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The interactions between soil type and earthworm species determine the properties of earthworm casts

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ABSTRACT

Earthworms are recognized to increase soil porosity, reorganize soil structure, and stimulate soil microflora and nutrient mineralization. The properties of earthworm casts should depend both on earthworm species or ecological group and on soil properties. Interactions between earthworm species and soil types have been suggested, but only poorly demonstrated. In order to better understand those interactions, two hypotheses led our study: (1) Soil type has a greater influence on cast properties than earthworm; (2) Earthworms from different species influence cast properties differently; (3) The intensity and direction of the impact of each earthworm species on cast properties vary with soil properties. Fifteen physical and chemical variables (N–NH_4^+, N–NO_3^-, total organic C and N, C/N ratio, $CaCO_3$, pH, P, K^+, Mg^{2+}, Mn^{2+}, Na^+, CEC, moisture, wettability) were measured in casts of three earthworm species (*Lumbricus terrestris*, *Allolobophora chlorotica* and *Aporrectodea rosea*) produced in three temperate soils. Univariate and multivariate analyses showed that earthworm species and soil types significantly impacted cast properties. pH, N_t, K and Mg contents were interactively altered by both factors. Multivariate analysis showed that a difference of soil type had a major impact on casts properties (62%) compared to the impact of a difference of earthworm species (10%). Cast properties were most impacted by *L. terrestris*, then by *A. chlorotica* and last by *A. rosea*. The response ratio (ratio of the properties of the casts to the properties of the bulk soil) was used to quantify the effect of earthworm species compared to the control soil. It showed a higher response of variables in casts in nutrient-rich soils, especially in casts of *L. terrestris*. The interactions between earthworm species and soil types on cast properties were discussed with regards to earthworm ecology, properties of the soil, and earthworm modifications of cast microflora.

1. Introduction

Earthworms significantly modify the physical, chemical and biological properties of the soils in which they live (Lavelle et al., 2006; Lee, 1985). They can increase soil porosity by creating burrows (Francis and Fraser, 1998; Shipitalo and Le Bayon, 2004), and they reorganize soil structure by ingesting and egesting the soil while rearranging linkages responsible for soil aggregate stability (Jouquet et al., 2008; Shipitalo and Protz, 1989). Soil passage through earthworm digestive system leads to the assimilation of organic matter by earthworms and bacteria ingested with the soil. This modifies the chemical properties of newly formed aggregates (Aira et al., 2003; Lavelle et al., 1995), i.e. earthworm cats. Cast chemical properties are also altered by changes in the microbiological activities that increase organic matter mineralization within casts, and therefore increase nutrient availability (Bityutskii et al., 2012; Chapuis-Lardy et al., 2010). These physical, chemical and microbiological modifications generally result in an increased plant growth, at least partially due to the release of mineral nutrients in earthworm casts (Chaoui et al., 2003; Scheu, 2003).

Cast properties should depend on the ingested soil material, on the life-traits of the earthworm that produced them, and probably on the interaction between both (Buck et al., 1999; Jana et al., 2010; Schrader and Zhang, 1997). Earthworm communities and activities depend on soil properties such as soil moisture, temperature, texture or soil organic matter (see Lavelle, 1988 for a review). The characteristics of the soil that they ingest are likely to be a primary factor influencing the chemical, physical and biological properties of egested casts (Jouquet et al., 2008; Lavelle, 1988; Shipitalo and Protz, 1989). Indeed, the cast content in, for example, organic matter, nitrogen or clay should depend on the corresponding soil characteristics. Additionally, casts produced by different earthworm species usually present different chemical and physical properties, especially if earthworms do not belong to the same ecological group (Zhang and Schrader, 1993; Schrader and Zhang, 1997; Aira et al., 2003). Indeed, anecic earthworms feed

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on decaying litter at the soil surface and fragments of this litter are found in their cast, while endogeic species feed on soil organic matter (Lee, 1985). Different earthworm species are also known to impact differently the communities of microorganisms found in their casts (Chapuis-Lardy et al., 2010; Decaëns et al., 1999; Lavelle et al., 1995). Taken together, soil type and earthworm species have been shown to impact cast properties but these two factors have rarely been studied together and compared.

A few studies have recently compared the properties of casts produced by several earthworm species in one soil (Bottinelli et al., 2010; Jouquet et al., 2008). Other studies compared the impact of mulch type on the properties of casts produced by one or several earthworm species (Buck et al., 2000, 1999; Flegel et al., 1998). However, experiments comparing the characteristics of casts produced by several species and in different soil types are still scarce. Schrader and Zhang (1997) used two horizons of a clay soil and a loam soil, and the two species *Lumbricus terrestris* and *Aporrectodea caliginosa.* They showed that casts had a higher organic carbon content than the bulk soil, especially in loam soil compared to clay soil, with higher values for *L. terrestris*. A larger C/N ratio was found in casts of *L. terrestris* compared to *A. caliginosa*, and the $CaCO_3$ content of casts varied with earthworm species and soil type. The authors concluded that differences in organic carbon and nutrient contents observed between species were due to a different substrate selection by earthworms and to differences in the efficiency of organic matter assimilation during the gut transit. Norgrove and Hauser (2000) also suggested that the food selectivity by earthworms might enable them to adjust their feeding regime to nutrient-poor soils. They reported a negative correlation between the nutrient and organic carbon concentrations in casts and in the surrounding soil.

It is relevant to study the interactive effect of earthworm species identity and soil properties on earthworm cast properties for three main reasons: (1) Earthworms are known to modify soil's physical and chemical characteristics at least partially through cast production (Lavelle et al., 1998; Lee, 1985); (2) Earthworm impacts on soil properties are known to influence, generally positively, plant growth (Jana et al., 2010; Scheu, 2003); (3) Earthworm casts have been found to host a high density of seeds (Decaëns et al., 2003), the germination of which is likely to be affected by cast properties. This should subsequently impact the composition and structure of plant communities (Forey et al., 2011; Willems and Huijsmans, 1994). Thus, analyzing the interaction between earthworm species and soil properties will help predict the way earthworms and soils interactively impact plant growth and seed germination (Roem et al., 2002). Jana et al. (2010) showed how *A. caliginosa* produces nutrient-rich casts in a poor soil and allows plants growing in a nutrient-poor soil to grow as well as plants in nutrient-rich soils. Doube et al. (1997) showed that the increased or reduced growth parameters of wheat, barley and faba beans in presence of *Aporrectodea trapezoides* or *A. rosea* were the result of interactions between the two earthworm species and different soil textures. However, Laossi et al. (2010a, 2010b) also showed that plant biomasses were increased by *L. terrestris* in the nutrient-rich soil only.

The objectives of our study were to evaluate through a microcosm experiment the differences between the cast physical and chemical properties of three earthworm species from two ecological groups, and to determine how these differences are affected by soil characteristics. Three hypotheses led our analysis: (1) Soil type has a greater influence on cast properties than earthworm, (2) Earthworms from different species influence cast properties differently, (3) The intensity and direction of the impact of each earthworm species on cast properties vary with soil properties.

2. Methods

2.1. Soil characteristics and preparation of microcosms

Soils were collected in February 2011 from the top layer (0–20 cm) of three different permanent grasslands in Upper-Normandy, France. Climate is temperate oceanic with a mean annual rainfall of 800 mm and a mean annual temperature of 10 °C. The soil from Saint-Adrien (N 49°22′22″, E 1°07′41″) is a rendzic Leptosol (IUSS, 2006) supporting vegetation dominated by *Brachypodium pinnatum* (L.), *Festuca lemanii* (L.) and *Carex flacca* (L.). The soil from Yvetot (N 49°36′37″, E 0°44′15″) is a NeoLuvisol-Luvisol (IUSS, 2006) supporting a vegetation dominated by *Agrostis capillaris* (L.), *Lolium perenne* (L.) and *Ranunculus acris* (L.). The soil from Yville-sur-Seine (N 49°25′11″, E 0°52′54″) is a Histosol (IUSS, 2006), where the vegetation is dominated by *Poa trivialis* (L.), *L. perenne* and *A. capillaris*. Names of soil types used here were Rendosol (Re), Luvisol (Lu) and Histosol (Hi).

All soils were hand-sieved within two days after collection with a 5 mm mesh sieve and air-dried for a week. Microcosms were cylindrical boxes (13.5 × 11 cm) filled with 750 g of soil watered with 115 mL water. When necessary, water was added to microcosms to adjust the soil water retention capacity to 65%. Microcosms were placed in the dark (17 °C) for a week to favor the establishment of naturally present microorganisms before the introduction of earthworms. Soil moisture was kept constant throughout the experiment.

2.2. Earthworms and cast collection

We used the anecic *Lumbricus terrestris* (L.) and the endogeics *Allolobophora chlorotica* (Sav.) and *Aporrectodea rosea* (Sav.), which are commonly found in grassland ecosystems of North-West France (Decaëns et al., 2008). Moreover, while casts of *L. terrestris* are commonly studied, casts of *A. chlorotica* (Sav.) and *A. rosea* (Sav.) have been subject to lesser attention. *A. chlorotica* individuals (AC; 0.32 ± 0.08 g, average fresh weight without gut content) were hand-sampled in April 2011 in neutral grasslands outside the university campus of Mont-Saint-Aignan. *A. rosea* individuals (AR; 0.23 ± 0.04 g) were hand-sampled in alluvial deposits near the Seine River and *L. terrestris* individuals (LT; 5.23 ± 0.73 g) were purchased in a fishing bait store. After voiding their guts for 24 h on moist filter paper in Petri dishes, three adult individuals from a single species were added to each microcosm leading to a total of twelve treatments: 3 soil types × (3 earthworm species + control without earthworm). Each combination of treatment was replicated five times and all 60 boxes were kept in darkness at 17 °C for the length of the experiment.

We collected casts form each microcosm once to twice a week for 180 days. This frequency was decided in order to collect fresh cast material for the time of the whole experiment. Casts had to be collected manually from the entire microcosm in order to obtain sufficient cast material for analyses. The repeated disturbance of the microcosms was also applied to microcosms with no earthworm. All samples (control and casts) were taken at the same time. Casts from each microcosm were air-dried and stored until analysis except for moisture, NO_3^- and NH_4^+ where fresh material was used. Two individuals of *L. terrestris*, three individuals of *A. chlorotica* and ten individuals of *A. rosea* died during the experiment (11%). New individuals of similar weight and species were used to replace the missing earthworms.

2.3. Physical analyses

In each microcosm, we measured the moisture content of aggregates from the weight loss of fresh material (Soil: 10 g; Casts: