

EARTHWORMS

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INTRODUCTION

Earthworms are perhaps the most important soil organisms in terms of their influence on organic matter breakdown, soil structural development, and nutrient cycling, especially in productive ecosystems. Aristotle called them the “intestines of the earth” and the eminent nineteenth century biologist, Charles Darwin, spent many years observing their major influence on the formation of humus and transport of soil (1). Despite the vast increase in scientific literature on earthworms in recent years, much remains to be known of their basic biology and ecology (2, 3).

EARTHWORM BIOLOGY AND CLASSIFICATION

Earthworms are terrestrial annelids with bilateral symmetry and corresponding external and internal segmentation. They have a thinly pigmented cuticle bearing setae on all segments except the first two. All earthworms are hermaphroditic. Their gonads are situated in specific segments, which vary among different taxa. When sexually mature, they develop a swollen area of the epidermis called a clitellum. This region produces a cocoon in which one or more eggs are deposited and then the cocoon is passed over the anterior segments and deposited in or on the soil. The young develop within the cocoon and newly hatched worms resemble adults. The time to hatching and reproductive maturity varies widely among different earthworm species and is influenced by environmental factors.

Earthworms are classified within the phylum Annelida and the class Oligochaeta, which consists of as many as 36 families worldwide. About two-thirds of oligochaete families comprise aquatic or semi-aquatic worms, and the remaining families comprise mostly or exclusively terrestrial worms or earthworms. There are over 3500 known earthworm species and it is estimated that the global total may be twice that number. Distinct taxonomic groups have arisen on every continent except Antarctica, and some groups are now distributed throughout the world.

EARTHWORM ECOLOGY

Ecological Groups

Earthworm species can be grouped according to behavioral, morphological or physiological adaptations that enable them to partition available resources in the soil. The three main life history strategies are termed epi, anecic, and endogeic (2, 3). Epigeic worms feed on plant litter, dwell on the soil surface or within the litter layer, tend to be heavily pigmented, and are small- to medium-sized. Anecic worms feed on plant litter and soil, live in nearly vertical permanent burrows, are dorsally pigmented, and large. Endogeic species are soil-feeders, are not heavily pigmented, form extensive horizontal burrow systems, and range in size from small to large. Endogeic worms have been further divided into polyhumic, mesohumic, and oligohumic groups, which are separated, respectively, by the descending importance of organic rich mineral soil in their diet and increasing size. Earthworm species do not always fall clearly into these three main categories and may even exhibit traits of different groups at different life stages or under different environmental conditions.

Earthworm Communities

Earthworm communities generally consist of from one to six species. The relative abundance and species composition of earthworm communities depends upon soil type, topography, and vegetation, and is also influenced by land use history and earthworm biogeography. Earthworms account for the majority of animal biomass in soil in a wide range of productive ecosystems, from temperate grasslands, pastures and forests to tropical pastures, savannas and rainforests, and many temperate and tropical agroecosystems. They generally do not occur in deserts and arid grasslands or in extreme alpine or boreal habitats. Earthworms are often absent from strongly acidic forest soils with poor litter quality, such as some northern coniferous forests.

Many earthworm communities consist of invasive exotic species. In North America, where approximately 100 native earthworm species have been described, at least 45 exotic species have been introduced. Lumbricid

earthworms of European origin dominate many North American agroecosystems. A worldwide survey of earthworms in tropical regions reported that a total of 51 exotic and 151 native species commonly occur in tropical agroecosystems (4).

EFFECTS OF EARTHWORMS ON SOIL PROPERTIES

The influence of a given earthworm species on soil properties depends upon that species' life history strategy. For example, the large vertical burrows of anecic earthworms, such as the common nightcrawler *Lumbricus terrestris*, can facilitate preferential flow of water through the soil profile, increasing the transport of water, nutrients, and agricultural chemicals into deeper soil layers (5, 6). Epigeic species facilitate the breakdown and mineralization of surface litter, whereas anecic species incorporate surface litter deeper into the soil profile. Anecic species also bring soil from deeper soil horizons to the surface, which over a long period of time can change the mineralogy of surface soil. Endogeic species feed on fragmented organic matter and mix it thoroughly through the surface mineral soil.

Effects on Organic Matter Breakdown and Nutrient Cycling

Earthworm activity accelerates the decomposition of plant litter, increases rates of nutrient transformation and plant nutrient uptake, improves soil aggregation and porosity, and enhances water infiltration and solute transport. Earthworms can consume and incorporate large amounts of organic matter into soil (Table 1). Such mixing is largely responsible for the formation of mull soils in which surface organic horizons are thoroughly mixed with underlying mineral soil.

Earthworms are a major influence on nutrient cycling in many ecosystems. Although they generally increase the mineralization of soil carbon, earthworms can also decrease mineralization of carbon by contributing to the formation of stable soil aggregates in which carbon is protected from further breakdown. Direct fluxes of nutrients through earthworm biomass can be considerable. For example, the turnover of nitrogen (N) through earthworm tissues can be up to $150 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (3). Earthworm casts contain elevated amounts of inorganic N relative to surrounding soil. As a consequence, earthworms can greatly enhance the mineralization of N and can stimulate other N transformations such as denitrification (7). By increasing bypass flow of infiltrating water, earthworm burrows can increase the amount N and other nutrients leaching from the soil profile (5). Alternatively earthworms can reduce the amount of nutrients lost in surface runoff by increasing rates of water infiltration into the soil (8).

Effects on Physical Properties of Soil

The effect of earthworms on soil structure results from the net outcome of their feeding and burrowing activities. Earthworms ingest soil particles and organic matter, mixing these two fractions together and egesting them as surface or subsurface casts. Estimates of annual rates of production of earthworm casts range from less than 5 to over 250 Mg ha^{-1} in various ecosystems (Table 2). Once egested, soil in casts can be eroded due to impact of rainfall or can form stable soil aggregates through a variety of stabilizing mechanisms (16).

Earthworms generally improve the aeration and porosity of soil through formation of burrows and by increasing the proportion of large aggregates in the soil, and their effects are especially important in poorly structured or reclaimed soil. By increasing rates of water infiltration, earthworms can reduce the amount of surface runoff. Alternatively, earthworms can increase erosion by

Table 1 Amount of organic matter ingested or incorporated into soil by earthworm populations in different environments

Ecosystem	Location	Type of organic matter	Amount consumed or incorporated (kg ha^{-1})	Reference
Maize field	United States	Maize residues	840	(9)
Orchard	England	Apple leaves	2,000	(10)
Mixed forest	England	Canopy tree leaves	3,000	(11)
Oak forest	Japan	Oak leaves	1,071	(12)
Alfalfa field	United States	Alfalfa residues	1,220	(13)
Tallgrass prairie	United States	Total organic matter	740–8,980	(14)
Savanna	Ivory Coast	Total organic matter	1,300	(15)

Table 2 The amount of earthworm casts produced and in different environments in various locations around the world

Environment	Location	Earthworm casts (Mg ha ⁻¹)
Arable	Germany	92
Arable	Switzerland	18–81
Arable	Nigeria	50
Arable/floodplain	Egypt	268
Pasture	England	19–40
Pasture	England	28
Pasture	Germany	91
Pasture	Switzerland	22–42
Grassland/tallgrass prairie	United States	24–94
Grassland	India	4–78
Savanna	Columbia	10–50
Tropical forest	Ivory Coast	32–50
Temperate forest	Germany	7–60

(Data from various sources)

removing the protective cover of surface litter, increasing surface sealing and depositing surface casts, which can be carried downslope during heavy rains. Some tropical species actually increase soil bulk density and decrease infiltration by producing compact soil casts. Overall, the effects of earthworms on soil structure are considered to improve soil fertility.

Effects on Plant Growth

The majority of studies examining the influence of earthworms on plant growth have reported that earthworms stimulate plant growth, although some studies have reported no effect or even a negative effect of earthworms on plant growth (2, 17). Earthworms have been shown to increase production of shoots and grain in a variety of field trials and greenhouse experiments. Introduction of earthworms into reclaimed polders in the Netherlands and in pastures in New Zealand resulted in large increases in forage quantity and quality (18, 19). Beneficial effects of earthworms on plant growth may be due to increased nutrient and water availability, improved soil structure, stimulation of microorganisms or formation of microbial products that enhance plant growth, or possibly through direct production of plant growth promoting substances.

Undesirable Effects of Earthworms

Despite the documented and putative beneficial effects of earthworms on nutrient dynamics, soil structure, and

fertility, some aspects of earthworm activities are considered undesirable (2). These include removing and burying surface residues that would otherwise protect soil surfaces from erosion; producing fresh casts that increase erosion and surface sealing; depositing castings on the surface of lawns and golf greens or irrigation ditches where they are a nuisance, or in pastures where they interfere with haying operations; dispersing weed seeds in gardens and agricultural fields; transmitting plant or animal pathogens; increasing losses of soil nitrogen through leaching and denitrification; and increasing soil carbon loss through enhanced microbial respiration. It is the net outcome of their positive and negative effects that determines whether earthworms are to be considered pests or benefactors in any given situation, and they are generally considered to be of great benefit to soil properties and fertility.

EARTHWORMS AND SOIL MANAGEMENT

Earthworms and Soil Reclamation

Introduction of appropriate earthworm species or encouraging natural population through the addition of suitable amendments can increase the rate of soil improvement and genesis of soil structure of reclaimed land. Introduction of European earthworms into pasture in New Zealand and Australia, as well as in Dutch polders, greatly facilitated improvements in soil structure and plant productivity (18, 19). There has also been some success in introducing earthworms into reclaimed mining sites and in reclaimed peat with beneficial effects on soil structural development, nutrient cycling, and productivity (2).

Influence of Agricultural Practices on Earthworm Populations

Earthworms can be affected favorably or adversely by different agricultural practices. Whereas heavy cultivation is detrimental to earthworm populations, reduced and no-tillage agricultural practices promote the growth of earthworm populations. Organic amendments, such as animal or green manures, also stimulate the growth of earthworm populations. Inorganic fertilizers may benefit earthworm populations by increasing the production of crop residues, but their effects are not as great as the effects of organic fertilizers. Long-term application of inorganic fertilizers may adversely affect earthworm populations due to soil acidification or other changes in the soil environment. Liming can benefit earthworm populations in some instances.

Effects of Pesticides and Soil Pollutants on Earthworms

Pesticides have widely varying effects on earthworm populations, with many chemicals having little or no toxicity toward earthworms and others exhibiting acute toxicity (20). In general, the carbamate insecticides and soil fumigants are very or highly toxic to earthworms. Herbicides in general show low toxicity toward worms, although there are some exceptions. Organochlorine and organophosphorous insecticides have varying levels of toxicity.

Soil contamination with organic pollutants, heavy metals, and acid precipitation can be detrimental to earthworm populations. Most toxic organic soil pollutants are highly toxic to earthworms. Heavy metals vary in their toxicity toward earthworms. In addition to acute negative effects of some heavy metals on earthworms, sublethal heavy metal concentrations can cause declines in earthworm growth and reproduction. Heavy metals can accumulate in earthworm tissues, which is potentially problematic for movement of heavy metals into higher trophic levels, because of the wide array of animals that prey on earthworms. Earthworm species vary in their tolerance of acid soil conditions but some reports have noted a decline in earthworm populations in response to large amounts of acid deposition.

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