Soil aggregation, ecosystem engineers and the C cycle

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HIGHLIGHTS

1. Invertebrates and roots are essential drivers of soil aggregation, but often overlooked.

2. Manual separation and NIR spectroscopy allow classifying macro-aggregates according to the physical or biogenic agents that produced them.

3. A simple field method is proposed to measure in situ rates of production and losses in the different macro-aggregate pools.

4. Stocks, inputs and losses of C in aggregate pools characterize their contribution to C cycling and conservation.

5. This simple and robust approach can support the identification of management practices that best store and conserve C in soils

Abstract: Soil aggregation and its effects on soil C storage have been addressed in thousands of research articles over the last 40 years. Research has been mostly focussed on the resistance of aggregates to mechanical disruption and the role of organic matter in aggregate stabilization. On the other hand, relatively little attention has been paid to identifying the microbial, plant root and macro-invertebrate actors and physical processes that continuously create and destroy aggregates. The sum and dynamics of these processes determines the ability of soils to store and conserve C. Understanding the interactions between aggregation dynamics and C transformations in soils therefore requires a precise identification of the agents that produced aggregates and knowledge of the rates of formation and persistence in the pools thus identified.

We propose to separate macro-aggregated components of different, physicogenic and biogenic origins from non-macro-aggregated soil on a morphological basis, using a simple visual technique. The specific biological or physico-chemical agent which produced each individual macro-aggregate can then be determined using Near Infrared Spectrometry (NIRS). A general description of the distribution and quality of organic matter among the

different groups of macro-aggregates can be made. Simple soil re-aggregation or dis-aggregation test conducted in field conditions further measure the production of different macro-aggregates with time and their mean residence times in the studied soil. Respirometry measurements on each recognized category of macro-aggregates evaluate the respective C losses through respiration. The methods described here will allow the dominant pathways of C flow at a given site to be characterized and possible management options to increase C storage identified. We finally discuss the different assumptions made to build this simple model and offer ways to test the methodology under field conditions.

1. Introduction

While improved soil management offers one of many promising approaches for climate change mitigation, soil scientists and technicians are increasingly faced with the challenge of proposing and testing viable strategies to enhance C sequestration in soils (Altieri et al., 2015; Poeplau and Don, 2015; Paustian et al, 2016; Powlson et al., 2016; Smith et al., 2016; Bedano et al., 2019). As a major C reservoir, soil organic matter on Earth is estimated to be 1500 to 2400 Gt C, that is more than twice the mass of the C contained in the atmosphere (860 Gt). In addition, soils currently sequester an additional 3.2 ± 0.7 Gt C annually, equivalent to 29.4% of the annual emissions from fossil fuel burning. However, this positive contribution is offset each year by 1.5 ± 0.7 Gt C emitted as a consequence of land use change and soil degradation (Le Quéré et al. 2018). We currently do not know whether soils will continue to store C as climate change accelerates, or lose it -as land degradation continues- and this represents a major uncertainty for climate change projections (Carvalhais et al. 2014). The international 4 per 1000 initiative proposes offsetting anthropogenic emissions by storing every year an extra 0.4 % in agricultural soils through adequate management options (Minasny et al., 2017). Such a challenge will require precise tools for implementation and monitoring at plot and farm scales. We argue that our understanding of the mechanisms involved in the stabilization of C in soils and ways to harness our knowledge under field conditions need to be improved.

The Importance of physical protection for organic matter conservation

Three processes allow organic matter conservation in soils: physical protection in aggregated structures, the association of transformed organic matter to mineral particles in organo-mineral complexes and chemical recalcitrance (Six et al., 2004). We argue that these processes are not independent and soil aggregation is expected to be a key process in facilitating all three (Amezketa, 1999; Sollins et al., 1996; Feller and Beare, 1997; Six et al., 2000a, 2002a and b; 2004; Von Lutzow et al., 2006). Physical protection is likely a first step in conservation, that slows down the mineralization process by isolation of microbes from their organic substrates and/or limits water and oxygen supplies; Kuzyakov et al., 2015; Negassa et al., 2015; Keiluweit et al., 2016). Suitable conditions are then created for the other two processes to occur and a great part of SOM storage in soils may be in the form of organo-mineral complexes (Cotrufo et al., 2019). Organic matter accumulation has positive feed backs on in turn is widely acknowledged as an essential component for aggregate formation and stabilization (Amezketa, 1999; Six et al., 2004; Abiven et al, 2009; Fultz et al., 2013; Gumus and Seker, 2015; Zhu et al., 2017).

However, a variable proportion of the leaf and root litter Carbon may have been mineralized before these complexes are formed. It depends on the suite of initial decomposition processes that associate physical processes like comminution, transfers in the soil profile, inclusion in aggregate structures and chemical transformations associated to digestion and humification (Lavelle and Spain, 2001). In determined conditions of climate, soil and plant cover, the stabilization of C in soils, in particulate (POM) or mineral associated (MAOM) forms thus depends to a great extent on the efficiency of physical protection of organic matter against decay at macro- or microsite scales (Parton et al., 1988, Lavelle, 2002; Jimenez and Lal., 2006; Kuzyakov et al., 2015).

The long admitted alternative option for accumulation in soils of C pools made recalcitrant because of their chemical compositions is now strongly challenged (Lehmann et al., 2015).

Priming effects triggered by water-soluble organic compounds migrating down the soil profile or released by roots and invertebrate soil ecosystem engineers actually allow the mineralization of substrates reputed to be highly recalcitrant (Martin et al., 1992; Trigo et al., 1999; Fontaine et al., 2007; Lehmann et al., 2015).

There is a relative dearth of knowledge, however, of the diversity of ways aggregates are formed and the consequences this has on the amounts and quality of C concentrated and conserved inside these structures.

What are soil aggregates??

Aggregates defined as "soil specific entities built from mineral and organic compounds with stronger bonds between building blocks than with neighbouring particles"….."have a size, form and stability that is typical for individual soils depending on parent material and texture, climate and vegetation, biological activity and management" (Yudina and Kuzyakov, 2018). Their classification and evaluation are still largely determined by the method used to view or isolate them.

Non-destructive viewing techniques require rather sophisticated approaches such as tomography or the realization and image analysis of soil thin sections (Tracy et al., 2015; Wang et al., 2016; Zhao et al., 2017; Scarciglia and Barca, 2017; Gutierrez-Castorena et al., 2018). Isolating techniques separate aggregates according to their resistance to physical rupture following dry or wet sieving or slaking in water or other liquid substrates (Elliott, 1986; Le Bissonnais, 1996). Isolating may provide different results from viewing techniques since the energy used to isolate may determine the size of elements separated (Ashman et al., 2003; Kravchenko et al., 2018).

Separation of macroaggregates according to their morphology is a simple method that associates viewing and isolating approaches (Topoliantz et al., 2000; Velasquez et al., 2007a). The major advantage is that it does not require sophisticated equipment and thus can be applied by non-scientific operators, school children, students, technicians and farmers to discover and quantify soil macro-aggregation.

Importance and diversity of macro-aggregates in natural soils

A wide range of possible mechanisms for aggregate formation exists, from the close association of mineral and/or organic particles in microaggregates, at microsite scales of a few tens of microns, to the production of highly organized long-lasting macro-aggregates made by soil ecosystem engineers such as ants, termites and earthworms (Lavelle et al., 1997; Tötsche et al., 2018, Zanella et al., 2018; Yudina and Kuzyakov, 2019). Aggregates frequently have a hierarchical organization and it is widely thought that microaggregates of a size < 250 µm, the most stable elements, are formed inside macroaggregates as part of their stabilization process (Six et al., 2014).

Many types of macro-aggregates of physicogenic or biogenic origin can be distinguished (Velasquez et al., 2007a; Zanella et al., 2018; Yudina and Kuzyakov, 2019. The simple visual separation of biogenic aggregates produced by roots and macroinvertebrate shows their importance in surface soil horizons: in natural soils of temperate (Pulleman et al., 2004) or tropical regions (Velasquez and Lavelle, 2019; Grimaldi et al., 2014), aggregates of biogenic origin, mainly produced by earthworm activities often represent 40 to 60% of the soil weight in the upper 15 cm of soil.

Energy cost of forming aggregates

When considering the effects of soil aggregation on the C cycle, the release of C by respiratory activities during their construction is often overlooked. It may be an important element to consider when designing management options aimed at storing C in soils. For example, populations of the earthworm *Reginaldia omodeoi* in savannas of Ivory Coast ingest every year an estimated 850 Mg eq. dry soil and transform it into casts that are compact and highly resistant macroaggregates with a rather complex general structure (Lavelle, 1978; Blanchart,1993; Blanchart et al., 1997). The mechanical work required to burrow, ingest soil particles, take them through the gut and release them as casts is allowed by the assimilation of 9% of the C contained in the ingested soil, that is 1.2 Mg C ha^{-1}yr^{-1} emitted as CO_2 through earthworm respiration (Lavelle, 1978). Energy cost derived from C mineralization is expected to be lower for macro-aggregates formed by fungal entanglement of particles since hyphae likely grow in the connected porous space of the soil and do not spend energy moving particles. Data to address this point however, are lacking. The creation of physicogenic aggregates by processes like wetting/drying or freeze/thaw alternances apparently has no direct C cost.

Temporal stability and turnover time of aggregates

Aggregates experience dynamic processes of creation, stabilization, ageing, destabilization and disruption (Marquez et al., 2019). A precise description of their spatio-temporal dynamics and turnover is therefore an obligate step in evaluating the effect of aggregation on C storage and conservation in soils. Assuming that C mineralization is either decreased or stopped in aggregated structures, we need to know how much C is protected in these structures, to what extent, in which forms and for how long time.

We actually know little of the temporal stability of aggregates of different origins and thus how long these structures will conserve C before they collapse. Macro-aggregates formed by entanglement of soil particles, by fine roots or mycorrhizal and other fungal hyphae, generally have rather short life times, from a few days to a few months (Plante and Mc Gill, 2002 ; De Gryze et al., 2005, Segoli et al., 2013); they tend to disaggregate when the fungal hyphae or root disappear and/or organic binding agents are mineralized. On the other hand, casts of the African endogeic species *Reginaldia omodeoi* can remain intact for long periods of time – from 20 to 28 months - depending on soil texture and activity of decompacting earthworm populations that feed on these structures and disperse them (Blanchart et al., 1993b). Stabilized macro-aggregates are actually estimated to last up to 10 or 20 years if no disturbed (Lobe et al., 2011, Koesters et al., 2013; Marquez et al., 2019).

Many studies have monitored the build-up or decrease of aggregation as a result of experimental conditions or changes in management options (Beare et al, 1994; Bronick et al., 2005; Calonego and Rosolem, 2008). However, the direct measurement of aggregate turnover under steady state conditions is difficult. It has only been achieved, to our knowledge, using labelling with very specific rare earth or isotopic tracers (Plante and Mc Gill., 2002; De Gryze et al., 2005), tomography (Roose et al., 2016) or by using rather complex mechanistic simulation models (Lavelle and Meyer, 1983, Martin and Lavelle, 1992; Segoli et al., 2013; Marquez et al., 2019). These approaches can help with understanding aggregate turnover dynamics, but also have a number of limitations.

A field-based conceptual model and methodological approach

The rarity and diversity of attempts to describe aggregate life histories and dynamics is a clear indication that the problem is complex. Actually, no simple conceptual or methodological approach have been proposed so far. While much is known on the aggregation process, its diversity and importance, we argue that a few critical elements are still lacking to allow us to evaluate and accurately model the effect of soil aggregation dynamics on C conservation. This exists as a serious impediment to identify management practices and accurately predict their potential effect on soil C sequestration in a context of climate change.

This paper starts with a general bibliometric analysis. The aim was to identify knowledge gaps, that impede the implementation of a dynamic modelling of the soil aggregation process and its effect on C conservation in soils. The lack of consideration of the role of soil ecosystem engineers in general soil processes, is one such possible gap indicated by several authors (Lavelle, 2000; Bottinelli et al., 2015; Filser et al., 2016; Jouquet et al., 2016). We then propose a simple conceptual model where the conservation of C in soil depends on its protection into macro-aggregates.

We finally discuss the coherence and feasibility of this approach in view of the assumptions made and identify research needs to improve it. Particular emphasis is set on providing concepts and methodologies accessible to non-specialized scientists, farmers and technicians.

2. Soil aggregation in the scientific literature

A search of the ISI Web of knowledge in November 2019, with the words ‘soil ‘and ’aggregat*’ in title provided 2,692 papers, with a clear exponential increase occurring in the rates of publication on these and related topics over recent years. With the same keywords in topic, we obtained 77,427 articles. The large number of citations (>77,000), further illustrates the enormous interest in, and the importance of, this topic.

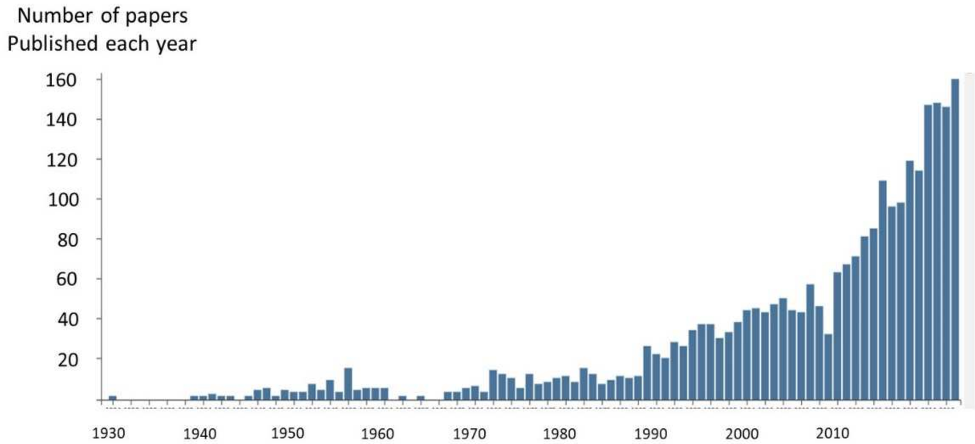

Figure 1: Number of papers published each year with words ”soil” and “aggregate” in title (source ISI Web) from 1900 to present.*

The frequency of associated words in titles showed the major themes studied. Organic matter or Carbon was the most important topic associated with soil aggregates, treated in 757 (28.1%) papers. This shows the strong association perceived between the aggregation process and soil organic matter cycling. Stability was the second topic in importance (572 occurrences, 21.2%), a very important attribute of aggregates that measures their resistance to breakdown by physical stress, especially by water (301; 11.1%). Soil management (or till* or crop*) considered in 430 papers (16%) reflects the ongoing concern for physical degradation in managed soils and interest to identify options for reverting degradation. Aggregate size (418; 15.5%) is an important morphological attribute, considered an indicator of aggregate stability. Water and erosion (358; 6.7%) and texture (clay or text* or sand) (198; 7.4%) are studied for their important role in aggregate stabilization. In comparison, biological actors of aggregation comprised a low proportion of the papers. Microbial relationships with aggregation (microb* or microor* or bact* or fung* or mycor*) were studied in only 307 (11.4%) papers, soil macroinvertebrates (earthworm* or lumbric* or termit* or ant* or formic* or macroinvert*) in 56 papers (2%), the same as roots (55; 2%). Finally, turnover of aggregates (7) or of organic matter in aggregates (9) have been very little considered in aggregate research.

3. An alternative approach to assess aggregate-associated C dynamics

In their seminal paper, Tisdall and Oades (1982) proposed a comprehensive conceptual framework to explain the origin, stabilization and dynamics of soil aggregation. They listed a number of key features that characterize the physical organization of aggregated structures and a diversity of mechanisms that provide stability against disruption. Such elements have been thoroughly described and discussed in later reviews (Elliott, 1986; Feller and Beare, 1997; Six et al., 2002a, 2014; Tötsche et al., 2018) and different elements have been introduced in recent modelling attempts (De Gryze et al.,2001, Marquez et al., 2019). Although this model has inspired a large number of studies, measuring the different compartments is still difficult and often requires rather high levels of expertise and equipment. Modelling the ageing and disruption dynamics of aggregates is even more difficult, partly because of the initial diversity of aggregate composition and structures that has not been considered so far in monitoring and modelling attempts. Stabilization or de-stabilization dynamics further depend on chemical, physical and biological processes associated with local soil conditions and the quality and quantity of organic material present in the aggregate.

3.1. General conceptual model

Our conceptual model is based on three simple assumptions:

1. Aggregate fractions should be separated according to their origin. This will prevent the mixing of very different aggregates into a single category based solely on their resistance to physical stress. We will recognize various pools of physicogenic or biogenic aggregates of root or invertebrate origin (Topoliantz et al., 2000; Velasquez et al., 2007a; Zanella et al.,2018). We expect each pool to have different dynamics

according to their initial diversity of compositions and structures (Hedde et al., 2005).

2. Microaggregates are mainly formed within macroaggregates (Six et al., 2004) and their dynamics are likely associated with the one of the larger structures that hosts them. We expect, however, that disaggregation of macro-aggregated structures will not go along with disaggregation of microaggregates and a pool of free microaggregates may be comprised in the non-macro-aggregated soil fraction (Tötsche et al., 2018).
3. Organic matter transformations are closely linked with aggregate dynamics. The incorporation of organic matter to the soil matrix is mostly a biological process associated with root growth, rhizodeposition, comminution, feeding and bioturbation processes. Flux of water-soluble organic matter that may transit through the porous space of the soil is expected to be negligible (Lavelle and Spain, 2001; Jimenez et al., 2006). Organic matter_is present in different forms and quantities in the different aggregated and non-macro-aggregated pools and associated to specific mineral components and porous spaces (Daniel et al., 1997; Capowiez et al., 2011; Arai et al., 2019). Mineralization rates are therefore likely determined by conditions that occur in aggregates.

In a given set of environmental - climate, soil and plant cover- conditions, macro-aggregates created by different processes and actors (see Fig. 2) accumulate in three compartments, which have different turnover times and mineralization rates and differently affect the overall C dynamics (Fig. 3).

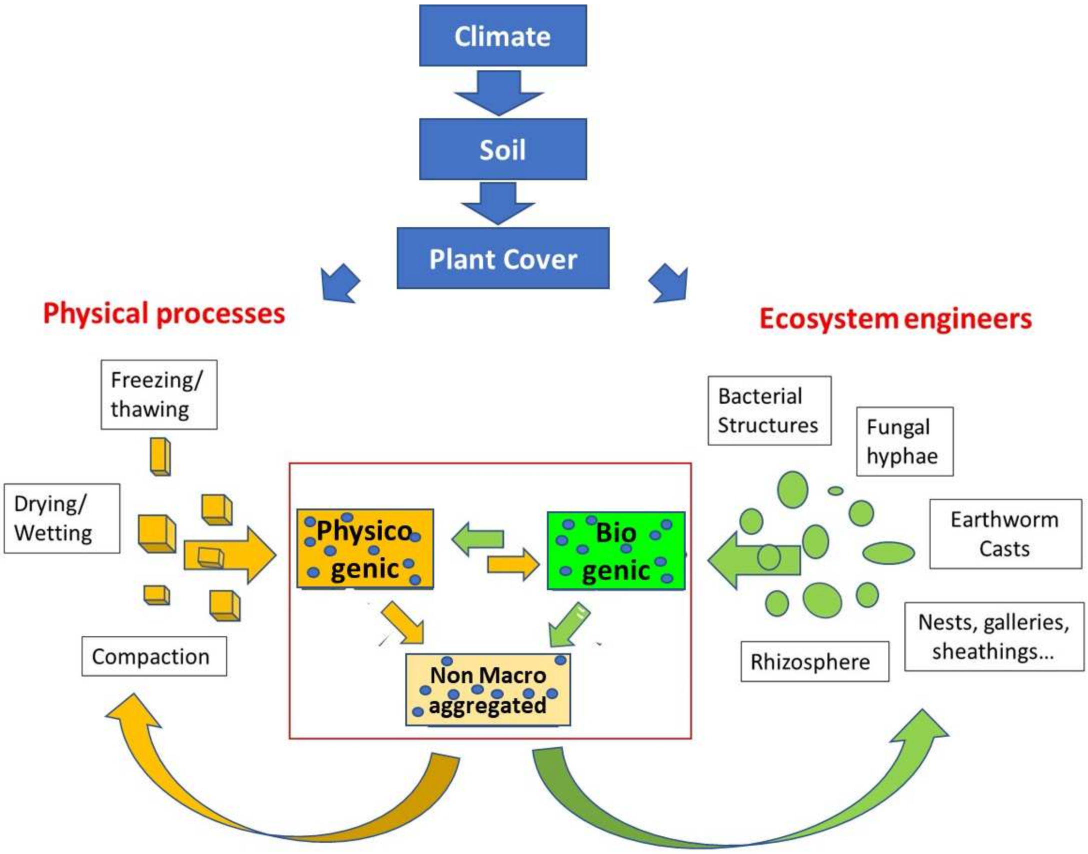

Figure 2: Conceptual framework for the diagnosis of soil macro-aggregation status and dynamics. Small circles in each category box symbolize microaggregates. Macroaggregates are classified in 3 categories, each of them having a definite number of sub categories indicated in boxes. Their dynamics involves creation from other aggregate pools, ageing and disruption that transfers their material to the non-macroaggregated pool, or a direct transformation into biogenic macroaggregates from the other 2 pools.

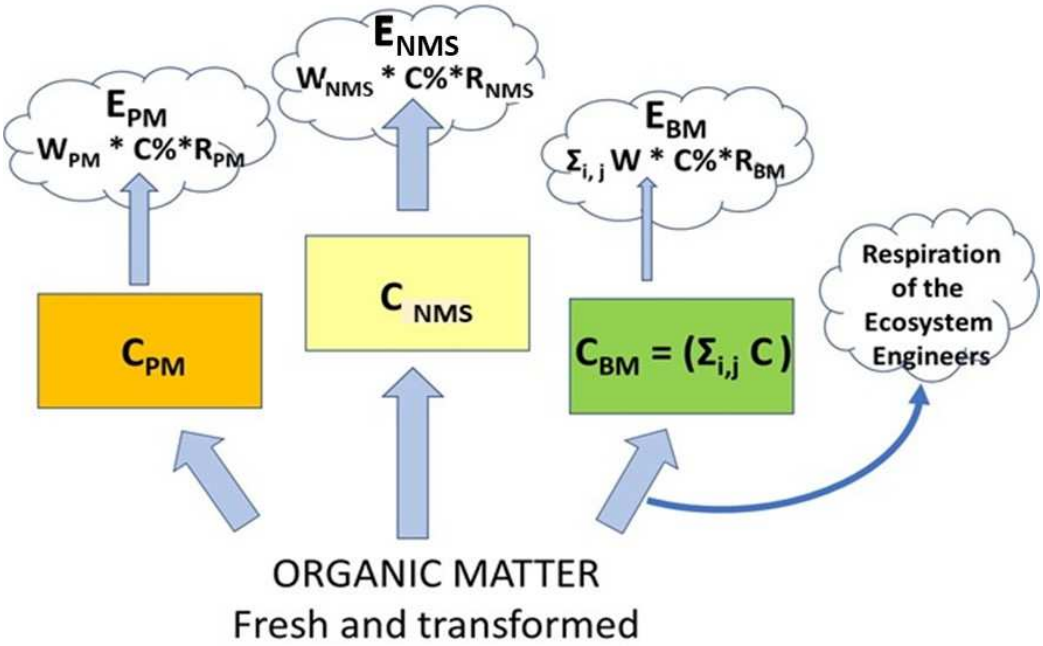

Figure 3: Flow of organic matter and gas emissions through the aggregated and non-macro-aggregated soil compartments.

Carbon in physical macro-aggregates (C_{PM}), non-macro-aggregated soil (C_{NMS}) and biogenic macro-aggregates (C_{BM}).
E_{PM}, E_{NMS} and E_{CBM} are gases released by respiratory activities from the C_{PM}, C_{NMS} and C_{BM} pools respectively. W: respective weights of the C_{PM}, C_{NMS} and C_{BM} pools: C%: % carbon contained in the respective pools; R_{PM}, R_{NMS} and R_{BM}: emission rate in %C of the different pools. Note that respiration of soil ecosystem engineers when they produce biogenic aggregates is an additional source of gas emissions.

Three major steps are necessary to run this general model of soil aggregation and associated C dynamics (Figure 2 and 3).

- Diagnosis of the aggregation status of the soil that considers the origins and relative amounts of the different types of aggregates (Fig.2);
- Assessing the production and turnover of aggregates by measuring the flows of materials among the different aggregated and non-aggregated fractions (Fig 2);
- C cycling and aggregate dynamics: an analysis of the quality and quantity of C pools contained within each macro-aggregate or non-macro-aggregated fraction, their mineralization rates in the respective pools and the C losses and gains associated with their production, stabilization, ageing and disruption cycles (Fig 3).

3.2 Diagnosis of aggregation status

Separation and identification of the origins of aggregates is the first step in our approach.

<u>Large macro-aggregated compartments</u>

Size limits. There is a general agreement that a 250 µm size separates macro- from microaggregates. Since it was first proposed by Tisdall and Oades (1982), this limit has dominated the research although sub categories have been proposed within each class. This paper focuses on the large macroaggregates > 2 mm sub category that can be easily separated and identified.

Origin and identity. Manual fractionation allows the separation of soil into three main fractions (non-macro-aggregated, physicogenic and biogenic macro-aggregates) based on their sizes and general morphologies (Topoliantz et al., 2000; Pulleman et al., 2005; Velasquez et al., 2007a). This method has been applied successfully to describe macro-aggregation in a wide range of soils, with sandy to clayey textures, in temperate and tropical areas. An example is provided in Figure 4. A great proportion of soils worldwide, protected by permanent vegetation and possessing suitable moisture contents, comprise large proportions of up to 60% macro-aggregates of both physical and biogenic types (Velasquez et al., 2019).

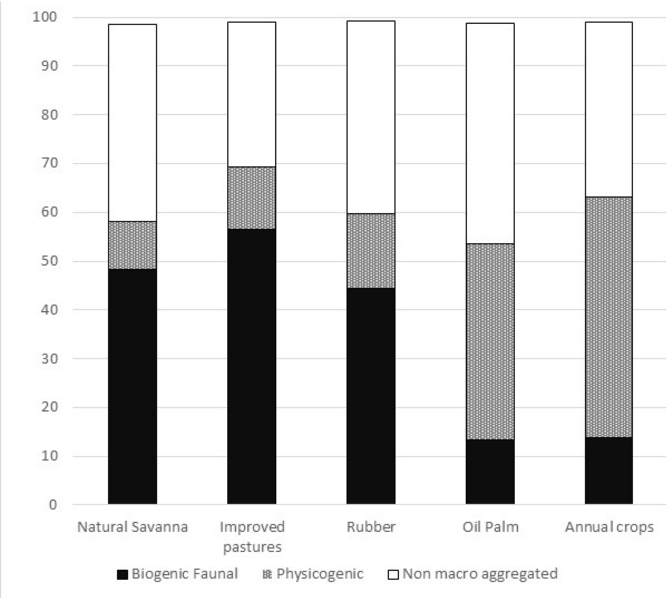

Figure 4: Relative proportions of biogenic, physicogenic macro-aggregates and non-macro-aggregated soil in different types of land use in the Eastern Plains of Colombia (Lavelle et al., 2014).

Physical aggregates are soil blocks produced by mechanical processes that create fissures in a continuous soil matrix (Boersma and Kooistra, 1994; Jongmans et al., 2001; Pulleman et al., 2005. They have angular blocky shapes with a dominance of sharp edges and plane surfaces. Particles within blocks are held together in a continuous matrix by organic and inorganic binding agents together with inter-particle binding due to Van der Waals forces (Hu et al., 2015). There is evidence that the same alternation of drying and rewetting events, that created these aggregates, may also activate the release of organic molecules, by microorganisms, that act as glues and consolidate these structures (Degens and Sparling, 1995; Cosentino et al., 2006). The addition of high molecular weight humic compounds may have similar effects (Piccolo et al., 1997; Yamaguchi et al., 2004). This set of aggregation processes when enhanced by physical compaction through use of tractors or cattle trampling in managed systems, tends to create very large clods and hard pans (Keen et al., 2013).

Biogenic aggregates are produced by organisms classified as ecosystem engineers for their ability to modify soil conditions through their physical activities (Blouin et al., 2013; Lavelle et al., 2016). Ecosystem engineers produce a wide diversity of macro-aggregated structures that differ significantly in their morphologies, chemical and biochemical compositions (Decaëns et al., 2001; Mora et al., 2003; Velasquez et al., 2007b) (Figure 5). Specific mineral compositions and organic matter contents and natures gives them rather specific spectral signatures when illuminated with Near Infrared light (Hedde et al., 2005; Dominguez-Haydar, 2018).

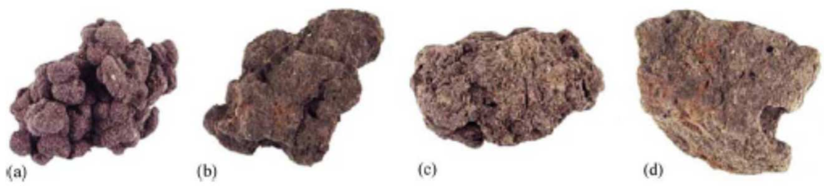

Figure 5: Different kinds of soil macro-aggregates: a. biogenic (fresh earthworm cast); b. biogenic (welded cast); c. intermediate (rounded aggregate); d. physicogenic (angular blocky aggregate) (Photo: Pulleman et al., 2005).

We recognize here four main categories which in turn comprise a large diversity of sub categories.

Fungal macro-aggregates are created when fungal hyphae entangle organic debris and mineral particles into stable aggregates that resist slaking and dispersion under the mechanical stresses applied in classical tests. They are usually not separated in soils with a permanent plant cover and are mostly seen in intensive cropping systems where communities of other ecosystem engineers are depleted.

Most of the macro-aggregation described in soils of cropped fields and laboratory tests is actually produced by this process (Tisdall and Oades, 1982; Plante and Mc Gill. 2002). Mycorrhizal fungi are considered major producers of this type of aggregation (Rillig and Mummey, 2006).

*Earthworms*_when present are major agents of soil bioturbation with widely different effects depending on their ecological strategies (Bouché, 1977; Lavelle and Spain, 2001). Epigeic earthworms live in the litter layers and are active composting agents that transform litter into largely organic pellets. Anecic species live in deep, subvertical galleries surrounded by zones of compacted soil that may behave as stable aggregated structures. Their casts are usually relatively loose structures stabilized by high contents of 20 to 40% on average (Judas, 1992) of little-decomposed particulate organic matter. Endogeic earthworms live within the mineral soil horizons and feed on soil, with different concentrations of organic matter depending on their specific – oligohumic, mesohumic or polyhumic- adaptive strategies (Lavelle and Spain, 2001). They are the major producers of biogenic macro-aggregates in many soils. They typically ingest from 1 to 10 and sometimes up to 30 times their own weight of soil daily and total values of up to 1150 Mg dry soil ha^{-1} have been measured, equivalent to a 10 cm thick soil layer (Lavelle, 1978). Their casts are either highly compacted structures, with bulk densities as high as 1.8 to 2.0 Mg m^{-3} (Blanchart et al., 1993), or loose structures, easily disaggregated, produced by the endogeic decompacting species (Blanchart et al., 1997).

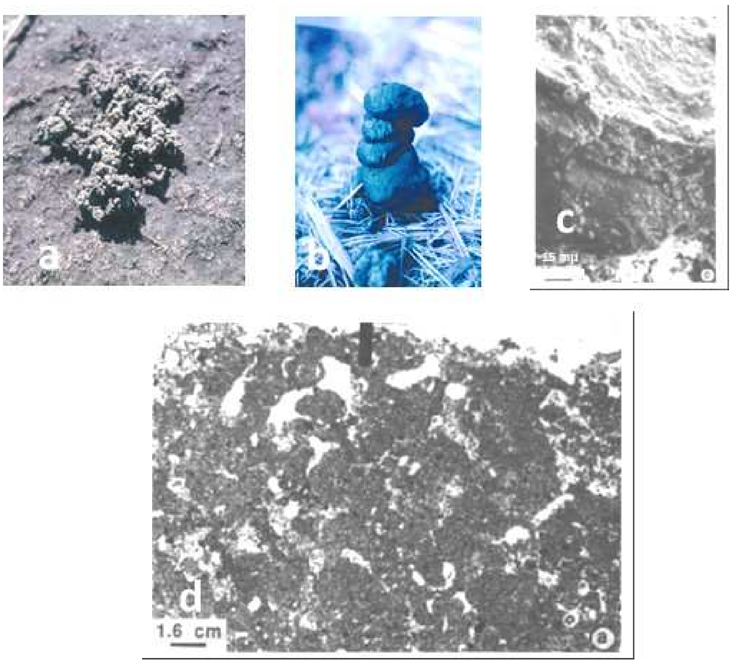

Figure 6: Loose (Chuniodrilus zielae) (a) and compact (Reginaldia omodeoi) (b) earthworm casts in African savanna (Lamto, Ivory Coast). (Photos P. Lavelle). Right: (c) Fracture of a surface cast of R. omodeoi observed with SEM. Observe the cortex made of fine particles that gives the surface of the cast a smooth and close aspect (Blanchart et al., 1993).
(d) Thin section in the 0-10 cm layer of a soil from a humid savanna (Lamto, Ivory Coast) showing accumulation of globular casts mainly produced by the earthworm Reginaldia omodeoi (Blanchart et al., 1997).

The destruction and reorganization of aggregates may actually be a product of earthworm activity itself in some soils.

*Social insect structures.*_Termites and ants may be active producers of soil macro-aggregates. Their bioturbation of several Mg ha^{-1} year^{-1} is the result of a mixture of digging, building and casting activities (Lobry de Bruyn & Conacher 1990; Folgarait, 1998; Jouquet et al., 2011). Aggregates formed that way vary from very loose deposits and faeces to very compact tunnel-shaped aggregates or complex nest structures that may last years to decades and even more (Rajagopal et al., 1982; Bonell et al., 1986; Mermut et al., 1994; Humphreys, 1994; Gorosito et al., 2005; Korb, 2011; Erens et al., 2015).

Maybe even more remarkable is the formation by humivorous termites of structures identified as pseudo-sand aggregates that end up comprising the entire volume of some tropical ferralsols (Wielemaker, 1984, Eschenbrenner, 1986; Balbino et al., 2002; Reatto et al., 2009; Millogo et al., 2011).

Root aggregates are structures that adhere to the roots. They are formed through five different processes: local compaction of soil, water regime alteration, rhizodeposition of gluing materials, decomposition of root material, and entanglement of soil particles by fine (0.2 to 1 mm in diameter) roots (Monroe and Kladivko, 1987; Miller and Jastrow, 1990; Morel et al., 1991; Materechera et al., 1992; Dorioz et al. 1993; Degens et al., 1994; Alami et al. 2000, Czarnes et al. 2000, Gale et al. 2000, Feeney et al. 2006; Demenois et al., 2018). An estimated 20% of plant photosynthesis is directly released at root tips with strong biological effects and induced aggregation (Miller and Jastrow, 1990; Lavelle and Spain, 2001). Macro-aggregation by root activities may be a rather fast process. In a five-week laboratory experiment, *Trifolium pratense* plants produced an average of 217.1 g and *Plantago lanceolata*, 142.1 g of macro-aggregates in pots that contained 800 g of dry soil moistened to field capacity (Zangerlé et al., 2011).

Mixed structures. Although some spectacular structures are produced by well-identified single actors in nature or laboratory experiments, aggregation seems frequently to be a cooperative process that involves different kinds of organisms, especially microorganisms. There is also evidence that fine roots often colonize fresh earthworm casts and thus possibly add their aggregative effects to those of the earthworm (Decaëns et al., 1999; Zangerlé et al., 2011; Fonte et al. 2012). Fungal hyphae likely participate in the consolidation of all sorts of other macroaggregates built by large ecosystem engineers.

Macro-aggregate specific identity and age

For a finer identification of physicogenic and biogenic macroinvertebrate or root macro-aggregates, Near Infrared Spectrometry (NIRS) has proven to be a very efficient and practical tool (Hedde et al., 2005). NIRS is a non-destructive method that reflects the texture and amount and quality of organic matter contained in a soil sample. For each sample, NIRS provides a spectrum that can be divided into separate ranges of wave length longitudes (Velasquez et al., 2007b). Manually separated biogenic, physicogenic and non-macro-aggregated aggregates exhibit significant differences (Dominguez-Haydar et al., 2018). The same method perfectly discriminated structures produced by different macro invertebrates (Hedde et al., 2005). Rather small samples of a few cg can be analysed separately. It is therefore possible to analyse individually all the macro-aggregates from a sample of a standard 10 x 10 x 10 cm size sample and group aggregates with similar spectral signatures into homogeneous categories. Using this method, Zangerlé et al. (2016) were able to separate eight categories of macro-aggregates from a forest soil in Luxemburg. They further identified the earthworm species that had produced the structure by comparing the spectral signatures with a bank of signatures established under laboratory conditions. In another experiment, the same authors observed changes in the spectral signature of casts as they aged (Zangerlé et al., 2014) showing potential of this method to identify different phases in the stabilization, ageing and disaggregation process of aggregates. Alternatively, enzymatic activities, microbial communities PLFA fingerprints or physical and chemical variables have been shown to discriminate among biogenic structures of different origins (Decaëns et al., 2001; Mora et al., 2003; Hedde et al., 2005; Jouquet et al., 2013).

3.3. Assessing the production and turnover of aggregates

Our literature survey has confirmed that very few studies have been devoted to aggregate production and turnover in natural or managed systems.

Field reaggregation or disaggregation tests

A simple way to approach the dynamics of aggregation can be obtained by applying an in-situ re-aggregation or disaggregation test as done by Blanchart (1992), Barros et al. (2001 and Gorosito (2007(). Blocks of soil from 10 x 10 x 10 cm to 25 x 25 x 30 cm depending on local conditions are taken in the field and a diagnosis of macro-aggregation is performed using the methodology proposed in section 3.1. Soil is then crushed and passed through a sieve with a 1 mm mesh size and taken back to fill the hole from which it had been excavated and reaggregation is monitored. The unit is covered with some litter taken from the surroundings and/or protected with a mesh to prevent the direct impact of rainfall that would create physicogenic macro-aggregates. Different sizes of mesh may be used to allow invertebrates and roots of different sizes to enter the experimental unit. Under these conditions, ecosystem engineers from the surrounding soil and natural physical processes will progressively form aggregates from the non-macro-aggregated soil. Experimental units are excavated at regular time intervals to follow the restoration of the macro-aggregated structure. In the experiment conducted by Blanchart (1992), the average percentage of macro-aggregates > 2mm was 12.9% when macroinvertebrates were not allowed to enter the unit, 49.9% when the mesh size allowed them to recolonize and 60.6% when the units had been inoculated with endogeic earthworms. The dynamics of disaggregation can also be observed putting the intact soil block, after fauna has been eliminated by a temporary drowning, in a net that will not allow roots and invertebrates to come in (Blanchart et al., 1997).

In some sites, macro-aggregate production can be measured using direct methodologies. Production of surface and subterranean casts by earthworms, root macro-aggregates and aggregated soil in the nest structures of termites and ants has been measured by ecologists in a range of laboratory and field situations (Lavelle, 1978; Lobry de Bruyn et al., 1990; Jouquet et al., 2013; Lavelle and Spain, 2001: Zangerlé et al., 2011) or simulated with mechanistic models (Martin and Lavelle, 1992). Data are still scarce because these measurements that require highly specific biological expertise are generally difficult and time consuming, especially when measuring structures produced in the soil matrix.

Spectral analysis of individual macro-aggregates

Macro-aggregates of biogenic root or invertebrate origin have a specific spectral signature that mostly reflect specific quality and concentrations of organic elements and texture (Hedde et al., 2005; Velasquez et al., 2007a; Zhang et al., 2009; Zangerlé et al., 2011). These specific signatures seem to progressively converge towards a common "bulk soil" signature as the structure ages. In a laboratory study conducted with the endogeic species *Aporrectodea caliginosa*, spectral signature of casts changed first rapidly, in the first 2 days after deposition and then slowly until day 45 to 60 when it was difficult to separate it from the bulk soil signature. This method allowed to separate casts aged less than 60 days and get an estimate of macro-aggregates of a given category during a 2-month period. (Zangerlé et al., 2016).

Turnover time in steady state situations

In a steady state situation, the amount of new structures created is expected to be compensated by the destruction of an equal amount. Based on reaggregation experiments conducted in natural environment, Blanchart (1992) was able to evaluate at 20 months and 28 months, in grass and shrub savannas respectively, the average residence time of casts of the earthworm *Reginaldia omodeoi* in a savanna of Ivory Coast. In this case, complementary studies have shown that macro-aggregated structures created by this

earthworm are eaten by another earthworm species from the Eudrilidae family that transform these highly compact casts into fragile erodible soil pellets (Blanchart et al., 1997). Very fast transformations of the soil structure have been observed with this method. In an experiment conducted in Amazonia, Barros et al, (2001) exchanged undisturbed soil blocks from a pasture and the natural forest to the other site. After one year, the heavily compacted soil of the pasture had recovered a macro-porosity close to that of the forest, while forest blocks inoculated in the pasture has almost attained the levels of compaction observed in this pasture. A similar experiment allowed Gorosito (200) to demonstrate that soil blocks from rice fields derived from a natural savanna were rapidly colonized, with similar abundances and diversities after one year and even higher values after 2 years.
Similar approaches developed with plants and other producers of biogenic aggregates might provide some estimates on the life duration of these structures. Further studies will then be required to identify the predominant disruption process and the fate of microaggregates that they contained.

4 C cycling and soil aggregation

Once recognized and measured the different aggregate pools in soil, the effect of soil aggregation dynamics on C cycling can be assessed using a simple conceptual framework (Figure 3). Assessing the effect of each recognized pool on soil C cycle first requires an evaluation of the energy cost (as mineralized C) of creating these macro-aggregates, if relevant. Then we need a precise knowledge of the amount and quality of the organic matter contained in this pool and an estimate of the persistence and general dynamics of the specific aggregate pool. In addition, one must have some ideas on the processes that lead to their disruption and transfer to the non-macro-aggregated pool or to another pool.

Soil C in aggregates and aggregation dynamics

Analysis of C contents separated among particulate organic matter (POM) and MAOM fraction associated to the soil mineral fraction will be applied to samples from the different recognized aggregate pools. This will allow measuring stocks of C associated to the

different pools. A number of studies has shown strong effects of plant cover and soil management on these stocks and their temporal variations (Dexter et al., 1999: Conant et al., 2001; Post et al., 2000; Martens, 2000; Zhang et al., 2013; 2016).
We hypothesize that transformations of particulate and mineral-associated organic matter are linked to those of the aggregated or non-aggregated mineral pools that comprise them. Dead fine and coarse root material and root exudates are transferred to the root biogenic macro-aggregated structures (CBM roots) through rhizospheric activities. Organic debris of root origin occasionally ingested by invertebrates will be further included in their faecal pellets as earthworm casts or as organic macro-aggregates of rhizophagous coleoptera larvae in other fractions of the CBM pool. Organic matter deposited in the leaf litter layer, the other source of organic materials, is first transformed by comminution and natural composting processes and progressively incorporated to the soil by digestion and bioturbation processes associated with macroinvertebrate feeding activities and leaching of dissolved organic matter. The decomposition rate of this organic matter is influenced by the same processes that lead to its incorporation in the aggregates, gut transit or burial below earthworm casts and insect deposits at the soil surface.

<u>Energy cost of macro-aggregate production</u>

As indicated before, the formation of certain biogenic macroaggregates has a significant cost in energy and C emission. This C loss may be evaluated by comparing C contents of the non-macroaggregated material originally used with the macroaggregates produced, or measuring the respiratory costs associated with the mechanical activities associated to their formation (Lavelle, 1978).

<u>Carbon emission from the aggregated and non-macro-aggregated pools</u>

A large number of studies have compared the respiration activity of aggregates of different size fractions and in different conditions of soil management (Dexter et al., 1999; Ashman et al., 2003; Zhang et al., 2013; 2016). Carbon from each pool is mineralized at different rates. For example, Martin (1991) showed that C mineralization proceeded at a much lower rate in casts of *Reginaldia omodeoi* than in the non-ingested soil sieved at 2mm. Digestion of the soil prior to cast release had decreased the C content of the soil by 9%, but mineralization inside the very compact cast had decreased microbial activity to such a low value that the non-digested soil and the cast had the same C contents after 100 days. With each day past this limit, the difference in C contents between macro-aggregated and non-macro-aggregated soil would increase. Where casts may persist from 20 to 28 months, the ability of this species and type of biogenic aggregate to conserve C may be very important.

The expected ´protection of C from mineralization however will likely depend on conditions created within the structure: aeration, temperature and moisture conditions, stoichiometric and other chemical environment conditions.

The major water-soluble organic sources, root exudates, earthworm intestinal mucus or termite saliva that represent inputs of several Mg C per ha per year are mixed with the mineral soil and soon become part of the macro-aggregated soil fraction, in the forms of earthworm casts, root macro-aggregates or termite constructions.

In the absence of invertebrate ecosystem engineers, leaf litter organic matter stays at the soil surface and the production of organo-mineral macro-aggregates is limited to root aggregate production. Water soluble organic matter leached from the litter layer may well circulate among macro-aggregated fractions as part of the soil drainage process and stimulate microbial decomposing activities creating priming effects (Fontaine et al., 2007). It should, however, not have a significant effect since it represents a rather limited flow as compared to other components of organic matter inputs (Lavelle and Spain, 2001; Jimenez and Lal, 2006). It is also expected to be rapidly flocculated in the presence of clay minerals (Toutain, 1981) or consumed upon entering the soil matrix and does not enter easily inside compact aggregates

Carbon in the non-macro-aggregated soil pool (C_{NMS}) may have been released from disaggregated biogenic or physical aggregates or be generated by flocculation or condensation processes of water-soluble organic matter occurring in the interaggregate space. Carbon of the physicogenic macro-aggregate pool (C_{PM}) may have been contained in the non-aggregated pool before it was transformed into physical aggregates.

5 Discussion

Our literature review confirmed that biological processes are severely undermined in aggregate studies was confirmed: only 11.5% of the papers considered microbial components, and 4% roots and invertebrate activities. This is clearly the result of restricted disciplinary focus where a holistic view is necessary (Lavelle et al., 2016; Briones, 2018). Five other important gaps, addressed below, appeared that are susceptible to hinder a global and practical understanding of processes at hand and ways to enhance their benefits in terms of ecosystem services. The approach that we propose to attain this goal is based on a number of assumptions, conceptual simplifications and the choice of technical options that often coincide with these gaps.

<u>Definition and classification of aggregates: The need for a comprehensive separation technique that combines viewing and isolating approaches.</u>

Soil macroaggregates may be seen in very different ways by scientists depending on the discipline they belong to. For soil ecologists, technicians and farmers, they often are visible and easily recognizable structures created by roots and invertebrate ecosystem engineers (Lavelle et al., 2006; Blouin et al., 2013; Jouquet et al., 2016). A severe drawback of using stress resistance of aggregates as a way to isolate them is that part of the resistance is provided by chemical and biological binding effects associated to the soil type, and not to the macro-aggregation process itself. On the other hand, a direct relationship between stabilization and conservation of C in soil conditions has not been proven to our knowledge. The manual separation technique that we propose is a combination of viewing and isolation techniques. This technique has proven very efficient at showing scientists, students and farmers the importance and vulnerability of the macro aggregation in soils. Synthetic indicators made with data provided with this method are always linked with other physical, chemical or biological attributes of soil fertility and ecosystem services provisioning (Velasquez et al., 2007b; Lavelle et al., 2014; Grimaldi et al., 2014; Velasquez ad Lavelle, 2019). When the objective is to show the importance of the macro aggregation process to students or farmers and differential effects of soil management options, no specific training is required since trainees will separate structures the same way, whatever it is, in different soils and perceive differences. Efforts should be done however, to better standardize this technique (Jouquet et al., 2009). Clear recommendations should be made on how to properly disrupt the soil matrix according to natural breaking surfaces, in different conditions of soil texture and plant root densities. Separation of root and other biogenic aggregates may require specific actions depending on their sizes and structures. Soil texture - especially when clayey- or effects of mismanagement -when soils are highly compacted- may complicate this technique in some situations. An important issue is the size of the elements that have been identified as macro-aggregates. When felt important, smaller sieves could be used to isolate fractions down to 1, or even 0.25 mm. In this case, the observation of subsamples with a stereo microscope may provide the accuracy required by specific scientific studies (Topoliantz et al., 2000).

<u>Macro vs. microaggregates. Can microaggregates be independent of macro-aggregates? And to what extent?</u>

The idea that microaggregates are formed inside macro-aggregates (Six et al. 2000) offers a welcome simplification in our approach. It is also in accordance with the self-organized soil model that proposes a hierarchical organization of soil, with successive functional units nested in each other as their size increases (Lavelle et al., 2016). While this view of soil organization is widely acknowledged and demonstrated by an important number of studies (Six et al., 2000; Bossuyt et al., 2004; Fonte et al., 2012), a few questions remain. First microaggregates are not a homogeneous category (Tötsche et al, 2018) although, there is some expectation that microaggregates have compositions derived from that of macroaggregates, although with generally less C and lower C:N ratio (Blanchart et al., 2000). Maybe more important is knowing what happens to microaggregates when macroaggregates get disrupted. In the model of aggregate dynamics proposed by Marquez et al. (2018), microaggregates may be either disrupted when the macro-aggregate that comprise them is disrupted or be part of a transient fractions that is further reincorporated into macro-aggregates.

<u>Identify aggregate origins to understand biological or other processes that determine their creation and further dynamics.</u>

The very low proportion of articles that consider root or invertebrate generation of macro-aggregates points at a very important gap. Specificities of composition, structure and microbial communities at species level of these macro-aggregates are very important determinants of their further stability and temporal dynamics (Hedde et al., 2005; Mora et al., 2003; Jouquet et al., 2013). NIRS has been showed to offer a cheap and efficient way to solve the problem. However, NIR spectral signatures have also proved to be unstable in ageing earthworm casts (Zangerlé et al., 2014). Changes in spectral signature probably reflect the rapid changes of microbial biomass and mineral N contents observed in freshly deposited earthworm casts (Lavelle et al., 1992). The Intriguing observation that casts aged >45 days have a signature similar to the bulk soil should be further investigated. Does this mean that the surrounding soil was actually mostly comprised of aged earthworm casts of the species considered? Or can we think of an alternative hypothesis? Fresh macro-aggregates are hotspots of microbial activity where some microbial species are enhanced, not the whole soil community. Would the specific signature observed in freshly created structures reflect important transient biomass of these components? And signature observed later on an indication that these populations have decreased to their initial abundance in the bulk soil? Comparable observations made by Blackwood and Paul (2003) show the importance of this question.

Interactions among physicogenic and biogenic agents in soil macro-aggregation dynamics

In a finite soil volume, formation of new macro-aggregates in a steady state formation has to be done at expenses of other pools of aggregated or non-aggregated soil. Stable macro-aggregates produced by a given set of invertebrates or roots can be destroyed by other invertebrates that may use them as food, or roots and invertebrates that just need to make their way through the soil to grow or develop their porous domains. Organisms may cooperate in forming macro-aggregates. This is the case for example for earthworms and roots, although cooperation may well be specific (Zangerlé, et al., 2011). The equilibrium among ecosystem engineers with opposite compacting or decompacting effects may be a critical element when considering soil management options (Blanchart et al., 1997; Chauvel et al., 1999). Research on this topic is virtually absent.

C loss and conservation associated to aggregation

While soil aggregation is largely associated with C accumulation in soils, detailed underlying mechanisms are far from being completely understood. The option of our model, considering C cycling as a discrete process split among different aggregate pools of different origins with different histories probably deserves improved theoretical and experimental foundations. In surface soil layers where biological activity is concentrated, aggregation seems to be the best option for limiting C mineralization. A better understanding and classification of biological aggregation processes would probably help. The overall effects of these aggregation processes on C cycling might well differ along a continuum from short term fungal hyphae particle entanglement observed in poorly aggregated agricultural soils to potentially long-lived earthworm casts stabilized by a drying event or aggregates associated with social insect nests. In both extreme cases, respiration of the organisms responsible for the creation of aggregates have very different energy costs that should be incorporated in models. One can hypothesize that in steady state conditions, the cost of creating aggregates is compensated by their protection effect on soil organic matter (Lavelle and Spain, 2001; Lubbers et al., 2017). Disaggregation of soils associated to intensive cropping practices may be explained by increased microbial mineralization in conditions where macro-aggregation by ecosystem engineers is deficient. In other cases, excessive activity of invasive ecosystem engineers, like European earthworm species in northern America forests, may well increase soil aggregation while soil C stocks decrease. Bioturbation activities then exceed the effect of physical protection in aggregates (Bohlen et al., 2004).

With soil depth, oxygen concentration naturally decreases and the mere rarefaction of biological activity is thought to favor C conservation. Mechanisms and conditions that allow migration of C in deep layers also require better understanding.

6 Conclusion

Synthesis of knowledges generated in different disciplinary fields led us to propose an alternative approach to evaluate the process of aggregate formation and its contribution to the conservation and accumulation of organic matter in soils. The methodology proposed is based on relatively simple and low-cost techniques that should be accessible to a large number of scientists, technicians and farmers. This condition is important to develop multi-functional agricultural practices that contribute to restore soil- based ecosystem services and especially soil critical contribution to the mitigation of global warming.

Explicitly considering biological mechanisms that determine soil aggregation will allow harnessing this process to ecosystem restoration practices and sustainable management options. In soils considered as self-organized systems, aggregates are constructed structures that have positive feedbacks on the communities that produced them (Lavelle et al., 2016; Bedano et al., 2019). Aggregation is part of the “potential” of the ecosystem as defined by Holling (2000), a capital that varies along adaptive cycles and that determines ecosystem evolution. In situ soil reaggregation tests, that indirectly evaluate the ability of organisms to collectively organize and improve their habitat, might well appear as a simple way to measure such an important attribute. This evaluation of potential combined with an assessment of the connectance, mostly linked to local diversity and abundance of plant and invertebrate ecosystem engineer communities, should allow progressing in the base line evaluation of ecosystems before initiating restoration practices.

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