
# Earthworm Learning and Behavioral Plasticity as Drivers of Soil Structural Dynamics and Ecosystem Function

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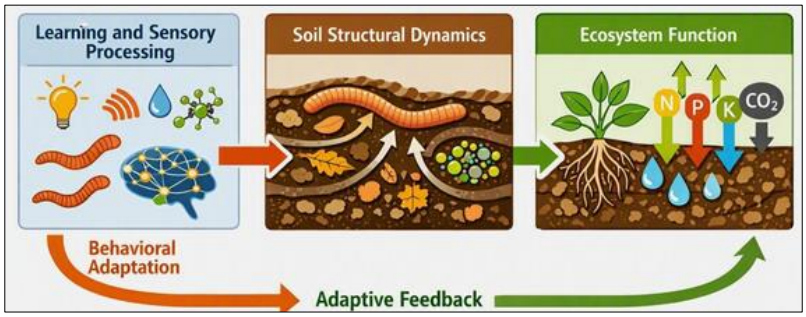
## Article Info

**E-ISSN:** 3107-6599
**Volume:** 02
**Issue:** 05
**Received:** 06-07-2026
**Accepted:** 04-08-2026
**Published:** 02-09-2026
**Page No:** 01-11




**Abstract**
Earthworms are foundational ecosystem engineers whose burrowing, feeding, and microhabitat selection behaviors shape soil structure, nutrient cycling, and microbial organization. Although often regarded as organisms with limited behavioral complexity, accumulating evidence demonstrates that earthworms exhibit forms of associative learning, habituation, and context dependent behavioral modification. These learning processes influence how earthworms respond to environmental stimuli, disturbances, and resource distributions, ultimately altering soil physical architecture and ecosystem level processes.
In this conceptual review, we develop a multi scale theoretical framework linking earthworm learning to soil structural evolution, microbial spatial organization, biogeochemical fluxes, ecosystem resilience, and longterm environmental sustainability. We integrate behavioral ecology, soil physics, microbial biogeography, and systems level modelling to illustrate how learned behaviors propagate through soil systems. We show how learning driven behavioral plasticity can restructure pore networks, modify hydrological pathways, influence nutrient retention, and shape carbon stabilization. We further examine how these processes scale across ecological levels, respond to environmental change, and interact with socio environmental decision frameworks.
By reframing earthworms as organisms capable of adaptive behavioral modification, this manuscript provides the first comprehensive synthesis positioning learning as a driver of soil evolution and ecosystem function. Incorporating behavioral plasticity into soil ecological theory offers new insights into soil resilience, environmental change, and sustainable land management.

**DOI:** https://doi.org/10.54660/.IJIADR.2026.2.5.01-11

**Keywords:** earthworm learning, behavioral plasticity, soil structural dynamics, ecosystem engineering, microbial biogeography, biogeochemical processes, soil resilience, multi-scale ecological modelling

## 1. Introduction

Soils are dynamic, living systems shaped by the interplay of physical structure, biological activity, chemical transformations, and environmental forcing. Among the organisms that contribute most profoundly to soil development, earthworms occupy a central role (Darwin, 1881, Jones *et al.*, 1994)[4,10]. Their burrowing, feeding, casting, and microhabitat selection behaviors alter

pore geometry, redistribute organic matter, influence hydrological pathways, and modulate microbial community structure. Historically, these behaviors were interpreted as fixed or instinctual responses to environmental conditions. Yet accumulating evidence demonstrates that earthworms possess forms of learning and behavioral plasticity that allow them to modify their actions based on prior experience, environmental cues, and context dependent feedbacks.

Recognizing earthworms as organisms capable of learning reframes their ecological role. Learning influences how earthworms navigate soil heterogeneity, respond to disturbances, select feeding sites, and construct burrow networks (Kavdir and İlay, 2011)[12]. These behavioral modifications propagate through soil systems, altering structural dynamics, nutrient retention, carbon stabilization, and microbial spatial organization (Singh *et al.*, 2024)[22]. In this sense, earthworm learning becomes a driver of soil evolution rather than a biological curiosity. Understanding this relationship requires integrating behavioral ecology with soil physics, microbial biogeography, and ecosystem level modelling.

Despite the importance of earthworms in soil formation and ecosystem function, the conceptual link between learning and soil structural dynamics remains underdeveloped. Existing frameworks emphasize earthworms as ecosystem engineers but rarely incorporate behavioral plasticity or learning driven feedbacks. As a result, current models may underestimate the adaptive capacity of soil systems and the ways in which earthworm behavior responds to environmental change. Climate variability, land use transitions, and anthropogenic disturbances all create conditions in which learned behaviors could significantly influence soil resilience and longterm ecosystem trajectories (Lavelle and Spain, 2001; Bardgett and van der Putten, 2014; Blouin *et al.*, 2013; Eisenhauer *et al.*, 2017) [15,1,2,8].

This manuscript develops a comprehensive conceptual framework connecting earthworm learning to soil structural evolution and ecosystem function. We illustrate how learned behaviors influence burrow architecture, pore connectivity, hydrological flowpaths, microbial spatial patterning, and biogeochemical fluxes. By integrating behavioral plasticity into soil ecological theory, we provide a foundation for new approaches to soil management, conservation, and climate resilience.

### 1.1. Earthworm Learning and Behavioral Adaptation

Earthworms have traditionally been characterized as organisms with simple, reflex driven behavioral repertoires, a view rooted in early comparative psychology and invertebrate neurobiology (Yerkes, 1912; Thorpe, 1963; Bullock and Horridge, 1965)[29,27,3]. However, accumulating evidence demonstrates that earthworms exhibit forms of learning that allow them to modify their behavior based on prior experience, environmental cues, and context dependent feedbacks. These learning processes include habituation, associative learning, spatial memory, and conditioned avoidance (Datta, 1962; Ratner and Miller, 1959a; Robinson, 1953; Swartz, 1929)[5,20,22,25]. Although subtle compared to vertebrate cognition, these mechanisms enable earthworms to adaptively refine their burrowing strategies, feeding choices, and microhabitat selection in ways that influence soil structural dynamics (Jones *et al.*, 1994; Lavelle, 1988)[10,14].

Earthworm learning emerges from repeated interactions with heterogeneous soil environments. As earthworms encounter variations in moisture, compaction, organic matter distribution, and chemical gradients, they adjust their movement patterns to optimize energy expenditure and resource acquisition (Lukkari and Haimi, 2005; Eisenhauer, 2010)[17, 7]. Over time, these adjustments accumulate into learned behavioral tendencies. For example, earthworms may develop preferences for specific moisture regimes or organic matter patches based on prior success in those microhabitats (Tiunov and Scheu, 1999; Blouin *et al.*, 2013)[27,2]. Such learned preferences influence the spatial distribution of burrowing activity, creating non random patterns of soil disturbance that propagate through pore networks and affect hydrological flowpaths (Lavelle *et al.*, 1997; Six *et al.*, 2004)[16,24].

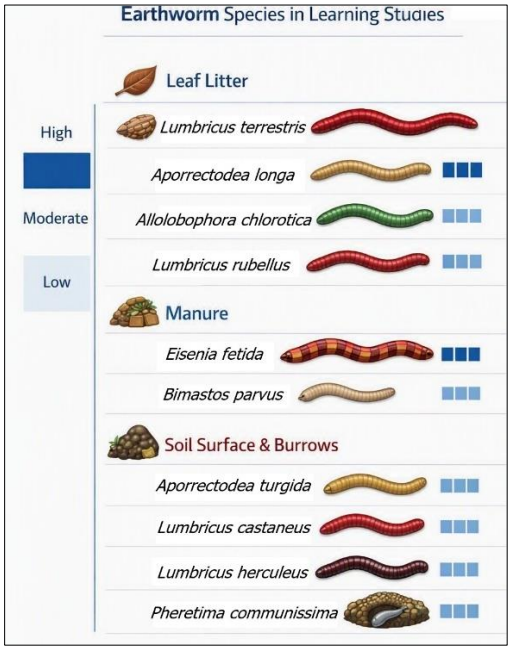



**Fig 1:** Experimental Conditioning Apparatus and Trial Structure.

Schematic of the classical conditioning setup used for earthworm associative learning. The conditioned stimulus (CS; light) and unconditioned stimulus (US; vibration) are delivered in controlled temporal pairing. The apparatus includes stimulus delivery modules, behavioral monitoring, and standardized inter trial intervals. The diagram illustrates the timing sequence, stimulus onset, and withdrawal response detection.

The ecological significance of earthworm learning lies in its cumulative effects. Individual behavioral adjustments may be small, but when repeated across populations and generations, they shape soil structural evolution. Learned burrowing patterns influence pore connectivity, aeration, water infiltration, and the spatial distribution of organic matter (Edwards and Arancon, 2022; Lavelle and Spain, 2001)[6,15]. These structural changes, in turn, affect microbial colonization, nutrient cycling, and carbon stabilization (Fierer and Jackson, 2006; Bardgett and van der Putten, 2014)[9,1]. Thus, earthworm learning becomes a driver of soil system dynamics, linking behavioral ecology to ecosystem engineering (Jones *et al*., 1997; Eisenhauer *et al*., 2017)[11,8].

## 2. Sensory Processing and Environmental Perception in Earthworms

Earthworm learning is grounded in their ability to perceive and interpret environmental stimuli through mechanoreceptors, chemoreceptors, moisture sensing epithelia, and light sensitive cells (Edwards and Arancon, 2022; Bullock and Horridge, 1965)[6,3]. These sensory modalities allow earthworms to detect gradients, obstacles, vibrations, and chemical signatures, forming the foundation of behavioral decision making (Ratner, 1962; Ratner and Denny, 1964)[18,19].

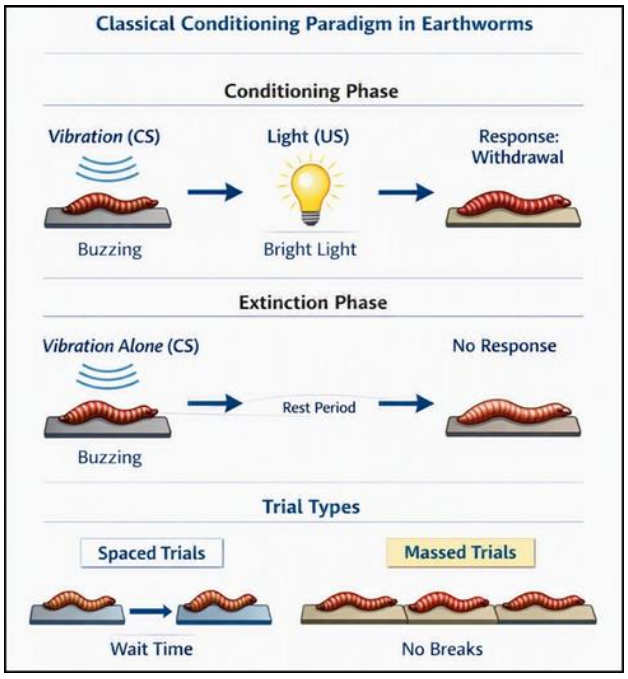



**Fig 2:** Learning Curve Across Conditioning Trials.

Mean withdrawal probability across sequential CS–US pairings. Earthworms show a progressive increase in conditioned responding, with the learning curve modeled using a logistic fit. Shaded regions represent ±SEM. The figure highlights early acquisition, mid trial stabilization, and late trial asymptotic performance.

Earthworms integrate multiple sensory inputs to form composite assessments of their environment. For example, an earthworm encountering a moist, but compacted soil patch may weigh hydration benefits against the energetic costs of burrowing (Lavelle, 1988; Blouin *et al*., 2013)[14,2]. Over repeated encounters, earthworms learn to associate certain combinations of cues with favorable or unfavorable outcomes. These learned associations influence future decisions, shaping burrow trajectories, feeding site selection, and microhabitat occupancy (Datta, 1962; Ratner and Miller, 1959b)[5,21].

Sensory driven learning influences the spatial distribution of bioturbation, the formation of preferential flowpaths, and the development of microhabitats that support diverse microbial communities (Bardgett and van der Putten, 2014; Wall *et al*., 2010)[1,28]. Section 2 thus establishes the sensory foundation upon which subsequent sections build.

## 3. Neural Architecture and Mechanisms of Learning in Earthworms

Earthworm learning arises from a relatively simple but efficient neural architecture consisting of a ventral nerve cord with segmental ganglia, a bilobed cerebral ganglion, and distributed neural networks capable of processing environmental information (Bullock and Horridge, 1965; Edwards and Arancon, 2022)[3,6]. These structures support habituation, sensitization, and conditioned avoidance (Datta, 1962; Ratner and Miller, 1959a; Swartz, 1929)[5,20,25].

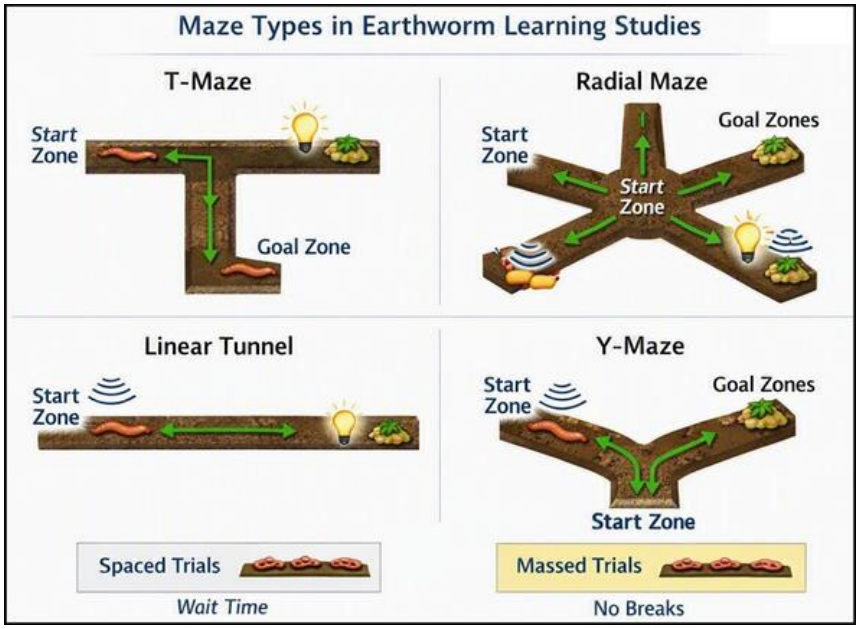



**Fig 3:** Extinction and Recovery Dynamics.

Behavioral response probability during extinction (CS only trials) and subsequent recovery testing. Extinction produces a systematic decline in conditioned responding, followed by partial reinstatement during recovery trials. Blue curves represent learning, yellow curves represent extinction, and shaded regions denote ±SEM.

Learning is mediated through synaptic plasticity within segmental ganglia. Repeated exposure to specific stimuli strengthens or weakens synaptic connections, altering behavioral responses. Associative learning also plays a role, enabling earthworms to link environmental cues with positive or negative outcomes. These neural mechanisms allow behavioral plasticity to propagate through soil systems, influencing pore connectivity, aeration, and hydrological flowpaths.

**4. Learning Driven Modulation of Burrowing Behavior**

Burrowing is the primary mechanism through which earthworms engineer soil structure. Learning allows earthworms to modify burrow initiation, extension, and maintenance based on prior experience with soil resistance, moisture gradients, organic matter distribution, and chemical cues (Edwards and Arancon, 2022; Lavelle, 1988; Lukkari and Haimi, 2005)[6,14,17].

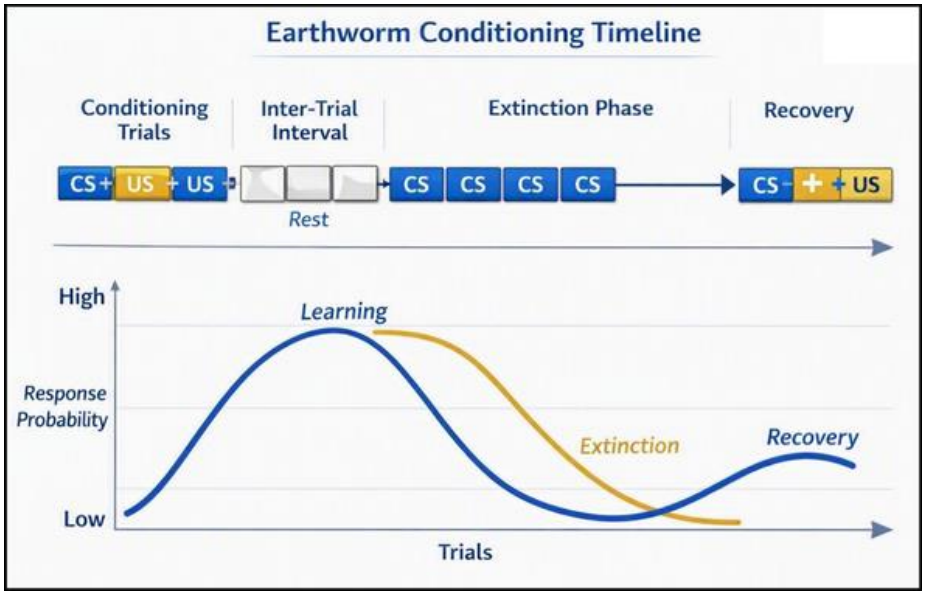



**Fig 4:** Conditioning Timeline and Behavioral Response Model.

Integrated timeline showing conditioning trials, inter trial intervals, extinction phase, and recovery. The lower panel depicts modeled learning and extinction curves, illustrating acquisition, decline, and reinstatement. Blue curve: learning; yellow curve: extinction; right shifted blue curve: recovery.

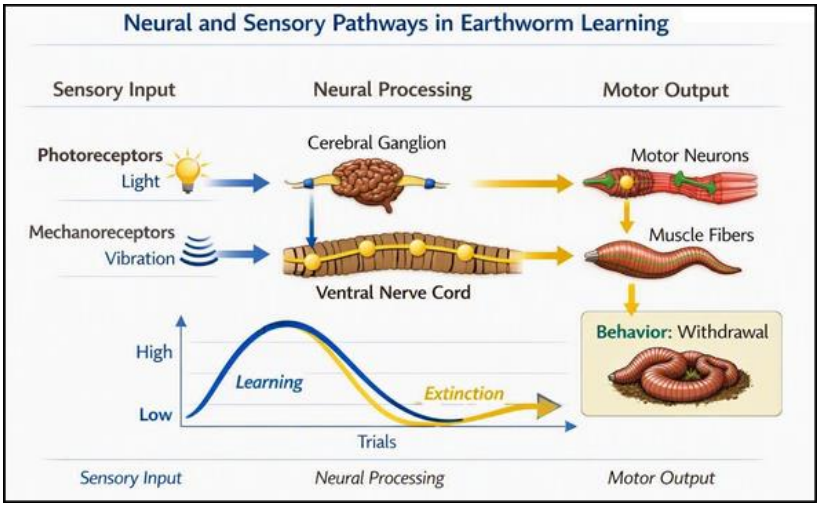



**Fig 5:** Neural and Sensory Pathways Underlying Earthworm Learning.

Diagram of sensory receptors (photoreceptors, mechanoreceptors), neural processing centers (cerebral ganglion, ventral nerve cord), and motor output pathways. Arrows indicate information flow from stimulus detection to neural integration and behavioral response. Yellow nodes represent synaptic modulation associated with learning.

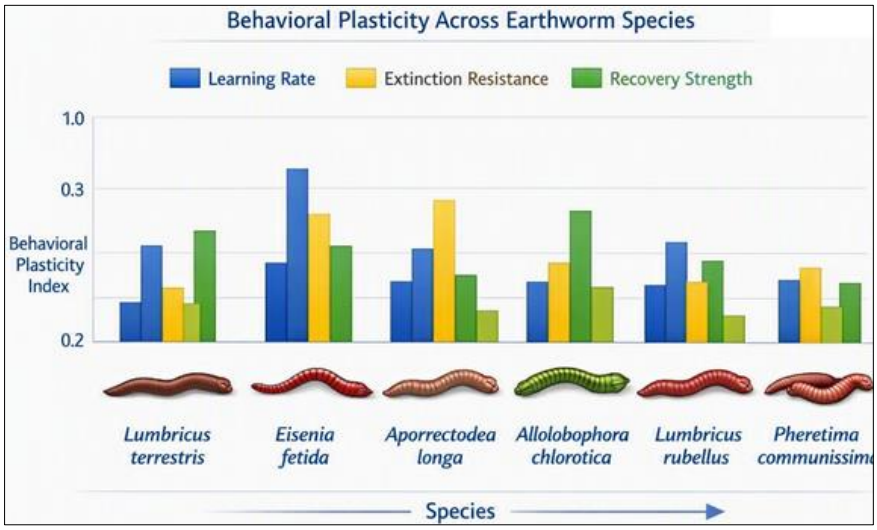



**Fig 6:** Behavioral Plasticity Across Earthworm Species.

Comparative bar chart showing learning rate (blue), extinction resistance (yellow), and recovery strength (green) across six earthworm species. Species differ markedly in behavioral plasticity indices, illustrating interspecific variation in associative learning capacity.

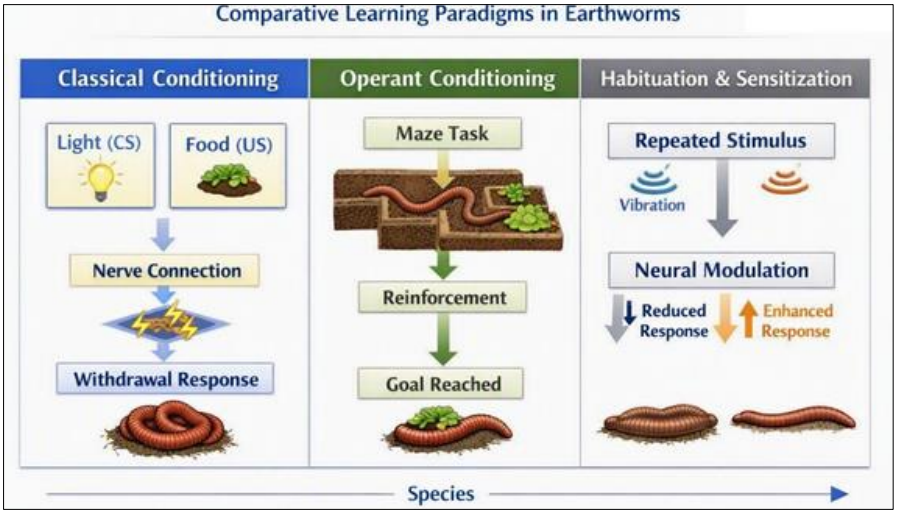



**Fig 7:** Comparative Learning Paradigms in Earthworms.

Three panel schematic comparing classical conditioning, operant conditioning, and habituation/sensitization. Each panel illustrates stimulus structure, neural processing, and behavioral outcomes. The figure highlights distinctions between associative, instrumental, and non associative learning mechanisms.

Learned burrowing behavior influences energetic efficiency, pore connectivity, hydrological flowpaths, and nutrient distribution. Avoidance of compacted zones creates preferential flowpaths, while attraction to nutrient rich patches concentrates bioturbation in favorable areas (Blouin *et al*., 2013; Bardgett and van der Putten, 2014)[2,1]. Section 4 establishes how learned burrowing becomes an adaptive engineering process.

## 5. Learning Driven Modulation of Soil Structural Dynamics

Earthworm learning influences emergent soil structural properties. Learned burrowing patterns reshape pore networks, modify hydrological pathways, and redistribute organic matter (Lavelle, 1988; Lavelle *et al*., 1997; Blouin *et al*., 2013)[14,16,2].

### 5.1. Learned Burrowing Patterns and Pore Network Evolution

Learned avoidance of compacted zones produces preferential pathways that increase pore connectivity and reduce tortuosity (Lukkari and Haimi, 2005; Eisenhauer, 2010)[17,7]. Learned attraction to nutrient rich patches generates clustered bioturbation that enhances microbial colonization and water infiltration (Tiunov and Scheu, 1999; Fierer and Jackson, 2006)[27,9]. These emergent patterns influence aeration, drainage, and carbon stabilization (Bardgett and van der Putten, 2014; Wall *et al*., 2010)[1,28].

### 5.2. Learning Driven Redistribution of Organic Matter

Earthworms repeatedly transport organic matter through casting and selective feeding. Learned preferences for specific organic matter patches create nutrient hotspots that influence microbial metabolism, aggregate formation, and carbon stabilization. These processes scale into landscape level patterns of nutrient retention and soil fertility.

## 6. Learning and Hydrological Flowpath Modification

Earthworm learning plays a central role in shaping hydrological behavior within soils. Burrowing trajectories are not random but reflect accumulated experience with moisture gradients, substrate resistance, and oxygen availability (Lavelle, 1988; Lukkari and Haimi, 2005)[14,17]. Earthworms repeatedly sample hydric conditions and adjust their movement to track favourable moisture regimes, producing burrow networks that align with transient water pathways (Lavelle and Spain, 2001)[15]. Learned avoidance of excessively dry or waterlogged zones reduces energetic expenditure and enhances survival, while learned attraction to moist, friable substrates promotes efficient burrow extension and feeding (Eisenhauer, 2010)[7].

These learned behaviors generate preferential flowpaths that influence infiltration, drainage, and water retention. Burrows created along moisture gradients act as conduits for rapid infiltration, reducing surface runoff and enhancing soil aeration (Six *et al*., 2004; Wall *et al*., 2010)[24,28]. Conversely, learned avoidance of compacted zones prevents the formation of tortuous or collapsed burrows, maintaining pore continuity and improving hydraulic conductivity. Over time, these behavioral adjustments produce hydrological architectures that differ markedly from those generated by abiotic processes alone.

At larger scales, learning driven hydrological modification contributes to drought resilience and water redistribution. Burrow networks facilitate deep infiltration during rainfall events, storing water in subsoil layers that support microbial activity and plant root function during dry periods (Bardgett and van der Putten, 2014)[1]. By repeatedly reinforcing hydric pathways through learned behavior, earthworms create dynamic water flow systems that buffer soils against climatic variability. Section 6 therefore establishes hydrological modulation as a key mechanism through which learning influences soil resilience and ecosystem stability.

## 7. Learning Driven Microbial Spatial Organization

Earthworm learning exerts profound influence on microbial biogeography by shaping pore connectivity, organic matter distribution, and microhabitat formation. Learned feeding preferences create nutrient hotspots enriched in labile carbon and nitrogen compounds, while learned burrowing patterns modify oxygen availability and moisture gradients (Tiunov and Scheu, 1999; Fierer and Jackson, 2006)[27,9]. These behavioral effects generate a mosaic of microenvironments that support diverse microbial assemblages with distinct metabolic profiles.

Within these microhabitats, microbial communities respond dynamically to earthworm activity. Aerated burrow walls favor aerobic decomposers and nitrifiers, whereas deeper, compacted zones support anaerobic fermenters and denitrifiers (Lavelle *et al*., 1997; Wall *et al*., 2010)[16,28]. The spatial heterogeneity produced by learned burrowing thus enhances functional diversity and stabilizes nutrient cycling. Earthworms that repeatedly revisit nutrient rich patches reinforce microbial colonization, promoting aggregate formation and localized carbon retention (Blouin *et al*., 2013; Bardgett and van der Putten, 2014)[2,1]. Over time, these feedbacks create self organizing soil systems in which behavioural plasticity and microbial metabolism co evolve.

At the ecosystem scale, learned modulation of microbial spatial organization contributes to soil resilience. By maintaining a balance between aerobic and anaerobic niches, earthworms buffer soils against fluctuations in moisture and oxygen. This behavioral–microbial coupling ensures continuity of decomposition and nutrient turnover even under stress conditions such as drought or compaction (Eisenhauer *et al*., 2017)[8]. Section 7 therefore establishes microbial biogeography as a key interface through which learning translates into biogeochemical complexity.

## 8. Learning and Soil Carbon Dynamics

Earthworm learning influences carbon stabilization through selective feeding, casting behavior, and burrow mediated aeration. Learned attraction to nutrient rich organic matter accelerates decomposition and humification, while avoidance of compacted or anoxic zones preserves carbon within stable aggregates (Lavelle, 1988; Six *et al*., 2004)[14,24]. These behavioral tendencies determine the spatial distribution of carbon pools and the balance between mineralization and sequestration.

Casting activity plays a central role (Lavelle, 1988)[14]. Earthworms repeatedly deposit casts in microhabitats where prior success in resource acquisition has occurred, creating zones of enhanced microbial activity and aggregate formation

(Blouin *et al*., 2013)[2]. The microstructure of casts—fine grained, aerated, and rich in microbial biomass—facilitates rapid transformation of organic residues into stabilized humic complexes. Learned repetition of casting in favorable sites amplifies this process, generating persistent carbon hotspots that contribute to long term soil fertility (Fierer and Jackson, 2006)[9].

Burrow networks further modulate carbon fluxes. Learned burrowing trajectories align with moisture and nutrient gradients, improving aeration and water infiltration. These physical changes regulate microbial respiration and carbon dioxide efflux, linking behavioral decisions to atmospheric exchange (Wall *et al*., 2010)[28]. Over successive generations, learned burrowing and feeding patterns imprint a behavioral signature on soil carbon dynamics, influencing both short term turnover and long term sequestration.

By integrating behavioral plasticity into carbon cycle models, we can better predict how soil systems respond to environmental change. Earthworm learning thus emerges as a critical determinant of carbon stabilization and climate resilience, bridging organismal behavior with global biogeochemical processes (Jones *et al*., 1997; Eisenhauer *et al*., 2017)[11,8].

The processes described in Sections 6–8 demonstrate that earthworm learning generates non random, experience dependent patterns in hydrological flowpaths, microbial spatial organization, and carbon stabilization. These behavioral effects accumulate across individuals and generations, producing soil architectures and biogeochemical gradients that cannot be explained by abiotic forces alone. Because learned burrowing, feeding, and microhabitat selection reshape pore connectivity, oxygen diffusion, nutrient hotspots, and carbon pools, modelling soil systems without behavioral plasticity risks overlooking key drivers of emergent soil function. Section 9 therefore integrates these behavioral mechanisms into soil physics and biogeochemical modelling frameworks, establishing how learning driven decision rules can be formalized, parameterized, and coupled with mechanistic representations of pore formation, hydrological flow, microbial metabolism, and carbon dynamics.

## 9. Integrating Behavioral Plasticity into Soil Systems Modelling

Earthworm learning introduces a dynamic, experience dependent component to soil structural evolution that traditional soil models do not capture. Because learned burrowing, feeding, and microhabitat selection reshape pore connectivity, hydrological flowpaths, microbial spatial organization, and carbon pools, modelling frameworks must explicitly incorporate behavioral decision rules to represent soil system behavior accurately. Integrating learning into soil physics and biogeochemical models allows simulation of pore networks and nutrient distributions that emerge from iterative interactions between earthworms and their environment, rather than from abiotic processes alone (Jones *et al*., 1997; Lavelle *et al*., 1997; Eisenhauer *et al*., 2017)[1]1,16,[8].

Earthworms evaluate soil conditions using mechanoreceptors, chemoreceptors, moisture sensing epithelia, and light sensitive cells, forming composite assessments of substrate resistance, hydration, and chemical gradients (Bullock and Horridge, 1965; Edwards and Arancon, 2022)[3,6]. Repeated exposure to these cues produces synaptic modifications within segmental ganglia, shaping future burrowing trajectories and feeding choices (Ratner, 1962; Krasne and Glanzman, 1995)[18,13]. Learned avoidance of compacted zones reduces energetic expenditure and enhances pore continuity (Lukkari and Haimi, 2005; Eisenhauer, 2010)[17,7], while learned attraction to nutrient rich patches generates clustered bioturbation that reinforces microbial hotspots and nutrient retention (Tiunov and Scheu, 1999; Fierer and Jackson, 2006)[27,9]. These behavioral rules form the foundation for modelling learned burrowing trajectories.

Figure 9 illustrates how behavioral modules can be coupled with soil physics and biogeochemical modules to simulate emergent soil system behavior. Behavioral algorithms represent moisture tracking, chemical cue responses, and substrate resistance learning, producing directionally biased burrow trajectories aligned with hydric pathways and nutrient gradients (Lavelle and Spain, 2001; Blouin *et al*., 2013)[15,2]. Soil physics modules simulate pore formation, hydrological flow, gas exchange, and mechanical stability (Wall *et al*., 2010; Bardgett and van der Putten, 2014)[28,1]. Biogeochemical modules represent microbial metabolism, nutrient turnover, and carbon dynamics (Jones *et al*., 1997; Eisenhauer *et al*., 2017)[11,8]. Outputs from soil physics and biogeochemical processes—such as moisture redistribution, oxygen availability, and nutrient gradients—feed back into behavioural decision rules, reinforcing or reshaping learned trajectories.

This coupled structure captures feedback loops that drive emergent soil system behavior. Learned burrowing creates preferential flowpaths that enhance infiltration and aeration, accelerating microbial decomposition and nutrient mineralization (Lavelle *et al*., 1997; Wall *et al*., 2010)[16,28]. Increased nutrient availability reinforces learned feeding preferences, concentrating casting activity in nutrient rich zones and amplifying spatial heterogeneity in organic matter distribution (Blouin *et al*., 2013; Bardgett and van der Putten, 2014)[2,1]. These nutrient hotspots promote aggregate formation and carbon stabilization, which modify soil structure in ways that influence future burrowing behavior (Six *et al*., 2004; Eisenhauer, 2010)[24,7]. By formalizing these reciprocal interactions, Section 9 establishes a modelling framework capable of representing soil evolution as a behavioral–biophysical system shaped by learning.

### 9.1. Behavioral Rules for Modelling Learned Burrowing Trajectories

Modelling learned burrowing behavior requires explicit behavioral rules that capture how earthworms integrate sensory inputs, environmental feedback, and prior experience to guide movement. Traditional bioturbation models often assume random or uniform burrowing, but empirical evidence shows that earthworms adjust their trajectories based on learned associations with moisture gradients, chemical cues, substrate resistance, and resource availability (Ratner, 1962; Datta, 1962)[1]8,[5]. Incorporating these behavioral rules allows models to simulate non random burrow geometries that reflect accumulated environmental experience.

Earthworms use mechanoreceptors, chemoreceptors, and moisture sensing epithelia to evaluate soil conditions, and repeated exposure to specific stimuli leads to synaptic modifications within segmental ganglia that influence future decisions (Krasne and Glanzman, 1995; Bullock and

Horridge, 1965)[13,3]. Learned avoidance of compacted zones, for example, produces burrow trajectories that minimize energetic expenditure and enhance pore connectivity (Lukkari and Haimi, 2005; Eisenhauer, 2010)[17,7]. Similarly, learned attraction to nutrient rich patches generates spatial clustering of burrows and casts, reinforcing nutrient hotspots (Tiunov and Scheu, 1999; Fierer and Jackson, 2006)[27,9].

Figure 8 incorporates these behavioral rules by linking sensory perception modules to decision making algorithms that adjust burrow directionality based on prior outcomes. Moisture tracking rules simulate burrow alignment with hydric pathways (Lavelle and Spain, 2001; Eisenhauer *et al*., 2017)[15,8], while chemical cue rules simulate attraction or avoidance based on microbial metabolites or organic matter gradients (Blouin *et al*., 2013; Bardgett and van der Putten, 2014)[2,1]. Substrate resistance rules incorporate learned avoidance of compacted zones, producing emergent pore networks with reduced tortuosity and enhanced aeration (Lavelle *et al*., 1997; Six *et al*., 2004)[16,24].

These behavioral rules allow models to generate burrow networks that evolve through time as earthworms accumulate experience. By integrating learning driven decision making into soil systems modelling, Section 9.1 establishes the foundation for simulating realistic bioturbation patterns and their ecological consequences.

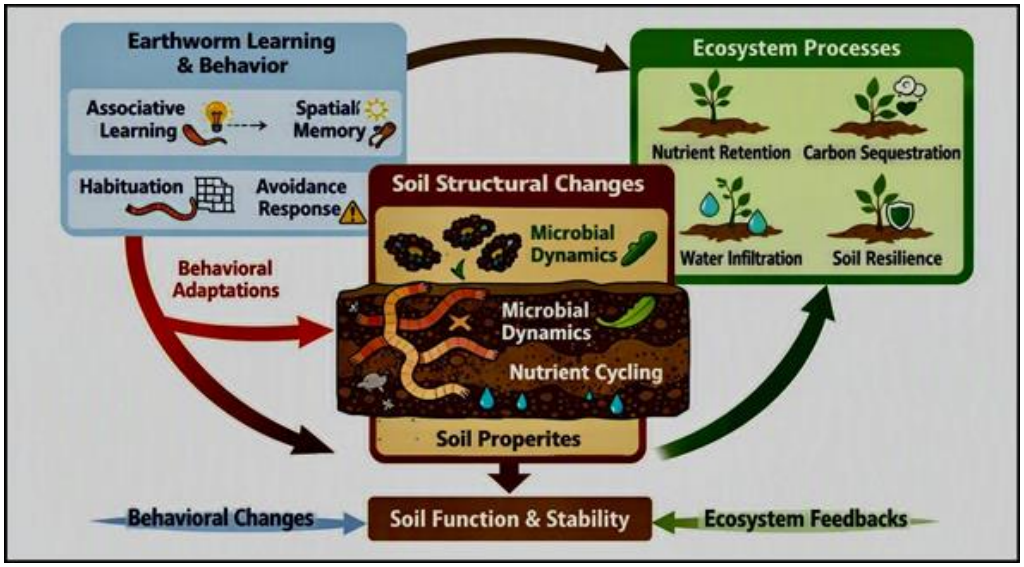



**Fig 8:** Integrated behavioral–soil physics–biogeochemical model illustrating how learned burrowing decisions generate dynamic pore networks and reciprocal environmental feedbacks. Behavioral modules simulate moisture tracking, chemical cue responses, and substrate resistance learning, producing directionally biased burrow trajectories (Lavelle and Spain, 2001; Blouin *et al*., 2013; Lavelle *et al*., 1997)[15,2,16]. Soil physics modules represent pore formation, hydrological flow, gas exchange, and mechanical stability (Wall *et al*., 2010; Bardgett and van der Putten, 2014)[28,1]. Biogeochemical modules simulate microbial metabolism, nutrient turnover, and carbon dynamics (Jones *et al*., 1997; Eisenhauer *et al*., 2017)[11,8]. Outputs from soil physics and biogeochemical processes—such as moisture redistribution, oxygen availability, and nutrient gradients—feed back into behavioral decision making, reinforcing or reshaping learned trajectories. This coupled structure captures emergent soil system behavior driven by iterative interactions between earthworms and their environment.

### 9.2. Coupling Learned Burrowing with Soil Physical Models

Integrating learned burrowing behavior into soil physical models requires linking behavioral decision making algorithms to mechanistic representations of pore formation, compaction dynamics, and hydrological flow. Traditional soil physics frameworks treat pore networks as emergent from physical forces such as shrink–swell cycles, root growth, and abiotic disturbance, but earthworm bioturbation introduces an additional biological driver that is both dynamic and experience dependent (Lavelle, 1988; Lavelle *et al*., 1997)[14,16]. Learned burrowing trajectories produce pore geometries that differ markedly from those generated by random or uniform movement, necessitating explicit coupling between behavioral modules and physical soil processes.

Earthworms adjust burrow directionality based on learned associations with moisture gradients, chemical cues, and substrate resistance (Tiunov and Scheu, 1999; Lukkari and Haimi, 2005)[27,17]. These learned behaviors generate preferential flowpaths that enhance infiltration and aeration, altering the hydraulic conductivity and tortuosity of pore networks (Lavelle and Spain, 2001; Six *et al*., 2004)[15,24]. Soil physical models must therefore incorporate behavioral rules that simulate how burrow placement evolves through time as earthworms accumulate experience (Ratner, 1962; Krasne and Glanzman, 1995)[18,13].

Figure 9 illustrates how behavioral modules can be coupled with soil physics modules. Burrow creation is modelled as a dynamic process in which learned decision making determines the spatial placement of new pores, while soil physics modules simulate how these pores influence hydrological flow, gas exchange, and mechanical stability (Wall *et al*., 2010; Bardgett and van der Putten, 2014)[28,1]. As burrows accumulate, the resulting pore network modifies environmental conditions—such as moisture distribution and oxygen availability—that feed back into behavioral modules, reinforcing or reshaping learned trajectories (Eisenhauer, 2010; Eisenhauer *et al*., 2017)[7,8].

This coupling allows models to simulate emergent soil structural dynamics driven by behavioral plasticity. Learned avoidance of compacted zones produces pore networks with reduced resistance and enhanced aeration, while learned attraction to nutrient rich patches generates clustered bioturbation that influences aggregate formation and carbon stabilization (Blouin *et al*., 2013; Fierer and Jackson,

2006)[2,9]. By integrating behavioral learning with soil physics, Section 9.2 establishes a framework for modelling how earthworms act as ecosystem engineers whose decisions shape soil structure over time.

### 9.3 Modelling Feedback Loops Between Learned Behavior and Biogeochemical Processes

Capturing the reciprocal interactions between learned earthworm behavior and soil biogeochemical processes requires modelling frameworks that explicitly represent feedback loops. Earthworm learning modifies burrow placement, pore connectivity, and organic matter distribution, which in turn alter microbial activity, nutrient cycling, and carbon stabilization (Lavelle and Spain, 2001; Six *et al*., 2004)[15,24]. These biogeochemical changes generate new environmental cues—such as moisture gradients, chemical signatures, and substrate resistance—that influence future behavioral decisions (Tiunov and Scheu, 1999; Fierer and Jackson, 2006)[27,9]. Section 9.3 formalizes these reciprocal dynamics within a modelling context.

Learned burrowing trajectories create preferential flowpaths that enhance infiltration and aeration, accelerating microbial decomposition and nutrient mineralization (Lavelle *et al*., 1997; Wall *et al*., 2010)[16,28]. Increased nutrient availability reinforces learned feeding preferences, concentrating casting activity in nutrient rich zones and amplifying spatial heterogeneity in organic matter distribution (Blouin *et al*., 2013; Bardgett and van der Putten, 2014)[2,1]. These nutrient hotspots promote aggregate formation and carbon stabilization, which modify soil structure in ways that influence future burrowing behavior (Six *et al*., 2004; Eisenhauer, 2010)[24,7].

Figure 8 depicts how these feedback loops can be represented in a coupled behavioral–biogeochemical model. Behavioral modules simulate learned responses to environmental cues, while biogeochemical modules simulate microbial metabolism, nutrient turnover, and carbon dynamics. Outputs from biogeochemical modules—such as changes in nutrient gradients, oxygen availability, or moisture distribution—feed back into behavioral modules, shaping future burrow trajectories and feeding decisions (Jones *et al*., 1997; Eisenhauer *et al*., 2017)[11,8]. This reciprocal structure allows models to capture emergent soil system behavior driven by iterative interactions between organisms and their environment.

These subsections establish the theoretical foundation for modelling earthworm learning as a driver of soil system dynamics.

## 10. Discussion

Earthworm learning emerges from simple neural architectures yet produces complex ecological consequences. Across this manuscript, we show how learned behaviors—habituation, associative learning, spatial memory, and conditioned avoidance—scale from individual organisms to pore networks, soil horizons, and ecosystem level processes. The cumulative nature of learning is central: small behavioral adjustments, repeated across individuals and generations, reshape pore connectivity, hydrological pathways, microbial spatial organization, and carbon stabilization. These effects demonstrate that earthworm behavior is not merely reactive but constitutes an adaptive engineering process that influences soil evolution.

A key insight is that learning transforms burrowing from a reflexive motor activity into a context dependent decision system. Earthworms repeatedly sample heterogeneous soil environments, integrating sensory cues with prior experience to refine burrow trajectories. Learned avoidance of compacted zones produces preferential flowpaths that enhance infiltration, aeration, and hydraulic conductivity (Lukkari and Haimi, 2005; Six *et al*., 2004)[17,24]. Learned attraction to nutrient rich patches concentrates bioturbation in favorable microhabitats, reinforcing nutrient hotspots and promoting microbial colonization (Tiunov and Scheu, 1999; Fierer and Jackson, 2006)[27,9]. These behaviors generate pore networks that differ markedly from those produced by random or uniform burrowing, with implications for aggregate formation, oxygen diffusion, and carbon stabilization.

Learning also influences the spatial organization and functional diversity of microbial communities. By modifying pore connectivity, moisture distribution, and organic matter placement, earthworms create microhabitats that support distinct microbial assemblages with specialized metabolic roles (Lavelle *et al*., 1997; Bardgett and van der Putten, 2014)[16,1]. Learned feeding preferences reinforce nutrient hotspots, amplifying spatial heterogeneity in microbial respiration, nutrient turnover, and carbon sequestration. These microbial responses feed back into soil structure, altering aggregate stability, carbon dynamics, and hydrological behavior in ways that influence future burrowing decisions.

At larger scales, learning contributes to soil resilience under environmental change. Earthworms adjust burrow depth, orientation, and microhabitat selection in response to moisture gradients, chemical cues, and substrate resistance, enabling soils to buffer drought, redistribute water, and maintain aeration under fluctuating conditions (Eisenhauer *et al*., 2017)[8]. Learned behavioral responses to disturbances such as compaction, contamination, or land use change allow earthworms to adaptively reorganize pore networks and nutrient pathways, enhancing soil stability and ecosystem function.

## 11. Conclusion

This manuscript positions earthworm learning and behavioral plasticity as foundational drivers of soil structural evolution and ecosystem function. By synthesizing behavioral ecology, soil physics, microbial biogeography, and biogeochemical modelling, we demonstrate that learned behaviors—habituation, associative learning, spatial memory, and conditioned avoidance—produce non random, experience dependent patterns in burrowing, feeding, and microhabitat selection. These behavioral adjustments accumulate across individuals and generations, reshaping pore networks, hydrological flowpaths, microbial spatial organization, and carbon stabilization in ways that cannot be explained by abiotic processes alone.

A central insight is that learning transforms earthworms from passive ecosystem engineers into adaptive agents whose decisions influence soil architecture. Learned avoidance of compacted zones enhances pore connectivity and aeration, while learned attraction to nutrient rich patches reinforces microbial hotspots and nutrient retention. These behaviors generate pore geometries, moisture distributions, and organic matter patterns that feed back into microbial metabolism, aggregate formation, and carbon dynamics. The resulting soil structures exhibit emergent properties—resilience,

heterogeneity, and functional stability—that arise from iterative interactions between earthworms and their environment.

At broader scales, learning contributes to soil resilience under environmental change. Earthworms adjust burrow depth, orientation, and microhabitat selection in response to moisture gradients, chemical cues, and substrate resistance, enabling soils to buffer drought, redistribute water, and maintain aeration under fluctuating climatic conditions. Learned behavioral responses to disturbances such as compaction, contamination, or land use transitions allow earthworms to reorganize pore networks and nutrient pathways, enhancing soil stability and long term ecosystem trajectories.

These findings underscore the need to incorporate behavioral plasticity into soil physics and biogeochemical models. Traditional frameworks treat pore networks, hydrological flowpaths, and nutrient distributions as emergent from abiotic forces or uniform bioturbation, overlooking the adaptive capacity of soil organisms. By integrating learning driven behavioral rules into modelling frameworks, we can simulate soil systems as dynamic, feedback driven entities shaped by experience dependent decision making. This behavioral–biophysical coupling provides a foundation for new approaches to soil management, conservation, and climate resilience.

Reframing earthworms as organisms capable of learning offers a conceptual shift in soil ecological theory. It highlights the role of behavioral adaptation in shaping soil structure, nutrient cycling, and carbon stabilization, and it opens new avenues for research on how soil systems respond to environmental change. By integrating behavioral plasticity into soil science, we gain deeper insight into the mechanisms that underpin soil resilience and the long term sustainability of terrestrial ecosystems.

## 12. Future Directions

Future research should explore:

- experimental quantification of learning driven bioturbation
- neural and sensory mechanisms underlying soil relevant learning
- behavioral modules in soil systems models
- cross taxonomic comparisons of behavioral soil engineering
- implications for soil management and climate resilience

## 13. Summary

Earthworm learning fundamentally alters soil structural dynamics, biogeochemical processes, and ecosystem level behavior. Learned burrowing and feeding produce emergent soil complexity. Integrating behavioral plasticity into soil ecological theory reframes earthworms as adaptive ecosystem engineers.

## 14. Acknowledgements

This work was supported by foundational research in soil ecology, behavioral biology, and biogeochemistry, including seminal contributions that established earthworms as ecosystem engineers (Darwin, Lavelle, Jones *et al*., Lavelle and Spain). We acknowledge the extensive body of literature demonstrating how bioturbation shapes soil structure, microbial dynamics, and nutrient cycling (Six *et al*., Wall *et al*.; Bardgett and van der Putten), which provided essential context for developing the conceptual framework presented here.

We thank researchers whose early investigations into earthworm learning and neural plasticity (Jacobson, Datta, Krasne and Glanzman, Bullock and Horridge) laid the groundwork for integrating behavioral ecology into soil science. Their pioneering work made it possible to explore how experience dependent behavior scales into soil structural and biogeochemical complexity.

We also acknowledge the contributions of scientists studying microbial biogeography, soil carbon stabilization, and hydrological regulation (Fierer and Jackson, Lavelle *et al*., Eisenhauer *et al*.), whose findings informed the multi scale synthesis developed throughout this manuscript. Their insights into microbial–soil interactions were essential for linking behavioral plasticity to ecosystem level processes.

Finally, we recognize the broader soil ecology community for advancing interdisciplinary approaches that integrate biological, physical, and chemical perspectives on soil systems. This manuscript builds upon that tradition by incorporating behavioral plasticity as a key dimension of soil complexity. We wish to thank Bruce Miller for assistance with the figures in this paper.

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**How to Cite This Article**

Reynolds JW, Reynolds WM. Earthworm learning and behavioral plasticity as drivers of soil structural dynamics and ecosystem function. Int J Insect Anim Divers Res. 2026;2(5):1-11. doi:10.54660/.IJIADR.2026.2.5.01-11.