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Earthworms and soil water regulation: A review

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Abstract

For a long time, soils were considered an inert substrate, however, now it is widely acknowledged that soils are a dynamic system comprising considerable biodiversity. Earthworms are an essential component of the biological activity in soils. These organisms contribute to plant productivity, plant and soil health and many other ecosystem services. Here, we review the contribution of earthworms to soil water regulation. We particularly synthesize our understanding of how earthworms affect soil water infiltration and movement and soil water retention and storage dynamics. We briefly review factors that impact soil water regulation, and we show a substantial knowledge gap related, in particular, to difficulties in identifying processes by which earthworms impact on soil water storage and how interactions of earthworms of different species with different plant rooting strategies impact water flow and storage. This review aims to provide guidance to obtain a general emerging framework of earthworm effects on soil water regulation.

Keywords: Earthworms, soil water infiltration, water holding capacity, soil water storage, earthworms, and plant interaction.

Vers de terre et régulation de l'eau du sol : Revue bibliographique

Résumé

Depuis longtemps, les sols ont été considérés comme un substrat inerte, mais il est maintenant largement reconnu que les sols sont un système dynamique constituant une grande biodiversité. Les vers de terre sont une composante essentielle de l'activité biologique des sols. Ces organismes contribuent à la productivité des plantes, à la santé des plantes et des sols et à de nombreux autres services écosystémiques. Nous abordons ici la contribution des vers de terre à la régulation des eaux du sol. Nous synthétisons en particulier notre compréhension sur la manière dont les vers de terre affectent l'infiltration et le mouvement de l'eau dans le sol et la dynamique de rétention et de stockage de l'eau dans le sol. Nous présentons brièvement les facteurs qui ont un impact sur la régulation des eaux du sol. Nous montrons également un manque de connaissances lié, en particulier, aux difficultés à identifier les processus par lesquels les vers de terre ont un impact sur le stockage des eaux du sol et comment les interactions des vers de terre de différentes espèces avec différentes stratégies d'enracinement des plantes ont un impact sur le flux et le stockage de l'eau. Cette revue vise à fournir des orientations pour obtenir un cadre général émergent des effets des vers de terre sur la régulation des eaux du sol.

Mots-clés : Vers de terre, infiltration de l'eau dans le sol, capacité de rétention d'eau, stockage de l'eau dans le sol, l'interaction de vers de terre avec les plantes.

ديدان الأرض وتنظيم مياه التربة: مراجعة

حلام جمال، مارك إدوارد هودسون

ملخص

لفترة طويلة، كانت تعتبر التربة مادة خاملة، الآن من المسلم به على نطاق واسع، أنها نظام دينامي يضم الكثير من التنوع البيولوجي. ديدان الأرض تعد العنصر الأساسي للنشاط البيولوجي في التربة. تساهم هذه الكائنات الحية في إنتاجية النبات وصحة (جودة) النبات والتربة، بالإضافة إلى العديد من خدمات النظام الإيكولوجي الأخرى. نستعرض هنا مراجعة حول مساهمة ديدان الأرض في تنظيم مياه التربة. لخصنا كيفية تأثير ديدان الأرض على تسرب مياه التربة وحركتها وديناميات تخزين مياه التربة واحتجازها. نستعرض أيضا وبإيجاز العوامل التي تؤثر على تنظيم مياه التربة، كما أظهرنا الفجوة المعرفية الجوهرية التي تتعلق، على وجه الخصوص، بالصعوبات في تحديد المناهج والعمليات التي تؤثر من خلالها ديدان الأرض على تخزين مياه التربة وكيف تؤثر تفاعلات الأنواع المختلفة من ديدان الأرض مع الإستراتيجيات المختلفة لتجذير النباتات على تدفق والتخزين المياه. تهدف هذه المراجعة إلى تقديم إرشادات للحصول على إطار عام لتأثيرات دودة الأرض على تنظيم مياه التربة.

الكلمات المفتاحية: ديدان الأرض، تسرب مياه التربة، سعة احتجاز المياه، تخزين مياه التربة، تفاعل ديدان الأرض والنبات.

Introduction

Because many ecosystem services are performed by organisms (Jax, 2005; Kremen and Ostfeld, 2005), Blouin et al. (2013b) conducted a bibliometric analysis which illustrates the growing interest in the use of earthworms in the management of ecosystem services. Blouin et al. (2013a) reviewed the link between earthworms as part of biodiversity and various ecosystem services and summarized different soil functions and ecosystem services that earthworms contribute to. They give examples of earthworms as drivers of soil functions such as soil formation and soil structure development, and ecosystem services including water regulation, nutrient cycling, climate regulation, pollution remediation, primary production, and cultural services. Amongst these many vital services, water regulation, and soil water, are fundamental in the soil-plant-water system and are of prime importance to modern agriculture.

The ability of earthworms to improve soil properties and the subsequent effects on soil hydrology were first recognized by White (1989). In the presence of earthworms, soil physical (Darwin, 1881; Zhang and Schrader, 1993; Bohlen *et al.*, 2004; Edwards, 2004; Drouin *et al.*, 2016; Hallam and Hodson, 2020) and hydraulic (Smettem, 1992; Bohlen *et al.*, 2004; Chan, 2004; Ouellet *et al.*, 2008; Yunusa *et al.*, 2009) properties are dynamic and affect soil water regulation (Blouin *et al.*, 2013a) through transfer and storage processes (Pitkanen and Nuutinen, 1998; Blouin *et al.*, 2007; Capowiez *et al.*, 2014b; Bertrand *et al.*, 2015; Hallam *et al.*, 2020). The Assessment Reports of the Intergovernmental Panel on Climate Change (IPCC, 2014, 2019) projected changes in the climate system as “it is very likely that heat waves will occur more often and last longer, and that extreme precipitation events will become more intense and frequent in many regions”. Therefore, modification of soil water flow and storage by earthworms would help to alleviate exposure of many human systems and ecosystem services to negative effects of extreme events due to current climate change (Wen et al., 2020; Rüdisser et al., 2021). Additionally, improved water storage and flux in the soils promote plant growth by increasing water availability to plants and diffusion of dissolved nutrient ions within the soil to the root surface, leading to higher crop yields (Chapman *et al.*, 2012; Hallam *et al.*, 2020). Further, earthworms support plant growth by increasing nutrient mineralization from residue and soil organic matter humification and by stimulation of soil microflora (Scheu, 2003; Cunha *et al.*, 2016). Meta-analysis of 57 published papers before 2013 showed an increase of plant shoot by 23% and roots by 20% in the presence of earthworms (van Groenigen *et al.*, 2014). The growth of plant roots will create further biopores and modify soil physical properties (Whalley and Dexter, 1994; Hallam *et al.*, 2020) which in turn influence soil water flow and storage (Figure 1).

The impact of earthworms on soil hydraulic properties differ according to their species or functional groups (Coleman and Wall, 2015). Anecic earthworms are usually associated with an increase in water infiltration due to their vertical burrowing which creates wide and continuous macropores that increase bypass flow through saturated soils (Coleman *et al.*, 2004). Endogeic species are generally linked with alteration of soil water retention and storage presumably due to their intense activity and highly branched and tortuous burrows of small diameter (Capowiez *et al.*, 2015), albeit contradicting results have been reported in the conducted studies (Stockdill and Cossens, 1969; Blanchart *et al.*, 1999; Blouin *et al.*, 2007; Ernst *et al.*, 2009).

The litter dwellers, epigeic earthworms, rarely burrow within the mineral soil (Shipitalo and Le Bayon, 2004) but are reported to enhance soil water retention (Smagin and Prusak, 2008; Ernst *et al.*, 2009).

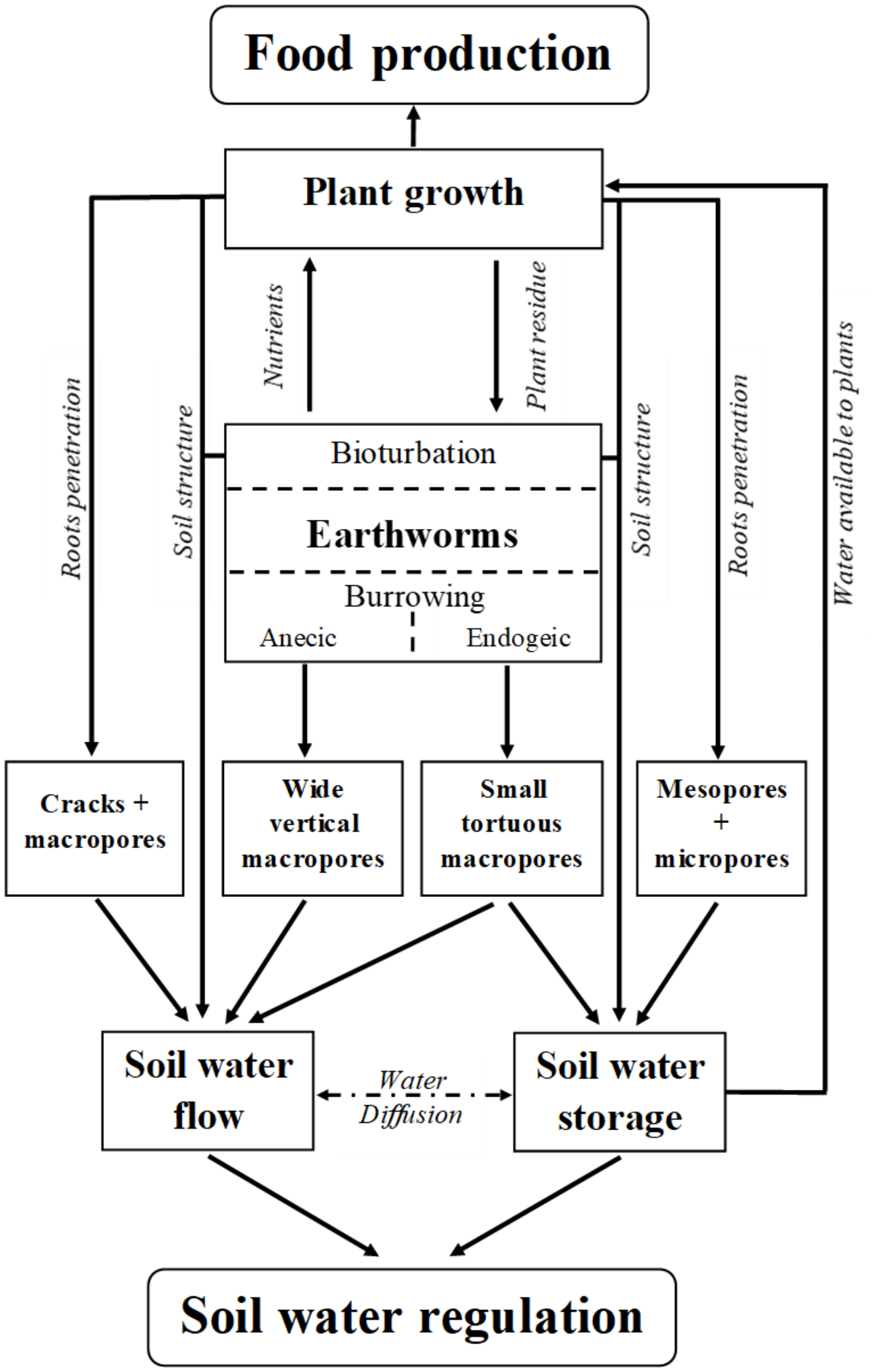

Figure 1. Schematic diagram of potential effects of the interaction between earthworms and plants on soil water regulation and food production services. Several factors affect soil water regulation and food production, including crop and soil management, soil erosion, seasonality, etc. These factors are described in the main manuscript (by Hallam, 2019, unpublished thesis).

In this paper we focus on one of the many important ecosystem services provided by earthworms, soil water regulation. This review will consider soil water regulation as the set of actions, interactions and processes controlling soil water flow and water storage during a given period to prevent floods, droughts, and erosion. Addition of earthworms to soil has a significant influence on soil water regulation by increasing/decreasing hydraulic conductivity and infiltration (Ehlers, 1975; Bouché and AlAddan, 1997; Capowiez *et al.*, 2009, 2014b; Hallam *et al.*, 2020), water retention (Ernst *et al.*, 2009; Milleret *et al.*, 2009; Bertrand *et al.*, 2015; Hallam and Hodson, 2020), risk of flooding (Edwards and Lofty, 1972) and erosion during runoff (Roth and Joschko, 1991; Blanchart *et al.*, 2004; Jouquet *et al.*, 2012b). To understand the influence of earthworm behaviour and burrows on soil water flow some authors have tried to model the system using soil physical properties (Bastardie *et al.*, 2002; Ouellet *et al.*, 2008; Schneider and Schroder, 2012; Capowiez *et al.*, 2015). However, despite this modelling work, this aspect of earthworm ecology is underrepresented in the literature compared to other aspects such as earthworm population dynamics and the morphological characteristics of earthworm burrows.

Thus, the aim of this review is to synthesise our understanding of how earthworms affect soil water regulation, particularly soil water infiltration and movement and soil water retention and storage dynamics. Many factors interact in a complex fashion to impact soil water regulation (Figure 2) such as earthworm species and biomass (Alegre *et al.*, 1996; Blouin *et al.*, 2007), bulk density (Blanchart et al., 1997; Capowiez et al., 2021), burrowing and casting activities (Bastardie *et al.*, 2003; Le Couteulx *et al.*, 2015), soil texture, soil structure and initial water content (Pérès *et al.*, 1998; Fischer *et al.*, 2014). In this paper we will briefly review each of these factors in turn, highlighting key findings. This review was conducted following a systematic review of the scientific literature by including leading authors from the different disciplines. We accessed to multiple databases that provide comprehensive citation data including Scopus (www.scopus.com), ScienceDirect (www.sciencedirect.com), Web of Science (www.webofknowledge.com), Google Scholar (www.scholar.google.com), Academia (www.academia.edu) and ResearchGate (www.researchgate.net). We searched for manuscripts focusing on earthworms and soil water regulation. We restricted our research to effects of earthworms on soil water infiltration and water storage, then we explored the impact of different species of earthworms and the main factors that influence soil water regulation by applying the following search string: ("Soil" OR "Soil water Regulation" OR "Infiltration" OR "Storage" OR "Hydrology" OR ‘’Water flow" OR "Holding capacity" OR "Physical properties") AND ("Earthworm" OR "Anecic" OR "Endogeic" OR "Epigiec"). We screened appropriate studies and reported key methodology information and their findings in Tables 1 and 2 and then identify relevant knowledge gaps, the filling of which would lead to an improved understanding of earthworm-water interaction in soils.

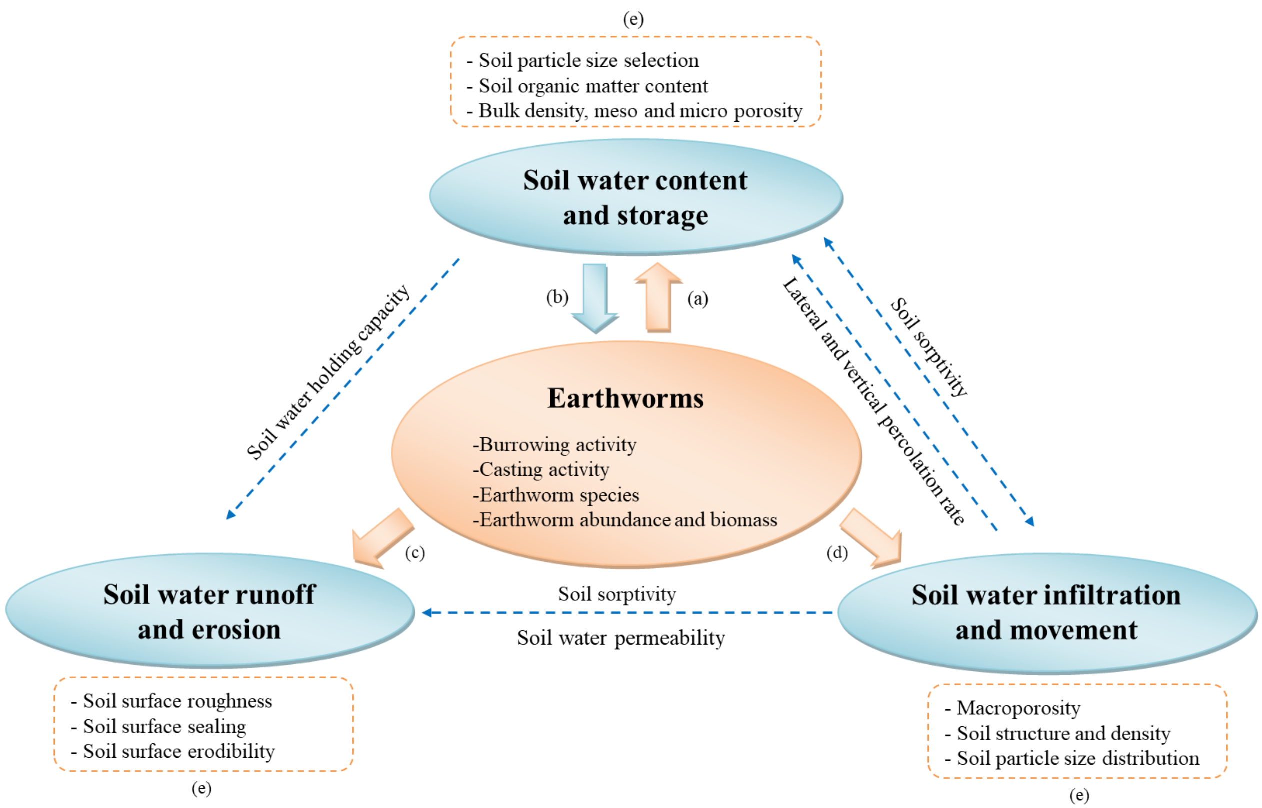

Figure 2. Potential influences of earthworms on soil water regulation (solid arrows) and the interactions between soil hydrological components (dotted blue arrows). (a): Earthworms affect soil water content and storage, (b): Soil water content affect life cycles of earthworms, (c): Earthworms affect soil water runoff and erosion, (d): Earthworms affect soil water infiltration and percolation, (e): the major variables affected by earthworms (by Hallam, 2019, unpublished thesis).

Earthworms and soil water infiltration and movement

Water infiltration influences hydrological flows by the transfer of water through the soil surface. Using dye and other tracers McCoy et al. (1994), Chan (2004), Shipitalo and Le Bayon (2004), Shipitalo et al. (2004), Holden and Gell (2009) and Schwartz et al. (1999) have shown that in soils with high populations of earthworms, burrows made by some earthworm species from the three main ecotypes can effectively conduct water and affect infiltration rate despite the volumes of the burrows not exceeding a few percent (0.2 %) of total soil porosity.

Earthworm ecotypes

Earthworms can be classified into three ecological groups, epigeic (litter dwelling), endogeic (shallow burrowing) and anecic (deep burrowing) (Bouché, 1977), and these have differing effects on water infiltration process (Figure 3). Most studies on the impacts of earthworms on infiltration rates have been conducted using anecic species and particularly *Lumbricus terrestris* (Shipitalo and Le Bayon, 2004; Spurgeon *et al.*, 2013). *L. terrestris* species are known to increase water infiltration rates and accelerate flow in soils (Willoughby and Kladivko, 2002; Fischer *et al.*, 2014) with several studies identifying rapid water flow through their burrows because of their large diameter, up to 12 mm, and deep penetration (by-pass flow), up to 240 cm, (Shipitalo and Butt, 1999). Bouche and AlAddan (1997) showed that in various soils the infiltration rate with 100 g m^{-2} of anecic species earthworm was close to 282 mm h^{-1} compared to a mean rate of 150 mm h^{-1} per 100 g m^{-2} of fresh earthworm biomass without anecic species. Chan (2004) estimated that the infiltration rate of water through a single burrow in 1 m^2 of soil was 1.9 times that of the remaining bulk soil (6.7 mm h^{-1} against 3.6 mm h^{-1}). Using medical X-ray tomography for the 3D characterization of earthworm burrow systems in natural soil dominated by the anecic species *Nicodrilus giardi*, Bastardie et al. (2005a) found that burrow systems provided a soil surface-accessible burrow volume ranging from 1400 to 10463 cm^3 and wall area ranging from 1069 to 7237 m^{-2} for 1 m^3 of soil. The accessible burrow volume and area would allow a good vertical water flow, through the burrows, and lateral water flow, within the soil matrix through burrow walls. However, Bastardie et al. (2005c) reported lower lateral water flow through *L. terrestris* burrows compared to that through soil fractures presumably due to high compaction of the burrow walls. In comparison to endogeic species, Capowiez et al. (2015) reported that the burrow systems of anecic species have fewer branched burrows (12.2 to 20.2 vs 28.2 to 37.2 branches m^{-1}) and were far more efficient regarding water infiltration rate (11. 03 to 12.42 vs 2.32 to 5.15 L min^{-1}) due to open burrows linking the top and bottom of the soil cores.

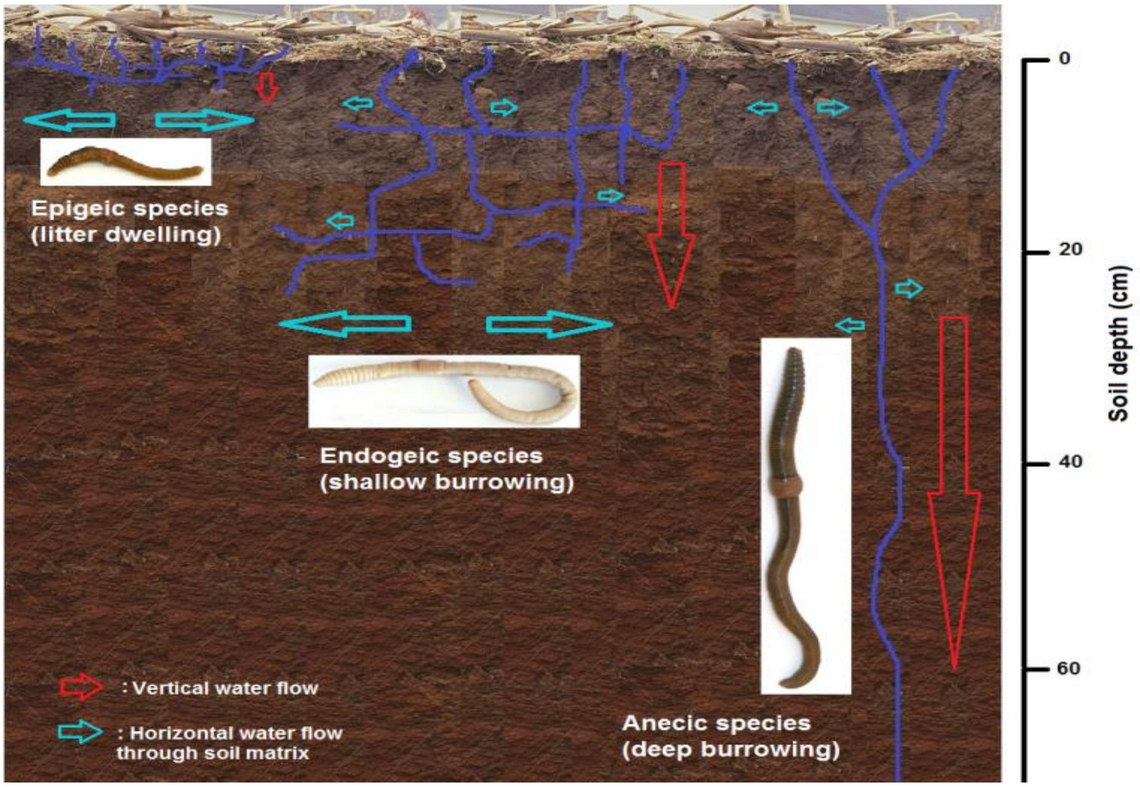

Figure 3. Potential effects of the three ecological groups of earthworms, epigeic, endogeic and anecic, described by Bouché (1977), on soil water flow. The blue lines are example of burrows filled with water. Arrow sizes are proportional to the impact of the earthworm species on water flow. (by Hallam, 2019, unpublished thesis).

A major concern with some of the field experiments (Ehlers, 1975; Edwards *et al.*, 1989; Shipitalo and Butt, 1999; Shipitalo *et al.*, 2004) and most laboratory experiments (Ela *et al.*, 1992; Bastardie *et al.*, 2005c; Capowiez *et al.*, 2015) designed to investigate the impact of earthworms on water flow through soil is that water movement through the burrows is over-estimated relative to natural conditions since, unlike many burrows in the field, the burrows in experiments do not terminate within the soil matrix (Smettem, 1992). In these situations, when it rains and the burrows fill with water, a constant flux of water can flow through the burrows at a rate proportional to the fourth power of its radius as described by Poiseuilles' equation (Figure 4). When earthworm burrows terminate within the soil matrix, and once they are water-filled, constant flow is not necessarily maintained; the water will flow through the burrow wall and through the soil matrix with the flux of water depending not strictly on burrow diameter (Sutera and Skalak, 1993; Singh *et al.*, 2013) but also on burrow length and on the permeability of soil matrix and its wetness (Smettem, 1986) (Figure 4). In addition, after initial infiltration, the pressure of encapsulated air in the burrow may reduce further water flow (Constantz *et al.*, 1988). Dead-end burrows also improve macropore-soil matrix interaction by increasing lateral water flow as the burrows are filling up (Cey and Rudolph, 2009).

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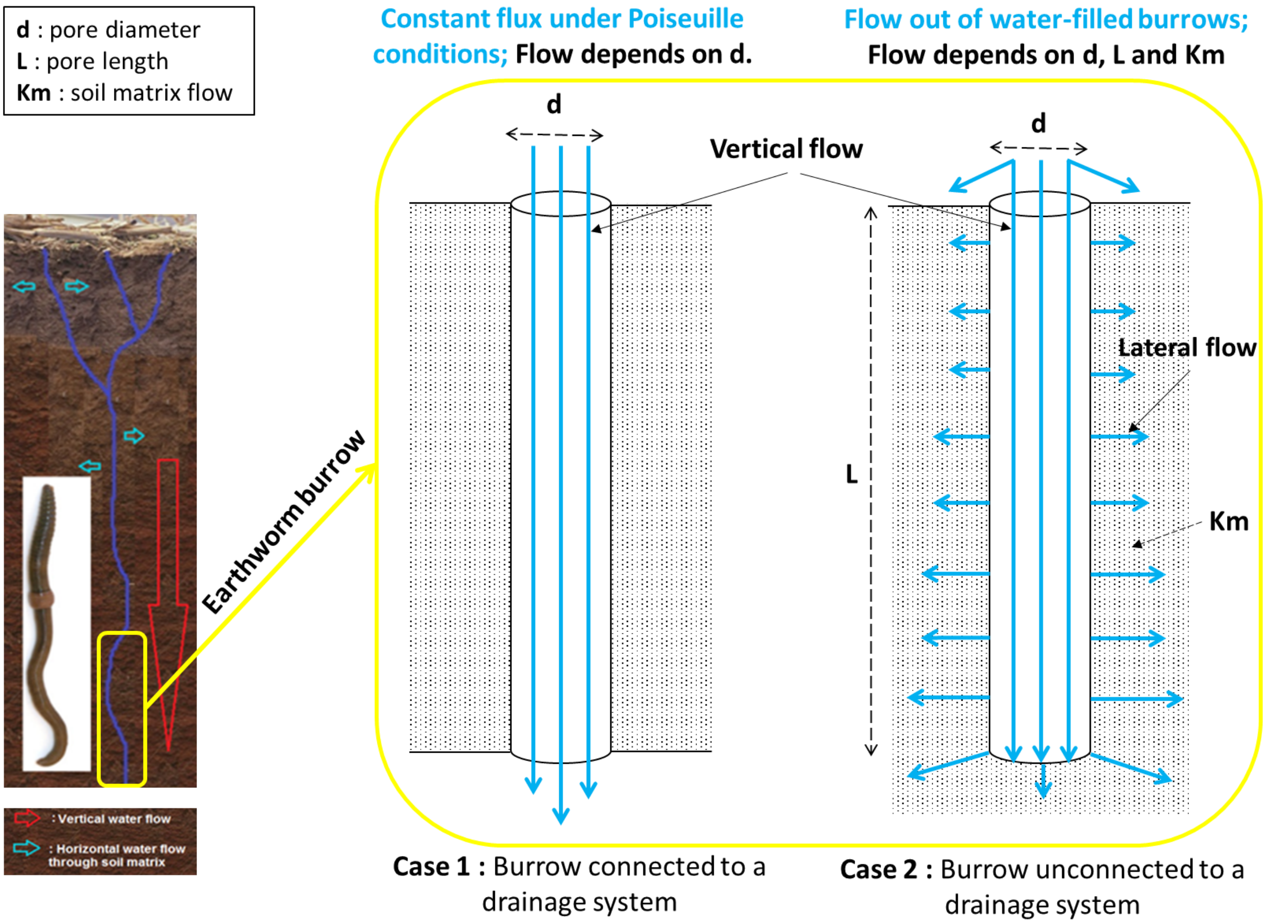

Figure 4. Empirical relationships between earthworm burrow characteristics and soil water flow. The schematic tubes are a simplification of the morphology of an earthworm burrow. Case 1: earthworm burrow is well drained (connect to field drains, or an underlying more permeable layer) and water flow depends on the burrow radius (Sutera and Skalak, 1993); Case 2: earthworm burrows terminate within the soil matrix and water flow depends on burrow radius, burrow length and soil matrix flow (Smettem, 1992). (by Hallam, 2019, unpublished thesis).

Unlike anecic earthworms, significant effects on soil water infiltration have not been widely reported for endogeic earthworms (Ela *et al.*, 1992; Spurgeon *et al.*, 2013). This may be because their burrowing activity is restricted to the topsoil horizons and their burrows are typically of a lateral-type (Bouché, 1972), as well as being sinuous and having a relatively small diameter (ranging between 2 mm and 5 mm compared to anecic earthworm burrows that have diameters up to 9 mm (Pérès *et al.*, 1998)). In addition, endogeic earthworms often block their burrows below the soil surface by casting. For example, Whalen et al. (2015) showed that macropore continuity can be reduced by endogeic compared to anecic earthworms when refilling no longer in-use burrows by ingested soil redeposited in burrows. Burrow refilling by endogeic earthworms was estimated to be up to 50 % compared to only 20 % for anecic earthworms assuming that all burrows should be connected (Capowiez *et al.*, 2014a). Le Couteulx et al. (2015) reported a greater percentage of burrowed area was refilled with casts in the presence of endogeic earthworms when organic matter was mixed into soil rather than being added to the surface. However, unlike Whalen et al. (2015), the authors showed that burrow refilling by endogeic earthworms does not depend on earthworm species and would result in low water movement due to burrow discontinuity. Refilling, caused by endogeic species, can also reduce burrows' life span due to the disintegration of no longer in use burrows (separated by casts) compared to anecic earthworms that repair and consolidate the burrows by reusing them (Capowiez *et al.*, 2014a).

In contrast to the above, some studies report an increase in soil water flow in the presence of endogeic earthworms. In column experiments, for example, saturated hydraulic conductivity as well as percolation rates were increased in the presence of the endogeic species *Allolobophora caliginosa* and *Allolobophora rosea* compared to the control (Roth and Joschko, 1991; Joschko *et al.*, 1992). Using the endogeic species *A. caliginosa*, Ernst et al. (2009), reported a larger water infiltration and faster water discharge through the soil column compared to anecic *L. terrestris,* probably due to the higher burrowing activity and connectivity between macropores of endogeic species. Capowiez et al. (2015) observed a positive linear relationship between burrow length and the water infiltration rate (R^2 = 0.49, p < 0.01) for endogeic species (*Aporrectodea rosea*, *Allolobophora chlorotica*, *Aporrectodea caliginosa*) but when *Aporrectodea icterica* was excluded from the experiment, the regression coefficient R^2 increase to 0.95 (p < 0.001). This increased correlation was explained by the low efficiency of water infiltration through *A. icterica* burrows due to lateral compaction or cast compressing along the burrow walls.

The studies that investigated the effect of epigeic species on water infiltration are contradictory. Although they have little effect on soil macroporosity and produce only shallow burrows in the litter layer or in the first 5 cm of soil compared to anecic species (Bouché, 1972; Fragoso and Lavelle, 1992; Bens *et al.*, 2007), the meta-data analysis by Spurgeon et al. (2013) showed that epigeic earthworms increased soil water infiltration significantly. This was attributed to their ability to: i) prevent soil surface crusting due to their surface activity, ii) form stabilized soil aggregates that helped soil water regulation and iii) form temporary deeper burrows when the earthworms are exposed to extreme climate conditions which helped to conduct water through the soil (Francis and Fraser, 1998). Compared to other earthworm ecotypes, Schutz et al.

(2008) reported a significant higher correlation between infiltration rate and epigeic earthworm density than anecic earthworms, but the results varied significantly for endogeic earthworms depending on their species. This was explained by the epigeic species *Lumbricus rubellus* preventing the blockage of burrows by mixing the soil litter with the topsoil or simply because anecic earthworm density was too low (25 to 65 ind m^{-2}) to have a significant effect on infiltration rates. Ernst et al. (2009) reported lower water infiltration rates and percolation in columns inoculated by the epigeic *L. rubellus* than in those containing the endogeic earthworms *A. caliginosa*. They assumed that the higher burrowing activity of *A. caliginosa* and the high connections between their burrows relative to epigeic earthworms had a big impact on soil water infiltration. In another study Francis and Fraser (1998) showed no significant differences between water flow in columns inoculated by *L. rubellus* and in earthworm-free controls, which was attributed to the lack of burrows in the subsoil that could conduct water.

Soil structure

By ingesting litter and soil, earthworms contribute to the increase of organic matter mineralization and to the development of soil aggregates and structure which have a significant impact on soil aeration and water infiltration (Jouquet *et al.*, 2012a). Earthworms affect soil structure by incorporating surface organic residues in the soil profile within cast aggregates or as coatings on their burrows (Bottinelli *et al.*, 2015). These biogenic aggregates (macroaggregates embedded one in another and produced by earthworms via casting) create a temporary structure composed of particles gathered by weak bonds through organic matter and clays (Puga-Freitas and Blouin, 2015). Larink et al. (2001) found that aggregates produced by *L. terrestris* and *A. caliginosa* showed ca. 10 % lower relative water stability and 10–20 % higher porosity than soil aggregates. The loose structure was attributed to the low quality of the organic matter eaten by the earthworms. Clause et al. (2014) reported that the high porosity and the particular microstructure of cast aggregates may enable a better water infiltration compared to soil aggregates. The porosity of casts can, initially, be greater than in other soil aggregates. However, they are less stable and, after breakdown and collapse during rainfall and infiltration, compaction can result in the soil porosity reducing by up to 50 % (Bottinelli *et al.*, 2010).

The activity of earthworms has the potential to compact the soil which is observed through an increase in density and a decrease in porosity of soil; this change in turn results in a decrease in water infiltration rates and sorption (Alegre *et al.*, 1996). The compacting effect of earthworms may be off-set by the decompacting effect of burrows and pores between casts that enhance water infiltration (Jouquet *et al.*, 2012a). Macropore size and number also affects infiltration rate (Smettem and Collis-George, 1985). The diameter of macropores created by earthworms ranges from 2 to 11 mm and a single macropore of 3 mm diameter per 30 cm diameter of soil area could contribute more to the steady infiltration rate through a soil than the cross-sectional area associated with the soil matrix (Ehlers, 1975; Smettem and Collis-George, 1985). Hallam et al. (2020) showed that pores> 1 mm diameter made a significantly greater percentage contribution to water flow in earthworm-present (98% contribution) than earthworm-absent (95% contribution) monoliths. This is why anecic species such as *L. terrestris* and adult endogeic species such as *A. caliginosa* (more than 2 mm in diameter) could contribute to a higher water infiltration rate, particularly the wider burrows of anecic species when water is supplied in large quantities (Fischer *et al.*,

2014). Soil macropores, as preferential pathways for water flow, depend also on the soil type and on the interactions between earthworm and soil type. Lower macroporosity was observed in sandy soils compared to soil of finer texture because of the low level, or absence, of earthworm activity and their lower organic matter content; this lower macroporosity may result in lower rates of water infiltration (Bens *et al.*, 2007; Luo *et al.*, 2010; Fischer *et al.*, 2014).

Land management practices

Further understanding of the functional links between earthworms and soil structure and their effect on infiltration requires consideration of land management practices, such as existing cropping and tillage management systems Previous research showed that no-tillage farming resulted in increases in soil water infiltration and percolation rates of up to 8 times compared to conventional tillage (Ehlers, 1975; Edwards *et al.*, 1990; Wuest, 2001; Chan, 2004; TerAvest *et al.*, 2015). The increased soil water flow was attributed to an up to 9-fold increase in earthworm abundance and activity which resulted in improved soil physical properties (Edwards *et al.*, 1990; Chan, 2004) and an increased number of earthworm burrows wider than 1 mm at the soil surface (Ehlers, 1975; Wuest, 2001). The increased earthworm abundance and activity in the no-till farming was due to an increase in soil residue cover (TerAvest *et al.*, 2015), favourable soil conditions and reduced earthworm mortality due to the cessation of mixing of the upper soil layers when ploughing (Chan, 2004; Spurgeon *et al.*, 2013).

The decrease of earthworm abundance and biomass in conventional tillage usually comes with an alteration of the species composition (Chan, 2001). Capowiez et al. (2009) and Nuutinen (1992) reported a significant influence of tillage system on ecological groups of earthworms and the abundance and continuity of soil macroporosity. They found less continuous pores, less abundant anecic species, *L. terrestris* and *Aporrectodea giardia*, and more abundant endogeic species, *A. caliginosa*, in conventional tillage compared to reduced tillage. Similarly, Spurgeon et al. (2013) reported a tendency of the dominating endogeic earthworm species in arable soil to be the first to increase in numbers in response to grassland conversion. The higher population of endogeic earthworms compared to other ecotypes was attributed to their easy access to decomposed organic matter when plant residues are buried during ploughing (Bertrand *et al.*, 2015). However, Capowiez et al. (2009) reported no significant effect of tillage management on water infiltration (mean values of 81.8- and 96.0-mm h^{-1} in conventional and reduced tillage, respectively; $p = 0.33$) even with the increase in macroporosity in reduced tillage; this high macroporosity was reported to be offset by a significant increase in soil bulk density which resulted in no effect on soil water infiltration rate. However, they reported a significant effect of the cropping system on water infiltration because of different compaction intensities depending on the crops rotation (119 mm h^{-1} in less compacted plots vs 79 mm h^{-1} in most compacted plots). Luo et al. (2010) on the other hand, found higher macroporosity and macropore length density in pasture compared to row crop land use because of greater earthworm activities and higher organic matter content in pasture lands which would probably increase soil water flow. Hallam et al. (2020) have shown that deterioration of soil properties in arable land can be reversed by adopting conservative land management systems. They reported a significant decrease in soil bulk density, and an increase in

organic matter content after only a year of arable to ley conversion, and that earthworms improved soil quality further, with a significant increase of soil hydraulic conductivity.

Seasonality

Various studies have reported variations in infiltration rates through the seasons of the year (Moujahed and Gifford, 1984; Angulo-Jaramillo *et al.*, 1997; Elhakeem *et al.*, 2018; Hallam *et al.*, 2020). In some cases, infiltration rates increased significantly during the summer compared to other seasons (Bertoni *et al.*, 1958; Cerdà, 1996, 1999; Sharma *et al.*, 2017) whereas in other studies infiltration rates decreased during the summer (Schumm and Lusby, 1963). These contrasting results are dependent on interactions between changes in soil properties, such as soil texture (swelling effect), dry bulk density and moisture (Fan *et al.*, 2013; Hesseltine, 2016), and external factors, such as land management practices, climate, and biotic factors (Starr, 1990; Azooz and Arshad, 1996; Willoughby *et al.*, 1997). Biotic factors, such as plants and earthworms, change through the different seasons of the year. Plants affect soil water flow through the growing season by creating new biopores via developing/ decaying roots, but their impact depends on the plant functional group with legumes increasing and grasses decreasing infiltration rates (Meek *et al.*, 1992; Fischer *et al.*, 2014). The proliferation and decay of the tap roots of legumes results in stable macropores and an increase in earthworm biomass because of an increase in organic matter content which increases water infiltration rate, whereas the fibrous roots of grass cause clogging of pore space and decrease water infiltration rate. Earthworm activity is seasonal with increasing activity in spring and autumn (Gates, 1961; Callaham and Hendrix, 1997). Their activity is a function of food availability and abiotic factors (Johnston *et al.*, 2014) but also of root growth that depends on plant functional groups (Eisenhauer *et al.*, 2009). From the few studies reporting seasonal effects of earthworm on soil water flow, Willoughby et al. (1997) showed that the presence of *L. terrestris* increases water infiltration rates gradually throughout the growing season in a no-tillage compared to a conventional tillage system. In arable land converted to ley, Hallam et al. (2020) reported a significant increase of saturated hydraulic conductivity in summer and spring and a decrease in winter with a significantly greater water flow (47%) in the presence of earthworms than in their absence. The increase in saturated hydraulic conductivity in summer was mainly attributed to changes in soil physical properties and to soil type prone to shrink-swell behaviours. Hu et al. (2012) also reported seasonal changes in soil water flow and attributed this to several factors including earthworm activity which contributed to the increase of saturated hydraulic conductivity in autumn compared to summer. Further experiments are, however, required to better understand the role of earthworms in changing soil water flow through time (under controlled conditions), or time of year (under field conditions).

To understand the interactions between earthworm and soil water flow, many interconnected factors should be taken into consideration. Regarding earthworms' species, most studies generally report an increased soil water infiltration and percolation in the presence of anecic species. The influence of endogeic species is highly debated and epigeics were considered in few studies with contrasting effects. Much current research is focussed on modelling using advanced technologies (e.g. X-

ray tomography) to visualize the hidden parameters of the bulk soil that affect water flows.

Table 1. Synthesis of the main reviewed literature on earthworm and soil water infiltration. Letters refer to type of experiment; R = Review, L = Laboratory experiment, F = Field experiment; and earthworm groups, AN = Anecic, EN = Endogeic, EP = Epigeic.

Authors	**Study objective**	**Study area**	**Type of experiment**	**Earthworm species**	**Earthworm group**	**Estimated population**	**Soil type**	**Soil density (g cm^{-3})**	**Cropping system / land management**	**Burrows description method**	**Infiltration method**	**Results**
Edwards et al. (1990)	Study the effect of *L. terrestris* burrows on no-till field Hydrology	Ohio, USA	R & F	*Lumbricus. terrestris*	AN	-	Silt loam	-	No-till / corn filed	Dye and chemical tracers	Subtraction of runoff and evapotranspiration from precipitation	Infiltration and ground water recharge could increase by more than 100 mm year^{-1} due to earthworm activity.
Bouche and AlAddan (1997)	Assessment of the effect of earthworms on soil physical functions.	Montpellier, France	F & L	*Scherotheca gigas*	AN	-	17 sites with large variety of soil types	1.1 to 1.3	Dry grassland	Dye	Double ring method (Müntz et al., 1905)	- Infiltration rate in soils with 100 g m^{-2} of earthworms is less than with 100 g m^{-2} of anecic species: (150 vs 282 mm h^{-1}); - Infiltration rate is correlated to earthworm biomass (*r* = 0.975) and to burrow length, surface and volume (*r* = 0.99); - Infiltration rate is not correlated with burrow diameter, tortuosity, earthworm number and soil profile depth.
Willoughby et al. (1997)	Seasonal variations in infiltration rate under no-till and conventional tillage systems	Indiana, USA	F	*Lumbricus. terrestris*	AN	Qualitative observations of earthworm casts on soil surface as an indication of their presence	Silt loam		No-till and conventional tillage / corn and soybean rotation.	-	Sprinkling infiltrometer (Zegelin and White, 1982)	- Before any tillage, the tilled treatment without casts had the highest infiltration rate than casts presence; - Infiltration rates increased through the growing seasons in no-till with casts presence on soil surface compared to the other treatments.

Chan (2004)	Impact of anecic earthworm burrows on soil hydrology	Central Tablelands, Australia	F	*Spenceriella. hamiltoni*	AN	-	Increase in %clay with depth starting from 25%	-	Permanent pasture	Dye	Twin ring method (Smettem and Clothier, 1989)	- Infiltration rate of 6.7 mm h^{-1} for single burrow vs 3.6 mm h^{-1} for bulk soil (macropores > 0.75 cm diameter excluded for bulk soil); - 53% of the burrow openings were transmitting water
Joschko et al. (1992)	Quantify the effect of earthworm burrows on soil hydraulic properties	Germany	L	*Allolobophora caliginosa*	EN	83 g m^{-2} fresh weight	Loamy silt	-	-	Columns with burrows were filled with gypsum	Constant head permeameter	-High correlation between *Ks* values and total burrow length for *A. caliginosa* (r_S = 0.943); -Increase of percolation rates with burrow length for both species but more for *A. caliginosa*.
				Allolobophora. rosea		60 g m^{-2} fresh weight						
Alegre et al. (1996)	Comparing changes in soil physical properties and their effect on water infiltration in the presence / absence of earthworms	Yurimaguas, Peru	F	*Pontoscole. corefhrurus*	EN	36 g m^{-2} fresh weight	Loam	1.12	Plots were cropped to maize-rice-cowpea-rice-rice-rice form March 1990 to January 1993	-	Instantaneous water ponding by driving a 110 mm i.d. and an open-ended steel cylinder into the soil	Earthworm inoculation induced: -An increase of macroaggregates (> 1 cm) from 25.1 to 32.7% in size and a decrease of small aggregates (< 2 cm) from 33.2 to 26.1%; - An increase of bulk density (from 1.12 to 1.23 g cm^{-3}); -A decrease of porosity (from 58 to 53%) and of sorptivity (from 0.45 to 0.15 cm $s^{-1/2}$).
Bottinelli et al. (2010)	Determine the impact of earthworm casting activity on soil porosity	Hanoi, Vietnam	L	*Metaphire posthuma*	EN	14 g m^{-2} fresh weight	Loam	0.8	-	High resolution image analysis	Water infiltration test using 2 syringes placed at 1 cm above the soil surface	After simulated infiltration the cast's porosity decreased by 50 % and was significantly lower than the surrounding soil aggregates.
Jouquet et al. (2012)	Assessment of the effect of earthworm on water infiltration depending on the initial soil bulk density	Hanoi, Vietnam	L	*Metaphire posthuma*	EN	92 ind m^{-2}	Loam	1.1 or 1.4	-	-	Decagon minidisk infiltrometer with a 40 mm diameter base	Earthworms significantly improved hydraulic conductivity at -0.05 kPa for two soil densities: 1.1 and 1.4 gcm^{-3}.

Le Couteulx et al. (2015)	Burrowing activity of endogeic species as affected by organic matter placed at different depths	Brittany, France	L	*Allolobophora chlorotica*	EN	170 ind m^{-2}	Silt loam soil	1.3	Soil from arable field	Drawings of burrows of sliced microcosm using a transparent sheet + digitization	-	- Regardless of earthworm species, there was a high percentage of burrow discontinuity (from 15 to 30 % vs 6-12 %) and fewer burrows (12 to 16 vs 18 to 40 burrows / section) in soil mixed with organic matter vs soil with a surface application of OM; - Burrows of *A. caliginosa* are affected by OM location.
				Aporrectodea caliginosa								
				Allolobophora icterica								
Bastardie et al. (2005a)	3D characterization of earthworm burrow systems of natural soil	Clermont-Ferrand, France	L	*Nicodrilus giardi*	AN	101 ind m^{-2}	Sandy clay loam	1.3	Agricultural research pasture	X-ray tomography	-	- Accessible burrows offer a volume from 1400 to 10463 $cm^3\ m^{-3}$ of soil; - Burrow length density: 687 to 1212 m m^{-3}; - Burrow volume density: less than 2.5% of total soil volume; - 9–43% of the volume was connected to the soil surface.
				Lumbricus. terrestris								
				Dendrobaena mammalis	EN							
				Aporrectodea caliginosa								
Capowiez et al. (2009)	Assessment of the effect of tillage type and cropping system on earthworm communities and on water infiltration	Estrees-Mons, France	F	*Lumbricus. terrestris*	AN	10.1-22.5 ind m^{-2} in conventional and reduced tillage	Silt loam	1.18-1.52	Conventional and reduced tillage coupled to three cropping system	Methylene blue dye tracer	Single-ring infiltration method (Braud et al., 2005)	- No significant effect of tillage management on water infiltration (increased porosity was offset by increased bulk density in reduced tillage compared to conventional tillage); -Significant effect of cropping system on water infiltration (high infiltration in crop system inducing less bulk density).

				Aporrectodea giardi		2.2-27 ind m^{-2}						
				Aporrectodea caliginosa	EN	54.2-23.9 ind m^{-2}						
				Aporrectodea rosea		16.6-19.6 ind m^{-2}						
Fischer et al. (2014)	Assessment of the effect of earthworm, soil texture and plant composition on water infiltration	Thuringia, Germany	F	*Lumbricus. terrestris*	AN	26.88 ind m^{-2}	Sandy loam to silt clay texture	-	Arable land / Grasses, small herbs, tall herbs and legumes	-	Hood infiltrometer (Schwärzel and Punzel, 2007).	- High earthworm populations and well-developed soil structure explain the higher water infiltration in silt clay soil compared to coarse soil; - Burrows of anecic species and of *Aporrectodea caliginosa*, which are larger than 2 mm in diameter, explain the effect of earthworm presence on water flow; -Legumes increased and grasses decreased soil water infiltration.
				Aporrectodea caliginosa								
				Octolasion tyrtaeum								
				Allolobophora chlorotica	EN							
				Aporrectodea rosea								
Capowiez et al. (2014)	Estimation of burrow system area and continuity	Montfavet, France	L	*Aporrectodea caliginosa nocturna*	AN	Earthworm collected at 450 ind m^{-2} from orchard and added to repacked cores at 200 ind m^{-2} in	Clay loam	1.1	Abandoned orchard	Drawings of burrows of sliced cores using a transparent sheet + digitization	-	-Anecic species burrow area was greater than that of endogeic species (c. 40 cm^2 vs c. 15 cm^2); - 40% to 50% of endogeic species burrows and about 20% of anecic species burrows were refilled by casts.
				Aporrectodea caliginosa meridionalis								

				Aporrectodea caliginosa icaliginosa	EN							
				Allolobophora chlorotica								
Capowiez et al. (2015)	3D characterization of reconstituted burrow systems of different earthworm species	Montfavet, France	L	*Aporrectodea nocturna*	AN	100 ind m^{-2}	Clay loam	1.26	Abandoned orchard	X-ray tomography	Single ring method (Braud et al., 2005)	Infiltration rates per core: 11.03 L min^{-1}
				Lumbricus terrestris		100 ind m^{-2}						12.42 L min^{-1}
				Aporrectodea rosea	EN	200 ind m^{-2}						2.32 L min^{-1}
				Allolobophora chlorotica		200 ind m^{-2}						4.41 L min^{-1}
				Aporrectodea caliginosa		200 ind m^{-2}						5.15 L min^{-1}
				Aporrectodea icterica		200 ind m^{-2}						3.76 L min^{-1}
Smettem and Collis-George (1985)	Prediction of steady-state infiltration rates through macropores in a soil under native pasture	Australia	F & L	*Eisenia rose*	EP	-	0-14 cm Sandy loam, 14-100 cm silty loam	1.33 - 1.42 cm^3 cm^{-3}	Pasture	-Resin peels & Methylene blue	-In the laboratory: matrix flow through field-core using permeameter method (Scotter et al., 1982) - In situ: infiltration through soil matrix by double-tube method (Bouwer, 1962) and Infiltration through individual macropores as described by Ehlers (1975)	-Single macropore of 3 mm diameter contribute greater to steady infiltration rate than the cross-sectional area associated with the soil matrix.

				Allolobophora caliginosa	EN							
Schutz et al. (2008)	Study of earthworm population and water infiltration rates in woodland flooding sites	Lange Erlen, Switzerland	F	*Lumbricus terrestris & others*	AN	from 25 to 65 ind m^{-2}	Fluvi-eutric Cambisol-	-	Floodplain (forest and grassland)	-	Bouwer Cylinder Infiltrometer (Bouwer, 1986)	- Low correlation was found between infiltration rate and anecic earthworm density but high correlation for endogeic and epigeic densities.
				Allolobophora chlorotica & others	EN	from 57 to 160 ind m^{-2}						
				Lumbricus rubellus & others	EP	from 11 to 29 g m^{-2} fresh weight						
Ernst et al. (2009)	Quantify the impact of earthworm species on soil water characteristics	Trier, Germany	L	*Lumbricus terrestris*	AN	100 and 113 ind m^{-2}	Sandy loam	1.5	Agricultural use soil	-	Modified infiltrometer according to Hills (1970)	The water infiltration rates were the highest and water discharge was faster in treatments with *A. caliginosa* compared to *L. terrestris* and *L. rubellus* treatments.
				Aporrectodea caliginosa	EN	350 and 370 ind m^{-2}						
				Lumbricus rubellus	EP	270 and 210 ind m^{-2}						
Wuest (2001)	Quantify biopores after long-term no-till compared to recently tilled soil	Pendleton, USA	F	-	-	-	Silt loam	-	No-till / spring and winter wheat rotation	Photographs of horizontal cross-sections of intact cores. + digitization	-	30 to 100% more biopores wider than 1 mm diameter in long-term no-till (17 years) in comparison to recently tilled soil.
TerAvest et al. (2015)	Investigate the effects of three cropping systems on soil–water relations and crop production	Nkhotakota and Dowa, Malawi	F	-	-	270 ind m^{-2}	Sandy loam	1.37-1.49	-Three cropping systems: continuous no-till maize, conservative agriculture rotation and conventional	-	Difference between rainfall applied and runoff collected using rainfall simulator as described by Thierfelder	In high potential evapotranspiration zone: - No-till and maize residue significantly increased earthworm abundance compared to conservative agriculture rotation and conventional tillage rotation;

									tillage rotation		and Wall (2009)	- Residue retention is positively correlated to infiltration and no till; - Conservative agriculture improved soil water content by 20 mm compared to conventional tillage.
Spurgeon et al. (2013)	Meta-analysis of the relationships between earthworm community change and soil structural properties		R	-	AN EN EP	-	-	-	Conventional / no & reduced tillage / grassland / woodland	-	-	-Positive correlation between earthworm numbers and soil water infiltration; - Epigeic and anecic species are a positively associated with an increased soil water infiltration, whereas endogeic species has no significant effect.
Francis and Fraser (1998)	The effects of earthworm species on soil macroporosity and hydraulic conductivity	New Zealand	F (monoliths)	*Aporrectodea caliginosa* and *Octolasion cyaneum*	EN	300 ind m^{-2}	Silt loam	1.2 - 1.3	Pasture soil	Analysing the binary images (using a standard image analysis system) of macropores filled with sand of a horizontal sectioned monoliths	Disc permeameters (Perroux and White, 1988) were used to measure unsaturated and saturated hydraulic conductivities	- *Lumbricus rubellus* created burrows in top soils; - Endogeic species created continuous burrows in both top and sub soil, but *Aporrectodea caliginosa* burrows were more connected to the soil surface; - *Aporrectodea caliginosa* showed the greatest *Ks* than other earthworm species; - No significant differences in *Ks* were observed between treatments with earthworms and control.
				Lumbricus rubellus	EP	600 ind m^{-2}						

Soil water storage and earthworms

While soil water infiltration implies the downward entry of water into soil (Richards, 1952), stored soil water is considered in this review as that part of the infiltrated water that is held by the soil matrix and that therefore does not flow downwards towards the water table (water redistribution and internal drainage are parts of water storage process in soil profile and determine the soil water balance). Soils that can retain more water support more plant growth and are less subject to leaching losses which is highly desirable for rainfed agricultural systems (Kramer and Boyer, 1995; Wang *et al.*, 2013). Soil water storage is known as being spatially variable and affected by many factors such as soil properties including water holding capacities and organic matter content, vegetation, topography, drainage properties, and meteorological conditions (Duan *et al.*, 2016).

Effect of earthworms on soil water retention and storage

Earthworms as biological actors impact soil proprieties that influence soil water retention and hence storage capacity (see Table 2). Earthworms support plant growth by increasing soil water retention and nutrient release because of improved soil aggregation and porosity through mineral and organic matter mixing (Darwin (1881) and White (1789) cited by Shipitalo and Le Bayon (2004)). Improvement of hydro-physical proprieties of soil such as porosity and capillary water capacity requires time. For example, in the presence of earthworm with an initial quantity of 0.1% of the soil mass the increase of soil water retention may take longer than the growing season (Smagin and Prusak, 2008). Comparison between sites on various soils with and without the endogeic earthworm *A. caliginosa*, showed a 17 % increase in soil moisture holding capacity, 27 % more available water and a near doubling of infiltration rate 10 years after the introduction of the earthworms (Stockdill and Cossens, 1969). The authors reported more water moisture held in high organic matter topsoil as result of an improved soil structure in the presence of earthworms. Earthworm absence was associated with high soil compaction which severely restricted moisture penetration. Furthermore, McDaniel et al. (2015) showed that *A. caliginosa* can change the soil water retention curves with soil depth with an improved soil residual water content from 33 to 41 % in the top 30 cm of the soil. Without giving any quantified measurements, they suggested that the higher concentration of fine soil particles in casts coated with hydrophilic surface layer may explain the increased residual water content in the top 30 cm of soil, where earthworms are most active. In the presence of the epigeic earthworm species *L. rubellus*, Ernst et al. (2009) reported an increase in soil water storage at 10 cm depth as a result of low rates of litter loss relative to *L. terrestris* treatment which reduced water evaporation at the soil surface. *L. terrestris* species buried surface litter leading to an increase in soil surface drying and aeration of their large burrows, resulting in lower water storage. Similarly, Hallam and Hodson (2020) reported a significant increase in soil water holding capacity (by 7–16%) through different depths of different soil types in the presence of *A. chlorotica* relative to *L. terrestris* (except for the upper 6.5 cm of the sandy loam soil where soil water holding capacity has increased by 11% in the presence of *L. terrestris*).

Effect of earthworm burrows and soil structure

Due to their burrowing activity, earthworms can improve water holding capacity (WHC) of the topsoil layers by modifying soil structure, porosity, and pore size distribution to a large range of pore sizes that can retain more water (Boyle *et al.*, 1997; Palm *et al.*, 2013; McDaniel *et al.*, 2015). Hallam and Hodson (2020) reported that earthworms significantly increased percent of water stable aggregates (%WSA) by 16–56% and 19–63% relative to earthworm-free controls for *L. terrestris* and *A. chlorotica*, respectively. Although differences in the magnitude of the impact were reported for the two species, a consistent linear regression was described between the % WSA and WHC increases for the two earthworm species. Also, cracks, smaller than surface holes, and burrows generated by earthworm activity could increase infiltration and help in water retention as the water in water-filled macropores diffuses into the soil matrix through macropore walls (Lee and Foster, 1991; Bastardie *et al.*, 2003; Edwards, 2004). Even though the volume of earthworm burrows accounts for only a few percent of total soil porosity (Schwartz *et al.*, 1999; Kördel *et al.*, 2008), Bastardie et al. (2005a) showed that the total surface of the burrow walls varied between 7721 to 12764 cm^2 m^{-3} with burrows that connected to the surface providing 1069 to 7237 cm^2 m^{-3}. The burrow walls provide an important surface for water diffusion into the soil matrix. In addition, the same accessible burrows offer a volume ranging from 1400 to 10463 cm^3 m^{-3} corresponding to 1–10 mm of a water storage capacity. This amount of water held by the soil matrix through the penetration of water into the earthworm burrow walls, in addition to water stored in water-filled burrows would help to increase soil infiltration and enhance water available for root absorption and uptake (Bastardie *et al.*, 2005c). Weiler and Naef (2003) reported that the macropores built by earthworms significantly affect water infiltration rate, but the flow into the surrounding soil matrix and its storage is mainly influenced by the soil properties and initial soil water content. Smettem (1992) and Bastardie et al. (2003) indicated that water diffusion from the burrow to the soil matrix is highly dependent on the burrow wall permeability. Indeed, Bastardie et al.(2005c) showed that the speed and volume of water that diffused through burrow walls of *L. terrestris* earthworms is less than that diffused through soil fractures due to low soil porosity because of the high compaction of burrow walls. In their experiment, the density values of artificial burrows (made by a metal rod) were 1.33 and 1.36 g cm^{-3} for the 0-3 mm wall layer and the surrounding soil respectively, whereas the values for burrows made by *L. terrestris* were 1.40 and 1.38 g cm^{-3} for the 0-3 mm wall layer and surrounding soil matrix respectively. Similarly, Rogasik et al. (2014) reported a 30 % increase (from 1.34 g cm^{-3} to at least 1.75 g cm^{-3}) in the bulk density of the burrow walls of *L. terrestris* compared to the soil matrix; from the burrow walls to their outer boundary the bulk density decreased. Since soil bulk density is a proxy for porosity and pore connectivity, high bulk density indicates a reduction of the transfer of water and solutes between burrows and the soil matrix. Anecic earthworms such as *L. terrestris* use their burrows for long periods of time and compress egested material onto the burrow walls, whereas epigeic and endogeic earthworms do not reuse their burrows and their casting influence on burrow wall permeability is assumed to be insignificant (Melnichuk, 2016). However, the presence of the compacting endogeic earthworm *Pontoscolex corethrurus* in three organic residue treatments resulted in a decrease in soil porosity (from 58 to 53 %) and sorptivity (from 0.45 to 0.15 cm $s^{-1/2}$) due to an increased soil bulk density (Alegre *et al.*, 1996). Similarly, Blouin et al. (2007) reported a decrease of soil water retention capacity by more than 6 % in the presence

of the endogeic earthworm *Reginaldia omodeoi* as a result of their compacting behaviour which may lead to a decrease in plant root growth.

Effect of earthworm casts

Soil water storage may be enhanced by the high water holding capacity of earthworm casts and the interstitial pores between casts (Bouché and AlAddan, 1997; Blanchart *et al.*, 1999). The hydroscopic swelling of plant remains in the casts and the increased capillarity of the highly porous aggregates produced by earthworms was reported to cause up to a 20 % increase in soil water holding capacity compared to the surrounding soil (Smagin and Prusak, 2008). The fine fraction of the soil is known to play an important role in soil water and nutrient retention (Saxton *et al.*, 1986; Yang *et al.*, 2014) and was found to be significantly higher in casts of endogeic earthworms compared to the surrounding soil (Duboisset, 1995; Asawalam and Johnson, 2007). During ingestion, the clay and silt fractions in earthworm guts are coated by an extra hydrophilic surface layer (Smagin and Prusak, 2008; McDaniel *et al.*, 2015). The high organic matter content mixed with the high proportion of fine particles in most earthworm casts would increase their ability to retain more water than the bulk soil (Lavelle, 1988). However, Lipiec et al. (2015) reported greater water repellency of old earthworm casts compared to the bulk soil. They suggest that this was due to the high hydrophobic layer of organic carbon that coated the surface of the casts during ingestion (1.99 vs 1.30 % organic carbon in casts vs in natural soil aggregates respectively). These contrasting effects could be dependent on organic matter quality and aging effect of casts on water retention.

Table 2. Synthesis of the main reviewed literature on earthworm and soil water storage. Letters refer to type of experiment; R = Review, L = Laboratory experiment, F = Field experiment; earthworm groups, AN = Anecic, EN = Endogeic, EP = Epigeic; and earthworm effect, N = negative, P = positive.

Authors	**Study objective**	**Study area**	**Type of experiment**	**Earthworm species**	**Earthworm group**	**Earthworm population**	**Soil type**	**Soil density ($g\ cm^{-3}$)**	**Cropping system / land manageme nt**	**Soil water retention / moisture / holding capacity method**	**Earthworm effect**	**Results**
Bastardie et al. (2005b)	Assessment of water diffusion through burrow walls	Clermont -Ferrand, France	L	*Lumbricus terrestris*	AN	One worm incubated per 2D terrarium (48 cm high × 33 cm wide)	Sandy clay loam	1.3	-	- Simplified sorptivity equation of Philip (1957) for water diffusion - Micro-tensiometers	N	- The amount of water transits (mean coefficient of sorptivity) through burrows of *L. terrestris* is lower than that transited through soil fractures; - Bulk density of *L. terrestris* burrows are higher than artificial burrows.
Rogasik et al. (2014)	Assessment of the structural changes of drilosphere by compaction	Braunsch -weig, Germany	L	*Lumbricus terrestris*	AN	105 ind m^{-2}	Silt loam	1.34-1.38	-	-	P/N	- Spatial heterogeneous earthworm effect on the bulk density (BD) (increased BD of inner burrows wall, 1.75, and decreased BD from the walls to drilosphere); - Earthworm compacting effect on burrow walls would have a potential impact on lateral water transfer between burrows and the surrounding soil matrix.
Stockdill and Cossens (1969)	Effects of earthworm activity on hydraulic properties of soil under pasture	New Zealand	F	*Allolobophora. caliginosa*	EN	-	-	-	Pasture	-	P	- Moisture holding capacity increased by 17%, and 27% more of available moisture in top soil with earthworm presence; - Increase of root development
Blouin et al. (2007)	Study of drought stress on rice in the presence of compacting	Humid savanna h, Cote d'Ivoire	L	*Millsonia anomala*	EN	127 g m^{-2} fresh weight	Sandy	0.8	Rice	Daily weight of soil mass after water saturation.	N	- Earthworm reduced soil water retention capacity by more than 6%; - No significant effect of earthworms on plant growth in drought condition;

	earthworm species											- 40% increase in shoot biomass production with the presence of earthworm in wet condition.
Lipiec et al. (2015)	Determine changes in pore size distribution, stability and water repellency of cast and natural aggregates	Lublin, Poland	L	*Aporrectodea caliginosa*	EN	-	Silt loam	1.33		Water drop penetration time method was used to measure water repellency (Chenu et al., 2000)	N	- One-week old casts collected next to the burrows showed greater repellency than the natural aggregates.
McDaniel et al. (2015)	Investigate the effect of earthworms on soil hydraulic properties	Colorado, USA	L	*Aporrectodea caliginosa*	EN	852 ind m^{-2}	Sandy loam	1.1	-	Bar Pressure Plate Extractor	P	- Water content increased by 33 and 41% in the 0-15 and 15-30 cm of column sections respectively in the presence of earthworm compared to control; - Reduction of pore-size distribution index (greater variety of pore sizes) in the presence of earthworm.
Smagin and Prusak (2008)	Study the effect of earthworm casts on the soil water retention curve	Moscow, Russia	L	*Lumbricus rubellus*	EP	0.1% of soil mass	Loam	-	-	Equilibrium centrifuging method (Smagin et al., 1998)	P	- The soil water retention capacity of casts increased within the entire range of the soil moisture contents compared to the surrounding soils up to 20 wt.% for 0 to –1000 kPa water potentials).
Boyle et al. (1997)	The effects of earthworms on grass growth and soil structure	Clonsant, Ireland	L	*Lumbricus terrestris* *Aporrectodea caliginosa* *Allolobophora chlorotica*	AN EN EN	250 ind m^{-2}	-	1.45	Perennial ryegrass in bucket and in glasshouse	Sand box method based on Stakman et al. (1969) procedures	p	- Grass yields were 89% and 19% higher in organically fertilized and inorganically fertilized buckets with earthworm presence respectively than without earthworms; - Soil from the organic fertilizer treatment with earthworm addition held the greatest

												volume of water than both treatments without earthworms and treatment using inorganic fertilizers. .
Bastardie et al. (2005a)	3D characterization of earthworm burrow systems of natural soil	Clermont-Ferrand, France	L (natural cores)	*Nicodrilus giardi*	AN	101 ind m^{-2} (in natural burrow cores)	Sandy clay loam	1.3	Agricultural research pasture	Estimation of water storage amount by X-ray tomography	P	- Accessible burrows offer a volume from 1400 to 10463 cm^3 m^{-3} of soil corresponding to 1–10 mm of a water storage capacity; - Surface diffusion from 1069 to 7237 cm^2 m^{-3}.
				Lumbricus. terrestris	AN							
				Dendrobaena mammalis	EN							
				Aporrectodea caliginosa	EN							
Ernst et al. (2009)	Quantify the impact of earthworm species on soil water characteristics	Trier, Germany	L	*Lumbricus terrestris*	AN	100 and 113 ind m^{-2}	Sandy loam	1.5	-	Tensiometers at 10 and 40 cm + FD-probes at 10 cm	P	- *L. rubellus* tended to enhance the storage of soil moisture at 10 cm depth; - *A. caliginosa* enhanced water infiltration rates compared *to L. terrestris* and *L. rubellus*
				Aporrectodea caliginosa	EN	350 and 370 ind m^{-2}						
				Lumbricus rubellus	EP	270 and 210 ind m^{-2}						
Palm et al. (2013)	Modelling distribution patterns of earthworms depending on soil proprieties, land management and topography	Baden-Württemberg, Germany	Modelling of collected field data	*Lumbricus terrestris*	AN	0 to 92 ind m^{-2}	Different texture containing clay from 9.3–23.6%	-	No till and reduced Ploughing	-	P	Distribution of epigeic earthworms are controlled by topographic features and endogeics species by soil moisture, clay content and organic matter.
				Octolasium cyaneum, Aporrectodea caliginosa and Aporrectodea rosea	EN	0 to168 ind m^{-2}						
				Lumbricus rubellus, Lumbricus castaneus	EP	0 to128 ind m^{-2}						

Knowledge and research gaps

Earthworms and soil water dynamics

Studies looking at the relationship between earthworms and soil water infiltration have considered both comparison between species and the effect of interactions between earthworm functional groups (Table 1). In the reviewed studies different earthworm population densities, initial soil bulk densities and methods of measuring infiltration were used. The studies have been conducted under many different climatic conditions across the globe and on soil textural classes ranging between sandy loam to clay loam. In manipulation experiments, anecic (*Lumbricus terrestris*), endogeic (*A. caliginosa* and *A. chlorotica*) and epigeic (*L. rubellus*) species are most frequently used. Epigeic species were considered in far fewer studies than anecic and endogeic species and have been found to have contrasting effects on soil water flow. Anecic species cause an increase in water infiltration rate in laboratory experiments and under conservation field management practices in field experiments. In these studies, the assessment of infiltration rate was coupled to physical descriptions and quantification of burrow morphology and characteristics of the population, such as earthworm abundance. Studies using endogeic species focus on the effect of casting and compacting activities of earthworms on soil water infiltration through modification of soil porosity, bulk density and macropore continuity. These studies were performed mostly in the laboratory, without any combined cropping system; increased, decreased or no significant effects of earthworms on water infiltration were reported. Studies investigating the combined effects of anecic and endogeic species focus more on the morphological characterization of the burrows and the effect of different cropping systems and land management on water infiltration. Under field conditions, earthworm burrows usually terminate in a dead-end, but most laboratory studies have investigated the effect of earthworms on soil water flow under the situation where earthworm burrows are well connected to a drainage system at their endpoint which would bias the estimated effects of earthworms during an experimental manipulation.

The relationship between earthworm activity and soil water infiltration has been extensively studied in the literature using a variety of laboratory and field experiments, however, we are still unable to say:

- How interactions of earthworms with types of crop impact water dynamics or more specifically how different root length / densities may enhance the activity of earthworms in increasing water flow?

- How earthworms influence the partitioning between macropore flow and micropores flow? and how the proportion of water flow through different pore size classes is different in the presence of plants with different rooting strategies which earthworms interact with?

- What is the way in which temporal changes in soil structure (e.g. due to crop development, seasonal weather changes and dry and wet cycles) are influenced by different earthworm species or as community and how this in turn can affect the stability of macropores and the potential consequences on water flow?

- How to relate earthworm to water dynamics in soils when shifting from conventional tillage-based agriculture to ecologically intensive or regenerative agriculture (agroecology, conservation agriculture etc)?.

It would be useful to consider these questions in situations where earthworm burrows terminate within the soil matrix to mimic the conditions found in most fields. This will allow the prediction of soil water infiltration and the sustainability of qualitative and quantitative beneficial effects of earthworms on soil water flows.

Earthworms and soil water storage

Compared to soil water infiltration, the impact of earthworms on soil water retention and storage is less well studied. Studies exist that consider all three ecotypes of earthworm, but most studies focus on endogeic species, particularly on *A. caliginosa* (Table 2). Studies either measure the water content of soils, the ability of earthworm casts to retain water under different soil water pressures or water repellency of earthworm casts. *L. terrestris* and *L. rubellus* are the main anecic and epigeic species studied. Studies that considered anecic earthworms focus on compaction due to burrowing activity and rates of water diffusion through burrow walls. Studies using epigeic earthworms stress their ability to maintain soil cover with low rates of litter loss which results in low water evaporation and the capacity of their casts to retain water. Studies in which earthworm numbers were manipulated reported a positive effect of the presence of earthworms on soil water storage and related this to burrow characteristics, cast age and levels of organic matter present. Most studies that consider the impact of earthworms on water storage are laboratory-based and used individual soils ranging in texture from sandy and silty loam to clays, though many studies used sandy and silty loams. Studies using suites of soils did not report textural information. Experiments conducted under a particular cropping system, or where soil water retention curves were drawn, are also infrequent.

The following are the identified knowledge and research gaps arising from the reviewed literature that should be pursued:

- There is currently little consideration in the literature as to how soil texture impacts on the effect that earthworms have on soil water retention when earthworm ecotype, earthworm density, soil density and soil organic matter content vary.

- Studies involving common earthworm species in Europe and globally are required, particularly *Lumbricus terrestris* (anecic) *Aporrectodea caliginosa* / *A. chlorotica* (endogeic) and *Lumbricus rubellus* (epigeic) to investigate their impact on soil water retention to better understand the role earthworms play in soil water regulation. The impact of ecotype/species could be evaluated both by comparison between and within ecotypes;

- Since different earthworms occupy different positions in the soil, water release curves for soils at different soil depth should be produced. Also, earthworm population density could be studied by comparing the influence of abundant, reduced and ambient densities in different soil types;

- Most experiments reported in the literature were performed in vegetation-free soil but most soils are vegetated. Carrying out experiments in the presence of different crop types would highlight the relative effects of crops and earthworms on water retention and any interactions that may exist;

- Organic matter (OM) pools in soils are modified by earthworms and this in turn may impact water retention. The composition of organic matter may affect the hydrophilic nature of casts and the location of OM in the soil may be relevant. Experiments where different organic matter compositions are used should emphasis the hydrophilic nature of casts (e.g., by measuring casts water repellency or water drop penetration time (Cosentino *et al.*, 2010) of different ecotypes of earthworm and its effect on soil water retention. Characterization of geomorphology and topography of the hydrophilic/hydrophobic surface layer coating soil particles of casts, using electronic microscopy for example, will help understand the processes;

- Most studies were undertaken in the laboratory; field experiments where treatments are exposed to natural condition would be more effective in transferring knowledge into practice;

- Earthworms are reported to improve crop growth through different processes (e.g. nitrogen mineralization, root aeration), it is likely that this is due in part to changes in water storage as a result of earthworm presence. This can be tested through experiments where soil water storage is measured in the presence of earthworm. Once the effects are established, crop growth could then be examined at different levels of soil water storage.

- It is necessary to develop new instruments and research design for studying earthworms in real situations and mainly to study diversity change and evolution as affected by land management scenarios and climate variability and change.

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