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Effects of soil and leaf litter quality on the biomass of two endogeic earthworm species

Simone Cesarz [a, b, c, *], Dylan Craven [a, b], Christoph Dietrich [a, b], Nico Eisenhauer [a, b]

[a] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[b] Institute of Biology, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany
[c] J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Berliner Straße 28, 37073 Göttingen, Germany

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ABSTRACT

Earthworms drive important ecosystem functions like decomposition and nutrient mineralization in many terrestrial ecosystems, which is why factors controlling their mass gain are of great scientific interest. We conducted a microcosm experiment using two common endogeic earthworm species (*Aporrectodea caliginosa* and *Octolasion tyrtaeum*) and two different soils (one from a beech-dominated forest and one from a mixed tree species forest in Germany) to test litter quality (different nutrient concentrations) and soil quality effects (low and high) on relative mass gain of earthworms. We hypothesized that mass gain of endogeic earthworms is driven by both soil and litter quality. Soil pH, carbon (C) and nitrogen (N) concentrations were used to characterize soil quality, while leaf litter N, phosphorus (P), calcium (Ca), and magnesium (Mg) concentrations were used as proxies for leaf litter quality. Forest soils were incubated with leaf litter of six common tree species in Central Europe (*Fagus sylvatica*, *Acer platanoides*, *Acer pseudoplatanus*, *Carpinus betulus*, *Tilia* spp., and *Fraxinus excelsior*) that span a gradient in leaf litter quality. In addition, we determined soil microbial biomass C as a potential food source of endogeic earthworms. After three months, relative earthworm mass gain of *A. caliginosa* and *O. tyrtaeum* was significantly higher in soil from the mixed tree species forest (high quality soil: +218% and +240%, respectively) compared to soil from the beech-dominated forest (low quality soil: +160% and +162%, respectively). Relative mass gain of *A. caliginosa* increased significantly with all leaf litter nutrients in low quality soil, whereas in high quality soil only leaf litter Ca positively affected relative mass gain. Similarly, relative mass gain of *O. tyrtaeum* increased significantly with increasing concentrations of leaf litter N, Mg, and Ca in the low quality soil. In the high quality soil, only leaf litter Mg significantly increased relative mass gain. Overall, our results indicate that leaf litter quality effects on endogeic earthworm mass gain were more important in low quality soil for both earthworm species. Notably, microbial biomass was significantly higher in high quality soil (506 ± 135 μg C g^{-1} soil dw) compared to low quality soil (217 ± 64 μg C g^{-1} soil dw), but microbial biomass was not significantly affected by leaf litter type and was a poor predictor of relative earthworm mass gain. This finding indicates that endogeic earthworms did not significantly depend on soil microbial biomass, but rather on the quality of dead organic material in the soil and surface leaf litter. As earthworms may prefer feeding on certain microbial taxa, and we only measured total soil microbial biomass, future studies could investigate if leaf litter quality effects on earthworms are mediated by changes in soil microbial community structure, micronutrients, and organic compounds.

1. Introduction

Earthworms play an important role in many terrestrial ecosystems as ecosystem engineers, by modifying soil structure via bioturbation as well as through their contribution to decomposition processes [1–3]. Furthermore, they often comprise, together with Protozoa, the largest biomass of soil fauna [4], and their functional

* Corresponding author. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.
E-mail addresses: simone.cesarz@idiv.de (S. Cesarz), dylan.craven@idiv.de (D. Craven), christoph.dietrich@idiv.de (C. Dietrich), nico.eisenhauer@idiv.de (N. Eisenhauer).

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significance, i.e., their effects on ecosystem processes, makes earthworms important study organisms in ecological and ecotoxicological research [5,6]. Moreover, some earthworm species are biological invaders in many ecosystems with major impacts on soil chemistry, plant communities, and soil microarthropod communities [7–9]. Consequently, it is vital to identify drivers that control earthworm mass gain.

Earthworms can be divided into three ecological groups: epigeic earthworms, which live in and feed on the leaf litter layer on the soil surface; anecic earthworms, which dig large vertical and permanent burrows and feed on surface leaf litter, and endogeic earthworms, which feed on organic matter in the mineral soil and build horizontal burrows in deeper organic and mineral soil layers [10]. Together with anecic earthworms, endogeic earthworms often dominate the biomass of soil invertebrates [2]. Endogeic earthworms have a very low assimilation efficiency (2%), resulting in high consumption rates of their poor quality diet, i.e., soil [11]. It has been suggested that endogeic earthworms feed on stabilized soil particles [12] as well on easily available compounds like glucose [13]. Rajapaksha et al. [14] demonstrated that endogeic earthworms were able to remove soil surface litter, which suggests that leaf litter may serve as potential additional food resource with both stable and soluble compounds. Direct or indirect litter feeding by endogeic earthworm has, however, rarely been investigated. Thus, exploring factors influencing the ecology of endogeic earthworms can help to improve species distribution models [15], understand their influence on the bioavailability of micronutrients [16], and increase our knowledge about their interactions with microorganisms that drive priming effects [17].

The quality of root and leaf litter inputs influence the quality of soil and organic matter and therefore the mass gain of endogeic earthworms [2,18–20]. Generally, low soil pH and low moisture negatively affect earthworm development [21,22], whereas high soil organic matter content positively affects earthworm nutrition and therefore mass gain [11]. Several studies have investigated the importance of soil microorganisms, mainly fungi, for earthworm nutrition but clear evidence is still lacking. Previous studies have suggested that endogeic earthworms consume microorganisms as bycatch during soil ingestion, as helpers to degrade recalcitrant compounds, but also as a direct food resource [11].

Food choice experiments have demonstrated a clear preference of earthworms for leaf litter with low C:N ratio and low concentrations of secondary compounds, and polyphenol content [14,23,24]. In addition, the availability of soil carbon (C) [13,25], and nitrogen (N) [26] have also been shown to increase earthworm mass gain. More recently, high calcium (Ca) concentration in soil was linked to reduced soil acidity and increased fertility, factors which positively affect both earthworm abundance and diversity [18]. While the effects of other leaf litter nutrients, such as phosphorus (P) and magnesium (Mg), on earthworm growth were not studied, a recent study by Resner et al. [27] showed that earthworms reduced the availability of Ca, Mg, K, and P when invading a North American forest.

Thus, factors affecting earthworm mass gain have generally been attributed to their feeding preferences and direct food sources. In doing so, effects of leaf litter quality were tested by using mainly anecic and epigeic earthworms, whereas soil quality was tested by using endogeic earthworms. Interactions of leaf litter and soil quality on earthworm mass gain have been largely neglected. Dechaine et al. [28] even suggested ignoring potential feeding relationships of endogeic earthworms on leaf litter material. However, feeding relationships in soil are complex and still poorly understood [29]. Investigating and understanding feeding relationships in soil is of particular importance to appreciate the consequences of anthropogenic environmental changes for species interactions.

The aim of the present study was to explore if the potential dependence of endogeic earthworm species on surface leaf litter material is contingent upon soil nutrient content. While surface leaf litter quality effects on anecic earthworms have already been investigated [11,30], the present study is one of the first investigating potential interaction effects of leaf litter and soil quality on endogeic earthworms. In this study, we investigated drivers of changes in earthworm biomass in soils of contrasting quality (low versus high quality) in combination with leaf litter types (beech, lime, ash, hornbeam, and two maple species) representing a broad gradient in nutrient concentrations and, therefore, leaf litter quality. We explored the relative mass gain of two endogeic earthworm species, *Aporrectodea caliginosa* and *Octolasion tyrtaeum*, as this ecological group often dominates the density and biomass of earthworm communities [31] and to determine if two functionally similar species exhibit similar responses to soil and leaf litter quality effects. As detailed above, endogeic species are considered to feed mostly on mineral soil, but leaf litter material could also have indirect effects on earthworm mass gain by altering nutrient availability and/or microbial community biomass and composition [32].

We hypothesized that endogeic earthworm relative mass gain would be significantly higher in high quality soil than in low quality soil (hypothesis 1) due to a higher pH value [2], higher nutrient availability (especially C, N, and Ca) [19], and higher soil microbial biomass [33]. Further, we hypothesized that leaf litter chemistry (C, N, P, Ca, and Mg concentrations) would influence relative mass gain of endogeic earthworms (hypothesis 2). Specifically, we expected increased leaf litter N and Ca concentrations to enhance earthworm biomass [18,34]. We also tested for effects of other leaf litter nutrients, such as P and Mg concentrations, on earthworm relative mass gain as these nutrients have rarely been considered in previous studies and could have significant effects on earthworm mass gain [35,36]. Finally, we hypothesized that negative effects on earthworm mass gain in low quality soil would be compensated by high leaf litter quality (hypothesis 3). Given correlations among different leaf litter quality properties and soil microbial biomass, we used partial least squares path modeling (PLS-PM) to identify the main drivers of earthworm mass gain [37].

2. Materials and methods

2.1. General design

A microcosm experiment was established to study the relative mass gain of the two endogeic earthworm species *A. caliginosa* and *O. tyrtaeum* in two different soils (where they naturally occur but in different densities [38]) and in different leaf litter treatments. The experiment was conducted using a two factorial design with two levels for the factor “soil” (low and high quality) and six levels for the factor “leaf litter” (one level for each tree species). Further, we used leaf litter concentrations of N, P, Ca, and Mg as proxies for leaf litter quality, which have been shown to determine essential processes like leaf litter decomposition [39], but other organic compounds like tannins and phenols may also be important for earthworm mass gain [14,23,24]. Every treatment was replicated seven times and the experiment ran for a total of three months.

2.2. Soil and leaf litter

Soil and leaf litter were taken from the Hainich National Park (Thuringia, Germany, annual precipitation: 600.5 mm and mean annual temperature: 9.0 °C). The soil was taken from a depth of 0–20 cm (without leaf litter layer) in forest plots with different