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Identification of earthworm burrow origins by near infrared spectroscopy: Combining results from field sites and laboratory microcosms

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ABSTRACT

A major obstacle to understanding feeding and burrowing behaviour of earthworms and their impact on soil structure in natural field conditions is that it remains impossible to identify the origins of burrows in the soil matrix. This gap in our knowledge makes it difficult to understand the roles of different earthworm species in creating the burrow network in soils. We tested the utility of near infrared spectroscopy (NIRS) as a new tool to overcome this obstacle. For the first time, we studied the ability of NIRS to detect specific chemical footprints left by different earthworms during the production of burrows, and thereby to identify the origins of burrows produced in the same soil matrix in the field, in terms of the earthworm species that produced them. The method was tested in three study sites (in sandstone, schist and marl geologies), differing in soil mineralogical composition and texture, with well-characterized and partially overlapping earthworm faunas. Burrows collected in the field were identified by comparing their NIR spectral signatures to the signatures of macroaggregates produced by the same earthworm species living in the same soil in laboratory conditions. We showed clearly that burrows of anecic and epi-endogeic earthworm species were characterized by specific NIR spectral signatures, resulting from quantitative and qualitative differences of OM in burrows among species. PLS-DA models conducted on NIR spectral data showed that NIRS technique allowed identification of a mean of 57.1% (±7.4) of burrows in soil monoliths at the sandstone site, 51.6% (±10.2) at the schist site and 46.5% (±8.1) at the marl site. Our study reveals some clear limitations in this method: low predictive abilities in surface soils, inability to discriminate among endogeic species and the requirement for a calibration procedure through the establishment of a site-dependent reference database.

1. Introduction

As ‘ecosystem engineers‘ (Jones et al., 1994; Jouquet et al., 2006), earthworms play an important role in soil structure and consequently in the regulation of soil ecological functions and ecosystem services (Lavelle et al., 2006; Birkhofer et al., 2008; Blouin et al., 2013). In particular, earthworms are known to influence water and solute transport by creating burrows in the soil matrix (McCoy et al., 1994). The quantities of water and solutes transported through earthworm burrows, and the patterns of transport, are highly variable (Shipitalo and Butt, 1999), depending mainly on the ecological type of earthworm (Shipitalo and Le Bayon, 2004) as defined by differences in burrowing and feeding behavior (Lee and Foster, 1991). Earthworm feeding behavior affects the amount and nature of organic matter in the burrow sidewalls, thereby strongly influencing the water repellence of the soil and the infiltration characteristics of the macropore-matrix (Leue et al., 2010). However, a major obstacle to understanding the feeding and burrowing behavior of earthworms and their impact on soil structure in natural field conditions is that it remains impossible to identify the origins of burrows in the soil matrix (i.e., the earthworm species that made each burrow). This gap in our knowledge makes it difficult to understand the roles of different earthworm species in creating the burrow network in soils and to model their effects on water and solute transport in the soil matrix.

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Understanding the effects of earthworms on soil properties and functioning requires taking into account the complexity of biological processes in the drilosphere. The drilosphere is defined by the soil ingested by earthworms, excreted in the form of casts, as well as the burrows that earthworms create through digging and soil ingestion (Lee et al., 1985; Brown et al., 2000 Brown et al., 2000). As earthworms ingest drilosphere soil, they simultaneously enrich it by the addition of saliva and intestinal mucus each time the earthworm passes through a burrow (Barois and Lavelle, 1986; Brown et al., 2000). As a consequence, soil microbial communities benefit from earthworm activity and are highly concentrated at the surfaces of burrow walls and within the surrounding concentric soil layer (Brown et al., 2000; Bundt et al., 2001). However, the microbial communities of the drilosphere – burrows and the surrounding soil – vary markedly depending on the earthworm species that produced the burrows. Earthworms have selective feeding habits and thus ingest preferred organic items (Bouché and Kretzschmar, 1974). Because feeding habits differ among species (Curry and Schmidt, 2007), organic matter in the casts and burrows they produce varies both quantitatively and qualitatively among species and ecological types, and this also leads to variation in microbial communities. For example, the microbial communities associated with anecic species, which remove litter from the soil surface and pull it into their burrows, enhancing its microbial degradation (Brown et al., 2000), differ in biomass and composition from those associated with endogeic species, which are geophagous.

Recent laboratory studies, using soil with homogeneous chemical and biological properties, have demonstrated the ability of Near Infrared Reflectance Spectroscopy (NIRS) to characterize earthworm casts, and aggregates associated with the roots of different plant species, by specific chemical fingerprints that reflect the amount and nature of organic matter and mineral particles, and how these soil components are associated (Zhang et al., 2010; Zangerlé et al., 2011, 2014). In field conditions, however, where soils show great heterogeneity of chemical and biological properties, studies have so far only tested whether NIRS can differentiate selected biostructures (surface biostructures, belowground earthworm casts) from the surrounding "bulk" soil (Cécillon et al., 2010; Jouquet et al., 2010; Bottinelli et al., 2013) and whether NIRS allows discrimination between biogenic soil structures produced by social insects and those produced by earthworms (Hedde et al., 2005; Hedde et al., 2005). Huerta et al. (2013) were able to characterize soil monoliths containing biostructures of different earthworm communities by spectral signatures specific to the earthworm community. However, the ability of NIRS to characterize single biostructures (for example, burrows) of each earthworm species by specific spectral fingerprints in field conditions remains unexplored. A next step would thus be to test whether NIRS allows identification, in natural field conditions, of burrows comprising a network in the soil matrix according to the earthworm species that created each of them. Achieving this goal requires taking into account the fact that NIRS signatures of soil macrofauna may be affected by variation in soil properties that are independent of these organisms. Applications of NIRS to characterize specific NIR signatures of biostructures in field studies have shown that "chemical footprints" of soil macrofauna are strongly dependent on the physical and chemical properties of the soil at the field site (Cécillon et al., 2010). Numerous studies have shown that NIRS measurements of soils are highly influenced by properties of the mineral fraction of the soil such as texture, mineralogical composition and clay content (Hunt, 1977; Stenberg et al., 1995; Clark, 1999; Chang et al., 2001).

In the present study, we developed a novel methodological approach to test the ability of NIRS to identify the origins of burrows in natural field conditions. This novel approach should allow us to identify origins of single field-collected burrows by comparing their NIRS signals with those of burrows produced by the same earthworm species kept in laboratory microcosms, and thereby allow the quantification of the respective contributions of different earthworm species to the burrow network of the soil matrix. Moving beyond previous studies, our experiment examines whether this discriminatory capacity is maintained under the variation in soil properties that characterizes real field situations.

Table 1
Density (individuals/soil monolith) and biomass of earthworms (fresh weight) ($g \times m^{-2}$), collected in the three field sites. The sizes (length and diameter) given for the earthworm species are those reported by Bouché (1972).

	Earthworm species size		Sandstone		Schist		Marles	
	Length (mm)	Diameter (mm)	Earthworm biomass/m^2	Individuals/soil monolith	Earthworm biomass/m^2	Individuals/soil monolith	Earthworm biomass/m^2	Individuals/soil monolith
Anecic species								
Lumbricus terrestris	130–250	6–10	19.2	0.6	83.2	2.6	32	1
Aporrectodea longa longa	130–170	4–9	51.2	1.6	–	–	32	1
Aporrectodea nocturna	90–180	4–5	17.9	0.8	–	–	9.0	0.4
Juveniles (all anecic and epigeic species combined)			28.8	3.6	12.8	1.6	44.8	5.6
Epi-endogeic species								
Aporrectodea caliginosa	50–80	3.5–4.5	–	–	53.8	4.2	15.4	1.2
Octolasion cyaneum	65–140	5–8	–	–	9.6	0.4	9.6	0.4
Endogeic species								
Aporrectodea icterica	70–90	3–6	2.6	0.2	–	–	7.7	0.6
Aporrectodea rosea	40–85	2–6	1.0	0.2	2.9	0.6	4.8	1
Allolobophora chlorotica	30–80	3–7	25.0	2.6	–	–	9.6	1
Juveniles (all endogeic species combined)			36.5	7.6	43.2	9	43.2	9
Total anecic species			117.1	6.6	96	4.2	117.8	8
Total epi-endogeic and endogeic species			65.0	10.6	109.4	14.2	90.2	13.2
Total			182.1	17.2	205.4	18.4	208	21.2

The symbol "-" indicates absence of a species in samples from a particular site.