



•综述•

# 放牧对蜜蜂的影响及其生态修复建议

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**摘要:** 过度放牧对全球大多数草地群落造成严重威胁。蜜蜂是草地群落中的关键传粉类群, 放牧可能引起群落中植物多样性和巢穴资源变动, 从而对蜜蜂多样性产生不利影响。然而, 在放牧历史较长和放牧管理良好的群落, 放牧对蜜蜂多样性也可能存在正面或中性的影响。因此, 放牧如何影响蜜蜂多样性及其在生态修复中的作用还需要深入研究。本研究整合已有文献资料以及近年来的研究实践, 提出通过整合蜜蜂物种丰富度、功能多样性、系统发育多样性, 以及传粉网络特征等与生态系统功能密切相关因素的研究, 能够更加准确地认识蜜蜂多样性在生态修复过程中的动态变化以及存在的问题。对于草地退化程度较低的地区, 建议通过有效的放牧管理, 利用草地群落自身的复原力实现蜜蜂的逐步修复。而对于草地退化严重的地区, 则需要在实行放牧管理的基础上, 通过人为干预的辅助再生策略加速生态修复进程, 如补播草种增加花多度和提供适宜蜜蜂的筑巢环境等。补播草种的筛选和组合要综合考虑其在传粉网络中的角色, 以及花特征和花期物候等因素, 确保蜜蜂在不同花期均能获得足够的食物。针对我国南北方不同草地类型开展蜜蜂丧失机制的调查, 并有针对性地制定蜜蜂的生态修复策略, 具有重要意义。

**关键词:** 草地; 过度放牧; 野生蜂类; 传粉网络; 生态修复

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Zhao QJ, Guo HJ, Meng GT, Zhong MC, Yin J, Liu ZC, Li PR, Chen L, Tao Y, Qiu S, Wang H, Zhao YH (2023) Effects of grazing on bees and suggestions for its ecological restoration. Biodiversity Science, 31, 23037. doi: 10.17520/biods.2023037.

## Effects of grazing on bees and suggestions for its ecological restoration

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### ABSTRACT

**Background & Aims:** Overgrazing poses a dominant threat to the biodiversity of most grassland communities. Bees are the primary pollinator group in the grassland ecosystem. Grazing has generally negative effects on bee diversity by affecting floral and nesting resources in grassland communities. However, in communities with long grazing history and reasonable grazing management, grazing may have a positive or neutral impact on bee diversity. Therefore, how grazing affects bee diversity and its role in ecological restoration needs further study.

收稿日期: 2023-02-09; 接受日期: 2023-04-18

基金项目: 中国科学院战略性先导科技专项(XDB31000000)、云南省基础研究专项重大项目(202101BC070003)、云南省基础研究计划面上项目(202201AT070633)、中央财政林业草原生态保护恢复专项和云岭学者项目和兴滇英才项目

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**Progress:** In this study, we integrate the recent literature and research practice, and propose that the efficacy of bee restoration can be more accurately assessed through the integration of bee species richness, functional diversity, phylogenetic diversity and full plant-pollinator interaction networks, which provide comprehensive and quantitative information on the structure and function of grassland communities. For grasslands with low degradation, bees can be gradually recovered by effective grazing management, which uses the natural recovery potential of the communities. For grasslands with greater degradation, it is necessary to accelerate the bee restoration through active interventions on the basis of grazing management, such as sowing wildflower species that cannot migrate into the restoration area without assistance and enhancing the availability of nesting habitat for bees. To ensure that bees can obtain enough floral rewards in different flowering periods, the selection and combination of the sown flower species should take into account their roles in the pollination network, floral traits and flowering phenology.

**Perspective:** It is of great practical significance to investigate the mechanism of bee loss in different types of grasslands in southern and northern China, and to guide the development of targeted ecological restoration strategies for bees.

**Key words:** grassland; overgrazing; wild bees; pollination network; ecological restoration

传粉昆虫是生物多样性的重要组成部分, 它们为植物提供传粉服务, 在维持遗传多样性、提高结实率等方面具有重要意义(Black et al, 2011)。广义的蜜蜂包括了蜜蜂总科的全部种类, 它们为地球上超过75%的被子植物传粉, 是最重要的传粉昆虫(Ollerton et al, 2011; Khalifa et al, 2021)。相较于其他传粉昆虫, 大部分蜜蜂因具有密集且分叉的体毛, 以及后足的携粉结构而具有更强的携粉能力(Michener, 2007)。据报道, 蜜蜂总科近2万种, 其中被驯养的仅有少数几种, 如西方蜜蜂(*Apis mellifera*)、东方蜜蜂(*A. cerana*)和欧洲熊蜂(*Bombus terrestris*)等, 而绝大部分种类都是野生蜜蜂(Michener, 2007)。野生蜜蜂通常受生存环境等因素影响而具有不同的生活习性, 并且与蜜(粉)源植物存在长期的协同适应, 提供着不可替代的传粉服务(Fenster et al, 2004)。

随着气候变化、物种入侵, 以及牧业生态系统管理实践活动等加剧, 蜜蜂种类和数量急剧下降(Kluser & Peduzzi, 2007; Stokstad, 2007; Potts et al, 2010; Meeus et al, 2018)。Bartomeus等(2013)对美国近500种蜜蜂的研究发现, 几乎所有蜜蜂种群数量都存在不同程度的降低, 其中熊蜂属(*Bombus*)物种的种群数量下降最为显著。虽然欧美以外地区的传粉昆虫监测数据较为薄弱, 但全球范围内野生和驯化的传粉昆虫种群数量下降是普遍存在的(Wagner, 2020)。传粉昆虫的减少可能导致传粉服务的丧失, 从而影响粮食安全、生物多样性的维持以及生态系统稳定性(Powney et al, 2019)。

放牧是一种普遍的草地利用方式, 地球上近

25%的陆地被用于放牧(Ramankutty et al, 2008; Ma et al, 2019)。畜牧业是牧民最主要的收入来源, 放牧不仅可以为人类提供生活及生产所必备的肉、奶和皮毛制品, 而且还被作为促进生物多样性和维持栖息地稳定的有效管理措施(Pykälä, 2000)。合理放牧施加的干扰对维持一个以草本植物为主的群落有积极作用, 同时也能够维持群落内更多样的传粉者, 并为传粉者提供更多的潜在筑巢资源(Black et al, 2011)。然而, 放牧行为通常仅在低至中等水平时有益, 过度放牧则对生态系统和畜牧业产生不利影响。牲畜过度取食可导致群落植被高度和生物量降低、植物多样性锐减、植物组成变化和土壤条件变化(如践踏作用、粪便沉积)等一系列的环境和生态问题(Enri et al, 2017), 这些改变会影响蜜蜂的食物(花粉和花蜜)和筑巢资源, 并进而影响传粉者的种群动态和多样性(Moreira et al, 2019; Wagner, 2020)。研究表明, 在北美和中国北方草地, 过度放牧已对生物多样性和生态系统功能产生较大威胁(Kimoto et al, 2012; 高二亮等, 2020)。

本文主要探讨放牧对蜜蜂的影响。蜜蜂在社会组织、体型大小、访花偏好和所需筑巢材料等方面呈现很高的多样性, 对放牧干扰的响应可能存在较大差异(Michener, 2007)。蜜蜂大都一年一代, 对筑巢环境有一定的选择性, 因此对群落变化更为敏感, 可以作为放牧对传粉者影响的指示物种(Odanaka & Rehan, 2019)。本文主要阐述放牧如何通过直接和间接作用影响蜜蜂的多度和多样性, 以及蜜蜂对放牧的响应及其生态修复建议。

## 1 放牧对蜜蜂的影响途径

### 1.1 放牧改变植物群落花报酬资源

由于群落中不同植物的生活史特征、营养水平以及对植食者防御能力等不同, 牲畜取食对蜜蜂的影响存在差异。Díaz等(2007)对世界不同牧场植物组成的研究发现, 放牧对多年生、植株高大和直立生长的植物具有更高的不利影响。在大部分牧场中, 放牧可能会导致适口植物多度和多样性降低或局部灭绝, 而物理和化学防御作用较强的非适口植物则逐渐泛滥和扩张(Vázquez & Simberloff, 2003; Mayer et al, 2006; Vavra et al, 2007; Zhao et al, 2021)。群落中植物组成的改变会导致花报酬发生相应的变化。植物花粉和花蜜是蜜蜂成虫和幼虫的能量来源(Kevan & Baker, 1983), 多项研究发现, 花报酬资源与蜜蜂多度和多样性正相关, 是影响蜜蜂在群落中种群变化的重要因素(Sárospataki et al, 2009; Roulston & Goodell, 2011)。研究表明花报酬的多度及组成的改变会影响蜜蜂访花行为(Hatfield & LeBuhn, 2007; Franzén & Nilsson, 2010; Roulston & Goodell, 2011)。当牲畜偏好取食禾本科等非虫媒植物时, 对蜜蜂产生的影响较小(Lázaro et al, 2016a; Tadey, 2016; Odanaka & Rehan, 2019)。而当牲畜偏好取食虫媒植物时, 可对蜜蜂产生多方面的负面影响。首先, 牲畜取食作用可能改变植物的开花物候, 导致植物和传粉者时间错配, 从而影响蜜蜂访花(Tadey, 2020)。其次, 蜜蜂偏向于不访问刚被牲畜取食过的植物的花, 因此牲畜高强度的取食对蜜蜂访花频率产生较强的不利影响(Bronstein et al, 2007)。再次, 牲畜取食可能通过影响植物的植株高度和花报酬多度而影响蜜蜂在单位时间内的报酬获取量(Davidson et al, 2020)。虽然一部分蜜蜂可以访问多种开花植物, 能够通过访问群落内其他植物缓解放牧带来的不利影响, 但如果这些植物花报酬量较低或存在花部特征限制, 则依旧会使蜜蜂取食效率下降(Zhao et al, 2022)。

蜜蜂获取花报酬数量和质量的降低会导致资源受限, 进而影响种群动态。由于专性取食的蜜蜂依靠少数植物提供报酬, 它们受放牧的不利影响可能高于取食多种植物的蜜蜂。据报道, 世界不同地区约有15%–60%的蜜蜂是专性取食者, 放牧可能导

致这些蜜蜂多样性快速降低(Minckley & Roulston, 2006)。但也有研究发现, 广食性蜜蜂也会受到食物短缺的不利影响。例如, 壁蜂(*Osmia lignaria*)受到资源不足的影响会使子代数量降低(Williams & Kremen, 2007)。花资源不足还会导致熊蜂产生更少且更小的工蜂个体(Pelletier & McNeil, 2003; Westphal et al, 2009)。另外, 蜜蜂幼虫营养不足会降低其对真菌、细菌和病毒疾病的抵抗能力, 存活率降低(Di Pasquale et al, 2013)。

然而, 牲畜植食作用对蜜蜂的影响也并不总是有害的。取食作用可以激发一些植物的补偿效应, 即在面对牲畜啃食后会加大对花资源投入, 访问这些植物的蜜蜂会由此获益(Schiestl et al, 2014)。另外, 牲畜的选择性取食会使非适口植物获得竞争优势而在群落中扩张, 这会使得以其为食的蜜蜂的多度增加(Zhao et al, 2021)。

### 1.2 放牧改变巢穴资源

蜜蜂是全变态昆虫, 其生活史的卵、幼虫和蛹期都在巢穴中度过, 成虫也会由于筑巢、储存花粉和花蜜、产卵等活动而在巢内停留较长时间。巢穴可以保护蜜蜂成虫和发育中的幼虫免受天敌、寄生者和极端天气的伤害(Roulston & Goodell, 2011)。虽然蜜蜂筑巢位置的选择具有较高多样性, 在土壤、石缝、墙壁、植物茎秆和腐木等位置中筑巢, 但是约有70%的蜜蜂在土壤中均可筑巢, 包括地蜂科、隧蜂科和准蜂科的几乎所有物种, 以及分舌蜂科、切叶蜂科和蜜蜂科的大部分物种; 另外30%的蜜蜂, 例如分舌蜂科和蜜蜂科部分物种, 在植物的髓茎和腐木上的虫洞中筑巢(Michener, 2007; 图1)。

蜜蜂的巢穴资源是有限的, 放牧可通过影响巢穴资源进而对蜜蜂产生影响。大部分在土壤中挖土筑巢的蜜蜂需要裸露的土地。已有研究发现, 在土壤中筑巢蜜蜂的多度和裸地的面积成正相关(Sardiñas & Kremen, 2014)。放牧活动中动物的啃食和践踏会导致植被盖度降低, 创造出新的裸露土地促进蜜蜂在土中筑巢(Vulliamy et al, 2006; Murray et al, 2012)。但牲畜的践踏作用也会压实土壤或直接破坏巢穴, 对蜜蜂筑巢不利(Murray et al, 2012)。例如, 放牧的践踏导致蜜蜂巢穴受损, 使成虫失去遮蔽所、幼虫直接死亡(Sjödin, 2007; Tadey, 2015; Lázaro et al, 2016a)。据报道, 在德国石灰质的草地



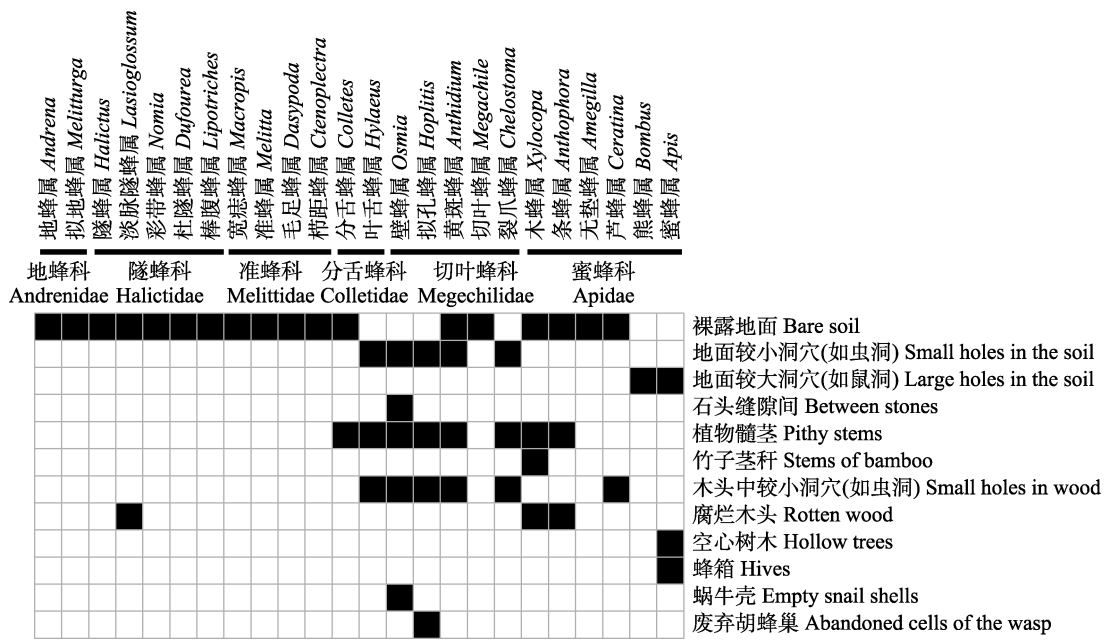


图1 蜜蜂总科主要类群筑巢环境。黑色方格: 蜜蜂可以使用的筑巢地点; 白色方格: 蜜蜂不可以使用的筑巢地点。数据来自 Michener (2007)和Harmon-Threatt (2020)。  
Fig. 1 The nesting sites of the main groups in Apoidea. Black cells: The nesting sites can be used by the bee genus; white cells: The nesting sites cannot be used by the bee genus. Data from Michener (2007) and Harmon-Threatt (2020).

上, 壁蜂(*Osmia* spp.)利用空的蜗牛壳建造巢穴, 但牲畜的踩踏会导致超过 1/3 的蜂巢受损 (Hopfenmüller et al, 2020)。

放牧对利用土壤中已有洞穴筑巢的蜜蜂的不利影响可能更大。熊蜂属大部分物种在兔形目和啮齿目动物废弃的巢穴中筑巢。切叶蜂科的壁蜂属 (*Osmia*)、拟孔蜂属 (*Hoplitis*)、黄斑蜂属 (*Anthidium*)、裂爪蜂属 (*Chelostoma*), 以及分舌蜂科叶舌蜂属 (*Hylaeus*)的部分物种依靠土壤中已有的虫洞筑巢。在对美国加州牧场的研究发现, 蜜蜂的多度和已有洞穴的数目正相关 (McFrederick & LeBuhn, 2006), 但羊的踩踏使多数废弃的洞穴不能被蜜蜂用于筑巢 (Sugden, 1985)。如果放牧使植物结实率降低, 会导致以植物种子为食的鼠类和昆虫洞穴减少, 从而使蜜蜂潜在可用巢穴资源降低。对于利用植物茎秆或树枝筑巢的蜜蜂, 由于其巢穴相比土中的巢穴更易暴露, 牲畜的踩踏和啃食行为对巢穴产生的影响可能更大 (Potts et al, 2009; Roulston & Goodell, 2011)。此外, 一些在土中和植物上筑巢的蜜蜂还需要叶片和树脂等作为筑巢材料, 放牧导致这些资源缺乏进而对蜜蜂产生不利影响 (Gess & Gess, 1993)。

## 2 放牧对蜜蜂的影响在不同研究中存在差异

放牧会显著影响蜜蜂多度和多样性已经得到广泛认同, 但放牧对蜜蜂群落的影响在不同研究中呈现较大差异。一些研究发现, 放牧降低了蜜蜂多度和物种丰富度; 而另一些研究发现, 放牧对蜜蜂群落存在中性甚至是积极的影响 (表1)。这些不同影响可能与不同研究中生境类型、放牧历史、牲畜种类、放牧强度和放牧季节等因素存在差异有关 (Kimoto et al, 2012)。

### 2.1 不同生境中放牧对蜜蜂的作用

不同生境中由于降水和土壤等环境因子的差异, 植物多样性、组成和植被有所不同, 对放牧可能存在不同的响应。放牧对植物物种的影响随着群落中降水量(或生产力)的增加而增加 (Cingo-lani et al, 2005; Lezama et al, 2014)。干旱地区植物对放牧的抵抗能力更强, 可能与其植株矮小、地下生物量比例高、具基部分生组织和较高的分枝密度等特征相关 (Herms & Mattson, 1992)。放牧通过影响植物而间接影响与其发生相互作用的蜜蜂, 这种影响可能在高降水地区更大 (Thapa-Magar et al, 2022)。已有研究发现, 湿润生境中放牧对蜜蜂多度和多样性的

**表1** 草地群落中放牧对蜜蜂多度和多样性的影响研究案例。放牧对蜜蜂多度和多样性存在正面(+)、中性(0)或负面影响(-)。  
**Table 1** Studies investigated the effects of grazing on bee abundance and species richness in grasslands. Livestock grazing could have a positive (+), neutral (0) or negative (-) effect on bee abundance and diversity.

研究区域 Study area	牲畜种类 Livestock species	蜜蜂类群 Functional groups of bees	放牧对蜜蜂多度的影响 Effect of grazing on bee abundance	放牧对蜜蜂物种丰富度的影响 Effect of grazing on bee richness	文献 Reference
美国西北部 Northwest United States	牛 Cattle	熊蜂 Bumblebees	-	-	Kimoto et al, 2012
美国西北部 Northwest United States	牛 Cattle	独栖性蜜蜂 Solitary bees	0	0	Kimoto et al, 2012
美国中西部 Midwest United States	牛 Cattle	蜜蜂总科物种 Apoidea	0	0	Stein et al, 2020
美国西南部 Southwest United States	牛、羊 Cattle, sheep	熊蜂 Bumblebees	0	-	Hatfield & LeBuhn, 2007
美国西南部 Southwest United States	牛 Cattle	蜜蜂总科物种 Apoidea	-	0	Minckley, 2014
美国西部 Western United States	牛 Cattle	蜜蜂总科物种 Apoidea	-	0	Kearns & Oliveras, 2009
英国威尔士 Wales, UK	牛、马、羊 Cattle, ponies, sheep	蜜蜂总科物种 Apoidea	-	-	Davidson et al, 2020
德国北部 Northern Germany	牛 Cattle	蜜蜂总科物种 Apoidea	+	-	Kruess & Tscharntke, 2002
德国西北部 Northwest Germany	羊 Sheep	独栖性蜜蜂 Solitary bees	0	0	Steffan-Dewenter & Leschke, 2003
匈牙利东南部 Southeast Hungary	牛 Cattle	蜜蜂总科物种 Apoidea	0	0	Batáry et al, 2010
瑞典中部 Central Sweden	牛 Cattle	蜜蜂总科物种 Apoidea	0	0	Sjödin, 2007
中国西南部 Southwest China	牦牛 Yak	熊蜂 Bumblebees	-	-	Xie et al, 2008

不利影响高于半干旱的生境(Herrero-Jauregui & Oosterheld, 2018)。在蒙古国东部半干旱地区, 高强度放牧虽然导致植物减少, 但对植物-传粉者物种互作数目没有显著负面影响(Yoshihara et al, 2008)。干旱地区蜜蜂受放牧的影响更小还可能与蜜蜂巢穴资源受到放牧影响较小有关。相比高降水牧场, 干旱地区牧场中较低的土壤含水量使其难以被牲畜践踏而压实, 这对在土壤中筑巢的蜜蜂更加有利(El-Swaify et al, 1985)。

**2.2 不同放牧历史草地中放牧对蜜蜂的影响**

放牧对蜜蜂的影响程度会受到草地和牲畜局部适应历史的影响。经历了牲畜长期取食的草场适牧性和耐牧性较高, 不会轻易被牲畜破坏。研究发现, 在被用作牧场使用的时间久远的草地, 植物可以通过快速再生的形式提高耐受性, 或以匍匐生长或提高二氧化硅含量的形式进行防御(Díaz et al, 2007)。对牲畜啃食有长期适应的草地, 群落的稳定会确保蜜蜂等种群不会发生剧烈的波动(Newbold et

al, 2014)。对美国不同牧场研究表明, 北美大平原相比其他牧区放牧历史更久, 放牧对传粉者的不利影响较小(Glenny et al, 2022)。如果草地和牲畜的演化史较短, 那么牲畜对草地生态群落是极大的威胁(Debano, 2006; Thapa-Magar et al, 2022)。

**2.3 不同牲畜种类放牧对蜜蜂的影响**

牛和羊是草地中最常见的反刍动物, 虽然二者消化系统类型相似, 但由于它们在体型大小、瘤胃容积、取食灵活性和取食偏好上存在差异, 会对草地植物群落和蜜蜂产生不同影响(Hanley, 1982)。羊在取食过程中能够更好地区分植物, 并偏好取食虫媒植物, 羊会优先选择植株上最有营养的花、果实和嫩枝(Rook et al, 2004; Redpath et al, 2010; Dumont et al, 2011; Ginane et al, 2015)。而牛对植物的取食偏好性较低, 并会取食更高比例的风媒植物, 如禾草等(Cutter et al, 2021)。另外, 羊在植物很矮的情况下依然可以取食, 而牛难以取食低矮的植物(Rook et al, 2004)。因此, 以牛为主和以羊为主放牧

导致植物组成存在差异(Dumont et al, 2011)。多项研究发现, 牧羊对蜜蜂多度、物种丰富度和功能多样性的不利影响均大于牧牛(Dumont et al, 2011; Enri et al, 2017; Glenney et al, 2022)。例如, 对美国西部内华达州和中部北达科他州牧场研究均发现, 牧羊相比牧牛对花多度、蜜蜂多度和蜜蜂多样性均有更强的负面影响(Hatfield & LeBuhn, 2007; Cutter et al, 2021)。有研究还发现, 在降水合适的年份, 牛可以通过抑制禾草和促进虫媒植物的生长, 使得蜜蜂受益于放牧(Kaminer et al, 2010; Enri et al, 2017)。

#### 2.4 不同放牧强度和放牧季节的影响

同一牧区即使牲畜种类相同, 但如果放牧强度存在差异, 对蜜蜂的影响也可能不同。根据中度干扰假说(intermediate disturbance hypothesis), 在中度放牧压力下, 由于牲畜对优势植物和多年生植物的抑制作用, 给竞争能力较弱植物创造出开放的空间, 可以形成一个物种更丰富的植物群落(Tadey, 2016; Wang & Tang, 2019; Gao & Carmel, 2020)。在对希腊蜜蜂的研究中发现, 蜜蜂多度和物种丰富度随放牧强度呈现先升高再降低的钟状曲线关系, 符合中度干扰假说的推断(Lázaro et al, 2016b)。然而, 更多的研究发现, 放牧强度和蜜蜂多样性存在负相关(Söderström et al, 2001; Xie et al, 2008; Thapa-Magar et al, 2022)或正相关(Vulliamy et al, 2006) (表1)。正相关的结果可能是针对放牧强度低的群落, 而负相关的结果可能是针对放牧强度高的群落。因此, 后续研究应尽可能覆盖较宽的放牧强度, 这样才能准确验证中度干扰假说是否能解释放牧对蜜蜂的影响。

不同季节为主的放牧也可能对蜜蜂产生不同影响。研究发现, 早春放牧会导致蜜蜂物种丰富度降低(Xie et al, 2008; Kimoto et al, 2012)。另外, 早春放牧导致的花资源降低引起蜜蜂种群的变化还会延伸至夏秋季的花期(Waser & Real, 1979), 而将放牧时间从早春推迟到夏季对蜜蜂多度和多样性均有正面影响(Sjödin, 2007)。

### 3 如何解决放牧对蜜蜂及其传粉植物产生的不利影响

适度放牧能够维持蜜蜂和植物多样性, 但过度放牧造成的蜜蜂种群下降和多样性丧失, 会对野生

植物和栽培作物的结实率以及遗传多样性产生不利影响(Potts et al, 2010)。生态修复是目前解决蜜蜂多样下降及其传粉服务丧失的重要途径。为实施已受到放牧不利影响的蜜蜂种群的生态修复, 首先应明晰放牧如何影响蜜蜂种群动态, 然后制定有针对性的措施来消除或减轻放牧对蜜蜂的负面影响(Goulson et al, 2008; Wagner, 2020)。

#### 3.1 加强对牧区蜜蜂群落的野外调查

对于蜜蜂的保护和生态修复工作, 首先应该对目标区域内蜜蜂现阶段的生存状况进行系统调查。这需要对蜜蜂种群开展长期且详尽的观测, 但以往的研究主要以蜜蜂科级水平为调查单元, 较少精确到属种水平(Hatfield & LeBuhn, 2007; Yoshihara et al, 2008; Kearns & Oliveras, 2009)。同属中的蜜蜂可能表现出不同的行为和生活史特征。例如, 熊蜂属物种可以在地面或地下筑巢, 也可以利用自身或其他熊蜂的工蜂哺育后代(盗寄生; Michener, 2007)。这些习性的差异会导致不同物种对放牧的响应不同(Sjödin, 2007)。因此, 后续对蜜蜂的调查研究应以种为单元, 这可以促进对放牧如何影响蜜蜂群落的认识, 并有针对性地制定出不同物种的保护和修复方案。目前, 我国对蜜蜂的分类学研究还较为薄弱, 已经出版的《中国动物志》中仅包括了蜜蜂科、切叶蜂科和准蜂科, 而有关地蜂科、隧蜂科和分舌蜂科的分类学资料还很缺乏(吴燕如, 2000, 2006)。另外, 为了便于生态学工作者使用, 一个地区的蜜蜂分类学信息应尽量包括物种目录、图像数据库和DNA序列库3个部分(Orr et al, 2022)。

#### 3.2 准确评估放牧对蜜蜂多样性和传粉服务的影响

经过详尽野外调查后, 需根据调查数据绘制放牧强度和蜜蜂多样性的相关性曲线对放牧造成的影响进行评估。其中放牧强度可以用载畜率、牲畜粪便量和围栏内外生物量比等确定(Yoshihara et al, 2008; 王梦佳等, 2017; Wang et al, 2019; Dara et al, 2020)。为了更准确地判断不同群落中蜜蜂受放牧影响的程度, 应将放牧强度作为连续变量并覆盖较宽的范围, 而不是仅考虑是否存在放牧行为。

描述蜜蜂群落多样性的指数包括物种丰富度、Shannon多样性、功能多样性和系统发育多样性等, 这些指数是生物多样性不同方面的统计表现(Grab et al, 2019; Banaszak-Cibicka & Dylewski, 2021)。在



放牧对蜜蜂影响研究中, 多样性指数的选择直接影响评估的可靠性。以往研究主要探讨放牧对蜜蜂物种丰富度的影响, 即认为物种丰富度和生态系统功能正相关(Davidson et al, 2020)。然而, 研究发现, 只有在物种多样性较低的群落中, 物种多样性才与生态系统功能正相关(Chapin et al, 2000)。在物种丰富度较高的群落中, 由于生态位重叠、功能冗余和种间竞争加剧, 物种丰富度和生态系统功能甚至存在负相关(Tilman et al, 1997)。因此, 仅用物种丰富度判断生态系统功能是否健康具有一定的局限性。

有研究发现, 功能多样性可以综合反映物种形态、生理和生殖等与生态系统功能相关性状的多样性, 这克服了物种丰富度指数同等对待每个物种的不足(Tilman, 2001)。另外, 系统发育多样性可以从进化维度进一步描述一个群落的生物多样性。具有较高系统发育多样性的群落能够促进更高营养级物种的维持(Wimp et al, 2005), 并加强群落对外来物种入侵和极端天气的抵御能力(Vellend et al, 2010; Cadotte et al, 2012)。如果蜜蜂的功能性状具有保守性, 维持较高的系统发育多样性还能保证群落有较高的功能多样性(Mouquet et al, 2012; Srivastava et al, 2012)。已有研究发现, 蜜蜂对环境变化的耐受性与其功能性状和系统发育相关(Williams et al, 2010; Bartomeus et al, 2013)。在健康群落中, 具有不同功能性状远缘物种的共存有利于资源利用和生态系统稳定性。而在退化群落中, 具有相似功能性状的近缘物种可能同时灭绝, 导致功能多样性和系统发育多样性显著降低。虽然功能多样性和系统发育多样性与生态系统功能之间具有更强的相关性(Winfree et al, 2018), 可以作为评估放牧对蜜蜂多样性影响更可靠的指标, 但目前的相关研究还很不足。

由于蜜蜂和植物间的互作蕴含传粉这一关键的生态系统功能, 物种互作也可以作为评估放牧对蜜蜂影响的核心指标之一(Cariveau et al, 2020; Genes & Dirzo, 2022)。近年来一些开创性的研究指出, 传粉网络不仅包含植物和传粉者物种丰富度信息, 还包括物种间的相互作用, 因此可以作为评估生态系统稳定性更可靠的综合性指标(Harvey et al, 2017; Moreno-Mateos et al, 2020)。传粉网络的结构特征会影响其对外部干扰的反应方式。传粉网络中

物种间由于常存在弥散性协同进化关系, 而具有较高的嵌套结构(Bascompte & Jordano, 2007)。传粉网络的这一属性赋予了群落抵御干扰的能力, 但在退化生态系统中嵌套结构则变弱或消失(Kaiser-Bunbury & Blüthgen, 2015)。已有实验研究表明, 放牧会使物种相互作用发生重排, 并导致整个传粉网络结构发生改变(Vázquez & Simberloff, 2003; Elwell et al, 2016)。

虽然功能多样性、系统发育多样性和生态网络物种互作多样性研究相比物种丰富度的统计要困难得多, 但应用这些指数可以综合考虑到物种之间的进化、功能性状、生态位重叠和功能冗余, 能够更好地反映蜜蜂多样性随放牧强度增加的变化规律。但值得注意的是, 如果不同群落降雨量、放牧历史和牲畜组成等因素存在较大差异, 那么会存在不同的放牧强度-蜜蜂多样性的变化。在我国, 北方和南方草地在自然环境、群落外貌、用作牧场使用的时间和物种多样性等方面存在明显不同, 因此放牧对蜜蜂的影响可能不同。今后需要加强放牧对我国南北方草地的比较研究, 以期更深刻地认识蜜蜂多样性丧失机制。

### 3.3 放牧导致退化草地中蜜蜂生态修复策略的制定

对于放牧导致蜜蜂丧失的草地, 生态修复能够顺利实施需要降低高牧压带来的不利影响。草地具有一定的自我修复能力, 植物物种可以通过土壤种子库或附近群落中种子的自然散布进行修复, 蜜蜂也可以从相邻群落扩散实现多样性提升。如果草地退化程度较低, 蜜蜂可在放牧压力减少的情况下实现自我修复。降低放牧压力可以通过一系列放牧管理措施实现, 包括控制牲畜种类(如提高牛而降低羊的比例)、控制放牧时间(如轮牧和季节性休牧)、控制载畜量等措施。围栏封育是降低放牧不利影响最经济且便捷的自然再生措施。研究发现, 花期围封禁牧和轮牧可显著提升群落内的花多度, 为蜜蜂和其他传粉昆虫提供更丰富的花粉和花蜜报酬, 从而促进其种群的修复(Scohier et al, 2013; Enri et al, 2017)。另外, 在一个区域内设置部分中等放牧草地和部分围封禁牧草地可增加生境异质性, 对蜜蜂多样性修复更为有利(Shapira et al, 2020)。

如果放牧对蜜蜂的影响较为严重, 可以在降低放牧干扰的基础上通过辅助再生的人为干预手段

进行生态修复(Gann et al, 2019)。大量研究发现, 放牧导致的食物缺乏是限制蜜蜂生态修复的重要因素(Xie et al, 2008; Davidson et al, 2020)。因此, 蜜蜂的生态修复可以通过在局域和地区水平补充食物资源实现(Haaland et al, 2011; Roulston & Goodell, 2011; Pywell et al, 2012; Baldock et al, 2019)。在耕地边界人工种植树篱和野花带以增强蜜蜂和其他传粉昆虫多样性是一种有效措施, 已经在欧洲多个国家农作物种植区实施(Haaland et al, 2011; Scheper et al, 2015)。蜜蜂修复程度和所种植植物的物种组成密切相关。研究发现, 群落中少数几种植物大面积开花就能维持较高的蜜蜂多样性, 因此增加蜜蜂偏好取食的植物的开花多度, 而非单纯增加植物多样性对蜜蜂种群修复更加有利(Carvell et al, 2007)。豆科植物是优质的蜜源和粉源植物, 是欧洲人工播种促进独栖性蜜蜂和熊蜂生态修复的首选物种(Scheper et al, 2015)。然而, 不同群落蜜蜂组成不同, 访花偏好也存在差异, 同一植物种植组合方案很难适用于所有群落。因此, 需要对计划种植的植物进行有针对性的筛选和组合才能实现更高效的修复。需要关注的是对传粉网络中物种担任角色进行分析可以甄别出群落中对蜜蜂多样性维持起关键作用的枢纽植物。枢纽植物的种群动态控制着蜜蜂群落的动态, 因此在修复计划中应优先考虑。由于一个花期内不同种蜜蜂成虫访花时间存在差异, 种植植物的选择还需考虑其开花时间和花期长度, 从而确保蜜蜂在不同花期均能获得足够的食物(Pywell et al, 2005; Pywell et al, 2006; Potts et al, 2009)。

巢穴资源是另一个维持蜜蜂多度和多样性的关键因素, 但相比增加食物资源, 蜜蜂生态修复还未受到足够关注(Harmon-Threatt, 2020)。大多数野生蜜蜂都是在土壤中筑巢(Michener, 2007), 因此其生态修复可以通过为蜜蜂提供更适合的筑巢地点实现, 如提供更多暴露在高温和高光照条件下的干燥土壤。对于在植物上筑巢的蜜蜂, 则可以提供枯木和巢管等“蜜蜂旅馆”提升筑巢资源(Buckles & Harmon-Threatt, 2019; Harmon-Threatt, 2020)。已有研究表明, 为蜜蜂创造这些筑巢生境会促进蜜蜂多度和多样性快速修复(Hernandez et al, 2009; Pawelek et al, 2009)。瑞士实行的农业环境改善计划会在农田附近保留面积不低于7%的生态保护区用

于蜜蜂筑巢, 此项措施对独居蜂和蜜蜂的种群修复有积极效果(Albrecht et al, 2007)。

## 4 结语

过度放牧导致的传粉者丧失在全球范围内普遍发生。近年来, 生态修复因可以缓解和扭转栖息地丧失和生物多样性下降而受到国内外学者的广泛关注(Perring et al, 2015)。我国草地占土地面积的41.7%, 而其中90%由于过度放牧和过度耕种等的影响发生退化(Waldron et al, 2010)。实施全国草地群落保护和修复意义重大。本研究认为蜜蜂是草原生态系统中重要的传粉昆虫, 应作为一个重要的生态修复目标。在过度放牧草地上, 蜜蜂群落修复应该如何设计并实施, 首先要评估放牧对蜜蜂多样性的影响程度。本研究建议优先分析功能多样性、系统发育多样性, 以及传粉网络这些与生态系统功能密切相关的特征, 因为这些特征能够更加准确地研究蜜蜂多样性随放牧强度增加的变化规律。退化程度较低的草地群落可以通过有效的放牧管理, 利用生态系统的自身复原力实现蜜蜂群落的逐步修复。退化严重的草地因其自我修复能力较低, 则需要实行放牧管理的基础上通过人为干预的辅助再生策略加速生态修复进程。补播草种增加群落中粉源和蜜源植物多度的辅助措施可作为首选。蜜蜂的生态修复还可以通过为其提供更适合的筑巢资源实现: 对于在土壤中筑巢的蜜蜂, 为其提供更多暴露在高温和高光照条件下的干燥土壤; 对于利用植物筑巢的蜜蜂, 提供巢管和枯木等筑巢资源。植物的筛选和组合要综合考虑其在传粉网络中的角色, 花特征、花期物候等因素, 确保蜜蜂在不同花期均能获得足够的食物。我国幅员辽阔, 对不同地区代表性草地类型制定有针对性的蜜蜂修复策略, 对草地群落健康发展将产生积极影响。

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