Earthworms and Humus Forms

Renée-Claire Le Bayon, Jean-François Ponge, and Augusto Zanella

Abstract Soils play a central role in global biogeochemical cycles and host plants and invertebrates whose engineering activities mainly occur in the upper soil layers, the so-called humipedon. This latter is the critical zone where most chemical, physical, and biological ecosystem processes arise. This chapter overviews the main definitions and concepts (diagnostic horizon, humus system, humus form) and functional approaches to humipedon intimately linked to ecosystem engineers, mainly plant roots and earthworms. Biological activities are decisive in integrating organic matter and forming soil aggregates and galleries. We highlight the relevance of studying humus forms based on field observations in various environments (grasslands, forests, mountains, floodplains) and pioneer ecosystems and underline that more research is needed on the role played by earthworms in the evolution of terrestrial biomes.

1 Exploring the Underground

The world's population reached a record eight billion people on 15 November 2022, according to the Department of Economic and Social Affairs of the United Nations (2022). Human population growth impacts the Earth's system in various ways, including the extraction of natural resources such as fossil fuels, minerals, trees, water and wildlife. Moreover, more than half of the world's population now lives in urban areas (Ritchie et al. 2024), and urbanisation is still in expansion. Such increased pressures endanger maintaining and expanding essential ecosystem

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Y. Kooch, Y. Kuzyakov (eds.), *Earthworms and Ecological Processes*,
https://doi.org/10.1007/978-3-031-64510-5_6

benefits and services required for human livelihood (Larondelle et al. 2014). These latter are commonly defined as the “benefits people obtain from the ecosphere and its ecosystems” (Millennium Ecosystem Assessment 2005) and listed into four broad categories: provisioning, regulating, cultural and supporting services (Dominati et al. 2010). To preserve as best as possible ecosystems’ services, the conservation and management of ecosystems appear crucial because this approach considers the entire communities of species and their interactions with the physical environment.

Usually, the most common and easiest way to understand terrestrial ecosystems is to study vegetation… provided you know botany and phytosociology! Vegetation relevés allow the establishment and monitoring of plant communities’ structure and composition using a percentage cover of species in each layer of phytocenosis (Braun-Blanquet’s scale). This approach is beneficial for preserving and predicting the ecosystems’ evolution due, for instance, to anthropic impacts such as climate change. To complement this descriptive vision, energy, water and nutrient fluxes provide a functional approach to ecosystems. However, more than staying at the level of the upper part of plants is required: we need to follow the plants’ dark side underground, which means their roots. This guides us to the most concealed part of the ecosystem, the underground black box and perhaps one of the last final frontiers of the research and knowledge: the soil (see the review in Science, Sugden et al. 2004).

As a three-dimensional effective, almost non-renewable system, soils represent the primary living matrix for many ecosystems and human activities (Dominati et al. 2010; Adhikari and Hartemink 2016; Blanchart et al. 2018; Sofo et al. 2022). They play a central role in global biogeochemical cycles and host the most extensive diversity of organisms (Smith et al. 2015). Among these organisms, plants and invertebrates are essential components of soil genesis, functions and properties. Their engineering activities mainly occur in the so-called humipedon, corresponding to the upper soil layers particularly enriched in organic matter, which are the core of the interactions between vegetation and soil (Zanella et al. 2018a, b). The activity of soil organisms is exceptionally high in humipedons and intensely involved in organic matter recycling and provisioning, as well as biogenic structures such as burrows, pellets and aggregates. Earthworms and plant roots mainly govern these latter: as allogenic engineers, they are responsible for physical modifications but may also be involved in biological and biochemical processes. In temperate ecosystems, they are thus the leading soil engineers creating habitats for other organisms, such as small arthropods such as springtails or mites (Eisenhauer 2010; Cameron et al. 2013; Liu et al. 2013). Both plants and earthworms also produce chemical substances, exudates (Bais et al. 2006) and mucus (Salmon 2001), which are enriched in water, carbon (C) and nitrogen (N). Plant roots interact with earthworms, and their concomitant activity increases aggregate stability (Fonte et al. 2012; Schomburg et al. 2018a, b). The critical zone where most chemical, physical and biological processes occur is the humipedon (Fig. 1).

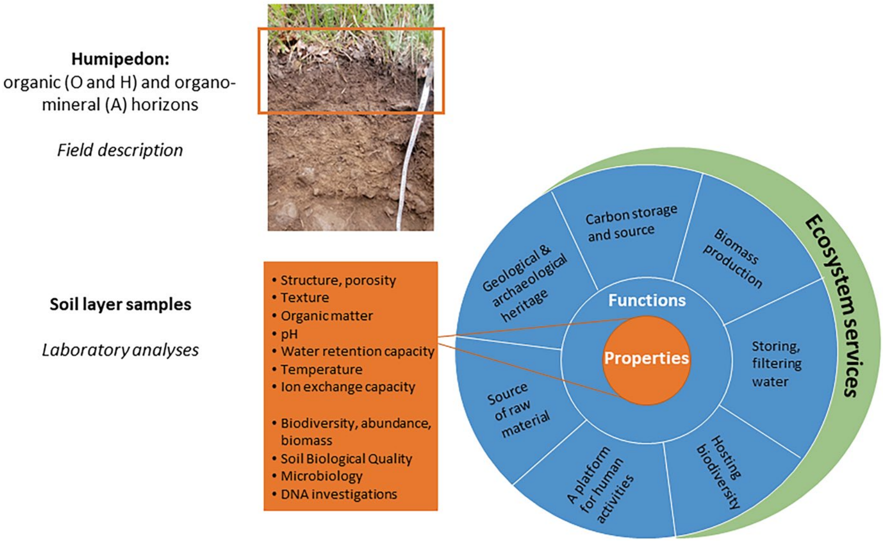

Fig. 1 The humipedon is crucial in ecosystem services as it interfaces between vegetation and mineral soil layers. The humipedon is involved in the carbon cycle, the hosting of biodiversity and the regulation of water and biomass production at the ecosystem level. Moreover, the humipedon has its own spatiotemporal functioning scale. Adapted from Adhikari and Hartemink (2016)

2 Humipedon, Humus Systems and Humus Forms: What Are We Talking About

2.1 Vocabulary

Since Zanella et al. (2018e), the “humipedon” represents the surface organic (O, H) and organo-mineral (A) soil layers, thus avoiding confusion with previous “top-soil”, “humus” or “forest humus” definitions. In terrestrial ecosystems, the humipedon organises into five *humus systems*: Mull, Moder, Mor, Amphi and Tangel, which can be eventually submerged a few days per year.

Humus systems differ by morpho-functional humus *diagnostic horizons* and are generated by specific groups of organisms. In each humus system, the thickness of diagnostic horizons defines some (3–4) similar *humus forms*.

The humipedon is made up of organic horizons (O, organic; OL, litter; OF, fragmented/fermented litter; OH, humic, i.e. transformed in rather organic minute droppings, small particle litter) and of organo-mineral A horizon (organic derivate integrated within a mineral layer). These horizons are placed on top of each other: OL at the surface, then OF, and OH, on A at the bottom of the humipedon. The OL layer is composed of recognisable leaves at different decomposition stages. The OF layer consists mainly of fragmented debris, and the OH layer contains a majority of holorganic droppings.

It is relatively easy to distinguish three zoogenic and one non-zoogenic type of organo-mineral A horizons:

1. Biomacrostructured A horizon (code: maA): at least one-third of the volume made by large (>4 mm) organo-mineral biogenic aggregates; origin: anecic or endogeic earthworms and microorganisms.
2. Biomicrostructured A horizon (code: miA): at least two-thirds of the volume made by small (≤1 mm) organic or organo-mineral faecal pellets; origin: arthropods, enchytraeids and microorganisms.
3. Biomesostructured A horizon (code meA): zoogenic horizon, not maA, not miA; origin: anecic or endogeic earthworms, microorganisms, insect larvae and large arthropods may also intervene in the Mediterranean environment. The appearance is that of a finer and very amalgamated maA aggregates.
4. Non-zoogenic A horizon: massive (code: msA, like clay organo-mineral blocky horizon) or single grain (code: sgA, sandy organo-mineral horizon, organic pellets ≤10%); origin: rather due to chemico-physical reactions and water transport of molecules and minerals, microorganisms may play an unknown role too.

For more information on diagnostic horizons and graphical illustrations, refer to Zanella et al. (2018f).

Table 1 is a revisited version of the synthesis made by Ponge (2003), which has been completed with Tangel and Amphi systems. From Tangel to Mor systems, a gradient of variations occurs, especially regarding the horizon sequences relative to the activity of soil organisms. The ecosystems and soil types differ, as do the recycling of organic matter and nutrient availability. At a finer level, in each humus system, diagnostic horizons' presence and thickness define several humus forms, differing slightly in between (i.e. Eumull, Mesomull, Oligomull, Dysmull; Zanella et al. 2018g).

In addition to plant roots, soil fauna and microorganisms (bacteria, fungi) are intensely involved and often used to discriminate the humus system at the inter- and intra-level. The same occurs for arthropods: while springtails and mites are the most common arthropods in the humipedon, enchytraeids and earthworms are the most efficient in organic matter recycling bioturbation processes (Table 1). In addition, arthropods and enchytraeids mainly live in O layers, while earthworms can live in soil surface layers or more profoundly. Figure 2 is an updated version of Zanella et al. (2018c), an extension of the presence of earthworms to a broader range of humus forms. New in situ observations revealed that epigeics are mostly ubiquitous in humus systems, while anecics range from Eumesoamphi to Eumoder.

2.2 The Amphi System: A Historical Overview

The introduction of Amphi forms in the classification of humus forms results from field observations and discussions within a consortium of researchers over the last two decades, as briefly described below.

In 1882, Peter Erasmus Müller (1887) described two humus forms in Germany: Mull (made by earthworms) and Torf (made by arthropods). In 1970, in the Austrian and Italian Alps, Franz Hartmann (1970) discovered that these two humus forms might overlap in what he called "Humus gemellare", literally "twin humus". This system was composed of a grey-brown organic-mineral layer made of large

Table 1 Main biological features of the five humus systems at the ecosystem level

	Tangel	Amphi	Mull	Moder	Mor
Ecosystems	Grasslands, coniferous woodlands, alpine meadows, cold and humid conditions	Deciduous and coniferous woodlands, transitional ecosystems such as abandoned pastures	Grasslands, deciduous woodlands with rich herb layer, Mediterranean scrublands	Deciduous and coniferous woodlands with poor herb layer	Heathlands, coniferous woodlands, sphagnum bogs, alpine meadows
Biodiversity	Medium	High in the A, low in O layers	High	Medium	Low
Productivity	Medium	Medium to high	High	Medium	Medium to low, adapted to acidophilic species
Litter horizons	OL, OF, OH	OL, OF, OH	OL, OF	OL, OF, OH	OL, OF, OH
Organo-mineral horizon	nozA, meA	miA, meA, maA	meA, maA	meA, miA	When present, nozA
Soil type	Holorganic soils, humo-calcic soils	Brown calcic soils	Brown soils	Grey-brown podzolic soils	Leached brown soils to podzols
Phenolic content of litter	Medium to high	Medium	Poor	Medium	High
Humification	Slow	Slow to medium	Rapid	Slow	Very slow
Humified organic matter	Slow but continuous degradation of plant debris	Holorganic faecal pellets in the O horizons, organo-mineral aggregates in the A horizon	Organo-mineral aggregates with clay-humus complexes	Holorganic faecal pellets	Slow oxidation of plant debris

(continued)

Table 1 (continued)

	Tangel	Amphi	Mull	Moder	Mor
Exchange sites	Organic (rich near the rock)	Organic (rich) to mineral	Mineral	Organic (rich)	Organic (poor)
Mineral weathering	Poor, except in the vicinity of the rock	Medium to high	High	Medium	Poor
Mineral buffer type	Carbonate range	Carbonate to silicate	Carbonate to silicate range	Silicate range	Iron/aluminium range
Impact of fire	High	Medium to high	Low (except in Mediterranean ecosystems)	Medium	High
Regeneration of trees	Poor	Medium, depending on A type (maA to meA)	Easy (permanent)	Poor (cyclic processes)	Young trees may develop on local degrading stumps or surface-stripped soils
Dominant mycorrhizal types	Ectomycorrhizae	VA-mycorrhizae to ectomycorrhizae	VA-mycorrhizae	Ectomycorrhizae	Ericoid and arbutoid mycorrhizae
Mycorrhizal partners	Unknown	Basidiomycetes	Zygomycetes	Basidiomycetes	Ascomycetes
Nitrogen forms	Protein	Protein, ammonium, nitrate	Protein, ammonium, nitrate	Protein, ammonium	Protein
Nutrient availability to plants	Direct from the OH horizon	Direct to indirect	Direct (through absorbing hairs)	Indirect (through extramatrical mycelium)	Poor
Nutrient use efficiency	Low to medium	Medium to high	Low	Medium	High
Fauna	Mesofauna (high), microfauna (high)	Macrofauna in the A horizon, mesofauna and microfauna in O horizons	Megafauna, macrofauna, mesofauna, microfauna	Macrofauna (poor), mesofauna (rich), microfauna	Mesofauna (poor), microfauna (poor)

	Tangel	Amphi	Mull	Moder	Mor
Earthworms: main ecological categories	Epigeics, some endogeics	Epigeics, endogeics, anecics	Endogeics and anecics	Epigeic, some endogeics	Some epigeics in thin mors
Faunal group dominant in biomass	Mites, springtails, a few earthworms, enchytraeids	Endogeic earthworms in the A horizon, macro- and microarthropods, epigeic earthworms and enchytraeids in O horizons	Earthworms	Enchytraeids, a few earthworms	Mites, springtails
Microbial group dominant in biomass	Fungi	Bacteria and fungi	Bacteria	Fungi and bacteria	Fungi
Affinities with polluted condition	Low	Low	Low	Medium	High

Adapted and revised from Ponge (2003)

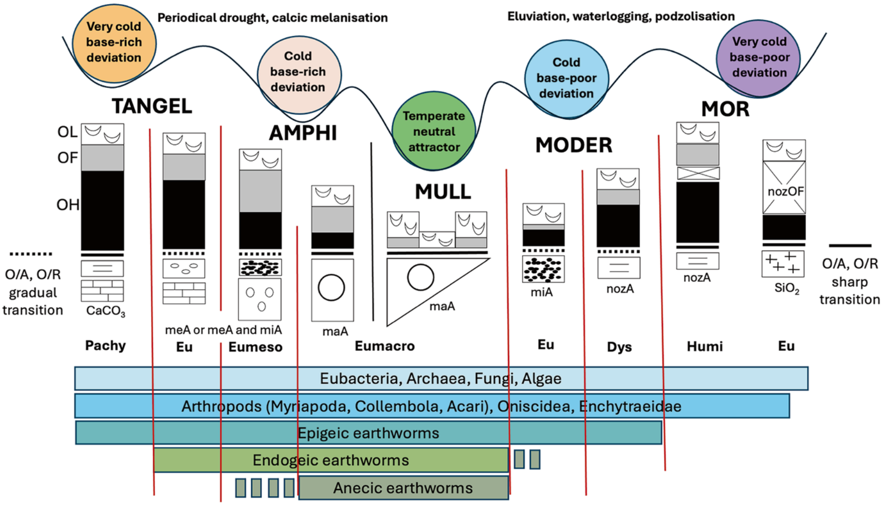

Fig. 2 An updated version of the simplified scheme of the terrestrial humus system classification (updated, from Zanella et al. 2018c). The scheme shows the main climatic and parent material determinants (top of the picture), diagnostic horizons (middle) and biological actors of organic matter transformation (bottom). OL, OF, nozOF, OH, maA, miA and nozA: diagnostic horizons described in Zanella et al. (2018f) transition between OH and A horizons: dashed line, gradual; continuous line, sharp; A horizon aggregates: two lines, non-zoogenic; small black circles, biomicrostructured; white small circles, biomesostructured; large white circles, biomacrostructured; lithopedon: bricks, base-rich substrate; +, base-poor substrate; Pachy, thick; Eu, typical; Dys, acid; Humi, rich in undecayed organic matter; Eumacro and Eumeso, large or medium biogenic structures in the A horizon. Humps and troughs of the continuous blue line refer to the hypothesis of humus systems as ecological attractors, with Mull as the "final" attractor

earthworms' dejections, overlapped by an organic black layer made of small aggregates generated by arthropods.

In 1995, Brêthes et al. (1995) set a similar humus form in their classification system; they called it "Amphimull" ("double Mull") and placed it in the Mull system. In 1996, Calabrese et al. (1996) revealed that such "twin humus" was relatively common in beech forests and Mediterranean ecosystems. This "Amphimull" evolved into "Amphimus" in 2009 (Jabiol et al., in Baize and Girard 2009), showing the importance of discriminating this system from the Mull one and the specificity of this particular humus form.

In 2003, 26 soil specialists met in Trento (Italy) and founded a Humus Group. After 3 years of exchanges, the Humus Group presented a poster at the World Congress of Soil Science in Philadelphia (USA, 2006) on which the Amphi reference was displayed aside from the well-known ones of Mull, Moder and Mor (Fig. 3). To provide a complete and updated framework in this chapter dedicated to earthworms, in Fig. 3, we added the Tangel system (bottom, in orange), which was not present on the drawing presented in Philadelphia because it was considered only in 2018.

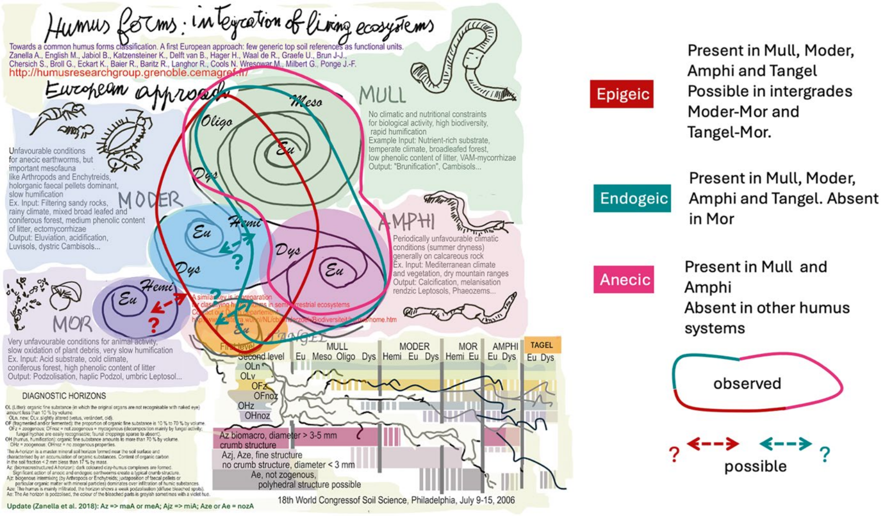

Fig. 3 Humus forms: integration of living ecosystems. Poster presented at the 18th World Congress of Soil Science at Philadelphia in July 2006, modified. Mull, Moder, Mor, Amphi and Tangel "humus form references" (corresponding to modern "humus systems") were represented as evolutionary holes in which the humipedon ecosystems fall driven by climatic, geological and vegetational relationships and constraints. In 2006, the Amphi "hole" was filled with two humus forms: Euamphi and Dysamphi. Since 2018, they became four: Leptoamphi, Eumacroamphi, Eumesoamphi and Pachyamphi. Moder did not change; Mor got a third Humimor form in 2018. In 2018, a Tangel fifth hole was added at the bottom of the picture, touching Amphi, Moder and Mor. This supplementary humus system, mostly generated by arthropods in calcareous or dolomitic high mountain environments, was first described by Walter Kubiëna in 1953 (Kubiëna 1953)

The group of *epigeic* earthworms has a habitat relegated to organic horizons (vOL, zoOF, zoOH; v, verbleit, bleached, old and packed litter; zo, zoogenic, with evident signs of the presence of animals that feed on litter, such as holes, bites, droppings, etc.). The epigeic earthworms produce small organic droppings (organic carbon > 20% by weight, measured with the elemental analyser) that remain in the organic part of the soil profile (Galvan et al. 2008). These earthworms initiate the biotransformation of litter but only indirectly participate in the genesis of organo-mineral aggregates, which are due only to endogeic and anecic groups; they are active in all humus systems presenting zoogenic organic diagnostic horizons, as in Mull, Moder, Amphi and Tangel (absent on Mor).

The *endogeic* group does not inhabit the organic horizons of the humipedon but prefers the superficial part of the organo-mineral horizon, feeding on organic horizons deposited above their habitat, but creating an organo-mineral horizon composed of their excrements. This also happens in environments of very superficial soils, as long as they are also covered by organic horizons, both in acidic and calcareous environments. The A horizon formed by endogeic earthworms is slightly smaller in size but very similar to that formed by anecics, made up of uniformly amalgamated organo-mineral aggregates (Zanella et al. 2018f). A transitional form of humus between Mull and Moder has been described, called Hemimoder (literally Half Moder). In it, the OH horizon is discontinuous. This means that juxtaposed surfaces with and without OH are observed in the field. On a more detailed scale, these are the Mull (without OH) and Moder (with OH) systems that developed in mosaic. Endogeic earthworms have been found in these areas. They would eat up the OH horizon and turn some of the area that was in Moder to Mull. This group may be present in the organo-mineral part of a Hemimoder but not on typical Moder and never present in a Mor system.

The *anecic* earthworms occupy a key place in the functioning of the Mull and Amphi systems. They form organo-mineral aggregates that make up the A horizon (fundamental matrix for plant nutrition) of all agricultural and forest soils in mild climate areas. Absent from Tangel and Mor humus systems, the importance of these earthworms in functioning Moder is null or marginal (transitional forms towards Mull or Amphi systems).

3 Earthworm Engineering: Opportunity or Threat?

Earthworms are known for a long time for the ecosystem services they provide through their engineering activity: litter decomposition (Bocock 1964), soil structure (Oades 1993), and nutrient cycling (Bohlen and Edwards 1995; Edwards and Arancon 2022), among many others, are improved under the influence of their multiple interactions with plants, microbes and other soil fauna (Brown et al. 2000), stemming in the formation of earthworm Mull (Zanella et al. 2018b). Less well-known despite of far-reaching consequences for global warming mitigation is the role played by earthworms in carbon sequestration in Mull humus systems in which organic matter is buried and mixed with mineral particles in physically and chemically stable aggregates (Zhang and Schrader 1993). Although more research on the subject is urgently needed, earthworm (macroaggregated) Mull and Amphi thereby might contain more organic carbon (although invisible to the naked eye) over their whole thickness and thus might sequester more carbon than Moder or Mor humus systems that visibly accumulate more organic matter at the soil surface (Andreetta et al. 2011; de Nicola et al. 2014). Another example of still poorly known ecosystem services provided by earthworms is the stimulation of forest regeneration through the building of humus forms favourable to tree seedling establishment(Ponge et al. 1998). As a consequence of benefits provided by earthworm activity, the colonisation of earthworm-free land by earthworms has been shown to favour crop production. Widely reported examples are the colonisation of Dutch polders by indigenous earthworm species and New Zealand pastures by exotic (European) earthworm species (Curry and Cotton 1983). In both cases, earthworms were considered as an essential tool for the successful development of agriculture.

However, and quite surprisingly, earthworm processes, e.g. casting deposition, may favour biodiversity by increasing heterogeneity at the soil surface and creating niches for plants (Milcu et al. 2006) and animals (Hamilton and Sillman 1989), but these same processes may also degrade the soil by favouring erosion along slopes (Le Bayon and Binet 1999; Le Bayon et al. 2002) or creating impervious crusts on the ground (Chauvel et al. 1999). Many reports have been done on detrimental aspects of earthworm activity. The most threatening is the still the incoming invasion of North American biomes by European (several lumbricid species) and Asian (several pheretimoid species) earthworms introduced in the past by European settlers (Nuzzo et al. 2009). In US northeastern forests, indigenous earthworm faunas, restricted to a few species living in their typical thick forest floors, are now outcompeted by invasive earthworms through changes in humus forms mediated by their mixing and digging activities, even if some cases of resistance have been observed (Hendrix et al. 2006). Dramatic changes caused by the establishment of exotic earthworm populations are also visible at the scale of forest vegetation (Hale et al. 2006). It might even be postulated that in a more or less near future tree populations will be affected, too, in particular if tree species favoured by Mull for their regeneration outcompete tree species favoured by Moder or even Mor.

In China, the introduction of the European manure worm *Eisenia fetida*, as yet commonly used for composting organic wastes, has been suggested as a mean to reclaim soils improper for agriculture (Zhang et al. 2015). This voluntary introduction, besides the expected development of agriculture, might have far-reaching detrimental consequences for the conservation of indigenous ecosystems, even if such deleterious effects are not purported at the beginning.

The main reason for these contrasted aspects of earthworm activity, whether opportunities of threats according to circumstances, is that earthworms, in particular those species capable of digging the soil and mixing it with organic matter (i.e. mull-forming species) create disturbances at a scale ranging from the drilosphere to whole forest or grassland ecosystems. These disturbances propagate themselves through scales by self-entertained chains of action and reaction, also called positive feedback loops until some equilibrium is reached and stabilised through negative feedbacks (Jouquet et al. 2006). Here, the Mull humus system can be considered as the climax, generating by itself the conditions of its own development, earthworm activity favouring the nutrient-rich vegetation favouring in turn the development of nutrient-eager earthworm populations (Ponge 2003; Arim et al. 2006). Detrimental effects of earthworm invasion can be alleviated only by changing the humus form, which is an unattainable task, or waiting enough time for a new equilibrium once the spread of invaders arrives to completion (Arim et al. 2006).

4 Let Us Go to the Field

Depending on the environment in which they form, there are different types of O and A horizons. In a mesophilic environment (plains, low mountains, rainy tropical), the O horizons last very little (animals eat them quickly); the OH horizon is rarely present. An earthworm biomacrostructured A horizon develops. This humipedon is said to belong to a Mull system. Anecic and endogeic earthworms make the whole A horizon of Mull and Amphi humipedons. When all organic horizons have been integrated in the A horizon, these animals eat their own matured in the soil droppings, living on the stock of organic molecules they previously set into the soil. In doing so, they function as natural refills of the soil, preventing it from being stripped and returning to an inert earth phase (Bouché 2014). It is known that the intense exploitation of agricultural soils produces the joint loss of organic carbon and earthworm populations (Pelosi et al. 2014).

4.1 Earthworms' Horizons in Grassland and Forest Ecosystems

Pedoclimatic conditions (temperature, humidity, acidity) regulate biological activities, especially for earthworms that are active most of the time in Spring and Autumn. Depending on the environment they form, there are thus different O and A horizons.

In a mesophilic environment (plains, hills, rainy tropical environments), the O horizon disappears quickly, the organic matter being swiftly decomposed by organisms. Moreover, the OH horizon is rare, and an earthworm biomacrostructured A horizon usually develops. The resulting humipedon ranges in the Mull system with anecic and endogeic earthworms as being the main ones responsible for forming the A layer. Humus forms, following a transition from mesophilic to aridic or colder conditions, may progressively be a Eumull (OL/maA), Mesomull (OL/(vOL)/maA; vOL being an old, whitish litter; brackets mean a discontinuous layer), Oligomull (OL/(OF)/meA) and Dysmull (OL/OF/meA) (Fig. 4).

Going from mesophilic (warm and humid climate) towards conditions less favourable to anecic and endogeic earthworms (drought, low temperature, acidity), we progressively encounter Eumull: OL, maA; Mesomull: OL, (vOL), maA; vOL is

Fig. 4 Pictures from two permanent grasslands (the two photos on the left) and beech forests in Switzerland (the two photos on the right). A sequence in a Mull system, from the best integration of organic matter to the lowest one: Eumull, Mesomull, Oligomull and Dysmull, respectively from left to right

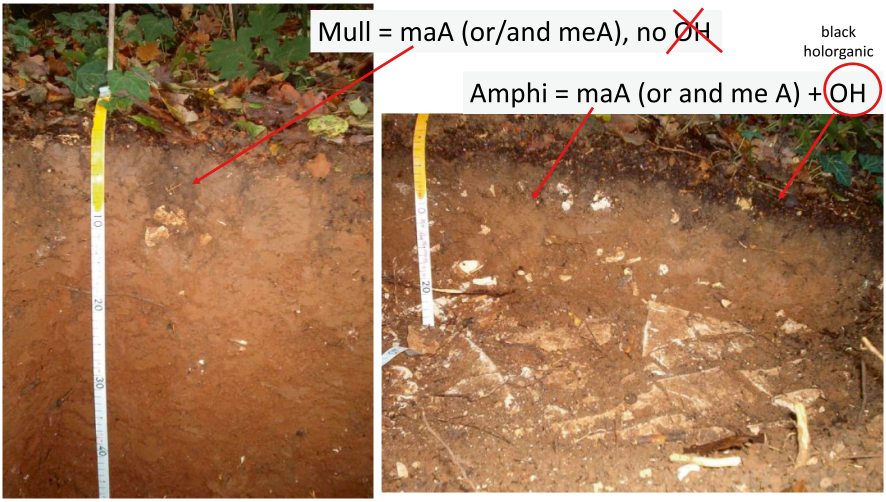

Fig. 5 Mull (left) and Amphi (right) on calcareous substrate. The OH horizon is present only in the Amphi humipedon. In the Amphi profile, earthworms are less active at the top, but can refuge in the cracks of the rock during dry periods

an old, whitish litter: brackets means that it is a discontinuous layer; Oligomull: OL, (OF), meA; Dysmull: OL, OF continuous, and meA.

If the climatic conditions become even more difficult, the genesis of humipedon knows a bifurcation:

1. On a basic substrate, the evolution goes towards an Amphi system (Fig. 5, right). Compared to a Mull (Fig. 5, left), anecic and endogeic earthworms are living deeper into the soil and cracks of carbonate rock. Progressively, less favourable conditions for anecic and endogeic earthworms lead from Leptoamphi (OH < 1 cm or discontinuous, maA) to Eumacroamphi (OH ≥ 1 cm, maA), Eumesoamphi (OH < 3 cm, meA) and finally to Eupachy amphi (OH ≥ 3 cm, meA).
2. On an acidic substrate, the evolution leads to a Moder system. An OH horizon appears above an A horizon no longer made by earthworms (Fig. 6, left). The sequence of horizons of a Moder system is as follows: OL, OF, OH and miA from arthropods or enchytraeids (presence of small lumps, mostly <1 mm) or non-zoogenic sgA or msA. Intergrades towards an Amphi system may show the presence of aggregates made by endogeic earthworms. A Mediterranean Amphi, with its typical maA horizon, is displayed (Fig. 6, right) as a comparison.

If the situation becomes even more difficult (high cold mountains, coniferous forests), the system moves towards Mor (acidic environment) or Tangel (limestone) systems:

1. On an acidic substrate, the sequence is OL, OF, OH and absence of A [the organic horizon lies directly on mineral horizons, generally an E horizon] (Fig. 7, left). A true Mor system (with a clear break between organic and mineral horizons,

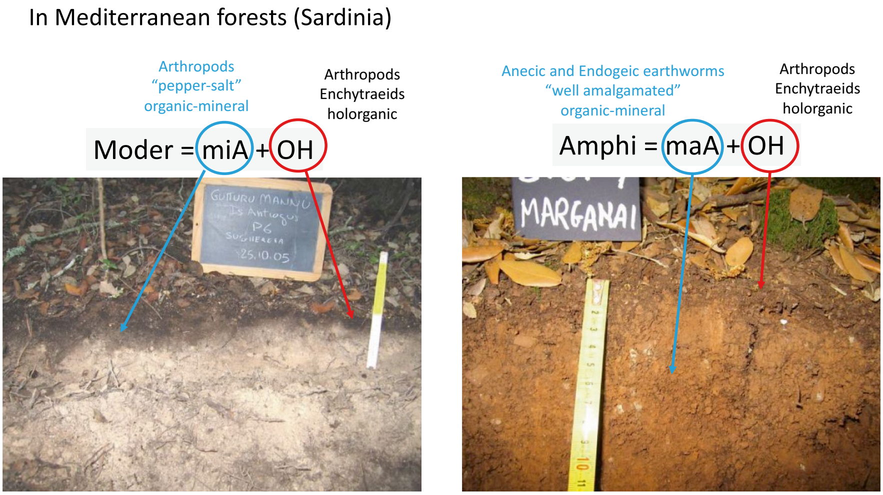

Fig. 6 Moder (left) and Amphi (right) in Mediterranean ecosystems. The Moder generates on an acidic substrate and the Amphi on a calcareous one. Under a black organic OH horizon, a thin (2–4 cm) grey arthropod' A horizon characterises the Moder system; under a brown OH horizon, a thick (>10 cm) red-brown earthworm' A horizon takes place in the Amphi system

Fig. 7 Mor (left) and Tangel (right) systems. The first lies on the acidic sand of Fontainebleau (Parisian region, France); consisting of a pack of dry moss and invaded by yellow fungal hyphae, this environment is not suitable for the development of earthworms. Although at 2000 m, on the slope facing east of the basin of Lake Misurina (Belluno, Alps, Italy), earthworms are instead numerous in the Tangel, which develops in the Swiss stone pine forest, and the water flows to the bottom and moistens a very organic soil, in the coldest and most unfavourable periods, earthworms are probably able to overwinter in deep shelters among the cracks in the limestone rock

with degradation of the litter due to fungi) is always devoid of any category of earthworms (or other pedofauna).

2. On a limestone or dolomitic rock, OL, OF, OH and sometimes a thin clay-humic A is in contact with the rock, due to endogeic earthworms' activity or by decarbonatation of the carbonatic rock. Superficial Tangel discovered at high altitudse in stone pine forests (>2000 m) were inhabited by numerous endogeic earthworms (Fig. 7, right).

4.2 Pioneer Ecosystems: Bryo and Rhizo Biological Connections

Biotic and abiotic factors condition the formation of the humipedon, as reviewed in Zanella et al. (2018a). At the same altitude, a southern exposure is hotter and drier than a northern one. The micromorphology plays also an important role and greatly influences the amount of water present in the soil. Earthworms generally love aerated soils that are well-fed with water. It is very easy to find earthworms in dried up anmoors, for example. Everyone knows that earthworms are plentiful in ripening manure. Anecic earthworms do not like high C/N litter. Many conifers produce such type of litter.

Earthworms are numerous in pioneer environments such as Bryo and Rhizo topsoils (Fig. 8). These humipedons exist as a single system in the high mountains, forming thin layers in contact with the rock; in forest and grasslands at a lower altitude, they may overlap other systems. They can also be found at low altitudes, in environments of initial soils, including anthropised ones such as the boundary walls, sidewalks edges and house roofs. A Bryo system typically develops under a carpet

Fig. 8 Top left and right: a Rhizo system at 2500 m in calcareous alpine mountains. The clod appears as it is just detached from the rock and pours out. In it, you can see the roots of the plants immersed in a brownish-grey mass (bryAOH) created by the young earthworm captured and set on the hand (do not worry, we released it immediately and put it back under the clod). Down left and right: a Bryo system, on Cambrian acid red schists. Beneath its surface living layer, this system typically shows an organic horizon of decomposing mosses and/or lichens (bryOF and thin bryOH), which rests on this more or less fragmented rock. In this fractured rock took refuge two epigeic earthworms

of mosses or lichens and shows organic horizons due the degradation of the low part of the thin-leaved steams of these plants; a Rhizo system takes place under a carpet of grasses and is characterised by the dense intertwining of secondary roots of these plants. In the high mountains, these systems form thin humipedons in contact with the rock; at lower altitudes, they lie son on other systems (often Moder systems for Bryo, Mull systems for Rhizo), in forest and grasslands as well. Endogeic earthworms are common in Bryo systems under mosses and/or lichens between the organic rests and the fragmented rock (that may be acidic or basic). Epigeic earthworms live in thin Rhizo systems at high altitude (2000–2500 m) in dolomitic and calcareous mountains. At a lower altitude, numerous endogeic and anecic earthworms are found in more or less humid Rhizo Mull systems all over the world, as explained in Domínguez et al. (2018).

4.3 Earthworms and Humus Forms in Alluvial Ecosystems

In near-natural floodplains, the high turnover of habitats and ecosystems due to the alluvial dynamics leads to rapid succession and community-assembly changes compared to other ecosystems (Corenblit et al. 2009; Milner and Tockner 2010). The discharge fluctuation and the frequency and intensity of flooding events cause erosion and/or deposition of sediments with a wide texture heterogeneity. The organic matter supply is also highly variable, either from autochthonous or allochthonous origin. Consequently, a wide diversity of soil layers and types occurs. In this context, the animal and plant communities follow topographic gradients where pedological changes occur from months to several hundred years (Petts and Amoros 1996; Gurnell 2007). The parental mineral material, as its granulometry (slab, blocks, stones,sand, etc.) and its nature (mineralogy, weathering resistance), play a crucial role in the formation and evolution of such humipedons. To improve the current classification, we propose to add new intergrades humipedons being the transition between Para, Terrestrial and Anthropogenic systems, called *Litho* (from Greek “λίθος”, rock), which decline in *Psammo* (“ψάμμος”, sand), *Peyro* (Πέτρος, stone, pebble) and *Stereo* (στερεός, hard). Discussion and thinking are still under investigation, and the systematic position will soon be clarified and published. In floodplains, most of the humipedons belong to these *Litho* intergrades, especially in the vicinity of the river bed where coarse sediments predominate (Fig. 9). In addition, Para systems such as Crusto and Bryo (Zanella et al. 2018d) and the current Mull, Moder and Amphi systems also coexist in floodplains. As for soils, terraces’ topography variability correlates to a gradient of humus systems from the river bed to the mature alluvial forest.

In this context, earthworms and plant roots are the primary ecosystem engineers that govern the formation of aggregates (Le Bayon et al. 2017; Schomburg et al. 2018b; Schomburg et al. 2018a, 2019a; Le Bayon et al. 2021a, b) .The earthworm communities’ distribution and composition depend on soil organic matter content, soil texture, altitude and flooding characteristics (Emmerling 1995; Salomé et al.

Fig. 9 Three soil types along an elevation gradient from the direct vicinity of the Sarine River to the mature forest situated onto a terrace at a distance of 150 m (FR, Grandvillard, Switzerland). Left: willow bushes, a Litho intergrade (Psammo Mull) and a Leptosol (Fluvic), with a J horizon (from French "jeune", young, where biogenic aggregates consist of organo-mineral aggregates, however less stable than those observed in an A layer; Baize and Girard 2009); middle: alder forest, an Eumull and a Calcaric Fluvisol; right: ash and beech mature forest, an Oligomull and a Fluvic Cambisol. Organic matter and sand particles are first juxtaposed (right), then the integration begins with the formation of aggregates (middle), and finally, resistant and stable aggregates are formed (right). The formation of aggregates and the integration of the organic matter progressively increase under the influence of earthworms. The dominant species of earthworms in the willow bushes is *L. rubellus*; in the alder forests, *O. tyrtaeum*, *A. rosea, A. caliginosa* and *L. terrestris*; and in the beech mature forest, *L. terrestris*, *A. longa*, *A. nocturna*, *O. cyaneum* and *O. tyrtaeum*

2011). Habitat research projects on earthworm communities in floodplains are few. Most of them were conducted at the hill level and focused on flooded meadows in northern Germany (Plum and Filser 2005), grasslands in river valleys in Estonia (Ivask et al. 2007) or short grass and herbaceous vegetation in the Netherlands (Zorn et al. 2008). In 2013, Le Bayon et al. synthesised several studies on earthworm communities in floodplains along an altitudinal gradient from the hill (350 m) to the alpine level (2300 m). Thus, overall in several Swiss near-natural floodplains, Guenat et al. (1999), Bullinger-Weber et al. (2007, 2012) and Salomé et al. (2011) found 27 species and subspecies from subalpine to hill levels (Table 2). This record corresponds to two-thirds of all inventoried earthworm species and subspecies in Switzerland, confirming that floodplains are among the most diverse terrestrial ecosystems. The earthworm distribution is widely heterogeneous within the same floodplain (Bullinger-Weber et al. 2007) and in the same vegetation unit (Bullinger-Weber et al. 2012). The texture and the organic matter are the main drivers of the presence and activity of earthworms. Epigeics are often associated with a coarse sandy texture in contrast to anecics that prefer deep soils and mature forest stages providing the highest carbon content and the finest soil texture (Salomé et al. 2011).

Table 2 Species and subspecies of earthworms recovered in near-natural floodplains in Switzerland at several altitudinal levels. For an update of genus and species names, see the world database DriloBASE on http://taxo.drilobase.org

Epigeic
Bimastos eiseni (Levinsen, 1884)
Dendrobaena octaedra (Savigny, 1826)
Dendrobaena pygmaea cognetti (Michaelsen, 1903)
Dendrobaena pygmaea pygmaea (Savigny, 1826)
Dendrodrilus rubidus rubidus (Savigny, 1826)
Dendrodrilus subrubicundus (Eisen, 1874)
Eiseniella tetraedra tetraedra (Savigny, 1826)
Eisenia andrei (Bouché, 1972)
Lumbricus castaneus (Savigny, 1826)
Lumbricus meliboeus (Rosa, 1884)
Lumbricus rubellus (Hoffmeister, 1843)
Octodrilus argoviensis (Bretscher, 1899)

Anecic
Aporrectodea caliginosa nocturna (Evans, 1946)
Aporrectodea giardi giardi (Ribaucourt, 1901)
Aporrectodea longa longa (Ude, 1885)
Aporrectodea longa ripicola (Bouché, 1972)
Aporrectodea longa ripicola viridis (Bouché, 1972)
Lumbricus terrestris (Linnaeus, 1758)

Endogeic
Allolobophora chlorotica chlorotica (Savigny, 1826)
Aporrectodea caliginosa alternitosa (Bouché 1972)
Aporrectodea caliginosa caliginosa (Savigny, 1826)
Aporrectodea handlirschi handlirschi (Rosa, 1905)
Aporrectodea icterica icterica (Savigny, 1826)
Aporrectodea rosea rosea (Savigny, 1826)
Octolasion cyaneum (Savigny, 1826)
Octolasion tyrtaeum lacteum (Oerley, 1885)
Octolasion tyrtaeum tyrtaeum (Savigny, 1826)

From Le Bayon et al. (2013)

This enormous diversity and vast abundance of earthworms in floodplains provide ideal conditions to study the very first steps of soil pedogenesis, especially aggregate formation. This is particularly the case in calcareous conditions where the presence of calcium ions enhances the binding of mineral particles to organic matter to form the clay-humus complex. At the hill and the mountain level, near the Thur

River and the Sarine River, we studied the implication of vegetation and earthworms on the soil structure in the context of how soils may prevent flood events. As a result, the more the distance and the elevation from the river bed occur, the more the earthworm activity supplants those of roots, but both of them are still involved in the structuring processes (Bullinger-Weber et al. 2007, 2012; Salomé et al. 2011; Schomburg et al. 2018a). In the presence of coarse sand, plant roots dominate the aggregate building. Still, when the texture becomes finer and in width layers of silt, anecics and endogeics activities contribute primarily to creating aggregates and burrows (Schomburg et al. 2018b, 2019a, b).

At the mountain level near Grandvillard (altitude: 750 m a.s.l., FR, Switzerland), earthworms are active for more than 8 months per year from March to December. The pedoclimatic conditions allow maintain their bioturbation activities: the tree canopy, leaves on the soil surface and the constant humidity in the soil create an ideal habitat for earthworms, which may explain the high diversity and abundance encountered (Fig. 10).

These optimal conditions favour the rapid integration of the organic matter and the formation of aggregates. Approximately every 2 years, we go into the field with students at the same place to monitor the evolution of vegetation, humus forms and soils. In one of our study plots, a permanent soil profile is described as a Calcaric Skeletic Pantofluvic Fluvisol (Geoabruptic) according to the IUSS Working Group

Fig. 10 Top of the figure, from left to right, several earthworms recovered in floodplains and belonging to different ecological categories: *L. rubellus* (epigeic), *A. chlorotica* (endogeic), *A. caliginosa* (endogeic), *O. cyaneum* (endogeic) and *A. longa* (anecic). Bottom of the figure: earthworm surface casts that may serve as nutrient pools for plants, here a young beech sprout

WRB (IUSS Working Group WRB 2022), and the humus form is an Eumull (Zanella et al. 2018g) . The A layer mainly comprises macroaggregates (maA) formed by earthworms and plant roots. In 2015, a flood occurred, and a sandy deposition of several centimetres was observed on the soil surface (Fig. 11, top left). After only a few days, earthworms built up surface casts. In 2016, no trace of the flood was visible anymore, and the thickness of the A has increased by at least 1 cm. In 2020, the maA showed a high density of plant roots highlighting the richness of nutrients and the water supply in this layer due to the intensive earthworm bioturbation activities.

The case of the Sarine River highlights how fast the formation of aggregates can be. An organo-mineral layer may be formed in only several years, and the evolution from sandy and silty raw deposits to soil macroaggregates occurs as one moves away from the influence of the river. The very first steps of aggregates' production in such a context are still under research. The X-ray micro-computed tomography helped us to show that the volume ratio of mineral grains within the aggregates is significantly different according to earthworm species (Le Bayon et al. 2021a, b). The organic matter can also be discriminated, and we showed in controlled mesocosms that plant roots could develop in sandy layers. In contrast, earthworms preferentially selected the organic matter and the silt layers (Schomburg et al. 2019a).

Fig. 11 The temporal evolution (2015–2020) of the humipedon is influenced by earthworms and deposits from the Sarine River (FR, Grandvillard, Switzerland). The sediment deposition did not alter the earthworm activity (see the surface cast and the presence of *L. rubellus*). The humus form is an Eumull following the key of Zanella et al. (2018a, b, c, d, e, f, g). Horizons sequence is [nOL-vOL]/maAca/Dca/IIMca-Dca/IIDca according to Baize and Girard (2009). The soil is a FLUVIOSOL TYPIQUE carbonaté, leptique, polylithique, according to the classification of Baize and Girard (2009), and a Calcaric Skeletic Pantofluvic Fluvisol (Geoabruptic), according to the IUSS Working Group WRB (2022)

Fig. 12 From left to right, progressive colonisation by earthworms of the organo-mineral A horizon of a stream bank (Grandvillard, FR, Switzerland). On the left, plant roots dominate in the formation of organo-mineral aggregates close to the river bed (J horizon, see Fig. 9, left); on the right, an A horizon very rich in earthworm aggregates

In floodplains, there is obviously a step between sediment and stable biogenic aggregates. After discussions and debates with soil and humus forms specialists, the J horizon was created in the French classification (Baize and Girard 2009) to describe the initial Fluviosols better (Fluvisols, according to the IUSS Group 2022). In a J horizon (from French “jeune”, young), biogenic aggregates are less stable than those observed in an A horizon (Fig. 9). Consequently, we can consider the J horizon as a functional soil layer that usually evolves towards a zoogenic (earthworms) A layer over time (Fig. 12).

This is typically the case we observed at the Sarine floodplain with the succession of soils, from the Leptosol (Fluvic) near the river to the Fluvic Cambisol in the mature and climacic forest. As these processes occur in the humipedon, the ultimate frontier would be to integrate this J layer in the classification key of humus forms, using a specific codification for the aggregates (jA in Psammo forms?). This would be very useful to describe better the transition between Prahumus systems and Terrestrial ones in environments containing vast amounts of sand and silt, as in floodplains. Ellen Desie (2020) encountered the same issue during her fieldwork in Belgium and the Netherlands. She found an accumulation of O layers (OL/OF/OH) directly deposited on sandy mineral layers and highlighted the need for intergrades.

In less active alluvial ecosystems, earthworms are implied in the formation of the humipedon, but they can be restricted to specific areas due to the permanent presence of water. Near the lake of Neuchâtel (St Blaise, altitude 440 m a.s.l., NE, Switzerland), a transect from the forest to the lake showed the influence of the water table on the vegetation and earthworm communities (Fig. 13). In the alluvial forest, all humus forms belong to the Mull system, most of them varying from Eumull to Oligomull. The biodiversity of earthworms is noticeable, with mainly endogeics and *L. terrestris* as the dominant anecic species. Going towards the lake, the

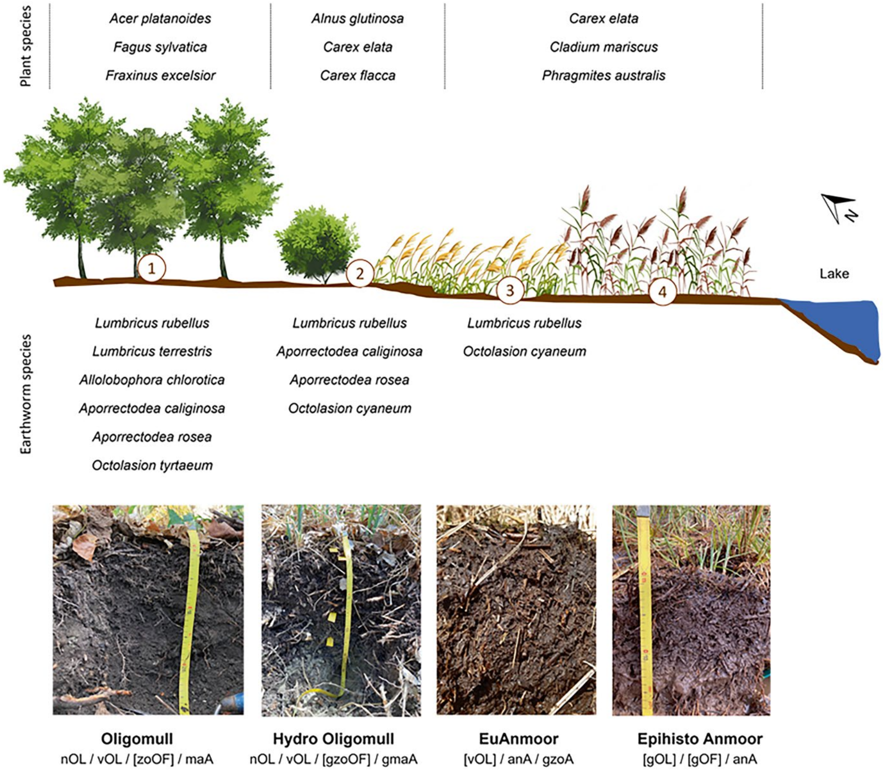

Fig. 13 Transect from the forest to the lake of Neuchâtel showing the humus forms and the horizons sequences, the main earthworm species and the dominant vegetation (St Blaise, NE, Switzerland). The humus forms indicate the progressive influence of the water (total distance: 60 m). The transect was made in the Spring of 2022. Photos credit: Maeder, Bovet, Bulliard and Guerra; scheme: Le Bayon and Semeraro

influence of water begins, the presence of *Carex flacca* being an indication. Earthworms are still numerous and active, and their casts can be easily seen in the A layer of the Hydromull. The increasing effect of water limits the presence and activity of earthworms in the third sampling point: *L. rubellus* (a pioneer species) and *O. cyaneum* (known for its affinity with humid soils) are active when the water level gets down due to the fluctuations of the lake, especially in drier periods of the year. Biogenic aggregates compose the A horizon and are especially observable in May and June. In the vicinity of the lake, no earthworms were observed because of the permanent presence of water. Such transects are pedagogic to students (and researchers!) to highlight how necessary humus forms are for explaining the complex relationships between soils and vegetation.

5 Earthworm Functional Domains as Extended Phenotypes: Eco-evolutionary Aspects

Earthworms, as soil engineers, transform the soil within their functional domain (Lavelle 2000, 2002), also called drilosphere (Brown et al. 2000) or in a few instances vermisphere (Hamilton and Dindal 1983). They create galleries (Amossé et al. 2015), incorporate organic matter to mineral particles (Stout and Goh 1980) and modify the composition of microbial (Dempsey et al. 2013), animal (Migge-Kleian et al. 2006) and plant populations (Hale et al. 2006), favouring or disfavouring species in the space of soil where they live as multispecies assemblages in spite of intense competition (Decaëns et al. 2008). As such they can be considered as agents of the building of ecosystems and communities (Ponge 2021), ensuring multiple ecosystem services far beyond their direct interactions with plants, animals and microbes (Liu et al. 2019). Here we suggest that the concept of extended composite phenotypes (Phillips 2009), covering the environmental properties durably modified by an organism, could be put in synonymy with the functional domain. This has strong consequences for eco-evolutionary issues (Bailey 2012). Considering the functional domain of an earthworm species as an extended composite phenotype means it has evolved and may continue to evolve with it.

This is reminiscent of the concept of niche construction (Odling-Smee et al. 2013), meaning that the niche durably created by an organism (in fact an ecosystem engineer) may, even after its death, be considered as a driving force of evolution. Like coral reefs of the Jurassic Period, the variety of which created various calcareous substrates influencing the composition and spatial distribution of present-day plant communities (Ricci et al. 2018), earthworm activities modify soil properties to an extent that survive their collapse, and even take part to global climate changes. A good example is the case of Mollisols (highly fertile soils with a deep homogeneous mineral-organic horizon), which accompanied the rise of Poaceae in the US Great Plains during the Neogene Period (Retallack 1997) and were thought to be responsible for further global cooling (Retallack 2013). According to what we can deduct from the micromorphology of mollic epipedons (Pawluk and Bal 2015), Mollisols (also called Chernozems) result from the mixing activity of soil engineers, mainly earthworms, although the presence in North America of digging and burying earthworm species (mostly lumbricids) before the first European settlements is still a matter of conjecture (Hendrix et al. 2008), contrary to the European framework (Dreibrodt et al. 2022).

The still postulated (because of the absence of fossils) coevolution of grasses with earthworms is mirrored in the present-day rich and diversified earthworm populations prevailing in permanent grasslands (Ponge et al. 2013). The well-known association of earthworms with the Mull humus system and arthropods with the Moder humus systems and the paucity of fauna in the Mor humus systems led Ponge (2003) to hypothesise that these three main terrestrial humus systems were linked by evolutionary relationships, from Mor (before the rise of arthropods) to Moder (before the rise of terrestrial annelids) and then to Mull. Much more research is needed on the role played by earthworms in the evolution of terrestrial biomes, like this has been fruitfully done in the coevolution of hosts with their parasites (May and Anderson 1990) and plants with their pollinators (Kiester et al. 1984). Here, the postulated processes resort to diffuse coevolution (Janzen 1980), including as a phenotypic set of traits the environment modified by earthworms in addition to signalling strategies (Puga-Freitas and Blouin 2015).

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