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蚯蚓在生态系统中的作用

张卫信[1,2*] 陈迪马[1,2] 赵灿灿[1,2]

1 (中国科学院华南植物园生态研究所, 广州 510650)
2 (中国科学院研究生院, 北京 100049)

摘要: 蚯蚓能够对许多决定土壤肥力的过程产生重要影响, 被称为“生态系统工程师”。它通过取食、消化、排泄和掘穴等活动在其体内外形成众多的反应圈, 从而对生态系统的生物、化学和物理过程产生影响。蚯蚓在生态系统中既是消费者、分解者, 又是调节者, 它在生态系统中的功能具体表现在: (1) 对土壤中有机质分解和养分循环等关键过程的影响; (2) 对土壤理化性质的影响; (3) 与植物、微生物及其他动物的相互作用。蚯蚓活动及其在生态系统中的功能受蚯蚓生态类群、种群大小、植被、母岩、气候、时间尺度以及土地利用历史的综合控制。蚯蚓外来种入侵与生态系统的关系以及蚯蚓对全球变化的响应和影响是两个值得关注的问题。土壤本身的复杂性, 蚯蚓自然历史和生物地理学知识的缺乏, 野外控制蚯蚓群落方法的滞后等都限制了蚯蚓生态学的发展。其他新技术如研究养分循环的碳氮同位素分析和揭示土壤微结构的图像分析等技术的应用是蚯蚓生态功能研究的迫切需要。

关键词: 蚯蚓, 生态功能, 蚯蚓生态类群, 蚯蚓入侵

Functions of earthworm in ecosystem

Weixin Zhang[1,2*], Dima Chen[1,2], Cancan Zhao[1,2]

1 *Institute of Ecology, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou* 510650
2 *Graduate University of Chinese Academy of Sciences, Beijing* 100049

Abstract: As one of the key soil invertebrates, earthworms can greatly impact soil processes, and thus was named as “ecosystem engineer”. Earthworm activities such as feeding, digestion, excretion, and burrowing, facilitate the formation of various drilosphere in their guts or soils around, through which they alter the biological, chemical and physical processes of the ecosystem. Earthworms act as consumer, decomposer and modulator in ecosystem. The ecological functions of earthworm include: (1) effects on key soil ecosystem processes such as decomposition of soil organic matters and nutrient cycling; (2) effects on soil chemical and physical properties; and (3) interaction with plants, microorganisms and other animals. Earthworm activities and their functions in ecosystem are determined by various factors such as ecological groups of earthworms, population size, vegetation, parent materials of soil, climate, time scale, and history of soil utilization. The development of earthworm ecology was constrained by the complex feature of soil, the scarce knowledge of natural history and biogeography of earthworms, and the low efficiency of approaches in field manipulation of earthworm community. We suggest that new technologies such as the C and N isotope technique for nutrient cycling and the image analysis approaches for soil micro-structure should be applied on earthworm ecological research in order to better understand the functions of earthworms.

Key words: earthworm, ecological function, earthworm ecological group, earthworm invasion

蚯蚓属于寡毛纲后孔寡毛目, 全球已记录的陆栖蚯蚓有12科, 181属 (Edwards & Lofty, 1977; 冯孝义, 1985), 约4,000种 (Edwards, 2004), 中国已记录的有9科28属306种 (黄健等, 2006)。人类仅仅对其中的大约40种蚯蚓的生物学特性和生态学功能有过不同程度的研究 (Edwards, 2004)。世界上大多

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* 通讯作者 Author for correspondence. E-mail: zwxjxyum@gmail.com

数生态系统中都有蚯蚓存在，但海洋是蚯蚓的天然屏障，沙漠区和终年冰雪区也很少见 (Edwards & Lofty, 1977; Edwards, 2004)。

依蚯蚓的习性及其在生态系统中的功能，蚯蚓一般被分为3种生态类群，即表栖类(epigeic)、内栖类(endogeic)和深栖类(anecic)，不同生态类群的食性和习性迥异 (Edwards & Bohlen, 1996; Rómbke *et al*., 2005) (表1)。内栖类又常被分为多腐殖质类(polyhumic)、中腐殖质类(mesohumic)、贫腐殖质类(oligohumic) 和内—深土栖类(endo-anecic) 等 (Hendrix & Bohlen, 2002)。三种生态类群并没有明显的分类学上的界限，经常有一些过渡类型出现，如表—内栖类(epi-endogeic)和表—深栖类(epi-anecic)。蚯蚓生态类群的概念已被广泛接受和应用。Rómbke等(2005)认为蚯蚓生态类群可用于土壤分类和评价。

蚯蚓通过取食、消化、排泄(蚯蚓粪)、分泌(粘液)和掘穴等活动对土壤过程的物质循环和能量传递作贡献 (Tian *et al*., 2000)，是对多个决定土壤肥力的过程产生重要影响的土壤无脊椎动物类群(主要是蚯蚓、螨和蚂蚁)之一，被称为“生态系统工程师” (Decaens *et al*., 1999)。蚯蚓在生态系统中的角色有三: 消费者 (consumer)、分解者 (decomposer)和调节者(modulator)。通常认为，它作为消费者在生态系统中的地位并不重要。进入分解子系统的能量一般只有3–6％被蚯蚓消耗；但若加上它在排泄物和蚓茧中所耗的能量，蚯蚓在系统能量传递中的作用会更大 (Edwards & Bohlen, 1996)。蚯蚓在生态系统中的功能主要表现在: (1) 对土壤有机质分解和养分循环等关键过程的影响; (2) 对土壤理化性质的影响; (3) 与植物、微生物及其他动物的相互作用。

1 对土壤关键过程的影响

1.1 对有机质分解过程的贡献

蚯蚓能破碎、分解和混合有机质。如在北美，蚯蚓*Allolobophora caliginosa*和*Octolasion cyaneum*每年能消耗浅层土壤(15 cm)中4–10％的土壤和10％的有机质(Edwards & Bohlen, 1996)。蚯蚓主要在4个尺度(scale)上影响土壤有机质动态和养分循环: (1) 蚯蚓肠道; (2) 新鲜排泄物; (3) 土壤中蚯蚓的陈旧排泄物; (4)土壤的长期发育(Lavelle & Martin, 1992)。热带休耕地上蚯蚓种群的恢复能加快凋落物的分解 (Tian *et al*., 2000); 北美森林中，蚯蚓活动也明显加快了森林地表物的周转，降低了森林地表物厚度和O层土壤中碳含量 (Hale *et al*., 2005)。蚯蚓的取食活动加强了植物残体分解中的生物过程，富含易水解氮的蚓粪又加快了周围凋落物的矿化过程 (Bezkorovainaia *et al*., 2001)。不同种类的蚯蚓取食偏好不同，故凋落物分解过程受其本身的物理化学组成和蚯蚓种类的共同影响 (Manna *et al*., 2003)。

蚯蚓活动能改变土壤有机质的空间分布，使土壤有机质呈斑块状分布(Shuster *et al*., 2001)。不同生态类群蚯蚓对碳分布的影响不同。在表—深栖蚯蚓如*Lumbricus terrestris*洞穴不同深度的管壁上，凋落物碳呈均匀分布; 但随着深度增加，深栖类蚯蚓*Aporrectodea giardi* 和内栖类蚯蚓*Aporrectodea caliginosa*孔道壁上的碳明显减少(Jeâgou *et al*., 1998)。Scheu (1997) 通过一年的室内凋落物分解实验发现，内栖类蚯蚓*Octolasion lacteum*使无凋落物的土柱中产生的CO_2显著减少，他认为蚯蚓的活动有利于该处理中受物理作用保护的碳库恢复。

土壤有机质的长期稳定性受土壤生物(如真菌、细菌、植物根和蚯蚓等)、土壤结构(如团粒)和它们相互作用的调控 (Six *et al*., 2002)。蚯蚓将有机质与矿质土混合，形成富含有机质的土壤微粒，为有机质提供物理保护，进而减慢有机质的周转，提高土壤潜在的碳吸存 (carbon sequestration) 能力 (Jongmans *et al*., 2003)。Decaëns等 (1999) 发现，在稀树草原中由于稳定的蚯蚓干粪对有机质的保护作用，大型内栖类蚯蚓*Martiodrilus carimaguensis*的粪中NH_4^+和NO_3^-的浓度在两星期后只有轻微变动。Ketterings等(1997) 发现在苜蓿地中，蚯蚓的活动提高了土壤结构的稳定性，增加了土壤碳氮在水稳定性团粒中的储存。Bossuyt等 (2005) 用^{13}C标记了高粱属植物*Sorghum bicolor*的叶片残体，研究蚯蚓*Aporrectodea caliginosa*对团聚体 (aggregates) 和相应的碳库的影响，发现蚯蚓的活动对土壤大团聚体 (macroaggregates)和微团聚体 (microaggregates)的碳有保护作用，有利于土壤碳的长期稳定。Pulleman等 (2005) 在永久牧场中的研究也发现，蚯蚓的活动是土壤中大量稳定微团聚体 (stable microaggregates) 存在的重要原因。这些稳定微团

表1 蚯蚓几种主要生态类群的特征(引自Edwards & Bohlen, 1996; Rόmbke *et al*., 2005)

Table 1 General features of the major ecological groups of earthworms (Adopted from Edwards & Bohlen, 1996 and Rόmbke *et al*., 2005)

	食物 Food	色素 Pigmentation	大小 Size	洞穴 Burrows	活动性 Mobility	寿命 Longevity	世代 Generation time	耐旱性 Drought survival	捕食 Predation	举例 Examples
表栖类 Epigeics	取食土表凋落物; 少量或不取食土壤 Decomposing litter on the soil surface; little or no soil ingested	深, 通常背腹均有 Heavy, usually both ventrally and dorsally	小到中型 Small to medium	无; 某些种类在表层几厘米土中有穴 None; some burrowing in upper few centimeters of soil	遇干扰快速运动 Rapid movement in response to disturbance	相对短 Relatively short-lived	短 Shorter	通常以蚓茧度过干旱 Survives drought in the cocoon stage	易被鸟类、哺乳动物和节肢动物捕食 Under high predation pressure, particularly from birds, mammals and predatory arthropods	*Lumbricus rubellus* *L. castaneus* *Dendrodrilus rubidus*
内栖类 Endogeics	矿质层特别是多有机质土壤 Mineral soil with preference for material rich in organic matter	无色或浅色 Un-pigmented or lightly pigmented	中型 Medium	连续而广泛但非永久性的水平洞穴, 常在10–15 cm 土层 Continuous, extensive, sub-horizontal burrows, usually in the upper 10–15 cm of soil	一般行动迟缓 Generally sluggish	中等 Intermediate	短 Shorter	遇旱滞育(diapause) Enters diapause in response to drought	不易被捕食; 有时被节肢动物和地栖鸟类捕食 Under low predation pressure, by ground-dwelling birds and predatory arthropods	*Aporrectodea caliginosa* *A. rosea* *A. chlorotica* *A. icterica*
深土栖类 Anecics	在土表分解凋落物, 有时将凋落物拖入洞穴; 有时取食土壤 Decomposing litter on soil surface, some of which is pulled into burrows; some soil ingested	较深, 常在背面, 至少身体前部色深 Medium-heavy, usually only dorsally	大型 Large	大、永久性的垂直洞穴, 可深入土壤 3 m Large, permanent, vertical burrows extending into mineral soil horizon for 3 m	遇干扰快速缩回洞穴, 但较表栖类动作慢 Rapid withdrawal into burrow but more sluggish than epigeics	相对长 Relatively long-lived	较长 Longer	遇旱休眠(quiescent) Becoming quiescent during drought	在洞穴外时易被捕食 Under high predation pressure, especially when they are at the surface; somewhat protected in their burrows	*L. terrestris* *A. longa* *L. polyphemus* *Dendrobaena platyura*

聚体可以给土壤有机质提供物理保护，从而减少分解。Bossuyt等 (2006) 发现，蚯蚓将新鲜有机质混合进土壤稳定微团聚体的过程因种而异；各蚯蚓种间的相互作用可能对此过程以及其对土壤碳的保护作用有重要的影响。

1.2　在土壤氮、磷循环中的作用

蚯蚓能提高土壤中可利用氮 (Callaham Jr & Hendrix, 1998; Domínguez *et al.*, 2004; Araujo *et al.*, 2004; Sheehan *et al.*, 2006) 和磷 (Le Bayon & Binet, 2006) 的水平。Wang等(2005) 的野外接种实验表明，蚯蚓活动促进了玉米残体氮的流失。Amador 和 Görres (2005) 报道*Lumbricus terrestris*的活动显著改变了玉米残体氮的分布，促进了氮向植物和土壤转移。Callaham Jr 和 Hendrix (1998) 发现提高蚯蚓 (Diplocardia, Megascolecidae) 的数量可导致植物地上和地下各部分氮含量的明显升高。Shuster等(2003)也发现在农业生态系统中，表—深栖类蚯蚓*L. terrestris*增加了氮的淋失。Schmidt 和 Curry (1999)报道在小麦－苜蓿间作系统中，蚯蚓能通过改变植物种内和种间的氮分配而影响小麦和苜蓿间生物量的平衡。Helling 和 Larink (1998)在室内和野外的实验都表明蚯蚓*L. terrestris*的活动能提高氮的矿化率。蚯蚓活动大大提高了土壤中无机氮(主要是NH_4^+-N)的浓度，促进了野外被标记分解物中氮的流失 (Cortez *et al*., 2000)。Araujo等 (2004)研究了在温室中添加蚯蚓对凋落物分解的影响，发现蚯蚓活动能提高土壤矿化氮的浓度，原因可能是蚯蚓消费了大量的土壤微生物，加速了微生物组织的矿化和周转。

蚯蚓对有机质的作用，因其自身及有机质的种类而异，蚯蚓与不同质和量有机物的相互作用不仅影响有机质被混入土壤的速度，也影响其中氮的矿化 (Bohlen *et al*., 1999)。Blair等 (1997) 发现，蚯蚓活动对氮的净效应因农业生态系统的管理方式的不同而变化。蚯蚓通过减少微生物对氮的固定而提高氮的矿化及可利用性，但在生长季末，土壤硝态氮以及土壤浅层氮浓度的升高会促进氮从非有机肥系统中大量流失。在中耕作物 (row crop) 农业生态系统中，蚯蚓虽然不影响无机态氮或溶解态有机氮的浓度，但能够提高深层土水和氮的沥滤 (leaching)，大大提高了土壤N淋出量，从而增加系统中氮的淋失 (Domínguez *et al*., 2004)。Shuster等 (2002) 发现在植物残体很多的农业生态系统中，蚯蚓对土壤碳氮的作用随着蚯蚓种群大小及群落种类组成的不同而不同。在草地向中耕作物系统转变过程的前几年，密集的蚯蚓种群，特别是*L. terrestris*种群，会使系统土壤及其中的碳氮更易流失。但是种群大小中等的内栖类蚯蚓，作用恰恰相反，能让土壤及其养分免于流失。氮在土壤中的转化及其可利用量也因蚯蚓群落组成而不同。当内栖类和深栖类蚯蚓多时，土壤淋出液中NH_4^+-N浓度一般较高；而在表栖类蚯蚓多时，NO_3^--N常较高 (Sheehan *et al*., 2006)。

蚯蚓是陆地生态系统N_2O排放的生物源之一, (Karsten & Drake, l997; 韩兴国和王智平, 2003)。Gudrun等 (1997) 发现在蚯蚓*Lumbricus rubellus*肠道物中可培养的去氮菌是相应土壤的256倍，达到73,107个/g (干重)。蚯蚓摄取土壤中的产N_2O细菌，其肠道给这些反硝化菌提供了有利的微环境 (Gudrun, 1995; Horn *et al.*, 2003, 2006; Ihssen *et al.*, 2003)。Borken等 (2000) 在野外实施了120 d的土柱实验，发现放养蚯蚓使得土壤CH_4氧化率比对照降低53%，而N_2O排放量提高57%。但是，蚯蚓并不是在任何生态系统中都提高N_2O排放 (Borken & Brumme, 1997)。例如，在施放了石灰的土柱中，加入*L. rubellus* 会使N_2O排放比对照降低8% (Borken *et al.*, 2000)。蚯蚓通过取食、排泄、掘土等影响土壤微生物及土壤碳、氮的矿化过程，改变土壤理化结构(如透气性、pH值等)进而影响其体内及土壤中的硝化和反硝化过程。蚯蚓对N_2O排放的正效应和负效应的平衡决定了其最终的贡献 (图1)。

Le Bayon和Binet(2006)的土壤微宇宙(microcosm)实验表明，蚯蚓*L. terrestris*的掘穴行为及取食偏好与土壤有机磷源的特性关系密切，蚯蚓的活动便于P向下移动，提高了P在土壤中的斑块分布，同时在蚯蚓粪或洞穴等“热点”区域显著改变P的状态，如可溶性、有机磷库、碱性磷酸酶活性等。

2　对土壤理化性质的影响

2.1　对土壤结构的作用

蚯蚓对土壤结构、团聚体形成以及植物生长和养分吸收所需的物理条件有十分重要的影响 (Hendrix, 1995; Edwards & Bohlen, 1996; Edwards, 1998; Scullion & Malik, 2000; Jongmans *et al*., 2001)。

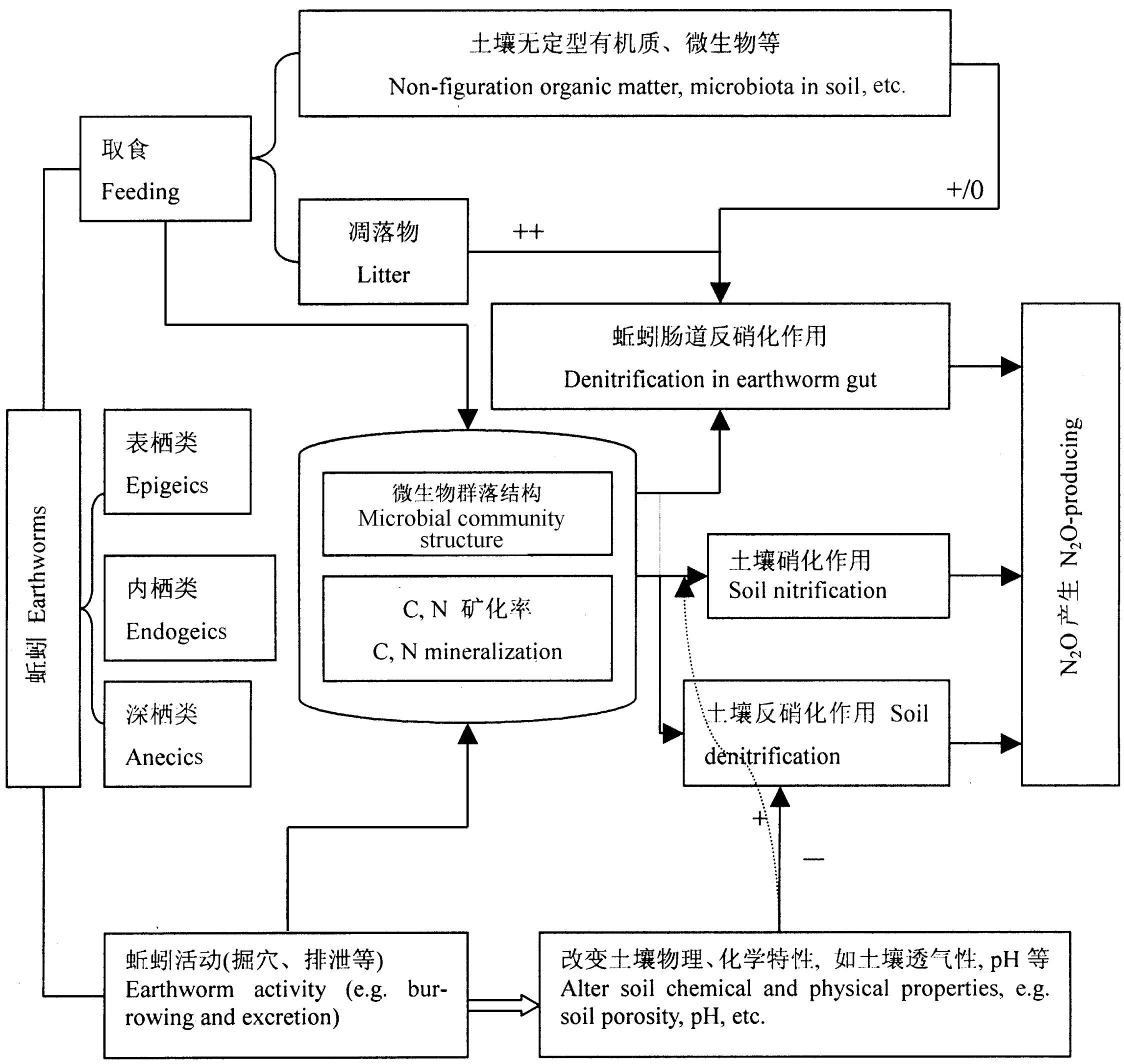

图1 蚯蚓影响土壤N_2O产生过程简图(“+”表示正效应，“++”表示强正效应，“－”表示负效应，“0”表示无效应，“---”表示可能产生的效应)

Fig. 1 The simple pattern that earthworm impact N_2O emission process. “+” means positive effects, “++” represent stronger positive effects, “－” negative effects, “---” potential effects and “0” zero effects.

Emmerling等 (2002) 指出蚯蚓主要通过其排泄物(cast) 及孔道影响土壤结构。Larink等(2001) 发现蚯蚓粪的溶胀值 (swelling values) 和孔隙度 (porosity values) 分别比对照的土壤高出50％和20％。Abdul 和Scullion (2003) 在严重退化的草地土壤中接种蚯蚓，结果显示蚯蚓促进了土壤团聚过程(soil aggregation)。Blanchart等 (1997) 在非洲稀树草原28个月的野外实验表明，蚯蚓*M. anomala*的活动形成土壤中粒径大于50 mm 的大团聚体，而另一种细长的蚯蚓的排泄活动则形成0–5 mm的小团聚体。Pérès等(1998) 在法国两葡萄园的实验也证实了蚯蚓群落组成越丰富，表土层中粒状生物扰动区(granular bioturbated areas) 及大孔隙 (macroporosity)愈多。当然，蚯蚓影响土壤团聚体形成和土壤孔隙大小及分布的同时，有时也会增加土壤流失的可能性，不同土壤类型流失的风险也不同 (Blanchart *et al*., 2004)。Vanden Bygaart等 (2000) 用一种图像分析法定量研究了蚯蚓对土壤结构特性的影响，结

果表明在免耕土中大于1 mm的孔隙数量比对照土的高两倍多，这可能缘于免耕土中存在有更大的蚯蚓种群。

蚯蚓的活动也并不一定总是有益于土壤结构的。Hallaire等 (2000) 报道，在中亚马逊河流域的氧化土中，过多的蚯蚓*Pontoscolex corethrurus*使草地土壤中大孔隙的数量减少，蚯蚓排泄物在土表形成一层壳状物，导致土壤结构退化。

2.2　对土壤调节因子(modulators)的影响

土壤调节因子(modulators)就是土壤中那些能影响生物活动，但又不会被生物消耗的土壤物理和化学特性，如pH值、氧化还原状态、温度等 (Hooper *et al*., 2005)。蚯蚓活动在影响生态系统物质循环过程及系统中的各种资源如碳、氮、磷和水等的同时，也对系统中上述各种土壤调节参数产生影响。蚯蚓排泄物的pH值明显高于周围土壤 (Basker *et al.*, 1994)。土壤调节因子又反过来影响森林土壤中的生物过程和碳氮循环 (Staaf, 1987; Reich *et al.*, 2005)。

3　与植物、微生物及其他无脊椎动物的相互作用

3.1　对植物的影响

蚯蚓对土壤中可利用氮、磷有重要影响，可以促进植物生长(van der Werff *et al.*, 1995; Wurst *et al*., 2004)。蚯蚓还可能使植物体内化学物质发生变化，进而影响植物与其他生物的相互作用(Wurst *et al*., 2004)。*L. terrestris* 对植物种子的散布、埋藏以及植物幼苗的恢复和空间分布有明显的影响，最终可能改变植物群落的组成 (Milcu *et al*., 2006)。Wurst等 (2003) 发现接种蚯蚓有利于植物从有机质和土壤中吸收氮，并且提高了非豆科植物*Lolium perenne*和*Plantago lanceolata*根茎的生长，但降低了*P. lanceolata*上蚜虫的繁殖力，说明蚯蚓活动可能间接改变植物的化学组成从而避免被取食。但也有蚯蚓的活动不利于植物对氮的吸收的报道。如Callaham Jr等(2001) 发现蚯蚓*Diplocardia* spp.的活动使植物*Andropogon gerardii* 对氮的吸收有负效应，原因不明。

目前，关于蚯蚓对植物生长影响的知识还很片面，以往的研究对象多集中在农作物特别是谷类和牧草上，关于自然群落中的树种与蚯蚓关系的研究很少；研究对象也多为欧洲蚯蚓 (Cheu, 2003)。

3.2　对微生物的影响

Zhang等(2000)报道，在有蚯蚓作用的土壤中微生物总量减少,而可利用的营养物质增加，真菌与细菌之比略高于对照土壤；而且通过蚯蚓肠道后，虽然微生物总量减少了，但有活性的微生物生物量 (active components of MB)增加了。Scheu等 (2002) 发现蚯蚓在降低微生物实际代谢活动的同时提高了其潜在活动力；蚯蚓种类和功能群数的减少都可能改变土壤微生物群落功能。Binet等 (1998) 在室内微宇宙控制实验中研究了蚯蚓对土壤微生物活性的刺激作用，结果发现微生物呼吸的升高并不像原先假设的那样是由于利用了蚯蚓的排泄物所致。于是他们假设微生物活性与蚯蚓间的关系并不仅仅依靠营养关联，还包含有某种催化机制。在农业生态系统中，蚯蚓与微生物的相互作用在调控土壤C通量和维持土壤肥力方面很重要，但是蚯蚓对微生物C同化的间接影响还没有被充分认识。蚯蚓粪中的微生物群落和周围土壤的微生物群落有功能上的差异，可能是由于蚯蚓粪的微环境中物理、化学特性和生物的共同变化所致 (Bohlen *et al*., 2002)。

蚯蚓甚至可以通过影响植物菌根的侵染力和形态而影响森林植物的养分吸收能力 (Lawrence, 2003)。但是, Pattinson (1997)发现蚯蚓*Aporrectodea trapezoides*对菌根真菌*Glomus intraradices*的传播并无帮助；但会影响菌根真菌的侵染，可能的途径有:干扰土壤和真菌菌丝网络、取食菌丝、消化或破坏真菌的繁殖体以及改变土壤的物理化学环境等。

3.3　对其他土壤生物的影响

蚯蚓的活动也常有利于其他土壤动物的生存，比如它能通过多种途径影响跳虫的丰度和多样性 (Salmon, 2004)。蚯蚓在土壤中创建的四通八达的孔道可以为跳虫提供众多的避难所 (Salmon, 2004)。但是，在酸性腐熟腐殖质中，蚯蚓的存在使小个体的跳虫密度下降。可见，除土壤孔隙大小外，其他因子也影响跳虫的分布 (Salmon *et al*., 2005)。蚯蚓的排泄物也可以对森林土壤中跳虫的分布产生明显影响 (Salmon, 2001)。Loranger等 (1998) 在法国一块种植了15年的草地上的调查表明，中型土壤动物的丰度和多样性至少部分是由大型土壤动物的活动决定的，他们发现在蚯蚓密度高的样点，小型节肢动物的密度也高；反之，密度也较低。但是，也

有研究发现，蚯蚓会使土壤中线虫和线蚓的生物量明显降低 (Räty & Huhta, 2003)。蚯蚓能通过很多途径，如直接摄食土壤和凋落物中的线虫，或通过蚓粪间接改变线虫群落结构；蚯蚓 (lumbricid) 粪中几乎没有植物寄生性线虫，但食细菌线虫比例明显升高 (Ilieva-Makulec & Makulec, 2002)。

4 蚯蚓外来种入侵对生态系统的影响

生物入侵在过去的10年里已经迅速成为生态学研究的一个热点。但是多数工作都是关注地上动植物群落的变化，特别是生物多样性的丧失，而土壤生物入侵少被关注，可能是由于土壤环境的“黑箱”效应及其入侵后果不易察觉所导致的 (Bohlen, 2006)。土壤生物入侵现象可能同样严重，不应忽视。

4.1 对土壤食物网的改变

4.1.1 外来种与本土种的相互作用

人类活动的干扰降低了蚯蚓本土种的数量和多样性，促进了外来种的定居。外来蚯蚓种主要生活在养分丰富的非自然生境中，而本土种在受干扰少的自然生境里占优势 (Bhadauria *et al*., 2000; Winsome *et al*., 2006)。Winsome等 (2006) 报道，外来蚯蚓 *Aporrectodea trapezoides*能阻止本土种蚯蚓 *Argilophilus marmoratus*进入其领地，但是，两者的竞争也限制了*A. trapezoides* 的扩张。Lachnicht等 (2002) 也发现本土种蚯蚓*Estherella* sp.会削弱外来种蚯蚓*Pontoscolex corethrurus*对碳氮矿化作用的影响。Bhadauria等 (2000) 报道在中喜马拉雅地区，森林采伐和退化导致本土种蚯蚓的减少和外来种的侵入。Sánchez-de León 和 Zou (2004) 认为，当热带森林变成草地时，本土种蚯蚓会被某些外来种如*Pontoscolex corethrurus*所替代，但随着森林因为次生演替而恢复，本土蚯蚓种群也会重新恢复。

4.1.2 与其他土壤生物的作用

Groffman等 (2004) 发现在温带森林中，蚯蚓入侵虽然极大地减少了森林地表土中微生物生物量库，但却更加显著地提高了矿质土壤(mineral soil)中的微生物生物量，从而导致被侵入区土壤微生物总生物量的升高。但是，氮循环过程(矿化和硝化)并没有随之得到加强。这样蚯蚓导致了矿层土中微生物的氮“沉积 (sink)”，把氮在土壤中储存起来。蚯蚓*Dendrobaena octaedra* 入侵松林后，破坏了真菌菌丝，进而降低了真菌群落的多样性和丰富度 (McLean & Parkinson, 2000; Bohlen *et al*., 2004a)。在不同条件下，入侵蚯蚓的活动也可能提高或减少甲螨的多样性和生物量 (Bohlen *et al*., 2004a)。Maerz等 (2005) 发现外来蚯蚓和气候的相互作用引起火蜥蜴(*Plethodon cinereus*)食物资源的剧烈波动，从而控制其繁殖力和生存率。

4.2 对凋落物分解和养分循环的影响

蚯蚓入侵后通过消耗森林地被物，并将它们与土壤混合等过程实现对土壤有机质的转化和再分布(Bohlen *et al*., 2004b)。Alban 和 Berry (1994) 报道在蚯蚓入侵14年后，森林地表凋落物的重量和厚度减少约85%，土壤 (0–50 cm) 总碳每年平均减少0.6 Mg/hm^2；同时，土壤E层[①]完全被A层代替，导致表层矿质土的碳氮浓度升高，但土壤pH值及C/N比没有明显变化。Suárez等 (2006) 报道在纽约中南部北方阔叶林中，外来蚯蚓的活动不仅明显促进凋落物分解，而且可以缩小不同种类凋落物间分解速率的差异；同样，不同蚯蚓群落组成对凋落物分解的作用不同，在540 d的野外试验中，以蚯蚓*Lumbricus terrestris*和*Aporrectodea tuberculata*为优势种的林地中，凋落物剩余量 (17%)明显比以蚯蚓*L. rubellus* 和*Octolasion tyrtaeum*为优势种的林地中的剩余量 (27%)要少。Burtelow等 (1998) 报道，在以外来种蚯蚓为主的美国东北部的前冰蚀区，有蚯蚓的土壤中有更多的活性的易矿化的有机质，蚯蚓活动使O层土壤中有机质含量减少36%；同时，土壤微生物生物量碳、氮，土壤反硝化酶活性分别是无蚯蚓土中的14, 24和27倍。Suárez等 (2003) 在北美温带阔叶林中的控制实验表明，不同生态类群的蚯蚓对土壤磷循环的作用不同。深栖种*Lumbricus terrestris*的活动提高土壤总磷，而表—内栖种*L. rubellus*的活动使上层土壤中可交换磷增加，导致磷随水流失。

4.3 对植物的影响

Fisk等 (2004) 认为外来蚯蚓未影响糖枫林 (sugar maple forests) 中土壤碳的净排放，但提高了根的养分吸收效率，也可能增加地下异养代谢碳的供应。Lawrence等 (2003) 报道外来蚯蚓种的活动

[①]E 层，有些学者在上层土(A)与下层土(B)之间划出一层，称为淋溶层(E)。

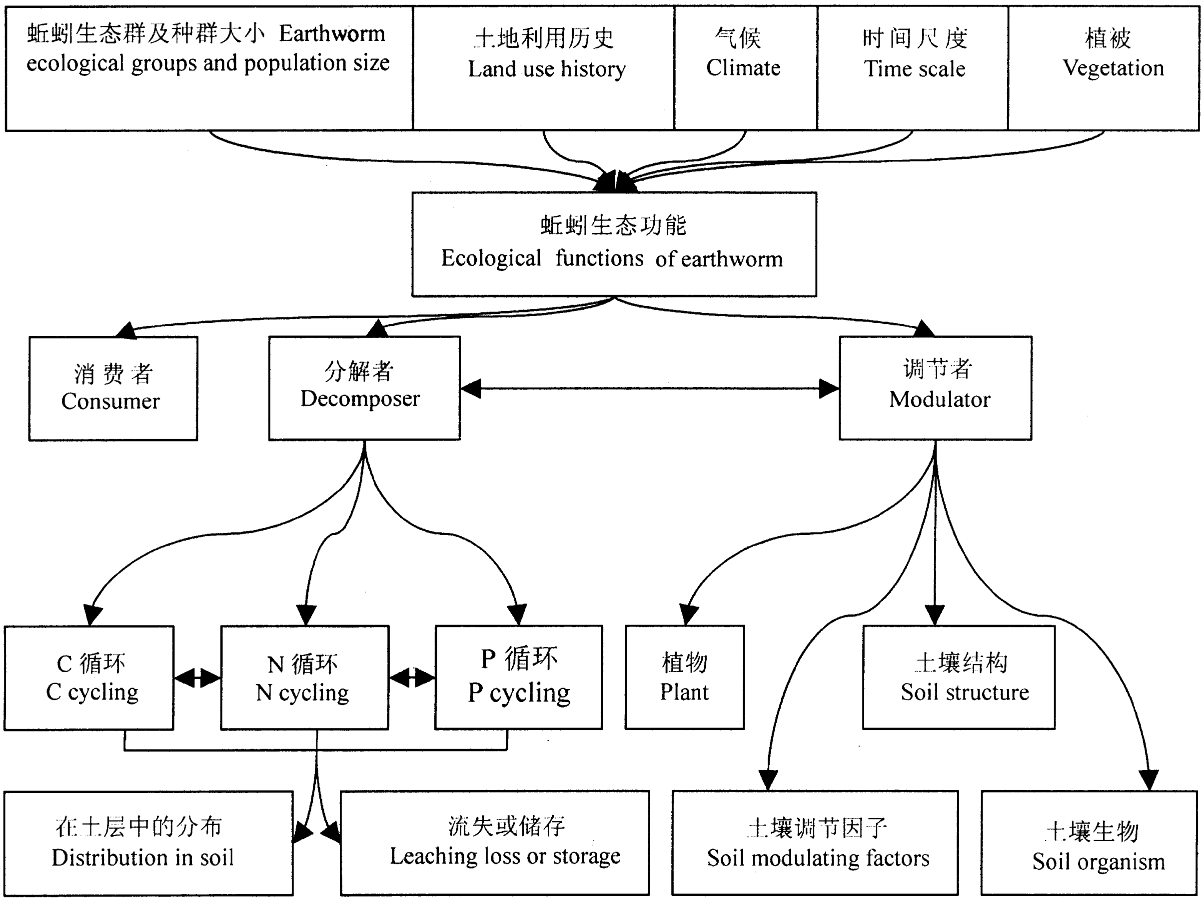

图2 蚯蚓在生态系统中的作用简图
Fig. 2 Simple model of earthworm functions in ecosystem

会改变或消除寒温带森林的地表有机质层。外来种蚯蚓活动还可以影响菌根的形态和侵染力，进而影响优势种植物的养分吸收能力。Gundale (2002) 发现*Lumbricus rubellus*的活动使O1和O2土层(即枯枝落叶层L和半腐层F)明显变薄，并且与蕨类植物*Botrychium mormo*的消亡紧密相关。Frelich等(2006) 报道，蚯蚓是重要的食碎屑者 (detritivores)，其对植物苗床环境、土壤特性、水文、养分和碳，以及植物–植食者的相互作用的影响最终可以影响森林的初级生产者。其影响程度取决于土壤母岩、土地利用历史和入侵蚯蚓的种类组成。在某些森林中，蚯蚓入侵导致可利用N和P的减少，使细根集中的土层中N和P的流失增加。在成熟糖枫林中，蚯蚓入侵显著降低草本植物的多样性和盖度以及树苗多度。随着蚯蚓的入侵，*Aralia, Botrychium, Osmorhiza, Trillium, Uvularia*和*Viola* 属的森林草本物种大量消失了。Ferilich等 (2006) 认为蚯蚓入侵改变植物群落的机制有: (1)去除土壤半腐层; (2) 直接影响种子和种子成活率; (3)改变菌根群落; (4)提高“植食者/植物”的比例; (5)改变养分状况和植物生产力。

5 小结

蚯蚓通过取食、掘穴和排泄等活动对生态系统的生物、化学和物理特性产生影响 (Bohlen *et al.*, 2004a)，这些因素也反过来影响蚯蚓本身。蚯蚓及其活动在其体内外形成众多的“蚓触圈”(drilosphere)，即蚓丘 (middens)、洞穴 (burrows)、滞育室 (diapause chambers)、地上和地下排泄物

(casts)，从而对土壤孔隙、团聚体的形成，成土作用(pedogenesis) 和凋落物破碎等过程产生影响(Brown, 1995)。一方面，蚯蚓活动对生态系统产生有利影响，包括加速凋落物的分解和氮的转化，促进植物对养分的吸收，在土壤中形成更多的微团聚体和孔隙，改善土壤结构，提高土壤渗透性和溶质的运移等。另一方面，蚯蚓活动也可能对系统产生有害的效应：如(1)蚯蚓将地表凋落物移走或埋入土中，蚓粪在地表的覆盖等都可能会增加水土流失；(2)蚯蚓也可能传播杂草种子或动物病原菌；(3)蚯蚓的活动在提高氮矿化的同时，容易造成氮的流失(Hendrix & Bohlen, 2002)。

蚯蚓对生态系统中凋落物分解和养分循环等关键过程的影响，受蚯蚓生态类群、种群大小、植被、母岩、气候、时间尺度以及土地利用历史的综合控制 (图2)。时间尺度的影响比较特别，如短期内蚯蚓的活动会提高碳的释放和氮的淋失，但从长远看，蚯蚓活动及其产生的大量微团聚体对土壤有机质有保护作用，有利于碳、氮在土壤中的长期储存(Helling & Larink, 1998; Decaëns *et al*., 1999; Jongmans *et al*., 2003)。

同理，蚯蚓入侵对生态系统的危害也因地而异。在人为干扰很少的地方，蚯蚓入侵造成的破坏会小得多 (Hendrix & Bohlen, 2002)。对蚯蚓入侵的研究，为人们提供了一个更好地了解蚯蚓对生态系统影响的机会。蚯蚓入侵对生态系统功能的影响是当前的一个热点，目前这方面的工作主要集中在北美。我国也有外来蚯蚓，但它对生态系统的影响还不清楚，开展一些外来种与本土种相互作用的研究是很有意义的。蚯蚓对全球变化的响应和影响是另一个值得关注的问题。

以往蚯蚓生态功能的研究多集中在农业生态系统，对森林生态系统的研究偏少。土壤本身的复杂性，人们对蚯蚓自然历史和生物地理学知识的缺乏，野外控制蚯蚓群落大小方法的滞后等都限制了蚯蚓生态学的发展。其他新技术如碳氮同位素分析，分子生物学技术和图像分析技术等的应用将有助于蚯蚓生态功能的研究 (Vanden Bygaart *et al.*, 2000; James & Olaf, 2007)。

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