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## 土壤动物与土壤健康\*

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**摘要:** 土壤动物与土壤健康息息相关, 土壤动物多样性和功能能够灵敏反映人类活动和气候变化引起的土壤扰动。同时, 土壤动物还通过与生物和非生物组分间的相互作用对地上生态系统产生反馈作用。当前土壤动物在土壤健康评价体系中的应用相对较少, 主要集中在土壤线虫、节肢动物和蚯蚓等类群, 仍缺乏基于土壤动物的系统性评价指标。因此, 本文围绕土壤动物在指示土壤健康方面的潜力, 系统总结了现有基于土壤动物的土壤健康评价指标, 强调未来应建立和完善土壤动物基因组信息数据库, 挖掘土壤动物的功能性状, 加强土壤食物网结构和生态功能的研究, 建立集成土壤动物物种多样性、功能性状和土壤食物网的指标体系, 从而促进土壤健康和生态系统的可持续发展。

**关键词:** 土壤健康; 土壤动物; 功能性状; 土壤食物网

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## Soil Fauna and Soil Health

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**Abstract:** Soil fauna play important roles in the maintenance of soil health. Soil biodiversity can sensitively reflect soil disturbances caused by human activities and climate change, and can also influence the above-ground ecosystem through interactions with other below-ground components. Inadequate knowledge on the taxonomy of soil animals as well as the complexity of soil food web greatly limit the research on the linkage between soil fauna and soil health. Thus, we review the recent advances in soil fauna as indicators of soil health, highlight the significance of soil fauna and soil food webs in the maintenance of healthy soil, and propose ways to improve the genome and functional traits database. Soil health assessment that integrates the diversity of soil fauna, functional traits, and soil food web structure is thought to be the most promising, and will

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promote soil health and sustainable development of the ecosystem.

**Key words:** Soil health; Soil fauna; Functional traits; Soil food web

土壤作为地球关键带的核心组成部分,其健康与大气、水环境质量密切相关,决定着植物、动物和人类的健康,同时也是保障农业可持续发展和支撑美丽中国的重要基础<sup>[1-2]</sup>。随着人口增长、气候变化、不合理的土地利用及环境污染等问题的加剧,土壤生态系统正面临着严峻的考验<sup>[3-4]</sup>,提升土壤质量和维持土壤健康成为我国土壤科学研究关注的焦点和前沿<sup>[5]</sup>。

土壤健康是指土壤履行生态系统服务功能的持续能力<sup>[6-7]</sup>,更加注重土壤质量随时间和管理而变化的动态特性,因此,需要通过一系列动态指标来评估土壤健康状况<sup>[8-9]</sup>。相比土壤理化特性,土壤生物学特性对环境条件的变化更敏感,目前常用的生物学指标主要包括土壤微生物生物量及活性、碳氮矿化速率、土壤呼吸作用和土壤生物网络复杂度等<sup>[9-10]</sup>,而对土壤动物相关指标涉及的较少<sup>[11]</sup>。土壤动物作为土壤生物多样性的重要组分,其种类丰富且高度多样化,具有广泛的生活史策略和摄食类型<sup>[12]</sup>,在生态系统功能、植物群落动态乃至人类健康中均发挥着至关重要的作用<sup>[13-15]</sup>。随着2020年全球土壤生物多样性现状报告的出版<sup>[16]</sup>,全球土壤动物学家相继在 *Nature* 和 *Science* 等刊物上报道了不同土壤动物类群(如线虫、蚯蚓和原生动物)在全球尺度上的分布及它们在土壤生态系统中的贡献<sup>[17-19]</sup>,进一步突显了全球变化背景下土壤动物多样性及其生态功能在生态系统中的重要性。

土壤动物几乎参与了所有重要的土壤生态过程,它们在有机质分解、养分循环和维持土壤结构和稳定等方面发挥重要作用<sup>[16]</sup>。土壤动物群落组成和多样性与土壤的物理、化学及微生物特性的变化密切相关<sup>[20-21]</sup>,是土壤健康变化的良好指示生物<sup>[22]</sup>。本文详细综述了土壤动物在土壤健康指示和评价体系中的潜力,尤其是土壤动物功能性状和土壤食物网指标的应用前景,以期能够推动土壤动物和土壤食物网在土壤健康评价和调控中的应用,促进土壤健康和生态系统可持续发展。

## 1 土壤动物对土壤健康的指示作用

土壤动物的种类繁多、数量庞大,在以往的生

态学研究中常根据体宽将土壤动物划分为小型土壤动物、中型土壤动物、大型土壤动物和巨型土壤动物<sup>[23]</sup>。小型土壤动物如原生动物和线虫等可通过捕食等作用改变土壤微生物群落的组成进而影响分解过程和生物地球化学循环<sup>[24-27]</sup>。例如原生动物通过取食细菌或真菌可以改变土壤微生物的群落结构,控制病原微生物群落,影响土壤有机质分解,从而影响养分周转及植物生长<sup>[17]</sup>。跳虫和螨类是中型土壤动物中的典型代表<sup>[28-29]</sup>,它们通过直接取食土壤微生物来调节其群落结构,同时还可取食凋落物并对凋落物进行破碎,增大微生物与凋落物表面的接触面积,间接促进凋落物的分解和养分循环<sup>[30-31]</sup>。蚯蚓和白蚁是常见的大型土壤动物类群,它们可通过穿梭、掘穴等非取食活动改变土壤结构,产生的生物孔隙可以增加土壤透气性,影响土壤有机质分布及腐殖质的形成<sup>[32-33]</sup>;同时,它们在取食土壤及凋落物的过程中还可摄入土壤微生物及其他小型土壤动物,进而间接影响土壤的养分循环过程<sup>[34]</sup>。蜘蛛、甲虫等捕食性土壤动物也会通过捕食环境中一些中小型土壤动物来影响它们的群落组成<sup>[35]</sup>。此外,一些巨型土壤动物如鼯鼠等的觅食和筑巢行为也会影响土壤理化性质及其他土壤生物群落组成<sup>[16]</sup>。

土壤动物的生命活动高度依赖于其所处的环境<sup>[36]</sup>。由于人类活动和环境变化等因素引起的土壤物理、化学或生物学特性的改变,能够直接导致土壤动物群落的变化(如物种组成、群落结构和个体数量等)<sup>[29]</sup>。因此,关注土壤动物对环境变化的响应有助于全面挖掘土壤动物类群对土壤健康的指示作用。目前土壤动物在土壤健康和质量的评价中应用较多的类群包括线虫、螨类、跳虫和蚯蚓等,它们对土壤环境的变化敏感且不同类群对于环境变化的响应程度不同<sup>[28, 37-39]</sup>。

在农业生态系统中,土壤健康的干扰因素主要是农药和化肥的使用、耕作和管理方式以及土壤污染等<sup>[11, 40]</sup>。近年来,在全球变化背景下农业土地集约化导致的频繁耕作、农药和肥料的过量使用降低了土壤动物多样性及丰度(abundance)<sup>[13, 41]</sup>,进而威胁土壤健康状况以及生态系统服务<sup>[42]</sup>。相比传统耕作,有机耕作和保护性耕作下土壤动物的多样性

和密度均有所提高<sup>[43-45]</sup>，能够显著提高土壤肥力从而促进土壤健康<sup>[46]</sup>。有研究表明，生物污泥的使用在增加土壤养分的同时也升高了土壤重金属的浓度，从而使土壤跳虫个体数量减少和食细菌线虫个体数量增加<sup>[47]</sup>。在自然生态系统中，土壤动物与土壤健康之间的关系也得到了广泛关注。土壤动物作为草地生态系统的重要组成部分，常用于监测草地退化及放牧管理对土壤质量的影响<sup>[48-49]</sup>。研究发现不同放牧强度会影响土壤动物多样性，随着放牧强度的增加，土壤中线虫和跳虫的密度也随之降低<sup>[50-51]</sup>；而燃烧因减少了输入土壤中的有机质对草地土壤动物群落产生了消极影响<sup>[52]</sup>。在森林生态系统中，森林砍伐和生态系统向耕地的转化会降低植物的生物量并导致土壤特性和土壤生物多样性的变化<sup>[53-54]</sup>。如森林砍伐增加了土壤线虫群落中食细菌线虫与食真菌线虫的比例，且短期内难以得到恢复<sup>[40, 54]</sup>；在亚马逊森林砍伐并建立牧场之后，单一的蚯蚓物种迅速繁殖，抑制了其他蚯蚓物种的生存<sup>[53]</sup>。因此，土壤动物多样性可指示环境变化下的土壤健康状况。

## 2 基于土壤动物的土壤健康评价

近年来，基于土壤动物开展土壤健康评价开始得到重视<sup>[21]</sup>，目前主要集中在线虫、节肢动物和蚯

蚓等类群（图 1）。

土壤线虫结构简单、数量多、分布广，世代周期较短且易于分离鉴定，在土壤食物网中占据多个营养级<sup>[55]</sup>，被认为是土壤健康的良好指示生物<sup>[22, 56-57]</sup>。目前基于土壤线虫的物种多样性、生活史特征及取食类型，研究人员提出了一系列相对成熟的土壤健康评价指标，其中物种多样性指标主要包括土壤线虫的物种组成、多度、生物量及均匀度等<sup>[40, 58]</sup>。荷兰学者 Tom Bongers<sup>[59]</sup>根据线虫不同的生活史对策将其划分为由 *r*-对策者向 *K*-对策者过渡的 5 个 c-p (colonizer-persister) 类群，并提出了可反映线虫群落演替状态的成熟度指数 (maturity index, MI)。成熟度指数可以表征土壤生态系统稳定性及其受干扰程度，通常越稳定的土壤环境中成熟度指数越高<sup>[40]</sup>。在此基础上，Ferris 等<sup>[60]</sup>2001 年根据线虫不同取食类型和生活史特征将线虫进一步划分为不同的功能团，并提出了基于不同功能团的富集指数 (enrichment index, EI)、结构指数 (structure index, SI) 和通路指数 (channel index, CI)。其中富集指数和结构指数分别用于评估土壤食物网对可利用资源的响应及食物网的结构变化<sup>[61]</sup>，而通路指数一般指示有机物的分解途径 (如细菌通道或真菌通道)<sup>[62]</sup>。在土壤健康评价体系中，可根据实际生态系统类型及研究目的选择相应的线虫生态指数。

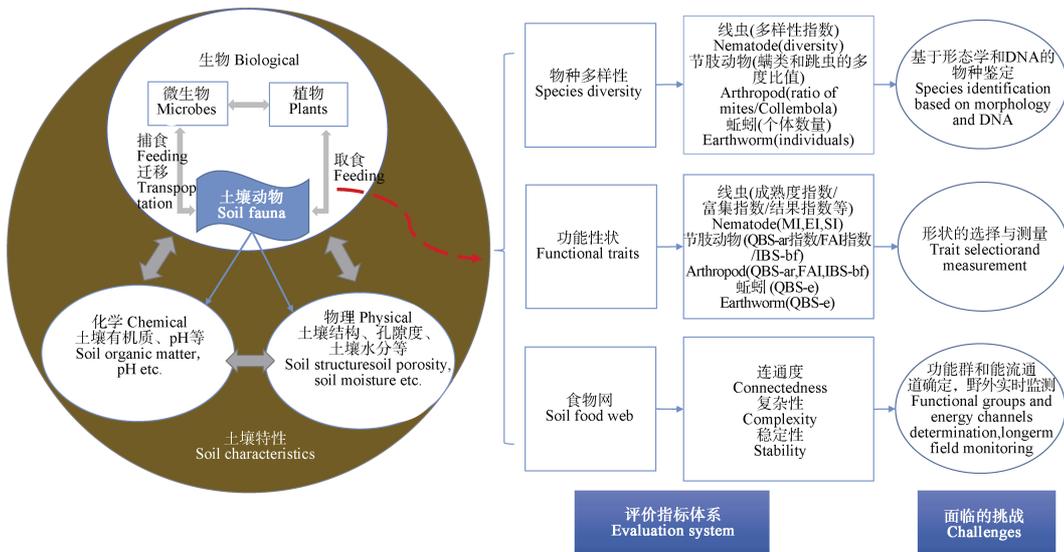


图 1 基于土壤动物的健康评价体系  
Fig. 1 Soil health assessment based on soil fauna

土壤节肢动物占所描述的土壤生物的大部分<sup>[37]</sup>，对土壤环境的变化响应迅速，在土壤健康指示研究

中也受到日益关注<sup>[63-64]</sup>。但由于该类群种类繁多而形态分类知识相对缺乏，直接对其多样性的量化存

在一定困难<sup>[64]</sup>。基于“在高质量土壤中,形态上能适应土壤环境的节肢动物类群数量更高”这一概念,反映土壤节肢动物群落多样性及脆弱性的 QBS-ar (Soil Biological Quality-arthropod) 指数被提出<sup>[63-64]</sup>。QBS-ar 指数根据土壤样本中节肢动物的形态类型进行生态形态评分 (EMI: Eco-morphological Index) 并求和<sup>[63-65]</sup>,常被用于评估土地利用及管理、重金属污染等干扰因素对土壤健康的影响<sup>[66]</sup>。QBS-ar 指数关注的是节肢动物适应土壤环境的形态特征,因此不需要在物种水平上的分类鉴定<sup>[64]</sup>。但是, QBS 指数的应用需依赖于土壤节肢动物的存在,并同时认为具有相同 EMI 值的节肢动物对土壤功能的影响相同,从而忽略了群落丰度差异对土壤功能的影响<sup>[10, 63]</sup>。为了克服这种局限性, Yan 等基于丰度提出了 FAI 指数 (Abundance-based Fauna Index)<sup>[63]</sup>。相比 QBS 指数, FAI 指数可以同时通过土壤动物群落和功能性状特征来衡量土壤保持生物多样性和实现土壤功能的能力,从而监测土壤健康<sup>[63]</sup>。为了可以更加灵活地选取土壤动物类群,基于节肢动物、腹足纲及寡毛纲类群提出了 IBS-bf 指数 (Soil Biodiversity Index-biodiversity friend)<sup>[66]</sup>。此外,螨类和跳虫丰度的比值也能很好地反映土壤退化程度,可作为衡量土壤健康状况的指标<sup>[65]</sup>。

蚯蚓作为“生态系统工程师”,其多样性和分布与土壤的健康状况密切相关<sup>[6]</sup>。它们对土壤环境的改变十分敏感,一旦环境压力过大,蚯蚓就会出现迁移或死亡,因此蚯蚓在土壤中存在与否及其数量多少常被直接作为土壤健康的生物指标<sup>[67]</sup>。以 QBS-ar 指数为模型,研究者相继提出了基于蚯蚓的土壤质量生物监测指标 (QBS-e: Soil Biological Quality-earthworm)<sup>[64]</sup>,该指标的运用不需要具备大量的分类学专业知识,因此可由农民或土地经营人员开展自主监测<sup>[68]</sup>。

### 3 土壤动物功能性状与土壤健康

生态系统多功能性是土壤健康评价的重要内容,土壤动物的功能性状是土壤动物对于周围环境的响应和适应性的直观表现<sup>[69]</sup>,在表征土壤动物群落、量化食物网结构及其对生态系统功能贡献方面具有很大的潜力<sup>[14, 70-71]</sup>。以跳虫为例,体型大小与资源可用性、代谢强度以及营养生态位有关<sup>[72]</sup>,食

性与物种的生长繁殖及生存能力有关<sup>[73]</sup>,弹器的发达程度与运动和扩散能力有关,体表色素沉着和眼睛的存在与否与居住环境偏好有关<sup>[74]</sup>,垂直分布状况与耐旱性有关(表土生的物种有良好的耐旱性,而真土生的物种易受干旱影响)<sup>[75]</sup>,生殖方式与环境适应性有关<sup>[73, 76]</sup>,等等。因此,土壤动物群落功能性状的组成和多样性会对土壤肥力、污染程度的变化做出响应<sup>[77]</sup>;同时基于功能性状的指数较基于物种多样性的指数更能精确地反映土壤的健康状况<sup>[41, 78]</sup>。在土壤健康评价体系中,受土壤动物物种本身以及功能性状认知程度的限制,基于土壤动物功能性状的相关指标尚未在土壤健康评价体系中得到有效推动。

土壤动物肠道内具有丰富的微生物类群,被认为是一个天然可移动的微生物存储库<sup>[79-80]</sup>。这些在土壤动物体内定殖的微生物类群在宿主长期进化、个体发育和环境适应等过程中发挥着重要的作用<sup>[81-84]</sup>,反映了宿主在土壤环境中的生态功能<sup>[85]</sup>,因此它们的群落组成和功能是表征土壤动物环境适应性的较好的功能性状。土壤动物肠道微生物与土壤动物一起,共同参与土壤凋落物的分解、养分循环、污染物的降解和迁移过程<sup>[80, 86-87]</sup>。例如,蚯蚓肠道中的营养丰富,有利于厌氧菌的定殖,从而将宿主肠道与其邻近的陆地环境相关联,这些肠道细菌在营养元素和污染物转化中(例如硝化作用和重金属解毒作用等)发挥着重要作用<sup>[88]</sup>。有研究表明鼠妇肠道微生物可为宿主提供消化陆地食物所必须的酶,从而促进宿主在陆地环境中的生存定殖<sup>[89]</sup>。有学者也发现土壤中抗生素的暴露增加了土壤动物肠道微生物组中抗生素的抗性基因丰度,抗性基因会在土壤食物链中进行传递,同时也可能通过土壤动物的活动扩散到土壤的其他区域<sup>[86, 90]</sup>。此外,(微)塑料污染和重金属污染也可显著改变土壤动物的肠道微生物组,同时也会对宿主本身的生长繁殖产生一定的负面影响<sup>[91-93]</sup>。土壤动物肠道微生物组能够同时反映土壤动物本身和其所处环境中的土壤健康状况,且高通量测序技术的突破和生物信息学的发展进一步推动了肠道微生物组群落组成和功能信息的获取。因此,肠道微生物组在土壤健康评价中具有很大的潜力。

### 4 土壤食物网与土壤健康

不同大小的土壤动物在土壤中以不同的方式发

挥各自的生态功能,但土壤动物之间、土壤动物与微生物及植物之间存在复杂的相互作用,它们通过取食和被取食关系构成了土壤食物网,从而维系着生态系统的结构和功能(图 2)。土壤食物网的特征可用来评价土壤质量和土壤生态系统服务功能,其连通度、复杂性和稳定性主要通过监测食物网中功能类群的组成和生物量、能流通道等参数的变化来实现<sup>[42]</sup>。根据基础资源(basal resource)的不同,土壤食物网

主要分为碎屑食物网和根际食物网<sup>[94-95]</sup>,其中碎屑食物网基于能流通道又可进一步分为细菌能流通道(以细菌和取食细菌的土壤动物为主)<sup>[96]</sup>和真菌能流通道(以真菌和取食真菌土壤动物为主)<sup>[97]</sup>。根际食物网以植物根系及植食性土壤动物为主,其能量通道为根际能流通道<sup>[96-97]</sup>。不同食物来源的能量通过不同的能流通道在土壤食物网各营养级间传递,从而维持土壤食物网的稳定和土壤环境的健康<sup>[98]</sup>。

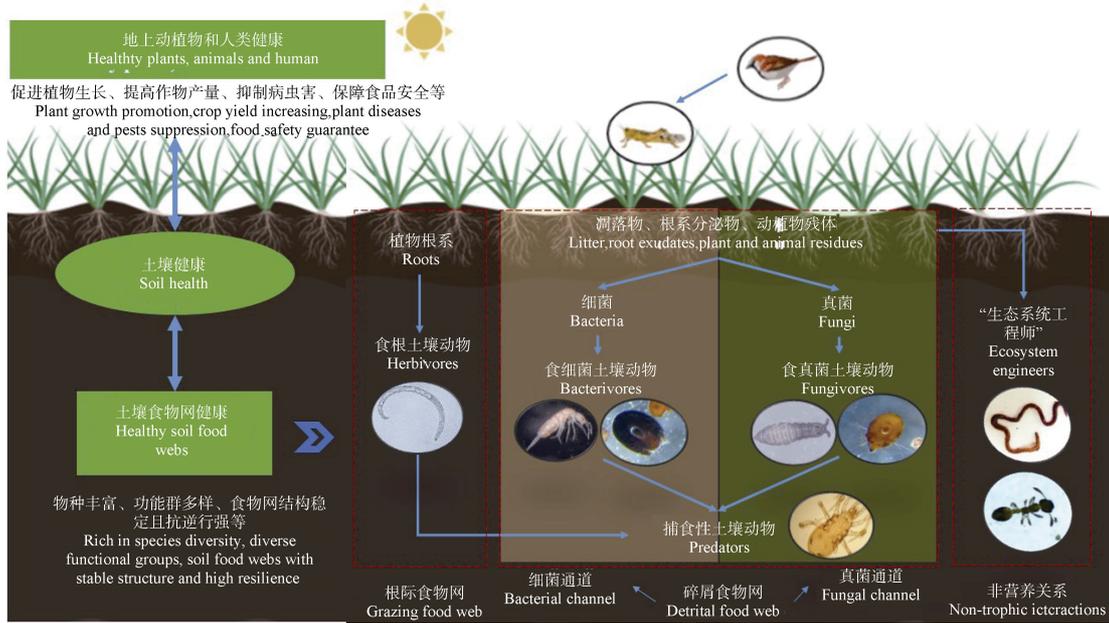


图 2 土壤食物网与土壤健康

Fig. 2 Soil food web and soil health

土地利用方式和强度、农业耕作措施、农田退耕修复等人类活动可引起土壤环境的变化,从而直接影响并改变土壤食物网的组成、结构和能流通道等<sup>[42, 99-101]</sup>。随着土地利用强度的增加,土壤生物多样性显著降低,从而改变了土壤食物网中各组分的生物量和能流通道<sup>[42, 102]</sup>。保护性耕作如免耕措施等可降低土壤有机质的分解速度并增加养分的固定,使土壤食物网以真菌能流通道为主<sup>[103]</sup>。此外,随着农田退耕修复年限的增加,食物网中的基础资源、低营养级的生物量以及各能流通道均显著上升。因此,土壤食物网的特征能够反映土壤环境的改变,并用于指示土壤的健康状况。

土壤动物可通过捕食或非捕食作用改变土壤食物网中的其他生物组分的群落结构,进而影响植物生长和土壤健康。例如,原生动物和线虫能够通过捕食作用影响丛枝菌根真菌的群落组成和生物量从而影响植物生长<sup>[104]</sup>,还可通过对微生物的捕食作用调节

凋落物的分解速率进而影响整个碳循环过程<sup>[105]</sup>;而蚯蚓等大型土壤动物还可通过非捕食作用如改变土壤的物理结构或竞争食物资源等改变中小型土壤动物的群落结构,从而影响土壤食物网的结构和功能<sup>[106]</sup>。同时,土壤动物可直接(如取食等)或间接(如分泌代谢产物、协助扩散等)地改变土壤病原菌的群落和功能,进而控制土传病害的发生<sup>[107-108]</sup>。此外,土壤动物与地上植食动物之间也存在复杂的联系,如原生动物的存在能够增加植物的生物量和繁殖率并提高植物对害虫的耐受性<sup>[109]</sup>。因此,土壤食物网结构和生态功能的研究对提高土壤肥力、促进植物生长和保持土壤健康具有重要的应用价值。

## 5 展望

人类活动正加速全球生物多样性的变化,并导致

生态系统服务功能受到严重威胁<sup>[16]</sup>。土壤承载了大部分的陆地生物多样性,但相比于地上生物多样性,对于土壤生物多样性的评估和保护仍十分有限<sup>[110]</sup>。随着土壤健康相关问题的提出,土壤动物多样性因其在土壤健康的指示和调节中发挥的重要作用受到日益关注<sup>[20, 111]</sup>。然而,由于种类繁多、食性复杂,土壤动物在土壤健康评价体系中的应用进展较慢,目前可用的评价指标也十分有限,未来应着重挖掘基于土壤动物的土壤健康评价指标,通过不同管理措施调控土壤动物及其构成的土壤食物网,提升土壤质量和生态系统功能。未来需重点关注以下几个方面:

1) 建立和完善我国土壤动物形态和基因组信息数据库。土壤动物多样性是土壤健康最直观的评价指标之一,但由于当前从事土壤动物形态学分类的研究人员较少,因此土壤动物的物种信息仍十分匮乏。得益于分子生物学技术的发展,基因测序成本大大降低,在大尺度上土壤动物多样性的研究也取得了重要的进展<sup>[17-19]</sup>。但受土壤动物基因组数据库不全的限制,该技术在土壤动物中的应用还没有得到有效的推动<sup>[112]</sup>。未来应重视土壤动物分类学和分子生物学技术的结合,建立和完善我国土壤动物形态和基因组信息数据库,从而更好地推动我国土壤动物多样性的研究。

2) 深入挖掘基于土壤动物功能性状的土壤健康评价指标。今后应在土壤动物微生物组、取食特性等方面深入挖掘更多具有生态功能表征能力的功能性状,解析土壤动物群落与生态系统功能之间的关联,以期更全面地获取基于功能性状的土壤健康评价指标。

3) 建立基于土壤食物网不同功能类群的综合评价指标体系。由于土壤动物食性复杂且随环境变化而改变,加上相关研究手段的限制<sup>[112-113]</sup>,土壤动物在土壤食物网中的位置和生态功能仍未得到一致的结论。未来在土壤健康评价中,应综合利用多种研究方法,如脂肪酸分析法、稳定同位素技术和DNA分子技术等,进一步明确土壤动物与其他土壤生物之间的营养关系,量化土壤动物在物质循环与能量流动过程中的贡献,建立基于土壤食物网不同功能类群的综合指标体系。

4) 对土壤食物网结构和功能的调控途径研究。土壤食物网是一个动态的网络,组成食物网的各功能群可通过上行效应、下行效应和营养级联效应对

食物网的结构和功能进行调控<sup>[114-116]</sup>,因此未来可通过适当的管理措施来调节土壤动物关键类群,从而调控土壤食物网的结构和生态功能,使土壤环境达到健康、稳定的状态,促进生态系统的可持续发展。

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