



## What determines earthworm cast fertility? A meta-analysis

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We have known for a long time that earthworms can beneficially affect plant growth. This is to a large extent due to the high fertility of earthworm casts. However, it is not clear how fertile casts exactly are, compared to bulk soil, nor how their fertility varies with earthworm feeding guilds and physico-chemical soil properties. We quantified the fertility of earthworm casts and identified its controlling factors using a meta-analysis including 405 observations from 81 published articles. We quantified cast fertility by determining the enrichment of earthworm casts relative to the bulk soil (“relative cast fertility”; RCF) for total organic carbon (TOC), total phosphorus (TP) and total nitrogen (TN) concentrations, as well as for plant available pools of N (AN: the sum of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) and P (AP: P-Olsen, P-Bray or comparable metrics), CN ratio and microbial biomass C. We also studied four additional variables: pH- $\text{H}_2\text{O}$ , clay content, cation exchange capacity (CEC), and base saturation. With the exception of CN ratio, microbial C and clay content, all studied response variables were significantly increased in casts compared to the bulk soil. Increases in total elemental concentrations (TOC, TP and TN), which are the result of preferential feeding or concentration processes, were comparable and ranged between 40 and 48%. Nutrient availability, which is to a large extent the result of (bio)chemical transformation processes in the earthworm gut, was increased more strongly than total elemental concentrations (241% and 84% for AN and AP, respectively). Increases in pH (0.5 pH units), cation exchange capacity (CEC; 40%), and base saturation (27%) were also large and significant. None of the soil-related possible controlling factors could satisfactorily explain the variation in RCF; plant presence (or other sources of organic C input such as residue application) was the only controlling factor that consistently increased RCF across soil properties. With the exception of AP, none of the studied response variables could be linked to earthworm feeding guild. Our results show that earthworm casts are much more fertile than bulk soil for almost all analysed cast fertility properties. However, these positive RCFs are to a large extent dependent upon the presence of plants. In general, earthworm feeding guild or specific physico-chemical soil properties could not explain the large variability in RCF for the various response variables. Therefore, we hypothesize that RCF effects depend on intricate interactions between earthworm species traits and specific soil properties. Understanding these interactions requires trait-based approaches combined with mechanistic modelling of biochemical processes in the earthworm gut and casts.