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•综述•

氮沉降对草地昆虫多样性影响的研究进展

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摘要: 昆虫是草地中数量和种类最丰富的生物类群之一, 占据食物网的不同营养级, 具有重要的生态服务功能。然而, 全球范围内昆虫数量和多样性持续降低, 对生态安全构成了潜在威胁。作为全球变化的主要组分, 不断加剧的氮沉降导致植物多样性下降, 但其对昆虫多样性的影响及机制尚不明确。由此, 本文梳理了近年来国内外相关研究, 发现氮沉降可以对昆虫种群数量和多样性产生正向、负向或中性影响, 其作用方向主要依赖于氮沉降持续的时间和强度、不同昆虫类群和草地类型。氮沉降能够通过改变植物多样性、植物生物量、植物营养、群落结构、微环境等多种途径影响昆虫的食物资源、生境适宜性以及种间相互作用, 进而对昆虫群落产生影响。未来从研究方法上应考虑氮沉降与其他全球变化因子的交互作用以及更大时空尺度的实验研究, 从研究内容上应加强氮沉降对草地昆虫食物网和多营养级关系作用的理解, 从研究机理上应重视昆虫关键功能性状对氮沉降的响应。本文有益于深入理解氮沉降对草地昆虫群落的作用规律及其调控机制, 并为全球变化背景下草地昆虫多样性的保护提供理论指导。

关键词: 养分富集; 氮添加; 全球变化; 节肢动物; 昆虫群落; 食物网

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Research progress on the impact of nitrogen deposition on grassland insect diversity

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ABSTRACT

Background & Aim: Insects are one of the most abundant biological components in grassland ecosystems, playing a critical role in the structure and function of the grassland food web. A systematic summary is lacking of the response patterns and regulatory mechanisms of insect communities due to the increasing severity of global nitrogen deposition.

Review results: This paper summarizes relevant research in recent years and finds that nitrogen deposition can exert positive, negative, or neutral effects on insect abundance and diversity. The direction of its impact mainly depends on the duration and intensity of nitrogen deposition, different insect taxa, and types of grasslands. Nitrogen deposition can affect the quantity and quality of food resources, abiotic conditions, and biotic interaction of insect communities

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through various pathways such as changing plant diversity, plant biomass, plant nutrition, community composition and structure, microclimate, and breeding habitat.
Suggestions & Perspectives: In the future, research should strengthen the understanding of (1) the multi-trophic interactions of grassland insects; (2) the interaction between nitrogen deposition and other global change factors; (3) the examination on a larger temporal and spatial scale; and (4) the role of key functional traits of insects to explain and predict the response to nitrogen deposition. A benefit from this study is to understand the impact of nitrogen deposition on grassland insect communities and provide theoretical support for the protection of grassland insect diversity due to global changes.
Key words: nutrient enrichment; nitrogen addition; global change; arthropods; insect community; food web

昆虫是草地生态系统中数量和种类最丰富的生物类群之一，涵盖不同的形态和生活方式，占据食物网的多个营养级(van Klink et al, 2020)。昆虫不仅在维持草地生态系统多样性和稳定性中发挥重要作用(Belovsky & Slade, 2000)，也可以提供一系列关键的生态服务功能(如授粉、害虫防控、物质分解等) (Losey & Vaughan, 2006; Stevens et al, 2018; David et al, 2019)。然而，由于气候变化、人类活动以及草地资源的不合理利用，昆虫的数量和多样性正在急剧下降(van Klink et al, 2020; Wagner, 2020; Wagner et al, 2021)，其多样性的下降速度远超植物与脊椎动物(Thomas et al, 2004)。在温带地区，近40%的昆虫物种正面临灭绝风险(Basset & Lamarre, 2019)。昆虫种群数量和多样性的衰减会严重威胁当地的生态安全，因此引起了人们的广泛关注。

工业革命以来，随着化石燃料的大量燃烧和农业化肥的广泛施用，越来越多的活性氮被排放到大气中并通过干湿沉降返回地球表面，从而导致全球范围内氮沉降总量及速率不断增加，对生物地球化学循环和生态系统稳定性产生了深刻影响(Galloway et al, 1995; Goulding et al, 1998)。目前亚洲已成为氮沉降增速最快的区域之一，中国氮沉降速率增幅最高可达111.5 kg N·km^{-2}·year^{-1} (Liu et al, 2013; Ackerman et al, 2019)。草地是全球分布最广、面积最大的陆地生态系统，覆盖了约24%的地球陆地表面(李建东和方精云, 2017)。氮沉降会显著影响草地生态系统的结构和功能。例如，氮沉降可以提高环境氮的可利用性，促进初级生产力(Borer & Stevens, 2022)；同时氮沉降可以提高多年生禾草等植物的优势度，通过加强植物对光和营养等资源的竞争，降低植物多样性(Stevens et al, 2004; Silvertown et al, 2006; Simkin et al, 2016)。虽然人们关于氮沉降对草地植物群落的影响已有了深刻理解，但对于昆虫群落受到的影响及作用机制尚不明确，缺乏系统性认识。本文结合已有相关研究，对氮沉降影响草地昆虫群落的作用模式及其调控机制进行梳理总结，有助于全面理解氮沉降背景下草地昆虫群落的变化规律，为保护草地生物多样性和维持草地生态系统健康提供理论依据。

1 氮沉降对草地昆虫群落的作用及其影响因素

植物和昆虫作为草地生态系统的重要组成部分，形成了相互制约与相互依存的协同进化关系(王德利, 2004)。由于氮沉降可以对植物群落产生强烈影响，因此可以间接地对更高营养级的昆虫群落产生深远影响(Nijssen et al, 2017; 孙玉诚等, 2017)。一些研究表明，氮沉降可以通过促进初级生产力，提高植物营养含量，引起昆虫数量和生物量显著提高(Richardson et al, 2002; de Sassi et al, 2012; de Sassi & Tylianakis, 2012; Grinath, 2021)。但也有研究显示，氮沉降可以通过降低植物适口性，或改变植物群落组成和结构，抑制昆虫种群数量(Chen et al, 2010; Cease et al, 2012; Asmus et al, 2018; Roth et al, 2021)。氮沉降会引起昆虫群落组成发生变化，对昆虫多样性产生正向、负向或中性的影响。大多数研究显示，随着环境氮浓度提高，昆虫物种丰富度呈下降趋势(Haddad et al, 2000; Asmus et al, 2018)。Nessel等(2021)近期的meta分析表明，氮富集使陆地昆虫多样性降低了33.8%。然而也有研究显示，氮沉降不会改变昆虫多样性(Cuevas-Reyes et al, 2011)。例如，Meza-Lopez等(2018)研究发现，氮沉降虽然提高了昆虫群落总多度，但不会对昆虫物种丰富度产生显著影响。

氮沉降对昆虫群落的作用方向受到不同因素的影响，包括模拟氮沉降处理水平的差异(氮沉降

持续时间和强度)、不同的昆虫类群(摄食类群和功能群)以及研究的草地类型(附录1)。

1.1 氮沉降持续时间和强度

短期氮添加会对昆虫个体性能(如繁殖和生存)产生显著影响, 但对昆虫种群或群落水平的影响较为有限(Williams & Cronin, 2004; Huberty & Denno, 2006)。随着氮添加时间累积, 氮沉降对昆虫群落的影响会逐渐增强。Murphy等(2012)对比了不同氮添加时间对昆虫群落结构的影响, 发现捕食者和植食性昆虫飞虱的数量比例随施氮时间逐年增加, 表明昆虫群落对氮添加的响应可能需要数年时间才能显现。研究表明, 长期氮沉降(> 10年)可以对昆虫群落的组成和结构产生更强烈的影响(Haddad et al, 2000; Asmus et al, 2018)。然而也有研究表明, 氮添加对昆虫的影响不随时间积累持续加强。Meta分析的结果表明, 氮沉降对陆地无脊椎动物数量的负面影响在短期(< 0.5年)内甚至要高于中长期(3–10年)施氮处理(Nessel et al, 2021)。此外, 不同昆虫功能群对施氮时间的响应并不一致。Cuesta等(2008)发现, 植食者的数量在施氮3个月和15个月后均显著增加, 而捕食者数量在施氮3个月后增加, 但在施氮15个月后呈下降趋势。

随着施氮浓度提高, 氮沉降对昆虫数量和多样性的影响会逐渐加强。Haddad等(2000)的研究表明, 随着施氮浓度的增加(5 g N·m^{-2}·year^{-1}增加到30 g N·m^{-2}·year^{-1}), 昆虫群落物种丰富度呈线性下降, 而昆虫数量呈线性上升。然而草地昆虫对氮添加的响应并不全是呈"线性模式", 有时也呈"单峰模式"(Westoby, 1978; Pöyry et al, 2006)。营养平衡假说(nutrient balance hypothesis)认为, 昆虫对食物营养具有特定的浓度需求, 营养过高或过低都会降低物种适合度(Raubenheimer & Simpson, 1993)。Raubenheimer和Simpson (2004)提出"几何框架"理论(geometric framework), 指出昆虫的营养需求具有种间差异性。例如, 亚洲小车蝗(*Oedaleus asiaticus*)偏爱碳水化合物含量高(低氮)的食物(Cease et al, 2012), 而棉铃虫(*Heliothis zea*)选择蛋白质含量高(高氮)的食物(Perner et al, 2005)。即使亲缘关系相近的昆虫也可能具有不同的营养需求(Braswell et al, 2019)。Zhu等(2023a)的研究表明, 不同强度氮添加处理会对两种同属的蝗虫(*Euchorthippus cheui*和*E. unicolor*)个体性能和种群数量产生相反的影响。因此, 昆虫的营养需求既取决于自身特定的发育阶段、性别和生理状态, 也是与环境长期协同进化的结果。

1.2 昆虫类群

不同昆虫类群具有不同的生活史, 以及不同的生理和生态学特征, 因此对氮沉降的响应具有显著差异。有研究表明, 氮沉降对半翅目(Gratton & Denno, 2003)及鞘翅目(Altfeld & Stiling, 2009)的物种存在正向影响, 而对鳞翅目(Roth et al, 2021)和直翅目(Cease et al, 2012)的物种存在负向影响。对于访花昆虫, 氮沉降会抑制植物群落中开花的杂类草类群, 减少这些昆虫的食物资源(主要为花粉/花蜜), 进而对其种群数量和丰富度产生负面影响(Potts et al, 2010)。Roth等(2021)通过分析瑞士383个地点的蝴蝶长期监测数据发现, 蝴蝶的数量(尤其是某些濒危物种)与氮沉降呈显著的负相关, 高氮沉降水平会显著减少当地蝴蝶的物种多样性。不同摄食类群的昆虫对氮沉降响应不同, 刺吸式昆虫(诸如叶蝉、飞虱、蝽、蚜虫)相比于咀嚼式昆虫, 对植物汁液的营养含量变化更为敏感, 因此施氮可以对其个体性能和种群数量产生更强的影响(Prestidge, 1982; Huberty & Denno, 2006; Cuesta et al, 2008; Altfeld & Stiling, 2009)。

氮沉降对昆虫的影响还依赖于昆虫的营养级位置。不同营养级昆虫的自身组织元素含量和摄入食物的元素含量具有差异(Sterner & Elser, 2003; González et al, 2018), 具有不同的养分需求, 因此对氮沉降具有不同的响应。低营养级昆虫受到的影响可能比高营养级昆虫更为强烈。例如, Asmus等(2018)发现, 昆虫群落受到氮沉降的影响主要体现在低营养级的植食者和分解者上, 这可能是由于低营养级昆虫对植物营养含量的变化更加敏感。相对于低营养级昆虫, 捕食者和寄生者与植物组织的氮含量差异较大, 因此对维持自身内稳态有更高的生理需求。有研究表明, 氮添加对植食者和分解者的数量和生物量产生积极影响, 但是对寄生者产生负面影响(Haddad et al, 2000)。

1.3 草地类型

氮沉降对昆虫群落的作用也会受到草地类型

的影响。不同草地类型具有不同的初级生产力、植物群落组成以及养分循环速率(Bowman et al, 2008; 韩其飞等, 2021), 因此会进一步影响氮沉降对昆虫群落的作用方向和强度。不同草地类型具有不同的植物优势种和功能群比例, 对氮沉降的响应具有差异。例如, 氮添加会显著提高小灌木沼桦(*Betula nana*)的优势度而降低草本植物(如禾本科、莎草科)的优势度(Asmus et al, 2018)。然而对于昆虫来说, 草本植物比灌木的适口性更强, 也能提供更合适的生境条件, 因此虽然氮沉降造成的灌木入侵导致了系统更高的初级生产力, 但是并没有提高昆虫群落总数量和生物量(Asmus et al, 2018)。而在典型草原和盐沼的氮沉降研究中, 施氮一般会通过提升植物生物量以及植物适口性来增加昆虫的数量或生物量(Haddad et al, 2000; Huberty & Denno, 2006)。具体而言, 氮添加可以使典型草地植物群落组成向适口性更强的C_3植物转变(Isbell et al, 2013), 对于单一植物米草属(*Spartina*)禾草占优势的盐沼系统来说, 氮添加不会改变植物群落组成, 但可以通过提高优势种的氮含量和适口性促进昆虫种群数量(Murphy et al, 2012)。Prather等(2021)在北美典型草原的研究样点发现氮添加会显著改变禾草的叶片氮含量而不会影响杂类草的叶片氮含量, 从而对昆虫群落产生影响。

此外, 不同草地所处的地理位置不同, 往往具有不同的气候条件(温度和降水)或氮沉降背景值, 导致氮沉降对昆虫的作用结果不一致。WallisDeVries和Van Swaay (2006)的一项关于欧洲的蝴蝶调查表明, 在氮沉降速率高的国家诸如荷兰、比利时, 蝴蝶多度下降的速度远超氮沉降速率较低的英国和爱尔兰。在不同气候条件下, 氮沉降会通过不同的作用途径影响植物和昆虫群落。瑞士的一项研究表明, 在低海拔地区, 氮沉降可以通过提高植物生物量、降低微环境温度, 引起蝴蝶物种丰富度下降; 而在高海拔地区, 氮沉降主要通过降低植物物种丰富度影响蝴蝶物种丰富度(Roth et al, 2021)。

2 氮沉降对昆虫群落的作用途径

氮沉降可以对昆虫产生直接的化学胁迫作用, 这一过程通常发生在水体或较为湿润的土壤环境中(Camargo & Alonso, 2006)。氮沉降引起的大量无机氮化合物(如NH_4^+、NO_2^-、NO_3^-等)增加可以对昆虫产生直接的毒性作用(Nijssen et al, 2017)。氮沉降也会降低土壤pH值, 引起土壤的酸化效应(Throop & Lerdau, 2004; Camargo & Alonso, 2006; 陈云等, 2021)。酸化效应会使土壤中H^+、Al和Mn等毒性元素浓度增加, 活性增强, 从而直接影响昆虫的生理代谢过程(Roem & Berendse, 2000; Horswill et al, 2008; Tian et al, 2020)。例如, 土壤酸化会扰乱昆虫体内的离子调节、呼吸和代谢(Leuven & Oyen, 1987), 降低昆虫的孵化率和蜕皮成功率, 抑制昆虫的采食行为, 最终影响生长速率(Økland, 1992)。

氮沉降对草地昆虫群落的影响主要来自间接作用(Nijssen et al, 2017)。氮沉降可以通过改变植物群落特征和非生物环境条件影响昆虫的食物资源和微生境适宜性, 进一步改变昆虫种间相互作用, 最终对昆虫种群数量和多样性产生影响(图1)。

2.1 食物资源

2.1.1 植物多样性

氮沉降造成的植物群落多样性变化在全球不同的草地生态系统中普遍存在(Stevens et al, 2004; Silvertown et al, 2006)。氮沉降可以降低土壤养分资源异质性, 诱发不同植物对光、水分和养分资源竞争, 使得植物间产生不对称的种间竞争: 促进喜氮的高大禾本科或灌木物种快速生长, 抑制矮小的竞争力较弱的禾本科和杂类草物种, 导致植物群落组成发生改变, 引起植物多样性下降(张世虎等, 2022)。植物多样性发生变化会对昆虫群落数量和多样性产生显著影响(Wan et al, 2022)。Haddad等(2009)的研究结果表明, 植食性昆虫和捕食性昆虫物种丰富度与植物物种丰富度呈强烈的正相关关系。资源专食性假说(resource specialization hypothesis)预测, 植食性昆虫多样性随植物多样性的增加而增加, 而捕食性昆虫多样性随植食者多样性的增加而增加(Keddy, 1984)。因此, 氮沉降导致的植物多样性下降会通过营养级联作用对昆虫群落产生强烈影响。

2.1.2 植物生物量

氮沉降导致的植物生物量提高和枯落物积累可以显著提高输入地上食物网以及地下碎屑食物网的资源数量, 进而增加昆虫多度和丰富度。更多个体假说(more individuals hypothesis)认为, 生产力更高的植物群落可以为消费者提供更丰富的食物

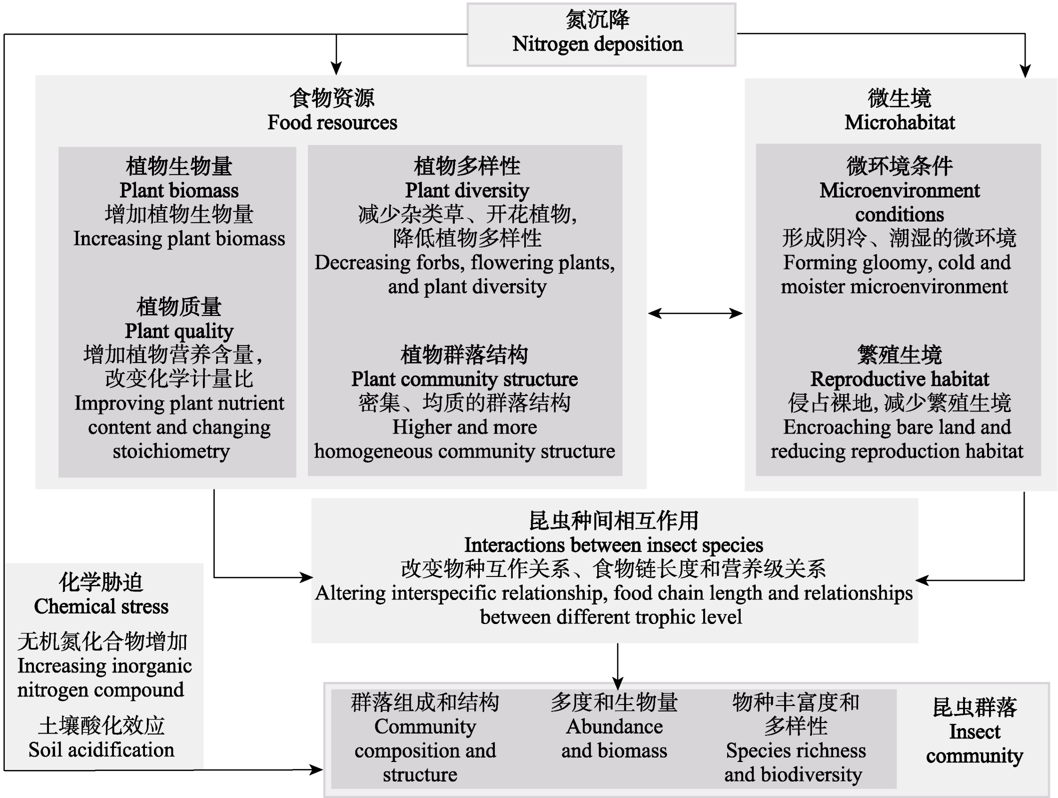


图1　氮沉降对草地昆虫群落作用途径的概念框架
Fig. 1　Conceptual framework for the impact pathways of nitrogen deposition on grassland insect communities

资源，进而支持数量更多的消费者，导致总体物种丰富度增加(Srivastava & Lawton, 1998)。然而许多昆虫物种依赖特定的植物物种或器官(植物鲜嫩组织、花蜜或花粉、种子等)生存，氮沉降引起的这些特定寄主植物的减少或丧失会对这些昆虫类群产生严重威胁(David et al, 2019)。Öckinger等(2006)发现蝴蝶物种数与氮沉降量存在负相关，并认为这种关系可能受寄主植物数量的调节。WallisDeVries等(2012)指出，由于氮沉降导致了植物群落组成变化、开花植物数量降低或是物候变化，导致访花昆虫的数量发生大规模的下降。专食性昆虫物种通常比广食性物种更容易受到这些变化的影响，因为它们的食物来源更加单一(Bernaschini et al, 2020)。虽然氮沉降可以引起食物资源数量发生变化进而影响昆虫多度，但是验证两者之间因果关系的证据十分缺乏(Nijssen et al, 2017)。

2.1.3　植物质量

氮沉降可以通过两种途径改变昆虫食物资源的质量。一方面氮沉降可以直接影响植株个体的营养、次生代谢物和元素比例，另一方面可以通过改变植物群落组成比例影响群落水平的植物质量(Nijssen et al, 2017)。氮含量被认为是表征植物质量的最佳指标，氮沉降可以提高植物组织氮含量，对昆虫个体性能和种群数量产生积极影响(Throop & Lerdau, 2004)。氮限制假说(nitrogen limitation hypothesis)认为，植物和昆虫氮含量具有很大差异(植物：2%–4%；昆虫：8%–14%)，因此氮沉降可以打破昆虫的氮限制，有利于昆虫的生存和繁殖(Mattson, 1980)。但也有研究认为，昆虫对植物氮含量具有特定的浓度需求，氮含量不足或过剩都会降低其适合度(Zhu et al, 2019)。例如，内蒙古草原的亚洲小车蝗(*Oedaleus asiaticus*)更偏向于选择采食低氮含量的食物，施氮会抑制其个体性能和种群数量(Cease et al, 2012)。除了提高植物营养含量，外源氮输入也会增加含氮次生代谢产物(如生物碱、非蛋白氨基酸等)的含量，对昆虫产生负面影响(Mattson 1980; Li et al, 2016; David et al, 2019)。氮沉降会影响植物和昆虫的化学计量比(张世虎等, 2022)。虽然昆虫较植物具有更高的化学计量内稳态(stoichiometric homeostasis)，但维持内稳态的同时

也会对其适合度造成负面影响。目前关于氮沉降对植物和昆虫化学计量关系的研究比较匮乏。有限的研究表明氮沉降可使草地从氮限制转向磷限制，但是这种转变对昆虫群落的影响还不清楚。从化学计量关系的角度探讨氮沉降对昆虫群落的影响为环境–植物–昆虫互作关系提供了新的视角。综上，氮沉降通过改变植物质量对昆虫产生的影响既受到植物特性(营养含量、防御水平、元素比例)的影响，也受到昆虫自身特性的调控(Persson et al, 2010)。

2.1.4 植物群落结构

植物群落结构可表征为植物群落的平均高度或植物高度的异质性(heterogeneity of plant height) (Joern & Laws, 2013)。植物群落结构会影响昆虫的生境条件、食物资源和捕食风险。相较均质化群落，复杂的植物群落结构可以支持更高的昆虫物种丰富度和数量(Jerrentrup et al, 2014; van Klink et al, 2015)。因为不同高度的植物可以满足不同昆虫类群对食物资源、微生境(繁殖或休眠)和躲避天敌的需求(Lawton, 1983; Treweek et al, 1997)。复杂的植物群落结构也可以缓冲外界环境的急剧变化，为昆虫在极端气候或严重干扰条件下提供生存庇护(Nijssen et al, 2017)。Aranda和Graciolli (2015)在巴西热带稀树草原的研究表明，植物群落结构驱动了膜翅目群落的变化。在中国东北松嫩草地的研究表明，植物高度的异质性是调控昆虫多样性的重要因素(Zhu et al, 2012)。一般而言，高大且复杂的植物群落结构可以为昆虫提供更多的生态位。因此氮沉降可以通过降低植物高度异质性对昆虫群落产生负面影响。

2.2 微生境

2.2.1 微环境条件

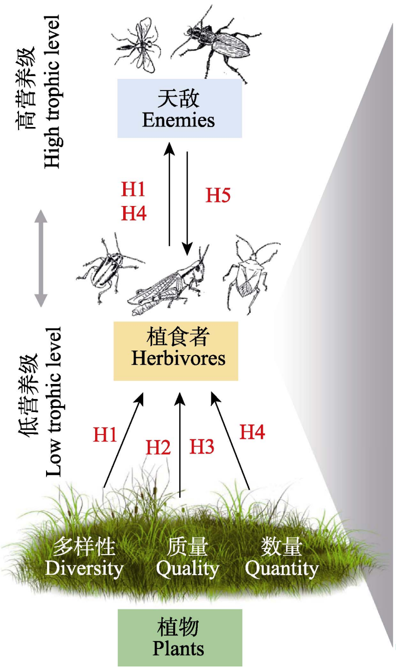
昆虫作为小型变温动物，需要依赖于外部热量进行体温调节，因此昆虫对微环境温度、湿度、光照的变化十分敏感(Jerrentrup et al, 2014)。氮沉降导致的微环境条件的变化会直接影响昆虫的发育、繁殖和生存(Nijssen et al, 2017)。氮沉降可以增加植物生物量，导致地表形成更厚的枯落物层，进而减弱光照辐射以及地表的空气循环，形成更为阴冷、潮湿的微环境，对昆虫产生不利影响(Klop et al, 2015; Nijssen et al, 2017)。在荷兰白垩草地(chalk grasslands)的研究表明，氮沉降导致的植被快速生长显著降低了微环境温度，抑制了切胸蚁(*Temnothorax albipennis*)的繁殖和种群数量(van Noordwijk et al, 2012)。在地表温度较低的条件下，草地毛虫(*Gynaephora alpherakjj*)个体性能显著下降(Yang et al, 2017)。微环境的湿度变化会影响昆虫身体组织的水分平衡，进而促进或抑制昆虫的生长发育速率(常晓娜等, 2008)。例如，较低的环境相对湿度会减少亮斑扁角水虻(*Hermetia illucens*)的孵化率和成虫羽化率，并延长其发育时间(Holmes et al, 2012)。昆虫的觅食行为和繁殖也受到光照条件(光强、光周期、波长)的强烈影响(Shi et al, 2017)。与短光照时长相比，长光照可以显著提高西花蓟马(*Frankliniella occidentalis*)的觅食行为和产卵数量(Whittaker & Kirk, 2004)。此外，氮沉降导致的微环境条件改变不仅会对昆虫生理和性能产生直接影响，也会通过改变食物或天敌数量对昆虫产生间接作用，但如何区分微环境变化对昆虫的直接和间接作用尚不清楚。

2.2.2 繁殖生境

氮沉降加剧也会影响昆虫的繁殖生境。氮沉降引起的植物生物量增加及枯落物累积，使得裸地生境迅速下降，可以对专门依赖这些特殊生境昆虫的繁殖(筑巢、求偶、交配及产卵)和生存产生重要影响(de Sassi et al, 2012; Streitberger et al, 2014)。氮沉降引起的繁殖生境丧失被认为是很多昆虫数量下降的主要原因(Nijssen et al, 2017; Sánchez-Bayo & Wyckhuys, 2019)。

2.3 昆虫种间相互作用

昆虫群落存在多种形式的种间相互作用(如竞争、捕食和互惠)。相互作用可以发生在相同营养级的物种间，也存在于不同营养级的物种间，如级联效应(cascade effect)。昆虫群落占据多个营养级，一个营养级的变化会对其他营养级乃至整个食物网产生复杂的影响(Schmitz, 2010; van Klink et al, 2015; 朱玉等, 2017)。氮沉降可以影响同一营养级内的物种互作关系，但研究案例多来自植物群落。例如内蒙古荒漠草原的研究表明，氮沉降显著改变植物的竞争关系(Ma et al, 2022)，而关于氮沉降对相同营养级昆虫的种间竞争或互惠关系的研究比较少见。氮沉降对昆虫多营养级的研究十分匮乏



序号 Number	假说 Hypothesis	描述 Description
H1	资源专食性假说 Resource specialization hypothesis	植食者多样性随植物多样性的增加而增加, 捕食者多样性随植食者多样性的增加而增加(Keddy, 1984) Herbivore diversity increases with increasing plant diversity, and predator diversity increases with increasing herbivore diversity (Keddy, 1984)
H2	氮限制假说 Nitrogen limitation hypothesis	植物和昆虫的氮含量具有很大差异, 因此提高植物的氮含量有利于昆虫的生存、发育以及繁殖(Mattson, 1980) Nitrogen content of plant is quite different from that of insects, therefore increasing the nitrogen concentration of plants is beneficial to the survival, development, and reproduction of insects (Mattson, 1980)
H3	营养平衡假说 Nutrient balance hypothesis	昆虫对植物质量具有特定的营养需求, 植物营养过高或过低都会降低昆虫适合度(Raubenheimer & Simpson, 1993, 2004) Insects have specific nutritional requirements for plant quality, and excessively high or low plant nutrition levels can reduce insect fitness (Raubenheimer & Simpson, 1993, 2004)
H4	更多个体假说 More individuals hypothesis	生产力更高的植物群落可以为植食者提供更丰富的食物资源, 进而支持更多的植食者及天敌(Srivastava & Lawton, 1998) Higher plant productivity provides a greater quantity of food resources for insect herbivores, thereby supporting more herbivores natural enemies (Srivastava & Lawton, 1998)
H5	天敌假说 Enemies hypothesis	昆虫群落内高营养级的天敌数量和多样性可以抑制低营养级的植食者数量和多样性(Russell, 1989) High trophic-level predators within insect communities can suppress the abundance and diversity of low trophic-level herbivores (Russell, 1989)

图2　植物调节不同营养级昆虫间关系的5种主要假说
Fig. 2　Five hypotheses regarding how plants regulate the relationships among insects at different trophic levels

(Nijssen et al, 2017)。根据理论假设, 氮沉降可能通过增加资源输入或提高植物营养水平对昆虫不同营养级产生正向效应, 增加食物链长度; 另一方面, 氮沉降也会引起寄主植物数量减少(如某些开花的杂类草), 降低植物多样性和群落结构异质性, 对昆虫不同营养级产生负面影响, 或者通过改变生境和食物资源适宜性抑制天敌数量, 从而缩短食物链长度(Nijssen et al, 2017)。例如, 氮添加通过降低寄主植食性象甲(*Mecinus pascuorum*)的数量, 显著地抑制了寄生蜂(*Mesopolobus incultus*)的数量(Hancock et al, 2013)。

氮沉降可以对昆虫食物网产生强烈的级联效应。级联效应可以通过上行作用(bottom-up effect), 即通过植食者数量的变化影响更高营养级的天敌数量, 也可以表现为下行作用(top-down effect), 即较高营养级的天敌数量可以控制植食者的种群数量(天敌假说, Russell, 1989)。一般认为草地食物网中植物驱动的上行作用占优势(Scherber et al, 2010; Wan et al, 2022)。氮沉降可以通过改变植物多样性(资源专食性假说)、植物质量(氮限制假说、营养平衡假说)、植物生物量(更多个体假说)影响昆虫不同营养级的种间相互作用(图2)。例如, Zhu等(2023b)的研究表明, 昆虫不同营养级受不同调控机制影响: 植食者对植物质量变化更为敏感, 地表捕食者对植物多样性变化较为敏感, 冠层捕食者对植物生物量变化较为敏感。而下行作用的研究案例相对非常有限。厘清氮沉降背景下上行作用和下行作用在调控草地昆虫群落及其相对贡献中的作用仍然是一项艰巨的挑战。未来亟需基于食物网的方法(food-web approaches)探究昆虫复杂的种间互作关系。

3　展望

综上所述, 当前氮沉降对草地昆虫群落的影响已积累了一定的理论认识和实验证据, 但仍存在诸多不足。第一, 外源氮输入可以同时改变植物群落的多个属性(包括物种丰富度、生产力、群落组成和植物质量), 因此在单一植物群落内很难分离植物群落不同属性对昆虫群落的影响。未来的研究应充分考虑草地植物群落中不同物种或功能群对昆虫群落的影响, 以厘清植物数量、植物质量以及其他植物性状对昆虫群落的独立和联合作用, 有利于梳理氮沉降对昆虫群落的作用机制。第二, 大多数研究关注了氮沉降对低营养级昆虫的影响, 但关于氮沉降对高营养级(如捕食者、寄生者)尤其是昆虫食

物网的影响及调控机制还十分薄弱。在自然环境下, 昆虫多营养级相互作用尤为复杂。随着研究者认识的深入, 尤其是食物网理论发展的需要, 亟需加强氮沉降对草地生物多营养级效应的探索。第三, 氮沉降可以通过改变土壤理化性质对生活在其中的昆虫类群产生影响, 然而氮沉降对土壤昆虫影响的研究比较少见。土壤昆虫与很多地下生态学过程有关, 在维持生态系统养分循环和能量流动方面发挥重要作用。未来应加强氮沉降对土壤昆虫以及地下食物网的影响及调控机制的研究。第四, 功能性状决定了生物的能量代谢、生长、繁殖、扩散等一系列属性并且可以有效指示环境变化或干扰对生物群落组成的影响, 对于研究群落构建机制具有重要的理论意义, 因此基于性状的研究方法(trait-based approaches)在过去几年发展迅速。但关于氮沉降如何影响昆虫功能性状还尚不清楚, 未来应该加强昆虫关键功能性状(如体型大小和移动特性等)对氮沉降响应的研究。第五, 未来的研究应更多考虑氮沉降的长期效应以及更大空间尺度的作用效应。因为氮沉降对昆虫的影响存在滞后效应, 尤其是高营养级昆虫物种对氮沉降的响应可能需要更长的时间才能显现。同时模拟氮沉降的处理多位于面积较小的样地内, 难以判定氮沉降对昆虫群落的影响是来自昆虫短距离内随机迁移的结果还是昆虫种群数量实际发生的变化。第六, 氮沉降和其他全球变化因子(如CO_2浓度升高、增温、降水变化等)存在复杂的交互作用。例如, 氮沉降和大气CO_2浓度增高的协同作用可以使植物产生更高的化学防御水平(同时增加氮基次级代谢物和碳基次级代谢物), 从而对植食性昆虫产生潜在的影响。氮沉降和增温的交互作用可能会加速昆虫的发育速率, 导致昆虫种群数量的暴发。因此未来需要综合考虑多种全球变化因子对草地昆虫群落的影响及机制。

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附录　Supplementary Material

附录1　氮沉降对草地昆虫群落的作用及其影响因素

Appendix 1　Effects of nitrogen deposition on grassland insect community and influence factors

https://www.biodiversity-science.net/fileup/PDF/2023130-1.pdf

附录 1 氮沉降对草地昆虫群落的作用及其影响因素

Appendix 1 Effects of nitrogen deposition on grassland insect community and influence factors

草地类型 Grassland types	施氮时间 Nitrogen application time	施氮强度 Nitrogen application intensity	昆虫类群 Insect groups	响应指标及作用方向 Response and effect direction	参考文献 References
草甸草原 Meadow steppe	4 个月 4 months	0, 10, 17.5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	直翅目(蝗虫) Orthoptera (grasshopper)	多度减少、性能降低 Decrease in abundance and performance	Zhu et al, 2019
	1 年 1 year	0, 13.3 g N m^{-2} $year^{-1}$ 有机肥 Organic fertilizer	鞘翅目(象鼻虫) Coleoptera (weevil)	多度减少 Decrease in abundance	Hancock et al, 2013
	2 年 2 years	0, 10, 30, 60, 90, 120 g N · m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(叶蝉) Hemiptera (leafhopper)	多度增加 Increase in abundance	Prestidge, 1982
	26 年 26 years	0, 2.5 g N m^{-2} $year^{-1}$ NPK 复合肥(Synthetic fertilizer)	膜翅目(熊蜂) Hymenoptera (bumblebee)	多度减少 Decrease in abundance	Villa-Galaviz et al, 2021
典型草原 Typical steppe	3 个月 3 months	0, 100, 200 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	膜翅目(瘿蜂) Hymenoptera (gall wasp)	多度减少 Decrease in abundance	Williams & Cronin, 2004
	4 个月 4 months	0, 10 g N m^{-2} $year^{-1}$ 尿素 Urea	直翅目(蝗虫) Orthoptera (grasshopper) 鳞翅目(毛虫) Lepidoptera (caterpillar) 半翅目(蚜虫) Hemiptera (aphid)	多度增加 Increase in abundance	Prather et al, 2021
	1 年 1 year	0, 5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	鳞翅目(毛虫) Lepidoptera (caterpillar)	多度、生物量增加 Increase in abundance and biomass	de Sassi et al, 2012a
	1 年 1 year	0, 17.5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	直翅目(蝗虫) Orthoptera (grasshopper)	多度减少、性能降低(生存率、生长率、体尺) Decrease in abundance and performance (survival rate, growth rate, body size)	Cease et al, 2012

草地类型 Grassland types	施氮时间 Nitrogen application time	施氮强度 Nitrogen application intensity	昆虫类群 Insect groups	响应指标及作用方向 Response and effect direction	参考文献 References
	2 年 2 years	0, 10 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	直翅目(蝗虫) Orthoptera (grasshopper)	多度增加 Increase in abundance	Loaiza et al, 2011
荒漠草原 Desert steppe	4 个月 4 months	0, 3, 6, 10, 16, 28, 50, 80 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(蝽 叶蝉 蚜虫) Hemiptera (mirid bug leafhopper aphid) 鳞翅目(毛虫) Lepidoptera (caterpillar)	多度增加 Increase in abundance	Strauss, 1987
	1 年 1 year	0, 5.6 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(蝽) Hemiptera (true bug) 鞘翅目(叶甲) Coleoptera (leaf beetle)	多度增加 Increase in abundance	Cuesta et al, 2008
	14 年 14 years	0, 1, 2, 3.4, 5.4, 9.5, 17, 27.2 g N m^{-2} $year^{-1}$ 尿素 Urea	植食性昆虫 Herbivores 腐食性昆虫 Detritivores	多度增加 Increase in abundance	Haddad et al, 2000
			寄生性昆虫 Parasitoids 捕食性昆虫 Predators	多度减少、丰富度减少 Decrease in abundance and richness	
灌丛草地 Shrub grassland	2 年 2 years	0, 7.5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目 Hemiptera	多度增加、丰富度增加 Increase in abundance and richness	Hartley et al, 2003
	9 年 9 years	0, 1, 2, 5, 5.6 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	鞘翅目(叶甲) Coleoptera (leaf beetle)	多度增加 Increase in abundance	Taboada et al, 2016
	9 年 9 years	0, 10 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(蝽 飞虱) Hemiptera (true bug planthopper)	多度增加 Increase in abundance	Richardson et al, 2002
	9 年 9 years	0, 0.5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(蚜虫 粉蚧 角蝉) Hemiptera (aphid mealybug tree hopper)	多度增加 Increase in abundance	Grinath, 2021

草地类型 Grassland types	施氮时间 Nitrogen application time	施氮强度 Nitrogen application intensity	昆虫类群 Insect groups	响应指标及作用方向 Response and effect direction	参考文献 References
高山草地 Alpine grassland	1 年 1 year	0, 5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	膜翅目(寄生蜂) Hymenoptera (parasitic wasp)	多度增加 Increase in abundance	de Sassi et al, 2012b
	2 年 2 years	0, 5 g N m^{-2} $year^{-1}$ 硝酸钙铵 Calcium Ammonium Nitrate	鳞翅目(毛虫) Lepidoptera (caterpillar)	生物量增加 Increase in biomass	de Sassi & Tylianakis, 2012
高寒草甸 Alpine meadow	1 年 1 year	0, 2.8 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	鳞翅目(毛虫) Lepidoptera (caterpillar)	多度减少、性能降低(生长和发育速率) Decrease in abundance and performance (growth, and development rate)	Yang et al, 2017
	8 年 8 years	0, 0.375, 1.5, 7.5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	鳞翅目(毛虫) Lepidoptera (caterpillar)	多度增加 Increase in abundance	Song et al, 2018
	8 年 8 years	0, 2.5, 5, 10 g N m^{-2} $year^{-1}$ 尿素 Urea	鳞翅目(毛虫) Lepidoptera (caterpillar)	多度增加 Increase in abundance	顾慧洁等, 2022
苔原 Tundra	24 年	0, 10 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(飞虱) Hemiptera (planthopper)	多度减少 Decrease in abundance	Asmus et al, 2018
盐沼 Salt marsh	3 个月 3 months	0, 10, 30, 60 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(飞虱) Hemiptera (planthopper)	多度增加、性能提高(存活率、体尺、发育速率) Increase in abundance and performance (survival rate, body size, growth rate)	Huberty & Denno, 2006
	1 年 1 year	0, 44.5 g N m^{-2} $year^{-1}$ 硝酸铵(NH_4NO_3)	半翅目(飞虱 盲蝽) Hemiptera (planthopper mirid bug)	多度增加 Increase in abundance	Gratton & Denno, 2003

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