The “*intestines of the soil*”: the taxonomic and functional diversity of earthworms – a review for young ecologists

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Abstract

Earthworms are some of the most important and popular soil organisms. Their essential roles in ecosystems have not only been recognized by Aristotle, Charles Darwin, and many active scientists around the globe, but also by land managers, farmers, and gardeners. However, many people do not know how diverse earthworms are in terms of their form and function. Here we summarize the current knowledge of the taxonomic, morphological, physiological, reproductive, and functional diversity of earthworms, their action as so-called “ecosystem engineers”, and their many interactions with other organisms below and above the ground. The ~7,000 described species range from a few cm to a length of up to 3 m and are categorized into three major ecological groups that reflect their life style. Taken together, this overview will help appreciate the surprisingly high diversity of a supposedly well-known soil animal group.

Keywords

Annelida, biodiversity, ecosystem engineer, functional diversity, soil ecology

The taxonomic diversity of earthworms

People often talk about "the earthworm". However, there is a huge diversity of earthworms in terms of species, even at a given location. When digging in a garden plot, a pasture, or a forest, one may find between 1 and 12 different earthworm species. Even in a small country like Germany, there are almost 50 earthworm species reported. However, there are many countries around the world, where the number of earthworm species is less well studied and described, such as in many areas of South America, Africa, and East Asia (Phillips et al. 2019). Globally, scientists have described roughly 7,000 earthworm species (Orgiazzi et al. 2016) and have made substantial advances in the last decade due to the development and application of novel molecular methods to differentiate species. However, scientists believe that this number is just the tip of the iceberg, and have estimated that the global number of earthworm species may be as high as 30,000 (Orgiazzi et al. 2016). Thus, there is still a lot of work to do for future generations of soil ecologists!

The reproductive, morphological, and physiological diversity of earthworms

Some earthworm species are mostly parthenogenetic, *i.e.* growth and development of embryos happens without fertilization. However, sexual reproduction is common in earthworms. Earthworms are hermaphrodites, which means that they have both male and female sexual organs, and each individual can thus produce offspring. These reproductive strategies allow earthworms to occur and thrive in many ecosystems around the globe. By the way, in contrast to the common myth that both parts of an earthworm will survive if cut into two pieces, only the front part of the harmed earthworm may survive this treatment, which is why cutting earthworms in pieces is not a successful strategy to increase their densities in your garden.

The thousands of different earthworm species can vary a lot in body size. Some adult earthworms can only reach a maximum size of a few cm, while others can reach a body length of a couple of meters. One prominent example is the giant earthworm (*Megascolides australis*) that can be as long as 3 m and lives in the south of Australia in an area that is only about 40 ha in size. Although this earthworm species mostly lives hidden in the soil, its presence can sometimes be recognized because of the gurgling noises it produces when moving through its underground burrows.

Earthworms occur in many ecosystems around the world. Given their dependence on water, *e.g.* for breathing through their skin, they have developed a range of clever strategies to tolerate or overcome adverse conditions, such as frost and drought. For instance, several species occurring at regions with long and cold winters have developed frost tolerance. Such species can accumulate compounds in their body fluids, which limit the formation of ice crystals that could otherwise destroy their body cells and harm their intestines. This strategy is very similar to the antifreeze people put in their cars. Some species are able to produce cocoons containing their offspring that can dehydrate and thereby avoid damage by freezing water. Other earthworms can curl up deep in the soil to enter a kind of hibernation or just move to deeper soil layers to endure dry soil conditions.

The functional diversity of earthworms

Although earthworms all live in or on top of the soil, they do differ substantially in their life styles. Soil ecologists have defined three major ecological groups of earthworms that have been very useful to describe their behavior, nutrition, and ecosystem effects: epigeic, endogeic, and anecic earthworms (Fig. 1).

Epigeic earthworms mostly live in the litter layer and feed on soil surface plant litter (Fig. 1). Some are also found under logs and stones as well as in and around patches of other animals' feces (some of them love pastures). By mostly feeding on litter material, epigeic earthworms play an important role in litter breakdown and fragmentation; this is why many of them are often referred to as "primary decomposers", because they initiate decomposition processes by nibbling on the litter, fragmenting it, and making the material accessible to other organisms. These species are mostly small in body size, and the whole body is pigmented and thus better protected against predators (because they have a body color similar to the plant litter) and UV light of the sun (with pigments functioning like a sun screen). Epigeic earthworms can occur in habitats that are not suitable for other earthworm species, such as some with acidic soils and long and cold winters, because they live on the soil surface and have developed strategies to overcome detrimental environmental conditions, respectively.

Endogeic earthworms are rather unpigmented earthworm species that range substantially in size, but share the behavior of living in and feeding on the top soil layers. They form non-permanent, horizontal burrows and feed on the organic material in the soil (Fig. 1). This feeding behavior is important for the further processing of organic material and the recycling of nutrients therein. This is why most of the endogeic earthworm species are referred to as "secondary decomposers", because they may feed on material that was already preprocessed, *i.e.* nibbled on, by primary decomposers like some epigeic earthworms.

While epigeic and endogeic earthworms mostly reside in their most favorite soil layer, anecic earthworms are the "connectors" between these soil layers. They live in permanent, vertical burrows that can go down to a depth of a couple of meters, but they do feed on litter on the soil surface (Fig. 1). Anecic earthworms pull leaves and other organic material into their burrows and transport soil from deeper layers to the surface, which is important for the mixing of soil layers and the decomposition of plant litter. Moreover, these vertical burrows provide an important channel system that is critical for soil aeration and water movements through the soil. Anecic earthworms often have a more pigmented front part and a less pigmented back part, because they mostly leave the soil headlong to collect litter material and to mate.

Earthworms as "ecosystem engineers" and the consequences for other organisms

Earthworms are known to have particularly strong effects on ecosystems, because of their manifold activities that change ecosystem structure. Because of these activities, they have often been referred to as ecosystem engineers. Ecosystem engineers structure the environment and thus influence the living conditions for a large range of other organisms (Jones et al. 1994, Eisenhauer 2010). Earthworms act as engineers by burrowing, casting, and mixing of litter and soil. This results in changes in the chemical (like nutrient mineralization and cycling) and physical properties of the soil (including soil stability, structure, water dynamics, and aeration), with important consequences for soil communities (Eisenhauer 2010).

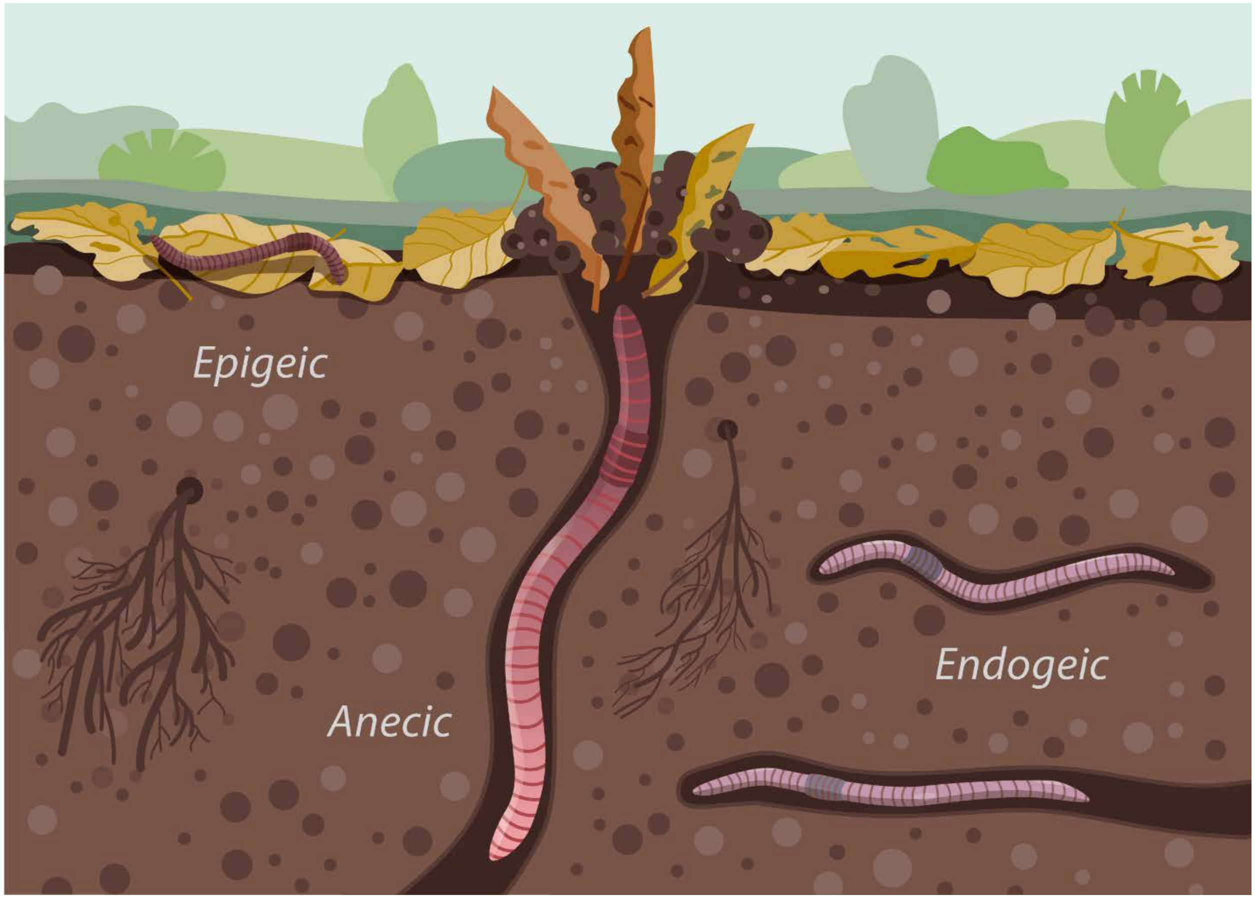

Figure 1 | The three main ecological groups of earthworms. Earthworms differ in their life style, and ecologists have defined these groups according to their burrowing and feeding behavior.

As outlined above, earthworm ecological groups differ a lot in their influence on ecosystems and thereby on other organisms. Recent studies have shown that earthworm effects, furthermore, depend on their densities and if the other organisms are used to the presence of earthworms (Eisenhauer 2010, Eisenhauer et al. 2019). Effects of epigeic earthworm species on other soil animals can be positive, *i.e.* increasing the densities and diversity of their neighbors, in the case of moderate earthworm densities, or negative in the case of high densities. While positive effects have been mostly ascribed to an increase in different living opportunities for other animals, negative effects were mostly explained by competition for food and the removal of living space. By contrast, impacts of endogeic earthworms may often be negative and primarily due to the competition with other animals for food. As a consequence, these detrimental effects intensify with more earthworms, which basically means more food competitors, being present. In contrast to endogeic earthworms, impacts of anecic earthworm species were shown to be neutral at larger spatial scales, *e.g.* in an area of 2 by 2 m, and positive at the small scale, *e.g.* in an area of 0.2 x 0.2 m. Such positive effects can be explained by the formation of stable living spaces that serve as homes for soil animals. In addition to interactions with soil organisms, earthworms also influence species living only partly in the soil like plants and aboveground species like many insects. Most of these effects have been ascribed to the fact that earthworms facilitate decomposition processes, which increases nutrient availability for plants that can then grow better and influence aboveground animals.

Conclusion

Earthworms are surprisingly diverse in form and function. While scientists may have only been able to describe a fraction of the global earthworm biodiversity, they have assembled very convincing information on how important earthworms are for how terrestrial ecosystems function, supporting Aristotle's analogy of the "*intestines of the soil*". So, the next time you find an earthworm in your garden, you may not want to cut it into two pieces (earthworms reproduce very well on their own), but have a more detailed look at its morphological traits and behavior, and remember Charles Darwin's conclusion: "*It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures.*"

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Author contributions

EE and NE jointly conceived and discussed the concept of this paper. NE wrote the first draft, and EE commented on all versions of the paper.

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