生物和土壤微生物等)和非生物(气候、土壤等)因子开展比较研究，也将有助于揭示植物入侵机制和效应的全貌，为有效制定预防和管理植物入侵的技术和对策提供科学和系统的理论指导。

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参考文献

Alexander JM, Diez JM, Levine JM (2015) Novel competitors shape species’ responses to climate change. Nature, 525, 515–518.

Allen WJ, Waller LP, Barratt BIP, Dickie IA, Tylianakis JM (2021) Exotic plants accumulate and share herbivores yet dominate communities via rapid growth. Nature Communications, 12, 2696.

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics, 3, 52–66.

Alvarez M, Ferreira de Carvalho J, Salmon A, Ainouche ML, Cavé-Radet A, El Amrani A, Foster TE, Moyer S, Richards CL (2018) Transcriptome response of the foundation plant *Spartina alterniflora* to the deepwater horizon oil spill. Molecular Ecology, 27, 2986–3000.

Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant–pollinator networks. Oecologia, 155, 761–770.

Bauer JT (2012) Invasive species: “Back-seat drivers” of ecosystem change? Biological Invasions, 14, 1295–1304.

Baynes M, Newcombe G, Dixon L, Castlebury L, O’Donnell K (2012) A novel plant–fungal mutualism associated with fire. Fungal Biology, 116, 133–144.

Bennett AE (2013) Can plant-microbe-insect interactions enhance or inhibit the spread of invasive species? Functional

Ecology, 27, 661–671.
Bezemer TM, Harvey JA, Cronin JT (2014) Response of native insect communities to invasive plants. Annual Review of Entomology, 59, 119–141.
Bhattarai GP, Meyerson LA, Anderson J, Cummings D, Allen WJ, Cronin JT (2017) Biogeography of a plant invasion: Genetic variation and plasticity in latitudinal clines for traits related to herbivory. Ecological Monographs, 87, 57–75.
Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. Journal of Ecology, 83, 887–889.
Blumenthal DM, Resco V, Morgan JA, Williams DG, Lecain DR, Hardy EM, Pendall E, Bladyka E (2013) Invasive forb benefits from water savings by native plants and carbon fertilization under elevated CO_2 and warming. New Phytologist, 200, 1156–1165.
Bunn RA, Ramsey PW, Lekberg Y (2015) Do native and invasive plants differ in their interactions with arbuscular mycorrhizal fungi? A meta-analysis. Journal of Ecology, 103, 1547–1556.
Callaway RM, Montesinos D, Williams K, Maron JL (2013) Native congeners provide biotic resistance to invasive *Potentilla* through soil biota. Ecology, 94, 1223–1229.
Callaway RM, Ridenour WM (2004) Novel weapons: Invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment, 2, 436–443.
Charlebois JA, Sargent RD (2017) No consistent pollinator-mediated impacts of alien plants on natives. Ecology Letters, 20, 1479–1490.
Chen EJ, Liao HX, Chen BM, Peng SL (2020) Arbuscular mycorrhizal fungi are a double-edged sword in plant invasion controlled by phosphorus concentration. New Phytologist, 226, 295–300.
Christianen M, Smulders F, Engel MS, Nava M, Willis S, Debrot A, Palsbøll P, Vonk J, Becking L (2019) Megaherbivores may impact expansion of invasive seagrass in the Caribbean. Journal of Ecology, 107, 45–57.
Copeland SM, Harrison SP, Latimer AM, Damschen EI, Eskelinen AM, Fernandez-Going B, Spasojevic MJ, Anacker BL, Thorne JH (2016) Ecological effects of extreme drought on Californian herbaceous plant communities. Ecological Monographs, 86, 295–311.
Corcos D, Cappellari A, Mei M, Paniccia D, Cerretti P, Marini L (2020) Contrasting effects of exotic plant invasions and managed honeybees on plant–flower visitor interactions. Diversity and Distributions, 26, 1397–1408.
Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion biology: Specific problems and possible solutions. Trends in Ecology & Evolution, 32, 13–22.
Cummings JA, Parker IM, Gilbert GS (2012) Allelopathy: A tool for weed management in forest restoration. Plant Ecology, 213, 1975–1989.
D'Antonio C, Flory SL (2017) Long-term dynamics and impacts of plant invasions. Journal of Ecology, 105, 1459–1461.
Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters, 14, 419–431.
Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. Journal of Ecology, 88, 528–534.
Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature, 592, 571–576.
Dickie IA, Bufford JL, Cobb RC, Desprez-Loustau ML, Grelet G, Hulme PE, Klironomos J, Makiola A, Nuñez MA, Pringle A, Thrall PH, Tourtellot SG, Waller L, Williams NM (2017) The emerging science of linked plant–fungal invasions. New Phytologist, 215, 1314–1332.
Du EW, Chen YP, Li YH, Sun ZX, Gui FR (2022) Rhizospheric *Bacillus*-facilitated effects on the growth and competitive ability of the invasive plant *Ageratina adenophora*. Frontiers in Plant Science, 13, 882255.
Duffin KI, Li SP, Meiners SJ (2019) Species pools and differential performance generate variation in leaf nutrients between native and exotic species in succession. Journal of Ecology, 107, 595–605.
Dyderski MK, Jagodziński AM (2019) Functional traits of acquisitive invasive woody species differ from conservative invasive and native species. NeoBiota, 41, 91–113.
Elton CS (1958) The Ecology of Invasion by Animals and Plants. University of Chicago Press, Chicago.
Enge S, Nylund GM, Pavia H (2013) Native generalist herbivores promote invasion of a chemically defended seaweed via refuge-mediated apparent competition. Ecology Letters, 16, 487–492.
Eppinga MB, Rietkerk M, Dekker SC, de Ruiter PC, van der Putten WH (2006) Accumulation of local pathogens: A new hypothesis to explain exotic plant invasions. Oikos, 114, 168–176.
Essl F, Dullinger S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kühn I, Lenzner B, Pauchard A, Pyšek P, Rabitsch W, Richardson DM, Seebens H, van Kleunen M, van der Putten WH, Vilà M, Bacher S (2019) A conceptual framework for range-expanding species that track human-induced environmental change. BioScience, 69, 908–919.
Fang K, Chen L, Zhou J, Yang ZP, Dong XF, Zhang HB (2019) Plant–soil–foliage feedbacks on seed germination and seedling growth of the invasive plant *Ageratina adenophora*. Proceedings of the Royal Society B: Biological Sciences, 286, 20191520.
Faulkner KT, Robertson MP, Wilson J (2020) Stronger

regional biosecurity is essential to prevent hundreds of harmful biological invasions. Global Change Biology, 26, 2449–2462.

Feng YH, Fouqueray TD, van Kleunen M (2019) Linking Darwin's naturalisation hypothesis and Elton's diversity–invasibility hypothesis in experimental grassland communities. Journal of Ecology, 107, 794–805.

Feng YH, van Kleunen M (2016) Phylogenetic and functional mechanisms of direct and indirect interactions among alien and native plants. Journal of Ecology, 104, 1136–1148.

Feng YL, Lei YB, Wang RF, Callaway RM, Valiente-Banuet A, Inderjit, Li YP, Zheng YL (2009) Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an invasive plant. Proceedings of the National Academy of Sciences, USA, 106, 1853–1856.

Feng YL, Li YP, Wang RF, Callaway RM, Valiente-Banuet A, Inderjit (2011) A quicker return energy-use strategy by populations of a subtropical invader in the non-native range: A potential mechanism for the evolution of increased competitive ability. Journal of Ecology, 99, 1116–1123.

Frevola DM, Hovick SM (2019) The independent effects of nutrient enrichment and pulsed nutrient delivery on a common wetland invader and its native conspecific. Oecologia, 191, 447–460.

Fu W, Wang N, Pang F, Huang YL, Wu J, Qi SS, Dai ZC, Du DL (2017) Soil microbiota and plant invasions: Current and future. Biodiversity Science, 25, 1295–1302. (in Chinese with English abstract) [付伟, 王宁, 庞芳, 黄玉龙, 吴俊, 祁珊珊, 戴志聪, 杜道林 (2017) 土壤微生物与植物入侵: 研究现状与展望. 生物多样性, 25, 1295–1302.]

Gao LL, Wei CQ, He YF, Tang XF, Chen W, Xu H, Wu YQ, Wilschut RA, Lu X (2022) Aboveground herbivory can promote exotic plant invasion through intra- and interspecific aboveground–belowground interactions. New Phytologist, doi: 10.1111/nph.18520.

Gao LL, Wei CQ, Xu H, Liu XY, Siemann E, Lu XM (2021) Latitudinal variation in the diversity and composition of various organisms associated with an exotic plant: The role of climate and plant invasion. New Phytologist, 231, 1559–1569.

Guyton JA, Pansu J, Hutchinson MC, Kartzinel TR, Potter AB, Coverdale TC, Daskin JH, da Conceição AG, Peel MJS, Stalmans ME, Pringle RM (2020) Trophic rewilding revives biotic resistance to shrub invasion. Nature Ecology & Evolution, 4, 712–724.

Haeuser E, Dawson W, van Kleunen M (2017) The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. Journal of Ecology, 105, 1698–1708.

Haeuser E, Dawson W, van Kleunen M (2019) Introduced garden plants are strong competitors of native and alien residents under simulated climate change. Journal of Ecology, 107, 1328–1342.

Heckman RW, Halliday FW, Mitchell CE (2019) A growth-defense trade-off is general across native and exotic grasses. Oecologia, 191, 609-620.

Hierro JL, Callaway RM (2021) The ecological importance of allelopathy. Annual Review of Ecology, Evolution, and Systematics, 52, 25–45.

Huang W, Carrillo J, Ding JQ, Siemann E (2012) Invader partitions ecological and evolutionary responses to above- and belowground herbivory. Ecology, 93, 2343–2352.

Huang W, Siemann E, Wheeler GS, Zou JW, Carrillo J, Ding JQ (2010) Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. Journal of Ecology, 98, 1157–1167.

Huang W, Siemann E, Xiao L, Yang XF, Ding JQ (2014) Species-specific defence responses facilitate conspecifics and inhibit heterospecifics in above–belowground herbivore interactions. Nature Communications, 5, 4851.

Inderjit, Callaway RM, Meron E (2021) Belowground feedbacks as drivers of spatial self-organization and community assembly. Physics of Life Reviews, 38, 1–24.

Jauni M, Hyvönen T (2012) Positive diversity–invasibility relationships across multiple scales in Finnish agricultural habitats. Biological Invasions, 14, 1379–1391.

Jeschke JM (2014) General hypotheses in invasion ecology. Diversity and Distributions, 20, 1229–1234.

Jin HF, Chang L, van Kleunen M, Liu YJ (2022) Soil mesofauna may buffer the negative effects of drought on alien plant invasion. Journal of Ecology, 110, 2332–2342.

Ju RT, Li H, Shang L, Qiu SY, Li J, Nie M, Li B (2017) Saltmarsh cordgrass *Spartina alterniflora* Loisel. In: Biological Invasions and Its Management in China (eds Wan FH, Jiang MX, Zhan AB), pp. 187–198. Springer, Singapore.

Ju RT, Li H, Shih CJ, Li B (2012) Progress of biological invasions research in China over the last decade. Biodiversity Science, 20, 581–611. (in Chinese with English abstract) [鞠瑞亭, 李慧, 石正人, 李博 (2012) 近十年中国生物入侵研究进展. 生物多样性, 20, 581–611.]

Kalisz S, Kivlin SN, Bialic-Murphy L (2021) Allelopathy is pervasive in invasive plants. Biological Invasions, 23, 367–371.

Kalisz S, Spigler RB, Horvitz CC (2014) In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. Proceedings of the National Academy of Sciences, USA, 111, 4501–4506.

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution, 17, 164–170.

Kempel A, Chrobock T, Fischer M, Rohr RP, van Kleunen M (2013) Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. Proceedings of the National Academy of Sciences, USA, 110, 12727–12732.

Kempel A, Nater P, Fischer M, van Kleunen M (2013) Plant–microbe–herbivore interactions in invasive and non-invasive alien plant species. Functional Ecology, 27, 498–508.

Koerner SE, Avolio ML, Chang CC, Gray J, Hoover DL, Smith MD (2015) Invasibility of a mesic grassland depends on the time-scale of fluctuating resources. Journal of Ecology, 103, 1538–1546.

Koorem K, Snoek BL, Bloem J, Geisen S, Kostenko O, Manrubia M, Ramirez KS, Weser C, Wilschut RA, van der Putten WH (2020) Community-level interactions between plants and soil biota during range expansion. Journal of Ecology, 108, 1860–1873.

Lei YB, Xiao HF, Feng YL (2010) Impacts of alien plant invasions on biodiversity and evolutionary responses of native species. Biodiversity Science, 18, 622–630. (in Chinese with English abstract) [类延宝, 肖海峰, 冯玉龙 (2010) 外来植物入侵对生物多样性的影响及本地生物的进化响应. 生物多样性, 18, 622–630.]

Levine JM, D'Antonio C (1999) Elton revisited: A review of evidence linking diversity and invasibility. Oikos, 87, 15–26.

Li H, Zhang XM, Zheng RS, Li X, Elmer WH, Wolfe LM, Li B (2014) Indirect effects of non-native *Spartina alterniflora* and its fungal pathogen (*Fusarium palustre*) on native saltmarsh plants in China. Journal of Ecology, 102, 1112–1119.

Li SP, Cadotte MW, Meiners SJ, Hua ZS, Shu HY, Li JT, Shu WS (2015) The effects of phylogenetic relatedness on invasion success and impact: Deconstructing Darwin's naturalisation conundrum. Ecology Letters, 18, 1285–1292.

Li SP, Cadotte MW, Meiners SJ, Pu ZC, Fukami T, Jiang L (2016) Convergence and divergence in a long-term old-field succession: The importance of spatial scale and species abundance. Ecology Letters, 19, 1101–1109.

Li SP, Jia P, Fan SY, Wu YT, Liu X, Meng YN, Li Y, Shu WS, Li JT, Jiang L (2022) Functional traits explain the consistent resistance of biodiversity to plant invasion under nitrogen enrichment. Ecology Letters, 25, 778–789.

Li WT, Zheng YT, Wang RF (2022) Extension of the EICA hypothesis for invasive *Chromolaena odorata*. Acta Oecologica, 114, 10383.

Li YJ, Gao YZ, van Kleunen M, Liu YJ (2022) Herbivory may mediate the effects of nutrients on the dominance of alien plants. Functional Ecology, 36, 1292–1302.

Li ZY, Xu CC, Wang JB (2020) Integrated physiological, transcriptomic and proteomic analyses revealed molecular mechanism for salt resistance in *Solidago canadensis* L. Environmental and Experimental Botany, 179, 104211.

Liu B, Yan J, Li WH, Yin LJ, Li P, Yu HX, Xing LS, Cai ML, Wang HC, Zhao MX, Zheng J, Sun F, Wang ZZ, Jiang ZY, Ou QJ, Li SB, Qu L, Zhang QL, Zheng YP, Qiao X, Xi Y, Zhang Y, Jiang F, Huang C, Liu CH, Ren YW, Wang S, Liu HW, Guo JY, Wang HH, Dong H, Peng CL, Qian WQ, Fan W, Wan FH (2020) *Mikania micrantha* genome provides insights into the molecular mechanism of rapid growth. Nature Communications, 11, 340.

Liu J, Li JM, Yu H, He WM, Yu FH, Sang WG, Liu GF, Dong M (2010) The relationship between functional traits and invasiveness of alien plants. Biodiversity Science, 18, 569–576. (in Chinese with English abstract) [刘建, 李钧敏, 余华, 何维明, 于飞海, 桑卫国, 刘国方, 董鸣 (2010) 植物功能性状与外来植物入侵. 生物多样性, 18, 569–576.]

Liu M, Pan YF, Pan XY, Sosa A, Blumenthal DM, van Kleunen M, Li B (2021) Plant invasion alters latitudinal pattern of plant-defense syndromes. Ecology, 102, e03511.

Liu MC, Dong TF, Feng WW, Qu B, Kong DL, van Kleunen M, Feng YL (2022) Leaf trait differences between 97 pairs of invasive and native plants across China: Effects of identities of both the invasive and native species. NeoBiota, 71, 1–22.

Liu WW, Zhang YH, Chen XC, Maung-Douglass K, Strong DR, Pennings SC (2020) Contrasting plant adaptation strategies to latitude in the native and invasive range of *Spartina alterniflora*. New Phytologist, 226, 623–634.

Liu YJ, Oduor AMO, Zhang Z, Manea A, Tooth IM, Leishman MR, Xu XL, van Kleunen M (2017) Do invasive alien plants benefit more from global environmental change than native plants? Global Change Biology, 23, 3363–3370.

Liu YJ, Speißer B, Knop E, van Kleunen M (2022) The Matthew effect: Common species become more common and rare ones become more rare in response to artificial light at night. Global Change Biology, 28, 3674–3682.

Liu YJ, van Kleunen M (2017) Responses of common and rare aliens and natives to nutrient availability and fluctuations. Journal of Ecology, 105, 1111–1122.

Liu YJ, Zhang XQ, van Kleunen M (2018) Increases and fluctuations in nutrient availability do not promote dominance of alien plants in synthetic communities of common natives. Functional Ecology, 32, 2594–2604.

Lu XM, He MY, Ding JQ, Siemann E (2018) Latitudinal variation in soil biota: Testing the biotic interaction hypothesis with an invasive plant and a native congener. The ISME Journal, 12, 2811–2822.

Lu XM, Siemann E, He MY, Wei H, Shao X, Ding JQ (2016) Warming benefits a native species competing with an invasive congener in the presence of a biocontrol beetle. New Phytologist, 211, 1371–1381.

Lu XM, Siemann E, Shao X, Wei H, Ding JQ (2013) Climate warming affects biological invasions by shifting interactions of plants and herbivores. Global Change Biology, 19, 2339–2347.

Lu XM, Siemann E, Wei H, Shao X, Ding JQ (2015) Effects of warming and nitrogen on above- and below-ground herbivory of an exotic invasive plant and its native congener. Biological Invasions, 17, 2881–2892.

Ma ZJ, Gan XJ, Choi CY, Li B (2014) Effects of invasive cordgrass on presence of marsh grassbird in an area where it is not native. Conservation Biology, 28, 150–158.

Malecore EM, Dawson W, Kempel A, Müller G, van Kleunen M (2019) Nonlinear effects of phylogenetic distance on early-stage establishment of experimentally introduced plants in grassland communities. Journal of Ecology, 107, 781–793.

Manrubia M, van der Putten WH, Weser C, Ten Hooven FC, Martens H, Brinkman EP, Geisen S, Ramirez KS, Veen GFC (2019) Soil functional responses to drought under range-expanding and native plant communities. Functional Ecology, 33, 2402–2416.

Mariotte P, Mehrabi Z, Bezemer TM, de Deyn GB, Kulmatiski A, Drigo B, Veen GF, van der Heijden MGA, Kardol P (2018) Plant–soil feedback: Bridging natural and agricultural sciences. Trends in Ecology & Evolution, 33, 129–142.

Maroli AS, Gaines TA, Foley ME, Duke SO, Doğramacı M, Anderson JV, Horvath DP, Chao WS, Tharayil N (2018) Omics in weed science: A perspective from genomics, transcriptomics, and metabolomics approaches. Weed Science, 66, 681–695.

Maron JL, Vilà M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos, 95, 361–373.

Mathakutha R, Steyn C, le Roux PC, Blom IJ, Chown SL, Daru BH, Ripley BS, Louw A, Greve M (2019) Invasive species differ in key functional traits from native and non-invasive alien plant species. Journal of Vegetation Science, 30, 994–1006.

Meiners SJ, Pickett ST, Cadenasso ML (2015) An Integrative Approach to Successional Dynamics: Tempo and Mode of Vegetation Change. Cambridge University Press, New York.

Mounger J, Ainouche ML, Bossdorf O, Cavé-Radet A, Li B, Parepa M, Salmon A, Yang J, Richards CL (2021) Epigenetics and the success of invasive plants. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 376, 20200117.

Moyano J, Rodriguez-Cabal MA, Nuñez MA (2021) Invasive trees rely more on mycorrhizas, countering the ideal-weed hypothesis. Ecology, 102, e03330.

Mozdzer TJ, Caplan JS (2018) Complementary responses of morphology and physiology enhance the stand-scale production of a model invasive species under elevated CO_2 and nitrogen. Functional Ecology, 32, 1784–1796.

Murphy SM, Vyas DK, Sher AA, Grenis K (2022) Light pollution affects invasive and native plant traits important to plant competition and herbivorous insects. Biological Invasions, 24, 599–602.

Parepa M, Fischer M, Bossdorf O (2013) Environmental variability promotes plant invasion. Nature Communications, 4, 1604.

Parra-Tabla V, Alonso C, Ashman T, Raguso RA, Albor C, Sosenski P, Carmona D, Arceo-Gómez G (2021) Pollen transfer networks reveal alien species as main heterospecific pollen donors with fitness consequences for natives. Journal of Ecology, 109, 939–951.

Parra-Tabla V, Angulo-Pérez D, Albor C, Campos-Navarrete MJ, Tun-Garrido J, Sosenski P, Alonso C, Ashman TL, Arceo-Gómez G (2019) The role of alien species on plant–floral visitor network structure in invaded communities. PLoS ONE, 14, e0218227.

Parra-Tabla V, Arceo-Gómez G (2021) Impacts of plant invasions in native plant–pollinator networks. New Phytologist, 230, 2117–2128.

Pauchard A, Milbau A, Albihn A, Alexander J, Burgess T, Daehler C, Englund G, Essl F, Evengård B, Greenwood GB, Haider S, Lenoir J, McDougall K, Muths E, Nuñez MA, Olofsson J, Pellissier L, Rabitsch W, Rew LJ, Robertson M, Sanders N, Kueffer C (2016) Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: New challenges for ecology and conservation. Biological Invasions, 18, 345–353.

Peng SJ, Kinlock NL, Gurevitch J, Peng SL (2019) Correlation of native and exotic species richness: A global meta-analysis finds no invasion paradox across scales. Ecology, 100, e02552.

Qiao HM, Liu WW, Zhang YH, Zhang YY, Li QQ (2019) Genetic admixture accelerates invasion via provisioning rapid adaptive evolution. Molecular Ecology, 28, 4012–4027.

Qin RM, Zheng YL, Valiente-Banuet A, Callaway RM, Barclay GF, Pereyra CS, Feng YL (2013) The evolution of increased competitive ability, innate competitive advantages, and novel biochemical weapons act in concert for a tropical invader. New Phytologist, 197, 979–988.

Qin WC, Tao ZB, Wang YJ, Liu YJ, Huang W (2021) Research progress and prospect on the impacts of resource pulses on alien plant invasion. Chinese Journal of Plant Ecology, 45, 573–582. (in Chinese with English abstract) [秦文超, 陶至彬, 王永健, 刘艳杰, 黄伟 (2021) 资源脉冲对外来植物入侵影响的研究进展和展望. 植物生态学报, 45, 573–582.]

Qiu SY, Liu SS, Wei SJ, Cui XH, Nie M, Huang JX, He Q, Ju RT, Li B (2020) Changes in multiple environmental factors additively enhance the dominance of an exotic plant with a novel trade-off pattern. Journal of Ecology, 108, 1989–1999.

Ramirez KS, Snoek LB, Koorem K, Geisen S, Bloem LJ, ten Hooven F, Kostenko O, Krigas N, Manrubia M, Caković D, van Raaij D, Tsiafouli MA, Vreš B, Čelik T, Weser C, Wilschut RA, van der Putten WH (2019) Range-expansion effects on the belowground plant microbiome. Nature

Ecology & Evolution, 3, 604–611.
Reinhart KO, Callaway RM (2006) Soil biota and invasive plants. New Phytologist, 170, 445–457.
Ren JL, Chen JS, Xu CL, van de Koppel J, Thomsen MS, Qiu SY, Cheng FY, Song WJ, Liu QX, Xu C, Bai JH, Zhang YH, Cui BS, Bertness MD, Silliman BR, Li B, He Q (2021) An invasive species erodes the performance of coastal wetland protected areas. Science Advances, 7, eabi8943.
Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters, 9, 981–993.
Richardson DM, Gaertner M (2013) Plant invasions as builders and shapers of novel ecosystems. In: Novel Ecosystems: Intervening in the New Ecological World Order (eds Hobbs RJ, Higgs ES, Hall CM), pp. 102–113. John Wiley & Sons, Chichester.
Robertson M, Schrey A, Shayter A, Moss CJ, Richards C (2017) Genetic and epigenetic variation in *Spartina alterniflora* following the deepwater horizon oil spill. Evolutionary Applications, 10, 792–801.
Schaffner U, Ridenour WM, Wolf VC, Bassett T, Müller C, Müller-Schärer H, Sutherland S, Lortie CJ, Callaway RM (2011) Plant invasions, generalist herbivores, and novel defense weapons. Ecology, 92, 829–835.
Schaffner U, Steinbach S, Sun Y, Skjøth CA, de Weger LA, Lommen ST, Augustinus BA, Bonini M, Karrer G, Šikoparija B, Thibaudon M, Müller-Schärer H (2020) Biological weed control to relieve millions from *Ambrosia allergies* in Europe. Nature Communications, 11, 1745.
Schultz EL, Eckberg JO, Berg SS, Louda SM, Miller TEX (2017) Native insect herbivory overwhelms context dependence to limit complex invasion dynamics of exotic weeds. Ecology Letters, 20, 1374–1384.
Seabloom EW, Borer ET, Buckley YM, Cleland EE, Davies KF, Firn J, Harpole WS, Hautier Y, Lind EM, MacDougall AS, Orrock JL, Prober SM, Adler PB, Anderson TM, Bakker JD, Biederman LA, Blumenthal DM, Brown CS, Brudvig LA, Cadotte M, Chu CJ, Cottingham KL, Crawley MJ, Damschen EI, Dantonio CM, DeCrappeo NM, Du GZ, Fay PA, Frater P, Gruner DS, Hagenah N, Hector A, Hillebrand H, Hofmockel KS, Humphries HC, Jin VL, Kay A, Kirkman KP, Klein JA, Knops JMH, la Pierre KJ, Ladwig L, Lambrinos JG, Li Q, Li W, Marushia R, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Morgan J, Mortensen B, O'Halloran LR, Pyke DA, Risch AC, Sankaran M, Schuetz M, Simonsen A, Smith MD, Stevens CJ, Sullivan L, Wolkovich E, Wragg PD, Wright J, Yang L (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. Nature Communications, 6, 7710.
Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, Dullinger S, Genovesi P, Hulme PE, van Kleunen M, Kühn I, Jeschke JM, Lenzner B, Liebhold AM, Pattison Z, Pergl J, Pyšek P, Winter M, Essl F (2021) Projecting the continental accumulation of alien species through to 2050. Global Change Biology, 27, 970–982.
Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, van Kleunen M, Winter M, Ansong M, Arianoutsou M, Bacher S, Blasius B, Brockerhoff EG, Brundu G, Capinha C, Causton CE, Celesti-Grapow L, Dawson W, Dullinger S, Economo EP, Fuentes N, Guénard B, Jäger H, Kartesz J, Kenis M, Kühn I, Lenzner B, Liebhold AM, Mosena A, Moser D, Nentwig W, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, Walker K, Ward DF, Yamanaka T, Essl F (2018) Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences, USA, 115, E2264–E2273.
Sheng M, Rosche C, Al-Gharaibeh M, Bullington LS, Callaway RM, Clark T, Cleveland CC, Duan WY, Flory SL, Khasa DP, Klironomos JN, McLeod M, Okada M, Pal RW, Shah MA, Lekberg Y (2022) Acquisition and evolution of enhanced mutualism—An underappreciated mechanism for invasive success? The ISME Journal, doi: 10.1038/s41396-022-01293-w.
Shi X, Li WT, Zheng YL (2021) Soil legacy effect of extreme precipitation on a tropical invader in different land use types. Environmental and Experimental Botany, 191, 104625.
Sorte CJB, Ibáñez I, Blumenthal DM, Molinari NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, Dukes JS (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecology Letters, 16, 261–270.
Speißer B, Liu YJ, van Kleunen M (2021) Biomass responses of widely and less-widely naturalized alien plants to artificial light at night. Journal of Ecology, 109, 1819–1827.
Stouffer DB, Cirtwill AR, Bascompte J (2014) How exotic plants integrate into pollination networks. Journal of Ecology, 102, 1442–1450.
Stricker KB, Hagan D, Flory SL (2015) Improving methods to evaluate the impacts of plant invasions: Lessons from 40 years of research. AoB Plants, 7, plv028.
Stricker KB, Harmon PF, Goss EM, Clay K, Flory LS (2016) Emergence and accumulation of novel pathogens suppress an invasive species. Ecology Letters, 19, 469–477.
Suding KN, Stanley Harpole W, Fukami T, Kulmatiski A, MacDougall AS, Stein C, van der Putten WH (2013) Consequences of plant–soil feedbacks in invasion. Journal of Ecology, 101, 298–308.
Sun KK, Yu WS, Jiang JJ, Richards C, Siemann E, Ma J, Li B, Ju RT (2020) Mismatches between the resources for adult herbivores and their offspring suggest invasive *Spartina alterniflora* is an ecological trap. Journal of Ecology, 108,

719–732.

Sun Y, Bossdorf O, Grados RD, Liao ZY, Müller-Schärer H (2020) Rapid genomic and phenotypic change in response to climate warming in a widespread plant invader. Global Change Biology, 26, 6511–6522.

Sun Y, Züst T, Silvestro D, Erb M, Bossdorf O, Mateo P, Robert C, Müller-Schärer H (2022) Climate warming can reduce biocontrol efficacy and promote plant invasion due to both genetic and transient metabolomic changes. Ecology Letters, 25, 1387–1400.

Tao ZB, Shen CC, Qin WC, Gui YF, Wang Y, Siemann E, Huang W (2021) Magnitude and timing of resource pulses interact to affect plant invasion. Oikos, 130, 1967–1975.

Tian BL, Pei YC, Huang W, Ding JQ, Siemann E (2021) Increasing flavonoid concentrations in root exudates enhance associations between arbuscular mycorrhizal fungi and an invasive plant. The ISME Journal, 15, 1919–1930.

Tomasetto F, Duncan RP, Hulme PE (2019) Resolving the invasion paradox: Pervasive scale and study dependence in the native-alien species richness relationship. Ecology Letters, 22, 1038–1046.

Valliere JM, Escobedo EB, Bucciarelli GM, Sharifi MR, Rundel PW (2019) Invasive annuals respond more negatively to drought than native species. New Phytologist, 223, 1647–1656.

van Boheemen LA, Lombaert E, Nurkowski KA, Gauffre B, Rieseberg LH, Hodgins KA (2017) Multiple introductions, admixture and bridgehead invasion characterize the introduction history of *Ambrosia artemisiifolia* in Europe and Australia. Molecular Ecology, 26, 5421–5434.

van Kleunen M, Bossdorf O, Dawson W (2018) The ecology and evolution of alien plants. Annual Review of Ecology, Evolution, and Systematics, 49, 25–47.

van Kleunen M, Schlaepfer DR, Glaettli M, Fischer M (2011) Preadapted for invasiveness: Do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? Journal of Biogeography, 38, 1294–1304.

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters, 13, 235–245.

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecology Letters, 14, 702–708.

Vlk L, Tedersoo L, Antl T, Větrovský T, Abarenkov K, Pergl J, Albrechtová J, Vosátka M, Baldrian P, Pyšek P, Kohout P (2020) Alien ectomycorrhizal plants differ in their ability to interact with co-introduced and native ectomycorrhizal fungi in novel sites. The ISME Journal, 14, 2336–2346.

Waller LP, Allen WJ, Barratt BIP, Condron LM, França FM, Hunt JE, Koele N, Orwin KH, Steel GS, Tylianakis JM, Wakelin SA, Dickie IA (2020) Biotic interactions drive ecosystem responses to alien plant invaders. Science, 368, 967–972.

Waller LP, Callaway RM, Klironomos JN, Ortega YK, Maron JL (2016) Reduced mycorrhizal responsiveness leads to increased competitive tolerance in an invasive exotic plant. Journal of Ecology, 104, 1599–1607.

Wan JL, Yi JH, Tao ZB, Ren ZK, Otieno EO, Tian BL, Ding JQ, Siemann E, Erb M, Huang W (2022) Species-specific plant-mediated effects between herbivores converge at high damage intensity. Ecology, 103, e3647.

Wang CY, Cheng HY, Wang S, Wei M, Du DL (2021) Plant community and the influence of plant taxonomic diversity on community stability and invasibility: A case study based on *Solidago canadensis* L. Science of the Total Environment, 768, 144518.

Wang LC, Li Y, Liu YJ (2022) Invasive herbaceous respond more negatively to elevated ozone concentration than native species. Diversity and Distributions, 28, 189–196.

Wang S, Chen JX, Liu MC, Arnold PA, Wang WB, Feng YL (2022) Phenotypic plasticity and exotic plant invasions: Effects of soil nutrients, species nutrient requirements, and types of traits. Physiologia Plantarum, 174, e13637.

Wang WB, Wang RF, Lei YB, Liu C, Han LH, Shi XD, Feng YL (2013) High resource capture and use efficiency and prolonged growth season contribute to invasiveness of *Eupatorium adenophorum*. Plant Ecology, 214, 857–868.

Wang WQ, Sardans J, Wang C, Zeng CS, Tong C, Chen GX, Huang JF, Pan HR, Peguero G, Vallicrosa H, Peñuelas J (2019) The response of stocks of C, N, and P to plant invasion in the coastal wetlands of China. Global Change Biology, 25, 733–743.

Wang Y, Chen C, Xiong YT, Wang Y, Li QJ (2021a) Combination effects of heavy metal and inter-specific competition on the invasiveness of *Alternanthera philoxeroides*. Environmental and Experimental Botany, 189, 104532.

Wang Y, Xiong YT, Wang Y, Li QJ (2021b) Long period exposure to serious cadmium pollution benefits an invasive plant (*Alternanthera philoxeroides*) competing with its native congener (*Alternanthera sessilis*). The Science of the Total Environment, 786, 147456.

Wei CQ, Gao LL, Tang XF, Lu XM (2021) Plant evolution overwhelms geographical origin in shaping rhizosphere fungi across latitudes. Global Change Biology, 27, 3911–3922.

Wilschut RA, Geisen S, Martens H, Kostenko O, de Hollander M, ten Hooven FC, Weser C, Snoek LB, Bloem J, Caković D, Čelik T, Koorem K, Krigas N, Manrubia M, Ramirez KS, Tsiafouli MA, Vreš B, van der Putten WH (2019) Latitudinal variation in soil nematode communities under climate warming-related range-expanding and native plants. Global Change Biology, 25, 2714–2726.

Wilschut RA, Geisen S, ten Hooven FC, van der Putten WH (2016) Interspecific differences in nematode control between range-expanding plant species and their congeneric natives. Soil Biology and Biochemistry, 100, 233–241.

Xu X, Zhang Y, Li SS, Chen HY, Liu M, Li B, Nie M (2022a) Native herbivores indirectly facilitate the growth of invasive *Spartina* in a eutrophic saltmarsh. Ecology, 103, e3610.

Xu X, Zhou CH, He Q, Qiu SY, Zhang Y, Yang J, Li B, Nie M (2022b) Phenotypic plasticity of light use favors a plant invader in nitrogen-enriched ecosystems. Ecology, 103, e3665.

Yan J, Zhang XY, Chen X, Wang Y, Zhang FJ, Wan FH (2016) Effects of rhizosphere soil microorganisms and soil nutrients on competitiveness of *Bidens pilosa* with different native plants. Biodiversity Science, 24, 1381–1389. (in Chinese with English abstract) [闫静, 张晓亚, 陈雪, 王月, 张风娟, 万方浩 (2016) 三叶鬼针草与不同本地植物竞争对土壤微生物和土壤养分的影响. 生物多样性, 24, 1381–1389.]

Yang Q, Veen GF, Wagenaar R, Manrubia M, ten Hooven F, van der Putten W (2022) Temporal dynamics of range-expander and congeneric native plant responses during and after extreme drought events. Ecological Monographs 10.1002/ecm.1529, e1529.

Yang Q, Wei SJ, Shang L, Carrillo J, Gabler CA, Nijjer S, Li B, Siemann E (2015) Mycorrhizal associations of an invasive tree are enhanced by both genetic and environmental mechanisms. Ecography, 38, 1112–1118.

Yin D, Meiners SJ, Ye Q, He F, Cadotte MW (2022) Positive interactions of native species melt invasional meltdown over long-term plant succession. Ecology Letters, doi: 10.1111/ele.14127.

Yu HW, He YY, Zhang W, Chen L, Zhang JL, Zhang XB, Dawson W, Ding JQ (2022) Greater chemical signaling in root exudates enhances soil mutualistic associations in invasive plants compared to natives. New Phytologist, 236, 1140–1153.

Zeiter M, Stampfli A (2012) Positive diversity-invasibility relationship in species-rich semi-natural grassland at the neighbourhood scale. Annals of Botany, 110, 1385–1393.

Zhang P, Li B, Wu JH, Hu SJ (2019) Invasive plants differentially affect soil biota through litter and rhizosphere pathways: A meta-analysis. Ecology Letters, 22, 200–210.

Zhang X, van Kleunen M, Chang CL, Liu YJ (2021) Soil microbes mediate the effects of environmental variability on plant invasion. bioRxiv, doi: 10.1101/2021.11.01.466853.

Zhang YH, Meng HY, Wang Y, He Q (2018) Herbivory enhances the resistance of mangrove forest to cordgrass invasion. Ecology, 99, 1382–1390.

Zhang YZ, Pennings SC, Li B, Wu JH (2019) Biotic homogenization of wetland nematode communities by exotic *Spartina alterniflora* in China. Ecology, 100, e02596.

Zhang ZJ, Liu YJ, Brunel C, van Kleunen M (2020a) Evidence for Elton's diversity-invasibility hypothesis from belowground. Ecology, 101, e03187.

Zhang ZJ, Liu YJ, Brunel C, van Kleunen M (2020b) Soil-microorganism-mediated invasional meltdown in plants. Nature Ecology & Evolution, 4, 1612–1621.

Zhang ZJ, Liu YJ, Hardrath A, Jin HF, van Kleunen M (2022) Increases in multiple resources promote competitive ability of naturalized non-native plants. Communications Biology, 5, 1150.

Zhang ZJ, Liu YJ, Yuan L, Weber E, van Kleunen M (2021) Effect of allelopathy on plant performance: A meta-analysis. Ecology Letters, 24, 348–362.

Zhang ZJ, van Kleunen M (2019) Common alien plants are more competitive than rare natives but not than common natives. Ecology Letters, 22, 1378–1386.

Zhang ZY, Zhang ZJ, Pan XY (2015) Phenotypic plasticity of *Alternanthera philoxeroides* in response to shading: Introduced vs. native populations. Biodiversity Science, 23, 18–22. (in Chinese with English abstract) [张紫妍, 张致杰, 潘晓云 (2015) 喜旱莲子草对遮荫的可塑性反应: 入侵地与原产地种群的比较. 生物多样性, 23, 18–22.]

Zheng YL, Burns JH, Liao ZY, Li WT, Li L (2020) Nutrient fluctuation has different effects on a tropical invader in communities from the native and non-native range. Environmental and Experimental Botany, 178, 104193.

Zheng YL, Burns JH, Liao ZY, Li YP, Yang J, Chen YJ, Zhang JL, Zheng YG (2018) Species composition, functional and phylogenetic distances correlate with success of invasive *Chromolaena odorata* in an experimental test. Ecology Letters, 21, 1211–1220.

Zheng YL, Feng YL, Zhang LK, Callaway RM, Valiente-Banuet A, Luo DQ, Liao ZY, Lei YB, Barclay GF, Silva-Pereyra C (2015) Integrating novel chemical weapons and evolutionarily increased competitive ability in success of a tropical invader. New Phytologist, 205, 1350–1359.

Zhu DH, Wang P, Zhang WZ, Yuan Y, Li B, Wang J (2015) Sampling and complementarity effects of plant diversity on resource use increases the invasion resistance of communities. PLoS ONE, 10, e0141559.

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附录　Supplementary Material

附录1　植物入侵生态学主要相关假说释义及参考文献

Appendix 1　Main hypotheses in plant invasion ecology and their corresponding references

https://www.biodiversity-science.net/fileup/PDF/2022438-1.pdf