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Original article

Soil invertebrates and ecosystem services

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Abstract

Invertebrates play significant, but largely ignored, roles in the delivery of ecosystem services by soils at plot and landscape scales. They participate actively in the interactions that develop in soil among physical, chemical and biological processes. We show that soils have all the attributes of self-organized systems as proposed by Perry (Trends Ecol. Evol. 10 (1995) 241) and detail the scales at which invertebrates operate and the different kinds of ecosystem engineering that they develop. This comprehensive analysis of invertebrate activities shows that they may be the best possible indicators of soil quality. They should also be considered as a resource that needs to be properly managed to enhance ecosystem services provided by agro-ecosystems.

Keywords: Soil invertebrates; Ecosystem engineers; Self-organized systems; Bioindicators

1. Introduction

Soils are essential sources of a wide diversity of ecosystem services defined as the goods and ecosystem functions that provide benefit to human populations [30,86]. They support most agro-sylvo-pastoral production systems (production services) through the beneficial services that they mediate: soil formation, nutrient cycling and primary production. Soils also participate in the provision of regulation services (climate regulation by controlling greenhouse gas fluxes and C sequestration; flood control, detoxification, protection of plants against pests) through their influences on organic matter dynamics and the wide-ranging effects on soil physical properties. Soils finally contribute to cultural services although to a rather minor degree given the surprisingly widespread lack of interest of many societies in the sustainable use of this key resource. These services are provided by a large range of organisms whose effects are still relatively poorly explored, especially for the smaller body-sized taxonomic groups ([19,38], this volume).

Soil invertebrates are enormously diverse. According to recent estimations, soil animals may represent as much as 23% of the total diversity of living organisms that has been described to date [38]. Their sizes range across three orders of magnitude. The smallest Nematodes and Protozoa (protists) of the microfauna less than 200 µm on average live in the water-filled porosity. Microarthropods, Enchytraeidae and the

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many groups of the mesofauna (0.2–2 mm) live in the air filled soil porosity. The largest arthropods, Mollusca, Annelida and Crustacea comprise the macrofauna that lives in the surface litter or in nests and burrows that they create in the soil [70]. In some places, vertebrates of the megafauna may become conspicuous elements of the soil fauna. This is the case for example for small rodents in deserts, pocket gophers in prairie ecosystems, moles and wild pigs in temperate grasslands and forests and other still poorly studied soil vertebrates in a large number of ecosystems [85,98].

In some ecosystems, the local diversity of soil fauna may be enormous: far above that of groups of aboveground plants or animals. For example, Schaefer and Schauermann [103] found 1000 invertebrate species in a temperate climate forest in Germany. In most sites of tropical or temperate areas of the world, a standard sampling of soil macrofauna (= invertebrates visible at the naked eye) in an area limited to a watershed of a few km^2 may yield 100–400 species [6,84,90]. This biodiversity is highly sensitive to any disturbance since the soil environment is their habitat and the source of all the resources they need ([11,25,56,58], this volume).

In this paper we first present a general conceptual overview of biotic interactions in soils to explain the intimate links among invertebrates and other soil organisms and their importance for the continued functioning of the soil environment. The concept of self organization is used to describe these links within and across scales and emphasize the role of soil invertebrates in this apparently complex web of interactions. We then present a synthetic review of the ecosystem services that are affected by invertebrate activities and broadly explain the mechanisms involved. We finally address the practical consequences of these findings for sustainable management of soils and in monitoring soil quality.

2. Evidence for self organization in soils

Soil ecosystem services are emergent properties—at the plot or landscape scale—resulting from the wide range of processes operating at much smaller scales, in which invertebrates are involved. These processes are mediated by biological interaction systems that develop at a limited number of discrete scales [73]. These interaction systems have the properties of self organized systems *strictly following the definitions* given by Kauffman [66] and Perry [95].

2.1. They are characterized by order where disorder would otherwise have been predicted

The organization of soil horizons, the distribution of pores among size classes and their spatial arrangement, the structure of invertebrate and microbial communities are among the many examples of structures and “order” in soils.

2.2. Structures and processes mutually reinforce one another

This is the case, for example, for the maintenance of structural soil porosity by invertebrates and roots that enhances their own activities, with positive feedback effects on the maintenance of suitable conditions of porosity to sustain biological activities.

2.3. The system maintains order within boundaries through internal interactions

Specific observations indeed tend to show that the functional domains of soil ecosystem engineers (that is, the volume of soil that is shaped by their activities [71]) have recognizable limits that can be defined, for example, from examination of the Near Infra Red spectral signatures of macro-aggregates [55]. At a large scale, populations of earthworms, termites and roots often occur in patches within which soils have notably specific characteristics and functions [33,79,99]. In spite of the current difficulty in rigorously classifying the types of interactions developed in these systems, they seem to be largely based on mutualism and/or non trophic relationships akin to ecosystem engineering [63,69].

2.4. Far from equilibrium, these systems are in a metastable equilibrium

Experiments by Blanchart et al. [9] and Barros et al. [6] show that soil physical function can be profoundly modified where disturbance affects the activities of invertebrates. Invasive species, for example, may exaggeratedly enhance one function (e.g. by producing large compact structures or mineralizing organic matter accumulated in the humus-rich layers) in such a way that the system no longer sustains its dynamic equilibrium [5, 80,81]. When eliminated by aggressive land management practices, the environmental conditions that they maintained in their sphere of influence may change drastically; one example may be the disappearance of control exerted by plant parasitic nematode communities on their most aggressive species when nematicides are applied ultimately leaving the most aggressive species with no competitors [72].

2.5. Finally, natural systems can be seen as comprising a hierarchy of self-organizing systems embedded within one another, stabilized by cooperative relationships and focused at spatial and temporal boundaries

Soil function is thus envisaged as a hierarchy of gearing effects that link small-scale, fast-developing processes to progressively larger scale and slower processes. This analogy to mechanical devices is supported by the observation of discrete scales for interactions in soils. It tends to invalidate models that would present soil function as complex webs of interactions with stochastic organization.

3. Discrete scales in soil function

Five relevant scales have been identified in soil function, and invertebrates are major actors at three of them. At each scale, interactions among organisms of one or several groups develop within the boundaries of such structures as bio films, micro aggregates or the functional domains of invertebrate ecosystem engineers [73].

3.1. Scale 1: microbial biofilms

The smallest habitat in soils is represented by assemblages of mineral and organic particles approximately 20 µm in size, called aggregates (Fig. 1, level 1).

Most chemical transformations that sustain organic matter cycling and soil chemical fertility are operated by microorganisms in microsites and biofilms. Microorganisms have very limited abilities to move and the rates of chemical transformations within soils are thus more probably determined by the occurrence of mechanisms that bring microorganisms into contact with organic substrates than by the amount of available substrates themselves. This paradigm known as the ‘sleeping beauty paradox’ is supported by a large set of experiments and observations [74].

3.2. Scale 2: micro-foodwebs

Microorganisms may live inside (e.g. in micropores filled with water) or outside soil micro aggregates, which in turn determines their access to resources, exposure to predators [54] and inclusion in micro-foodwebs (level 2; [73]). Different strategies among micro organisms may lead them to renew rapidly their

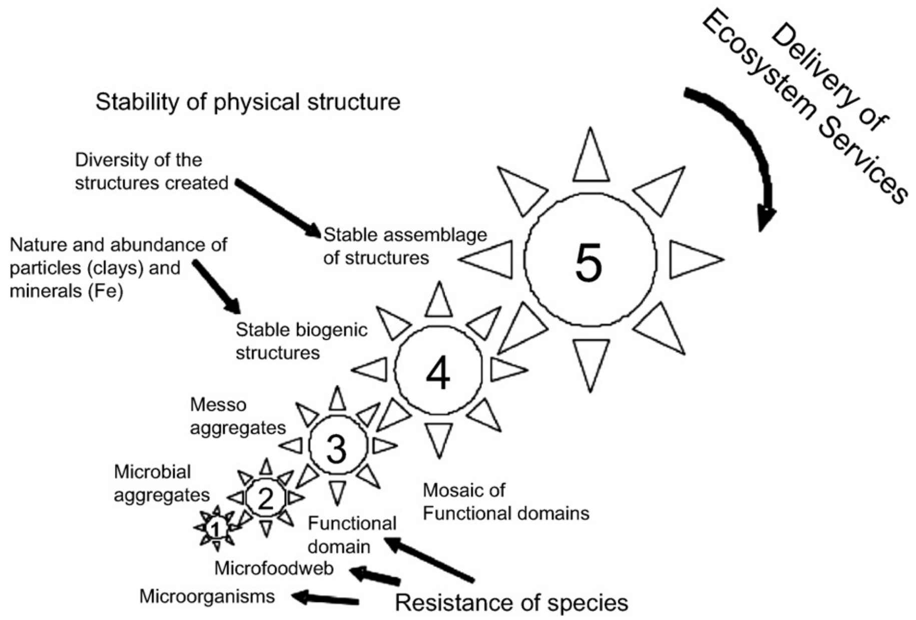

Fig. 1. Self organizing systems in soils at different scales from microbial biofilms—where most microbial transformations occur—to the landscape, where ecosystem services are delivered. The stability of delivery of ecosystem services at scales > 5 is supported by the resistance of species to disturbances and/or the stability of physical structures and other effects of invertebrates that may extend their effects when they are temporarily absent (modified from [73]).

populations in the "outside environment", a relatively rich medium trophically where predation and environmental instability exert constant pressure on their populations. A contrasting strategy is to avoid predation by soil microfauna as much as possible by living within micropores and therefore inaccessible to predators although this limits the trophic resources available [97].

3.3. Scale 3: functional domains of ecosystem engineers [71]

At the scale of centimeters to decimeters, ecosystem engineers (a functional group that also includes plant roots) and abiotic factors determine the architecture of soils through the accumulation of aggregates and pores of different sizes. These spheres of influence (= functional domains) (level 3) extend horizontally over areas ranging from decimeters (e.g. the rhizosphere of a grass tussock) to 20–30 m (drilosphere of a given earthworm species) or more, and from a few centimeters up to a few meters in depth, depending on the organism [35,61,99,100].

3.4. Scale 4: mosaics of functional domains at plot scale

Functional domains are distributed in patches that may have discrete or nested distributions and form together a mosaic of patches (level 4). Such a mosaic has been described, for example, by Rossi [99] who observed the distributions of two groups of earthworms with contrasting effects on soils. The 'compacting' group stimulates soil macro aggregation through the accumulation of large (ca. 1 cm) compact casts and reduces soil macroporosity leading to high soil bulk density values [9]. The other 'decompacting' group has the opposite effect, breaking large aggregates into smaller pieces leading to a decrease in bulk density and consequently an increased density of fine roots that find a more suitable environment in these patches. More complex effects incorporating the joint activities of termites, ants, earthworms and plant root spatial domains probably exist, although their structures and the relationships between their different components have seldom been addressed.

3.5. Scale 5: landscape/watershed

At the landscape level, different ecosystems coexist in a mosaic with clearly defined patterns (level 5). The pattern observed in the mosaic may result from natural variations in the environment and/or human land management. Soil formation processes, for example, are very sensitive to topographical changes and lead to the formation of catenas of different but related soils from upper to lower lying areas. Significant differences in such soils often result in different vegetation types and the formation of a mosaic of ecosystems [102]. In savannah regions of Western Africa, plateaus that have thick soils and a gravel horizon are often covered with open woodland. Slopes have shallower soils and fewer trees while low-lying areas have fine-textured soils resulting from the transport and accumulation of fine elements from the upper lying areas. The latter are also moister environments and the vegetation may comprise grasses and other herbaceous components. In riparian zones of river catchments, gallery forests may utilize the constant water available from near-surface water tables [17].

Soil formation at regional scales is one of the ecosystem services that integrate processes over all scales; it extends over long periods of time and is largely determined by climatic conditions and the nature of the parent material. In temperate areas, for example, it may take 20,000 years to transform alumino-silicate parent material into a 1 m thick soil, but it takes half that time to develop carbonate rich material [26]. Most soils in Northern Europe and America that formed after the retreat of glaciers 20,000 years ago still have the characteristics of relatively young soils, as compared to soils from Australia and some parts of Africa that began forming millions of years ago [46].

4. Invertebrates, the engineers of self organized systems in soils

Soil invertebrates are key mediators of soil function for the diversity of ecosystem engineering processes in which they partake. The comminution and incorporation of litter into soil, the building and maintenance of structural porosity and aggregation in soils through burrowing, casting and nesting activities, the control of microbial communities and activities, plant protection against some pests and diseases, acceleration of plant successions are among the many effects they have on other organisms through their activities [7,37,65,72]. In so doing, they develop multiple interactions with other organisms, at different scales and across the whole range of chemical, physical and biological processes that sustain the provision of soil ecosystem services. These interactions generally generate positive feedback effects on their own fitness; this is particularly the case for "extended phenotype" engineers that modify the environment with positive effects for themselves as opposed to "accidental" engineers that do not seem to get positive feedback from their mechanical effects on soil [65].

Ecosystem engineers of any kind have the potential to enhance ecosystem function in soil, probably more than in any other ecological medium. This is due to the unique constraints faced by life in the subterranean environment [70]. Compaction tends to severely limit movement, aeration and water storage unless porosity is created by powerful physical or biological processes. Furthermore, the general quality of feeding resources and/or access to nutrients is low, limiting their assimilation drastically, unless complex processes, mainly based on multispecies biological interactions, allow the constraint to be lifted.

For these reasons, the occurrence and activity of invertebrates in soils must firstly be interpreted as clear evidence of important processes at work; the diversity and complexity of life forms observed in soils are testimonies of millions of years of co-evolutionary processes that need to be preserved even though we barely understand even a very small fraction of them.

Invertebrates participate in the regulation of ecosystem processes and the delivery of ecosystem services at the usually large scale at which they are perceived, from parcels allocated to one type of land use to landscapes or watersheds (Table 1). These effects remain mostly unseen since they generally operate two or three scales below that at which services are delivered. For example, most physical activities of soil invertebrates consist in bioturbating soils at the scale of their functional domains, i.e. a few cm^3 or less for most individuals. The accumulation of these effects over time and space, however, creates a continuous structure that provides soils with emergent properties at scales 4 (land use unit in a landscape mosaic) and 5 (local and regional landscapes). An example is provided by the biological formation of stable soil aggregates, which promotes the sequestration of C at the scale of landscape or entire biomes (see review by Jiménez and Lal [60]).

Jones et al. [63] called ecosystem engineering any physical transformation in the environment that modifies the resources for other organisms. Soils host a number of such organisms among which earthworms, termites and ants are the most commonly cited examples [2,57,62,65,73,85]. One feature common to all these organisms is the disproportionate magnitude of their

Table 1
Contributions of soil invertebrates to the provision of ecosystem goods and services by soils

Service types	Goods/services	Ecosystem process	Soil invertebrate contribution	Indicator of faunal contribution
Production	Water supply	Infiltration and storage of water in soil pore systems	Building and maintenance of stable porosity through bioturbation and burrowing	Proportion and arrangement of biogenic structures in soil Water-holding capacity
Support	Nutrient cycling	Decomposition Humification Regulation of nutrient losses (leaching denitrification)	Comminution, selection/ activation of microbial activities	Litterbag decomposition assessments Profile of soil organic matter Measure of Organic matter content in the different soil fractions
	Soil formation	Pedogenesis	Bioturbation Surface deposition Particle selection	DNA and NIRS analyses in biogenic structures
	Primary production	Stimulation of symbiotic activity in soil	Selective microbial enhancement in functional domains	Soil and humus morphology
		Indirect production in the soil of molecules recognized by plants as hormones	Control of pests through biological interactions; enhanced capacity of plant response	Soil DNA assessments
		Protection against pests and diseases communities		Soil faunal communities Indices of plant vigor
Regulation	Flood and erosion control	Regulation of water runoff	Creation of surface roughness by biogenic structures	Production of biogenic structures
		Infiltration and storage of water in soil	Building and maintenance of stable porosity through bioturbation and burrowing	Soil and humus morphology
	Climate regulation	Production/consumption of greenhouse gases	Organic matter sequestration instable biogenic macro-aggregates	Stable biogenic macro-aggregates
		Organic matter storage in soil and biomass	Enhanced formation of resistant humic compounds	

effects in terms of their biomasses and the way that their activity modulates soil resource accessibility for other soil organisms. Examples also include the modification of microbial and soil invertebrate communities by earthworm activities at different scales [34,78], or the impact of ants or earthworms on soil seed banks and seedling recruitment [32,37,87].

Based on the same principle, we can define chemical and biological engineers in terms of their possibly disproportionate effects on the fitness of other organisms through the emission of specific chemical compounds (e.g. allelopathy in plants or the production of phytohormones) or selection of species in communities (e.g. selection of microbial communities in biogenic structures of termites or earthworms [43,74].

4.1. Physical engineering

Physical engineering is thus the ability of organisms to alter the environments of other organism through their mechanical activities. In soils, this effect of invertebrates is now largely acknowledged and many examples have been proposed across all scales. At scale 1, the effect of microbial biofilms in stimulating soil microaggregation and creating microtubules by fungal hyphae are examples of micro engineering carried out by microorganisms [118]. At larger scales, fungal hyphae can create rather dense networks that link soil particles into rather fragile macro-aggregates [96].

Effects at scale 2 have been widely described in the literature. Significant effects of such small invertebrates as Enchytraeidae on physical properties have been frequently observed in soils. Invertebrates of the soil mesofauna (on average 0.2–2 mm in size) are well known for their physical effects on humic material: the Ah horizons of moder humus types are comprised of accumulated faecal pellets and the size and diversity of species that participate in this process give this material its specific microgranular characteristics [59].

The effects of the three major groups of soil ecosystem engineers (scale 3)—ants, termites and earthworms—have been widely described and documented [1,70].

Many experiments have shown how fast a soil that had been previously dispersed into units <2 mm can be enriched in large aggregates by endogenic earthworms [9,47]. In tropical soils, this effect can be particularly intense and the whole soil of the upper 10 cm may be bioturbated within a few years. The distribution of communities among different functional groups (for example 'compacting' vs. "decompacting") therefore becomes critical to soil functioning. In Amazonian oxisols near Manaus (Brazil), diverse communities of soil engineers in natural forests produce a large diversity of biogenic structures (voids, pores, fabrics and aggregates of all sizes) which provide these soils with highly favorable hydraulic properties. When deforested, these soils tend to lose the greater part of this diversity and invasive species may even severely impair their physical function by producing excessive amounts of a single type of structure [5,6,25].

Effects of soil invertebrate engineers have been sometimes described at scale 5 (landscape). In sloping environments in West Africa [92], earthworms have been report to trigger soil creep through the continuous erosion of surface casts and down-slope transport of their materials. Jones et al. [64] describe rather sophisticated contributions of Isopods to the regulation of physical (soil erosion) and chemical (soil desalinization) soil processes at the scale of watersheds in the southern Negev Desert Highlands, Israel. The roles of termites and ants in shaping geomorphology and soil profiles at landscape levels have been well documented [2,116].

4.2. Chemical engineering

Some organisms may trigger effects that are disproportionate to their size and activity by producing chemical substances with hormone-like or other physiological effects.

An example of this effect is the release of organic acids in faecal pellets of invertebrates that live in temperate forest litters. Soil invertebrates produce two kinds of feces within which contrasting reactions occur. The casts of anecic earthworms (those that ingest a mixture of soil and surface litter and inhabit galleries) are macro-aggregates of 2.5–10 mm in diameter and form 'macro aggregate closed systems' in which intense microbial activity favors a rapid flocculation of soluble organic compounds that have no effect on mineral weathering.

Arthropods that live in the surface litter and holorganic horizons produce small (<100 μm) and unstable faecal pellets. Microbial activity is generally low and these aggregates are subject to intense leaching. The aggressive organic compounds released promote intense weathering and the loss of clay minerals [8].

Production of hormone-like and energy-rich substances such as root exudates, earthworm and termite mucus and saliva has been indicated in a number of publications [76]. Research on this topic is still in its infancy and the general hypothesis is that the effects observed are often due to an intermediate effect on microorganisms that, when activated, further release plant-growth-promoting, allelopathic and other substances. Intestinal mucus plays a significant role in the selection and stimulation of microbial activities in the earthworm guts [4] and the effects of earthworm cutaneous mucus on microbial selection have also been demonstrated [74]. Termite saliva has comparable effects and large numbers of similar cases are expected to be discovered in future research.

4.3. Biological engineering

We propose to group under this term the consequences of changes in communities due to invertebrate activities. Interactions of below ground communities with plants and other above-ground communities often result in significant modifications to successional dynamics. This may sometimes be a consequence of a general effect of invertebrates on nutrient cycling: Bernier and Ponge [7] thus described how the intense activity of earthworms in the senescent and early phases of natural succession in alpine spruce forests boosts the growth of tree seedlings and prevents the forest from being replaced by *Myrtilus* shrub communities.

De Deyn et al. [39] also showed how plant parasitic Nematodes may accelerate plant successions by successively weakening plant populations that have arrived at a transitient dominance situation, and facilitate their replacement by plant of another species still not attacked by parasites.

The effects of earthworms and ants on selective seed dispersal and growth stimulation are other still little explored processes whereby biological engineering mediated by soil invertebrates may ultimately affect the provision of ecosystem goods and services. Earthworms for example may ingest large amounts of viable seeds, which are later deposited in their casts within the soil profile or at its surface [37,82,109]. In so doing, they generate vertical seed movements and may alter the composition of the soil seed bank [117]. Surface casts may also constitute a regeneration niche (sensu Grubb [50]) for some plant species, as their seeds may have a greater chance to germinate than those of the soil seed bank [37].

5. Invertebrates as promoters and indicators of the provision of ecosystem services

The engineering activities developed by invertebrates contribute significantly to the production and delivery of soil ecosystem services in many ways (Table 1).

5.1. Water supply

The contribution of soil invertebrates to water storage and detoxification is rarely if at all acknowledged. However, their participation in intermediate, small-scale processes that support this service are well known. Invertebrates tend to decrease surface runoff by their effects on surface roughness [24,77] and water infiltration and they create structural porosity in soils [70]. The diversity of pore shapes and sizes may allow soils to store water at a wide range of potentials. These effects have been reviewed and synthesized in major textbooks and articles but still no global figure on amounts of water infiltrated and stored in soils as a consequence of invertebrate activity has ever been proposed. Indicators of these activities are available [111, 112] and there is no real obstacle to comprehensive assessments of their contributions at large scales.

5.2. Nutrient cycling

The effects of invertebrates in support services have been extensively described although mainly at their own scales. Their contributions to nutrient cycling have been extensively studied and modeled: their principal contribution seems to result from the comminution of litter and the selective activation of microbial activities [74,108]. In addition to their instantaneous enhancement of mineralization and humification of organic substrates, they create biogenic structures that may act as incubators of microbial activities (the ‘external rumen strategy’) or microsites for carbon and nutrient sequestration [10]. This ability to affect nutrient cycling at several scales of time and space is an important attribute of soil invertebrates as regulators of nutrient cycling [69]. Indeed, these effects have different importances and have been unevenly supported by scientific experimentation, depending on specific nutrients. Much is known of invertebrate effects on C and N cycling, much less on P and virtually none on that of K, Ca and other important macro and micro nutrients. Invertebrates are generally considered key actors in the buffering systems that allow efficient local recycling of nutrients and prevent leakage from impaired ecosystems towards low-lying aquifers, streams and oceans [75]. This effect however has never been quantified in any ecosystem or large landscape unit.

5.3. Primary production

Primary production is greatly affected by soil invertebrate activities, directly and indirectly. Many experiments have shown significant enhancements of plant production in the presence of Protoctista [15,16], Nematodes and Enchytraeidae [105], Collembola [28, 29,52] combinations of these organisms [105], termites or ants [93]. Last but not least, several hundred experiments have shown significant effects of a wide diversity of earthworm species on many different plant species [18,104]. Enhanced primary production has been generally attributed to five main processes: 1. Enhanced nutrient release in plant rhizosphere. 2. Stimulation of mutualistic micro-organisms, mycorrhizae and N-fixing micro organisms. 3. Enhancement of plant vigor and protection against pests and diseases, above and below ground. 4. Positive effects on soil physical structure. 5. Production of plant-growth promoters (the 'hormone-like effect') by micro organisms. Although the mechanism precisely responsible for such effects are generally not known [13], these five effects seem to represent the multiple facets of interactions among plants and soil organisms. They are likely to result from million of years of co-evolution and research is only starting to unravel the mechanisms for such interactions, often based on sophisticated chemical communication. The selective effects of earthworms on the expression of stress genes of rice plants described by Blouin et al. [12] is an indication that invertebrates might play a significant role in adjusting plastic plant phenotypes to current environment conditions in soils. This evidence that invertebrates adjust plant phenotypes through gene expression manipulation is another reason for considering the management of these organisms and not expecting too much from plant genetic manipulations that would create totally artificial GMOs that have never been exposed to interactions with the soil community.

In spite of these observations, the attention of farmers has been principally focused, until recently, on those invertebrates that become pests in agro-ecosystems as a result of practices that drastically reduce invertebrate activities [51,67]. Nematodes are one group of these plant parasites, causing damage evaluated at 10 billion Euros each year to the most intensive industrial crops. Research has shown that outbreaks of these parasites are most often enhanced by the mere application of pesticides. In West African fallows, competition within soils among diverse plant parasitic nematode populations seems to maintain the most dangerous species at a density that allows plants to tolerate them [21,22,72]. Settle et al. [106] also showed that systematic application of pesticides in rice fields enhanced damage due to plant parasites since their natural enemies had been decimated by unnecessary pesticide applications and were not sufficiently active when the pest started to appear. The challenge is therefore not to find a way to eradicate a pest but rather develop management practices that enhance the activities of their competitors and natural enemies. There is much to discover in this respect regarding interactions in soils and the multiple roles that invertebrates may play in controlling pests and diseases.

5.4. Soil formation

Soil formation is another long term process for which soil invertebrate activities have not been much considered. In spite of the acknowledged role of earthworms in the creation of "vermisols" and the belief expressed by a few authors that micro aggregates observed in oxisols have been formed by termites, the consequences of 1000 or more years (i.e. time to create 1 m of soil in temperate areas) of faunal activities accumulated over time and spatial scales 4–6 orders of magnitude lower is mostly ignored. There are a few known examples, however, where drastic changes in soil macrofauna communities occur following forest clearing, or the explosion of populations of invasive species, have significantly changed the soil profile in surprisingly short periods of time. In Amazonia, for example, invasion of pastures derived from the original forest by the earthworm *Pontoscolex corethrurus* triggered a very fast evolution of oxisols towards gleysols, with appearance of deep anoxic horizons in which Fe reduction shifts soil color from red to grey [6,25]. Invasion of North American forest soils by the European earthworm *Dendrobaena octaedra* is profoundly effecting many parameters of soil function and humus profiles [20,45,78,80,81]. Darwin [31] emphasized the effect of earthworms in the burial of stones and human constructions. An average annual deposition of 10 Tonnes of fine soil per ha at the soil surface by ants, termites, earthworms and other ecosystem engineers results in an approximate 1 mm downward movement of gravels and stones. Figures for total deposition provided in literature are very often greater than this minimal figure [76].

5.5. Climate regulation

Climate regulation is clearly influenced by soil invertebrate activities, through the accumulation over large periods of time of small-scale effects. Soil aggregation and enhanced humification are the main mechanisms involved in this process. Sequestration of C in compact and stable aggregates is regarded as an important process whereby soils accumulate C thus preventing its rapid release in the form of green house gases [83]. Enhanced humification also tends to transform large amounts of relatively labile C into forms that are much more resistant to further decomposition and hence to slower green house gas release from soils.

It is largely believed—and repeated in many an article—that organic matter inputs and/or cover plants in no-till systems improve soil physical structure and aggregation [44,49,96,110]. Organic matter itself however does not create aggregates and the observed aggregation is mostly due to the use of organic inputs by invertebrates that transform it until roots and large invertebrate ecosystem engineers use part of the nutrients and energy contained in organic matter to build the solid and persistent aggregates that play multiple roles in soil function [10,48]. Without this macrofauna, aggregates formed by the trapping of soil particles into networks of fungal hyphae and/or gluing of particles by bacterial mucilages associated with roots, have rather weak stabilities and short life spans as compared to earthworm casts or termite fabrics [41,96].

5.6. Soil invertebrates as indicators of soil function and quality

Soil invertebrates are clearly important components of soil function and any change occurring in soil properties is likely to affect them. Their effects in different land use types have been widely studied during the last decade and no less than 18 papers in this special issue detail the many effects of land use management on the community structure of diverse soil invertebrate groups (see for example [23,53,56,87–89,113,119]). Consequently, they may be considered highly responsive indicators of many aspects of soil quality [94]. Comprehensive indicators based on the composition and abundance of their communities are currently being developed [14,68,91,101,111].

6. Conclusion

Despite many decades of intensive research, initiated by such great scientists as Gilbert White or Charles Darwin, invertebrates are still poorly acknowledged as mediators of soil function and the delivery of ecosystem services. The recent publication of a number of specific textbooks and synthesis papers in journals with large overall scientific impact may however mark the start of a significant change in thought and practice [3,27,76,114,115,140]. Traditional textbooks of Soil Science and Ecology still pay very little—if any—attention to their effects and no mention is made of the management of their diversity and/or activities in strategic plans of all major research centers of agricultural research.

Conventional agricultural scientists mostly consider only that fraction of the invertebrates that have negative effects on crop plant-growth and usually try to eradicate them using drastic chemical methods. By so doing they usually worsen the problem since many chemical control methods may only achieve the selection of the most resistant and aggressive pests. Natural enemies of pests, at first weakened by the degradation of their environment generally disappear as “non-target” victims of strategies focused only on the symptoms (presence of the pest) since they ignore the mechanisms that favor pest development.

Soil scientists quite often acknowledge microbial activities as the mediators of over 90% of nutrient mineralization and dominant actors in biogeochemical cycles. They pay much less attention to the roles of roots and invertebrates: the real conductors of microbial symphonies that shape their communities and tune their activities in complex multi scale interactions.

Soil invertebrates are however located at a strategic position in the continuum of structures and processes that link basic microbial processes carried out by their colonies and biofilms to the scale of fields and landscapes where ecosystem services are produced. They interact with other soil organisms to form self organized systems that regulate the fluxes of different ecosystem services.

Plants, invertebrates and microorganisms have coevolved over several hundred million years within soils. Highly complex and intimate interactions have developed resulting in three different categories of engineering mediated by invertebrates and roots. This organization gives high resistance and resilience to soils that allows them to retain some favorable hydraulic properties long after the mechanisms that generated and maintained these properties have been destroyed by inadequate management practices. We know that this resilience has limits: threshold effects manifested as landslides, massive erosion events or soil compaction, indicate that such limits have been exceeded.

The major lesson to be learned from soil invertebrate ecological studies is the need to consider all the levels in the hierarchy of biological systems that link single microbial chemical functions and individual microphysical features, to ecosystem services, the emergent ecological functions at the scale of landscapes as mosaics of types of land cover and land uses.

The natures and qualities of the interactions that occur among all the constituents progressively reveal their importance as studies move from the first step of a gross evaluation of processes to finer scales and long-ignored micro-processes[36,40,42,88,107].

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