Soil Organic Matter Dynamics and Structure

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Abstract

Soil ecosystem functions have significantly deteriorated due to agricultural intensification with dramatic consequences on carbon loss, loss of soil biodiversity, erosion, compaction as well as unsustainable use of water and mineral resources. Sustainable agricultural practices are necessary if we are to face the challenge of food security while preserving the integrity of soil and aquatic ecosystems. Conservation agriculture which is comprised of zero or minimum tillage, carbon amendments and crop rotations holds great promise in delivering higher yields, using water and soil resources in a sustainable manner and increasing soil biodiversity. This paper presents a synthesis of current knowledge on soil ecosystem processes and modeling with a focus on carbon and nitrogen dynamics and their link to soil structure, and proposes a conceptual framework for model parameterization capable of predicting critical soil functions and potential shifts.

We reviewed the dynamics of carbon, nitrogen and soil structure with an emphasis in elucidating predominant state variables and the interaction with plants and food web dynamics. Existing models that simulate the dynamics of organic matter and structure in soils at various scales were evaluated for their ability to simulate the functions of soil ecosystem. Current modeling approaches treat carbon, nitrogen and soil structure for the most part separately without incorporating feedback mechanisms. The synergistic and antagonistic processes between bacteria and plants and fungi and

plants are partially understood and more importantly the community lacks the knowledge to predict if and when these processes fail and any related potential ecosystem shift. A conceptual modeling framework is proposed, developed along the following three axes: incorporate emerging ecosystem state variables, account for the ecology of life in soils, and model processes from first principles. A synthesis of the carbon and nitrogen cycles is suggested in which the dynamics of the two cycles are interlinked. State variables in soil ecosystem models that link carbon and nitrogen dynamics with soil structure and the biological community are recommended. Plant feedback mechanisms with the physical, biochemical and biotic soil components and the symbiotic relationship between bacteria, fungi, and plants should be modeled using principles from the ecological succession theory that would relate the taxonomic structure with function and nutrient fluxes. A conceptual model of soil structure and soil stability is suggested that links the soil organic matter sub-model to an aggregation sub-model and a dynamic soil structure sub-model. The development of new generation soil ecosystem models is a necessary step to better quantify soil functions, assess possible soil tipping points, and develop methods to restore soil functions.

Keywords: Soil carbon; Soil nitrogen; Soil structure; Model; Feedback mechanisms

Contents

Abbreviations

POM   Particulate Organic Matter

SOM   Soil Organic Matter

1. Introduction

Food security, our ability to feed the ever increasing human population as well as satisfy the increases in the standard of living in developing countries, has been one of the great challenges of our times (FAO, 2011). The loss of fertile agricultural land to urbanization, in conjunction to pressures to increase biomass production for energy use, biofuel, has caused an expansion of agricultural lands to marginal areas unsuitable for cultivation. Soil ecosystem functions, food and biomass production, biodiversity, carbon sequestration, filtering and transformation, raw material and landscape, and heritage have significantly deteriorated worldwide during the past century due to agricultural intensification with dramatic consequences on carbon loss, loss of soil biodiversity, erosion, compaction as well as unsustainable use of water and mineral resources (Stagnari et al., 2009; Sapkota, 2012). Fig. 1 visually illustrates the impacts of tilling and agricultural practices in a olive grove in Crete, Greece. Similarly, lack of terrace maintenance combined with livestock grazing have caused failure of the terraces, soil erosion and general deterioration of the landscape (Fig. 2).

Conventional agriculture maintain yields by extensive use of fertilizers and energy (Heller, 2009; Tillman, 2010) which makes it overall unsustainable. Significant recycling of NPK nutrients is necessary to sustain global food production (Nikolaidis, 2011). Sustainable agricultural practices are necessary if we are to face the challenge of food security while preserving the integrity of soil and aquatic ecosystems. Conservation agricultural practices which are comprised of zero or minimum tillage, carbon amendments and crop rotations (Aune, 2012; Stagnari et al., 2009; Sapkota, 2012), holds great promise in delivering higher yields, using water and soil resources in a sustainable manner and increasing soil biodiversity (Saha, 2010).

An ecosystem is a dynamic complex of plant, animal and microorganism communities and the non-living environment interacting as a unit (Alcamo et al., 2006). Ecosystem shifts due to climate and land use changes have abrupt, long-lasting impacts to ecosystems and should be averted by

defining critical thresholds that provide sufficient response time for management (Biggs et al., 2009). The importance of improving the forecast reliability of ecosystem state, services and shifts has been highlighted by Clark et al. (2001) a decade ago and has since been the subject of many scientific and policy related manuscripts (Schroter et al., 2005; Butler and Oluoch-Kosura, 2006; Nelson et. al., 2006; Tallis and Kareiva, 2006; Carpenter et. al., 2006; Cowling et al., 2008; Steffen 2009; Allen et al., 2010; Kutilek, 2011).

There are two fundamental factors that impede our ability to detect and forecast ecosystem shifts: lack of monitoring data and scientific gaps regarding thresholds in the function of ecosystems. The limitation in the availability of monitoring data is best illustrated in the case of land use conversion. Limited chronosequence carbon and nitrogen data obtained after land use conversion from forest or grassland to crop land indicate rapid loss of bio-available carbon and nitrogen and deterioration of soil stability during the first few years after the conversion (i.e. Olson et al., 2005) suggesting a significant ecosystem shift. Soil-water-plant models have traditionally simulated conditions where the impacts of land use changes have reached a near-steady state condition and have not been tested adequately to evaluate the processes during the shifts (Nelson et al., 2006; Dawson and Smith 2007). Similarly, the models have failed to predict global shifts such as tree mortality due to climate change or account for the impacts of inorganic fertilization on soil plant and microbial biodiversity. Our inability to predict tree mortality has been associated with gaps in the understanding of the physiological thresholds and mechanisms of tree mortality as well as the inability to adequately model plant-soil interactions and feedback mechanisms (Allen et al., 2010). Similarly, plant species decline has been related to both high (U.K. grasslands - Stevens et al., 2004) and low-level (Minnesota prairie-grasslands - Clark and Tillman, 2008) atmospheric nitrogen inputs suggesting a narrow range of ecosystem thresholds (Rockstrom et al., 2009) that have neither been fully understood nor the respective processes incorporated into soil ecosystem models. These examples suggest that a new generation of soil models should be developed if we are to understand how to

reverse the impacts of land use conversion, redesign agricultural practices, and quantify the impacts of climate change to terrestrial ecosystems.

During the past decade, there has been an "explosion" in the number of review articles published in the scientific literature on terrestrial processes and modeling suggesting a growing demand within the scientific community for a better understanding of the unifying principles of soil ecology (Fierer et al., 2009). The objective of this review is to provide a synthesis of current knowledge on soil ecosystem processes and modeling with a focus on carbon and nitrogen dynamics and their link to soil structure, and propose a conceptual framework for model parameterization capable of assessing critical soil functions and potential shifts. It is not our intent to cite the thousands of articles of primary research, but rather to focus on review articles that discuss critically and in detail original research and synthesize the acquired knowledge of these reviews from the view point of modeling soil ecosystems.

2. Soil carbon and nitrogen dynamics

Carbon and nitrogen dynamics in terrestrial environments have been reviewed extensively in recent years (i.e. Jastrow et al., 2007; Trevenot et al., 2010; Sinsabaugh, 2010; McGuire and Treseder, 2010; Kuzyakov, 2010; Blagodatskaya and Kuzyakov, 2008; Gardenas et al., 2011; Schimel and Bennett, 2004; Nannipieri and Eldor, 2009; Geisseler et al., 2010; Knicker, 2011; Wu, 2011; Szanser et al., 2011). The following is a synthesis of the literature with an emphasis on elucidating the predominant state variables of the system and bridging the gap between scientific knowledge and manner in which organic matter is modeled.

2.1 Carbon dynamics in soils

Carbon dynamics in soils are driven by photosynthetically derived plant litter inputs and organic amendments to the soil system (Fig. 3). Plant litter is physically fragmented into Particulate Organic Matter (POM) which is composed of lignin, cellulose and hemi-cellulose (Trevenot et al., 2010).

Lignin is connected to cellulose and hemicellulose in the fiber walls of the vascular system of plants providing strength and rigidity. Lignin consists of aromatic rings that are chemically resistant to degradation and thus influence carbon turnover. Cellulose are polysaccharide, glucose chains, $(C_6H_{10}O_5)_n$, that comprise the structural material of the cell wall. On average, one third of all plant matter is comprised of cellulose, although there is high variability in the composition among vascular plants (i.e. Cotton has 90% cellulose content and trees 40-50%). Hemicellulose contains several short chain sugar monomers and binds together with pectin, a structural polysaccharide, to cellulose to form a network of cross-linked fibres (Trevenot et al., 2010).

Lignin degrades primarily through biotic, aerobic and co-metabolic processes although a few studies suggest anaerobic biodegradation and abiotic processes (Trevenot et al., 2010). Saprotrophic fungi and a few bacteria have been shown to degrade lignin, a process that is catalyzed by unspecific, extracellular enzymes like lignin or manganese peroxidase. Accumulation and stabilization of lignin in soil has been observed and attributed to clay-lignin binding, however, this process has not been elucidated adequately. Rapid turnover of lignin has been observed in agricultural soils suggesting large variability in degradation rates and the existence of two pools. Trevenot et al. (2010) concluded that there are gaps in our knowledge of the fate of lignin in soils associated with their stabilization in clay particles and that lignin should be considered as a state variable in carbon dynamic models.

The major pathways of POM decomposition and creation of humic substances has been reviewed in depth by Jastrow et al., (2007) and Wardle (2002). POM undergoes a biochemical alteration into smaller molecules mediated by fungi, bacteria and enzymes. The products of decomposition are sugars, polyphenols and quinones which are derived from the microbial decomposition of lignin. The products from microorganism lysis and released exudates are amino compounds, acids and sugars as well as nucleic acids and structural cell polymers. Linear chains (>250) of amino acids form proteins which are essential parts of microorganisms and plants participating in all processes within their cells. Amino acids are bonded together with peptide bonds (CO-NH amide moiety) to form the

protein chains. Many proteins are enzymes with specific roles in catalyzing chemical reactions within the cell or outside the cell which correspond to metabolic reaction and substrate utilization respectively. Other proteins are involved in signaling processes or as structural components of the cell. Rillig et al. (2007) classified proteins into two categories, the detrital proteins that are released after cell lysis and the functional proteins that include microbial surface-active proteins and extracellular enzymes. Finally, mycorrhizal fungi contribute glycoprotein complex molecules to the soil organic carbon pool through the release of exudates and products of fungal lysis. Condensation and polymerization reactions between the amino compounds, the sugars and the quinines and the lignins produce humic substances. Humic substances are associations of low molecular weight compounds stabilized by hydrophobic interactions and hydrogen bonds (Sutton and Sposito, 2005). Stevenson (1994) proposed four major humification pathways: i) the sugar-amine pathway, ii) the polyphenol-quinone pathway, iii) the lignin-quinone pathway, and iv) the modified lignin pathway. Further microbial degradation of humic substances results in CO_2 which closes the cycle.

The released enzymes mediate key carbon and nitrogen cycle processes involved in the decomposition and humification of organic matter (Sinsabaugh, 2010). Plants and microorganisms produce enzymes to mitigate oxidative stress, detoxify phenolic compounds and utilize carbon sources. Environmental factors such as oxygen availability, soil pH, mineral and organic matter composition as well as nitrogen enrichment regulate the overall enzyme activity in soils. The interactions between the biological and environmental factors produce positive and negative feedbacks that control the content of organic matter in soils.

Plant roots release exudates that can "prime" microbial activity (Kuzyakov, 2010; Blagodatskaya and Kuzyakov, 2008) and the phenomenon is especially significant in microbial hotspots where the activity is intense. The priming sequence involves: i) exudation of organics by the roots, ii) activation of microorganism (r-strategists, organisms that have the ability to reproduce quickly) by the availability of organics, iii) activation of fungi (k-strategists, organisms that have the ability to

compete successfully for resources), iv) production of enzymes by fungi to catalyze the decomposition of SOM, v) production of organics and nutrients, and vi) uptake of nutrients by roots (Kuzyakov, 2010). Gardenas et al., 2011 identified rhizosphere priming as one of the five most important knowledge gaps in our understanding of carbon and nitrogen interactions in soils.

Sorption of organic and organo-mineral compounds on clays and oxides is a significant chemical protection mechanism in the carbon cycle. Organic compounds bind to mineral surfaces through cation bridges, hydrogen bonding and van der Waals forces (i.e. Kleber et al., 2007). A number of factors such as pH, redox conditions, and the characteristics of mineral surfaces and of organic matter affect the degree of sorption and surface complexation of organics with mineral surfaces. The negatively charged surfaces of clay minerals bind with the negatively charged organic compounds through cation bridges (Jastrow et al., 2007). The availability of multivalent cations plays an important role in the formation of clay-cation-organic complexes. Similarly, the availability of iron and aluminum oxide surfaces bind organic compounds via electrostatic forces. Kleber et al. (2007) suggested a conceptual model of organo-mineral interaction in soils that consists of three layers, the contact zone, the hydrophobic zone and the kinetic zone. In the contact zone, organic functional groups form inner sphere complexes by binding directly to the surface. The hydrophobic zone is formed due to hydrophobic interactions of the organic functional groups in the contact zone and those in solution and the kinetic zone is formed due to cation bridging and hydrogen bonding between organics. Chemical protection of carbon is one of the mechanisms that increases carbon turnover time in soils. The other is physical protection in the soil aggregates and it will be discussed later in this review.

2.2 Nitrogen dynamics in soils

A new conceptual cycle of nitrogen dynamics in terrestrial systems is emerging based on the research conducted during the past two decades (Fig. 1). The following is a synthesis of several recent review

papers (Schimel and Bennett, 2004; Nannipieri and Eldor, 2009; Gardenas et al., 2011; Geisseler et al., 2010). Soil organic nitrogen being part of the humic substances is comprised of proteins, peptides and amino acids (40%), amino sugars (6%), heterocyclic N compounds (ie. Pyrines, 35%), and ammonia (19%) (Schulten and Schnitzer, 1998). The traditional view of the nitrogen cycle is that soil organic nitrogen is being mineralized to ammonia and ammonium ion due to microbial activity in the soils (Mineralization-Immobilization-Turnover route). Ammonium is then converted to nitrite and then to nitrate through the microbial assisted nitrification process. Denitrification converts nitrate to nitrogen gas and nitrous oxide. Microbial cell synthesis requires primarily ammonium uptake creating an immobilization mechanism, while plants uptake nitrate and ammonium for the development of plant tissue. Schimel and Bennett (2004) reviewed the literature of mineralization studies and suggested the need to revise the conceptualization of the N cycle by including the enzyme catalyzed de-polymerization of soil organic nitrogen into light molecular weight Org-N such as amino-acids and amino-sugars. They also suggested that plants uptake directly these monomeric Org-N compounds corresponding to an alternative direct route (Schimel and Bennett, 2004; Wu, 2011). This pathway of N immobilization appears to be very important in low-N systems. This uptake is facilitated by mycorrhizae (Manzoni and Porporato, 2009; Wu, 2011). Gardenas et al., (2011) have identified plant utilization of organic N priming as one of the five most important knowledge gaps in our understanding of carbon and nitrogen interactions in soils. Many field studies suggest that organic N utilization is a ubiquitous capacity of plants, being more important in cool and wet environments than hot and dry (Gardenas, 2011; Jamtgard et al., 2010; Ramirez et al., 2010). Nannipieri and Eldor (2009) focused on reviewing the mineralization-immobilization processes of N in soil and attempted to relate N turnover to the biota that conduct the transformation. They extended the view of Schimel and Bennett (2004) by identifying three pathways of org-N transformation: i) direct mineralization of org-N to ammonium by microorganisms, ii) release of org-N due to micro-organism lysis and exudates, and iii) excretion of ammonium by bacterial-grazing protozoa and nematodes. Two

additional processes have been suggested as being important in the microbial N transformation in soils: Nitrifier denitrification which is the oxidation of ammonium to nitrite followed by reduction of nitrite to nitrogen gas and anaerobic ammonia oxidation or Anammox (oxidation of ammonium to nitrite followed by reduction of nitrite to hydroxylamine; hydroxylamine then reacts with ammonium to form hydrazine which is oxidized to nitrogen gas and the released electrons are used to reduce nitrite). Geisseler et al., (2010) reviewed the pathways of nitrogen uptake by microorganisms in terrestrial environments and examined the relative importance between the direct route of org-N uptake versus the mineralization-immobilization-turnover route. Three factors were identified that determine the relative importance of the two routes in various ecosystems: the form of available N, the source of C, and the availability of N relative to C.

A synthesis of these reviews resulted in the following terrestrial nitrogen cycle. POM is decomposed by saprotrophic fungi to soil organic nitrogen. Microorganisms uptake and decompose POM. The products of decomposition contribute to the soil organic nitrogen pool as well as products from microorganism lysis and released exudates. Plant roots on the other hand release exudates that can "prime" microbial activity. Mycorrhizal fungi contribute to the soil organic nitrogen pool through the release of exudates and products of fungal lysis. Microorganism and fungal exudates include enzymes that catalyze the de-polymerization of soil organic nitrogen to amino-acids and amino-sugar type compounds. These compounds can be up-taken directly by the microorganisms and the mycorrhizal fungi/plants or follow the mineralization-immobilization-turnover process to ammonium. The nitrification process converts ammonium to nitrite and nitrate while denitrification nitrate to nitrogen gas. Ammonium and nitrate can then be up-taken by both microorganisms and mycorrhizal fungi/plants. To complete the list of nitrogen transformations in soils, one could add the two processes of ammonium conversion to nitrogen gas, nitrifier denitrification and anaerobic ammonia oxidation.

The interaction of the various nitrogen compounds with mineral surfaces should also be taken under consideration because it plays a role in the regulation of nitrogen transformation in soils by limiting its availability. Plant and microorganism exudates include protein N and peptide N which can absorb readily to clays due to their hydrophobic domains. Jamtgard et al., (2010) found that the concentration of bound amino acids in unfertilized soils were 50 times higher than the free amino acids in solution as well as higher than the ammonium and nitrate concentrations suggesting the importance of soils in regulating the availability of enzymes for soil organic matter decomposition.

2.3 Impact of bacteria, fungi, invertebrates and plants on the C and N dynamics

The role of bacteria and fungi in the dynamics of carbon and nitrogen cycles has already been discussed. They utilize and decompose organic matter and produce enzymes that assist in the humification process. In addition, they metabolize carbon and nitrogen for biomass formation. The lysis products of bacteria and fungi are very different in nature. Fungal cells are composed of complexes such as melanin and chitin (amino sugars) whereas bacterial cells primarily of phospholipids and peptidoglycan (Lorenz et al., 2007). Melanin and chitin do not degrade easily, while phospholipids are metabolized rapidly by other bacteria and grazers. Soil invertebrates such as protozoa and nematodes contribute significantly to plant litter decomposition and microbial population control through grazing (Jastrow et al., 2007). A detailed discussion of soil food web structure and dynamics is given by Wardle (2002).

A conceptual representation of the symbiotic relationship between ectomycorrhizal fungi and plants in a forested ecosystem has been reviewed by Courty et al. (2010). In addition to participating in the carbon and nitrogen cycles, mycorrhizal fungi contribute to soil functions by linking trees together through common mycorrhizal networks. Mycorrhizal community taxonomical structure and growth depends on the quantity and quality of tree photosynthetic activity, soil water, nutrient content and mineral composition. The taxonomic structure and the soil properties determine the functional

structure of the mycorrhizal community which in turn affects the mineral nutrition of the tree. The nutritional status of the tree controls its photosynthetic activity, closing in this way the feedback mechanism. Recent research (Bonfante and Genre, 2010) has identified selective transporters located in the fungal membrane that facilitate the translocation of carbon, nitrogen and phosphorous from the soil to the plant tissue, supplying the plant with nutrients. Fungi produce hyphal branching in the direction of root exudates in search of new root colonization suggesting direct signaling communication. Intracellular and intercellular hyphae colonization of the root provides large surface area for nutrient exchange. Plant growth-promoting bacteria that colonize the rhizosphere and the plants (endophytic colonization) compliment the role of fungi in the plant nutrition cycle. In addition, the endophytic bacteria have been shown to be capable of degrading contaminants (phytoremediation of organic pollutants) and contributing in this way to the defense mechanisms of plants (Compant et al., 2010; Cheng et al., 2010). Bacteria use extracellular (quorum-sensing) and intracellular signaling to assess the external conditions and react to environmental changes (Camilli and Bassler, 2006). Similar biochemical signaling exists between plant and microbe interactions (Baker et al., 1997). Feedback mechanisms in the plant-soil system (in terms of the physical, biochemical and biotic components of the soil) were reviewed by Ehrenfeld et al. (2005) in an attempt to critically appraise the system and identify new research directions (Table 1). There is strong evidence of feedback mechanisms in the plant-soil system which become more apparent in extreme environments and systems involving trophic interactions. There is a need to further study the feedback between soil structure and plant growth as well as the role of plant-microbial plasticity in enhancing or attenuating feedbacks.

2. 4 Modeling of carbon and nitrogen dynamics

In general, carbon models divide SOM into several pools one of which is the soil microorganism pool. Carbon in these pools is degraded as a first order process. This approach is also used in eco-

hydrological models (i.e. SWAT, Debele et al., 2008 or SWIM, Post et al., 2007) that simulate carbon, nitrogen and phosphorous dynamics at the watershed scale. They have been using a simplified parameterization of carbon and nitrogen in the soil that consists of recalcitrant and labile organic pools as well as the mineral pool. The use of the first order exponential model to describe the dynamics of carbon degradation even though it "fits the data" in many cases, it does not accurately reflect the dynamics of the process and alternate models have been proposed. These alternate models are based on the assumption of time-variable decomposition rate (Rovira and Rovira, 2010) or the incorporation of logistic functions, recognizing the existence of competitive strategies in soil (Gillis and Price, 2011). Carbon and nitrogen mineralization is considered the dominant process that drives the system. The most comprehensive parameterization regarding soil formation is presented in the SoilGen1 model (Finke and Hutson, 2008). SoilGen1 is an integration of a transport and speciation of inorganic anions model and a carbon cycle model. The one dimensional transport Richards' equation for transient flow is coupled with heat flow and the advective-dispersive equation for solutes. Major anions and cations are simulated and chemical speciation determines the precipitated and exchanged phase based on thermodynamic considerations. The carbon cycle model considers five carbon pools, the resistant and decomposable plant material, the microbial biomass, the humified organic matter and the inert organic matter. Mass changes due to bioturbation, organic carbon and precipitates are used to calculate changes in bulk density and porosity and thus soil evolution. In the models described above, the microorganism communities have been modeled in terms of biological carbon content using a static physiological state. Even though modeling of several bacteria and fungi communities shifting in composition or transition from an active to dormant state is still at its infancy, the approach holds great promise and should be further developed (Ingwersen et al., 2008).

To more accurately account for the turnover of carbon in arable soils, Kuka et al. (2007) developed Carbon turnover In Pore Space (CIPS) model. The model assumes that the biological activity is not distributed evenly in the pores which results in uneven oxygen distribution and

differences in decomposition rates. It considers three pore sizes, the micro-pores, meso-pores and macro-pores and four carbon pools corresponding to fresh, active, refractory and dissolved organic matter. In this way, soil carbon turnover time was related to physical measures of the soil system.

Modeling of carbon and nitrogen dynamics in terrestrial environments has also been reviewed extensively in recent years (i.e. Fallon and Smith, 2000; Manzoni and Porporato, 2009; Battle-Aguilar et al., 2010; Shibu et al., 2006; Minasny et al., 2008). Fallon and Smith (2000) reviewed 98 agro-ecosystem models in order to identify the shortcomings in modeling refractory soil organic matter and set priorities in research areas for future development. They concluded that processes of refractory SOM formation and protection are not clearly understood and models were limited in their ability to predict refractory SOM content and turnover because refractory SOM pools cannot be directly related to field measurements. Models need to account for carbon turnover with depth as well as for carbon stabilized on charged surfaces of iron oxides and clays. Manzoni and Porporato (2009) reviewed and classified 250 biogeochemical models in terms of their mathematical approaches to soil carbon and nitrogen dynamics. In addition, they analyzed the relationship between model structure and the temporal and spatial scale of its respective application. They identified the following theoretical gaps: i) mechanistic and scale dependent description of microbial mass and activity using dedicated state variables, ii) link decomposer activity and metabolism, nutrient availability, vegetation growth and climate dynamics using stoichiometric links, iii) soil food web dynamics instead of aggregated variables, iv) mechanistic and rigorous representations of small-scale processes that account for spatial heterogeneity, v) physical processes that affect soil structure (tillage, wetting and drying cycles and aggregate turnover) in the biogeochemical models, and vi) need to develop novel modeling approaches for scaling up pore scale dynamics to observational scales. Battle-Aguilar et al. (2010) reviewed carbon and nitrogen models for their ability to simulate land-use change conditions. The most common features of the mechanistic compartment based carbon and nitrogen models were the number of C and N pools, plant growth parameterization, parameterization of physical soil

parameters, simulation time step, interconnectivity of C and N cycles and simulation of hydrology and soil temperature. An example was used to illustrate the predictive ability of a model to simulate scenarios of carbon and nitrogen turnover in forested and agricultural land uses in different climatic conditions. They concluded that such models are a promising tool in the design of new soil practices and predicting the effects of the practices on soil fertility. Shibu et al. (2006) reviewed 20 process-based SOM dynamics simulation models in terms of their ability to simulate long term carbon and nitrogen dynamics in rice-based cropping systems. They concluded that no existing SOM model simulates properly lowland anaerobic conditions or alternate flooded and non-flooded conditions. It is suggested that the biochemical characteristics of SOM should be modeled explicitly in relation to their effect on yield. Finally, Minasny et al., (2008) reviewed the applicability of existing quantitative models for pedogenesis and suggested that an integration of state factor empirical models and energy and mass balance models could provide the analytical framework to model how soil horizons and profiles evolve in the landscape.

3. Soil structure modeling

Soil structure and in particular soil particle aggregation formation stability and turnover play a catalyzing role in soil erosion, nutrient cycling and soil fertility. There are tens of literature review manuscripts published during the past decade that review scientific work that supports overwhelmingly the relationship between soil structure and soil fertility (i.e Fallon and Smith, 2000; Manzoni and Porporato, 2009; Batlle-Aguilar et al., 2010; Abiven et al., 2009; Jastrow et al., 2007; Bronick and Lal, 2005; Ehrenfeld et al., 2005). The following is a synthesis of the literature with an emphasis on elucidating the predominant factors affecting soil structure, its relation to the carbon and nitrogen cycles and modeling approaches.

3.1 Factors affecting soil structure

Many factors play a significant role in the formation of soil aggregates and their stability such as the primary particles (clays-silt-sand) and their surface charges, organic matter available for decomposition (hydrophobic nature – attached to surfaces); bacterial biomass that utilizes the organic matter and produces exudates that catalyze the breakdown and transformation of organic matter; plant roots that also produce exudates, organic matter for decomposition and control the availability of water in the soil system, and fungi and other organic fauna such as invertebrates and worms (Ehrenfeld et al., 2005). There are two basic mechanisms of aggregate formation (Abiven et al., 2007; Abiven et al., 2009). The first mechanism proposes that microaggregates (<250 μm) consist of organic molecules that are bound to clays and polyvalent cations to form an organo-mineral complex. Organo-mineral complexes then combine to form macroaggregates. The second mechanism proposes that macroaggregates are formed around particulate organic matter (POM). As POM is decomposed bacterial colonies form and bind clay particles with their exudates. Particle enmeshment to the macroaggregate is facilitated by roots and fungal hyphae that release exudates that bind particles. In this way, stable microaggregates are formed within the macroaggregate and as decomposition (carbon turnover) progresses they are released. The stability of aggregates and their turnover greatly depends on the quantity and quality of organic matter and plant litter added to the soil (Abiven et al., 2007; Abiven et al., 2009). However, abiotic factors such as soil texture are more important for determing soil aggregation than biotic factors (Barto et al., 2010). Earthworms contribute greatly to soil aggregation by utilizing plant litter together with soil, passing it through their gut and excreting casts (Six et al., 2004). Casts mediate both microaggregate and macroaggregate formation in soils the stability of which depends on the quality of organic material consumed by earthworms. In addition, earthworms contribute to aggregate formation due to burrowing activities where they deposit mucus on the burrow walls which together with the soil clays can form a stable structure (Six et al., 2004). Roots influence soil aggregation through entanglement of soil particles with the mycorrhizal-root system as well as through root exudates (Jastrow et al., 2007; Six et al., 2004). Table 2 presents an

overview of the factors (Bronick and Lal, 2005) that must be considered in the formulation of soil stability and soil fertility models. Microaggregates and macroaggregates provide a physical protection from decomposer activity to the soil organic carbon and nitrogen incorporated in them and influence carbon and nitrogen turnover in soils. Decomposer activity is limited in the aggregate structures due to oxygen and water availability, and enzyme accessibility (Jastrow, 2007). Fig. 4 is a photograph of macroaggregates developed in an uncultivated olive grove in Crete, Greece. Fungal hyphae and roots participate in the aggregate formation and they are visible in the upper part of the photograph.

A critical review of the scientific literature (Bronick and Lal, 2005; Allen et al., 2010; Six et al., 2004; Alaoui et al., 2011) suggests that even though there has been significant progress in the understanding of soil processes, a comprehensive understanding of how these factors contribute to soil aggregation is lacking. For instance, a fundamental framework that would explain why some crops are more effective in structural development than others or how insecticides and fungicides affect aggregate formation is lacking. The link between soil structure and agricultural practices should be approached from a fundamental perspective if we are to make progress in developing sustainable crop management systems.

3.2 Soil structure modeling

During the past decade, there were five papers that dealt explicitly with soil aggregate modeling (De Gryze et al., 2005; Plante et al., 2002; De Gryze et al., 2006; Abiven et al., 2008; Malamoud et al., 2009). The models can be classified into four classes: empirical, mechanistic, deterministic soil aggregate models and deterministic soil structure models.

3.2.1 Empirical models

De Gryze et al. (2005) developed two empirical models, a linear regression and a 3-parameter sigmoidal curve model to fit the rate of increase of water stable aggregates due to POM addition. Abiven et al. (2008) following a different approach developed an empirical model where Monnier's

conceptual description of variations in aggregate stability for different organic substrates was formalized and applied to field conditions. The following log normal function was fitted to the field data: $AS(t)=A \exp\{-0,5 \exp[\ln(t/C/B)]^2\}$ where A is a function of the lignin content, B of the polysaccharide content and C of the cellulose and hemicelluloses content. In order to apply the model to field conditions, factors that account for the effect of soil moisture, soil temperature and soil N availability on carbon decomposition were used to adjust the aggregate stability function. These models represent the first attempt to model aggregate stability dynamics after the incorporation of organic residues.

3.2.2 Mechanistic models

Plante et al. (2002) assumed four water stable aggregate classes (<1 mm, 1-2 mm, 2-4 mm, and >4 mm) and described the flows between the classes using first order kinetics. They assumed six potential aggregation (outward flows) and six breakdown (inward flows) movements between the four classes as part of the "fully developed" conceptual model. The model was calibrated using data for two soils after tilling. De Gryze et al., (2006) used this model to calculate micro-aggregate and macro-aggregate turnover times. The soil sample was homogenized with rare earth powders as tracers to test the assumptions involved in modeling. Mechanistic models were shown to provide valuable information on the microaggregate and macroaggregate stability and turnover, confirming the assumptions that microaggregate turnover is higher than the macroaggregate one.

3.2.3 Deterministic soil aggregate models

De Gryze et al. (2005) wrote a mass balance on the rate of soil aggregation by assuming that the rate of aggregation is proportional to mass of non-aggregated soil minus the mass of aggregate breakdown that is proportional to the aggregate mass: $dM/dt = fU-bM$ where M is the macroaggregate content of the soil, U is the non-aggregated soil content, f is the rate of formation and b is the rate of breakdown. Mass conservation is assured by M+U=100%. The solution of the mass balance is an "exponential increasing to maximum" curve. As an alternative to this model, the authors assumed that the rate of

aggregate formation is proportional to microbial activity in the soil, C. f=kC(t-t_0), where t_0 is a time lag between microbial activity and aggregate formation. A measure of microbial activity can be considered the respiration rate.

3.2.4 Deterministic soil structure models

Malamoud et al. (2009) modified the RothC-26.3 model (Coleman and Jenkinson, 1999) to accommodate the concept of size hierarchy for the physical protection of aggregates and developed aggregation and porosity sub-models in order to model aggregate fractionation and carbon content, aggregate turnover time and changes in the porosity of the soil. The new model, named Struc-C, was then used to model data from an agricultural land and a woodland located in temperate climate with significant oceanic influence (UK) in the first and to a lesser extent (Australia) in the second (Paul et al., 2002). The model defined three aggregate fractions with corresponding three aggregate carbon types and complexed clay distributed in these three fractions assuming constant partitioning with soil organic carbon for each fraction. Once the organo-mineral aggregates have been calculated, the porosity submodel estimates the bulk density of each of the three aggregate types assuming pyramidal, tetragonal and cubic packing respectively and then the new porosity of the soil. The major limitations of the model as outlined by its authors relate to the following: i) the relation between input residue and soil organic carbon is not linear and the quality of the input is not addressed, ii) geochemical factors that influence soil structure such as type of clay, iron oxide sorption, pH etc are not included in the formulation, and iii) aggregate parameters do not vary with space and time. Even though these are significant limitations of the model, Struc-C is the most comprehensive model regarding soil aggregate stability and turnover as well as soil structure in the scientific literature thus far.

So far models have aimed at describing the rates of aggregate formation and turnover. A number of processes that are significant and affect aggregate formation and stability have not been included (Malamoud et al., 2009; Ehrenfeld et al., 2005) such as:

- Explicit formulations of aggregate stability as a function of residue type

- Cations and charged surfaces explicitly (acid-base chemistry, CEC, pH)

- Soil moisture impacts and wet-dry cycles

- The concept of Water Stable Aggregate

- Plant and bacterial exudates

- POM composition and decomposition products (lignin, cellulose, polysaccharides)

- Plant and fungi impact to Water Stable Aggregates due to moisture re-distribution

- Antagonistic and synergistic effects on Water Stable Aggregates

- Feedback mechanism

Bacterial communities, soil fauna and plants participate in both synergistic and antagonistic ways in "building" (aggregate formation) their soil micro-environment as well as in the "quality" (aggregate stability) of the construction. If one considers that the rate of microbial reproduction is at the 20 minute time-scale, then the life-cycle of the aggregates which corresponds from weeks to months is very long. In order to model aggregate stability, the soil ecosystem state variables should include the "building materials" such as lignin, cellulose, polysaccharides, acid-base and interfacial chemistry concepts and the synergistic and antagonistic effects of the terrestrial ecology fauna.

4. Future directions of soil ecosystem modeling

The complexity of the soil-water-plant-organism system is overwhelming, and even though ecological and biogeochemical research has made significant strides during the past decades, we still have significant knowledge gaps in understanding the fundamental functioning of the system (Gardenas et al., 2011). This has been stressed in a special issue of the journal of Science, where soils have been identified as "the final frontier" (Science, 2004). There is an emerging consensus that the diversity of life in soil is a key factor determining soil functions and the life-sustaining processes (Crawford et al., 2005). The synergistic and antagonistic processes between bacteria and plants and

fungi and plants are partially understood and more importantly the community lacks the knowledge to predict if and when these processes fail and any related potential ecosystem shift. Current modeling approaches treat carbon, nitrogen and soil structure for the most part separately without incorporating feedback mechanisms. For instance, recent research (Ramirez et al., 2010) suggests that inorganic nitrogen fertilization directly affects microbial respiration rates by up to 60% regardless of the form of nitrogen addition and that fertilization influences the C and N pools in the aggregates (Chen et al., 2011). Such common perturbation of soil systems as agricultural fertilization, cannot be modeled properly because the cause and effect relationships have not been determined. A revised modeling framework is necessary to be developed that would synthesize current understanding of soil functions. We propose this modeling framework be developed along the following three axes:

Emerging ecosystem state variables – A synthesis of the carbon and nitrogen cycles emerging from this review is presented in Fig. 1. Carbon and nitrogen dynamics are interlinked and can only be separated after the production of humic substances by condensation and polymerization reactions (Batlle-Aguilar et al., 2010). The enzyme catalyzed de-polymerization of humic substances separate the nitrogen from the carbon cycle by creating light molecular weight organic nitrogen compounds that can be mineralized into ammonium and follow the remaining reactions in the known nitrogen cycle. State variables in soil ecosystem models should be selected in a way that link carbon and nitrogen dynamics with soil structure and the biological community. We propose that carbon and nitrogen state variables be linked directly with the composition and quality of plant litter and organic matter input to soil. Soil ecosystem state variables should be comprised of the following:

- the components of the decomposition of particulate organic matter such as lignin, quinone, polyphenols, sugars, amino compounds, glycoprotein, humics, light molecular weight organic N compounds, ammonium ion, nitrite and nitrate,
- the biomass of the soil food web such as microorganisms, saprotrophic fungi, mycorrhizal fungi and other terrestrial species and

- the enzymes produced by microbial and fungal lysis and root exudates.

The adaptation of the proposed state variables in the new generation soil models would be a strategic decision by the soil science and agricultural engineering community because it will require extensive modifications in the design and execution of field studies since current approaches do not measure specifically for these variables.

Modeling ecology of life in soils – Biological diversity dynamics and their interaction with the physical and chemical microenvironments are emerging as the principal factor determining soil functions Barot et al., 2007; Wu et al., 2011; Zhang and Xu, 2008). Plant feedback mechanisms with the physical, chemical and biotic soil components are critical processes especially in extreme environments that should be considered in soil ecosystem models. The symbiotic relationship between bacteria, fungi, and plants should be modeled using principles from the ecological succession theory that would relate the taxonomic structure of the various species with their respective function in the ecosystem and the necessary nutrient fluxes to maintain it. It is necessary to view the ecology of life in soils as an "intelligent" living system within which each species actively functions towards building its own niche, understanding the symbiotic and antagonistic relationships with other species in terms of their own survival and the survival of the system and participate fully in sustaining soil ecosystem functions (Gillis and Price, 2011). It is also important to assess the capability of soil microbial communities to adapt to changing environmental conditions and the dynamics of turnover at different time scales (Schmidt et al., 2007). Soil ecologists and biologists should join their experiences and propose modeling approaches that would capture the complexity of the life in soils.

Modeling from first principles - Modeling soil structure and relating soil stability to carbon and nitrogen dynamics would require a first principles approach where the interaction within and between the various components of the system (clay particles, organic matter, terrestrial organisms etc.) are modeled using the fundamental principles that govern the system. Fig. 5 presents a conceptual model

of soil structure and soil stability similar to the one developed by Malamoud et al. (2009). The SOM sub-model (Fig. 1) should be linked to an aggregation sub-model and a dynamic soil structure sub-model. The particle distribution of the original mineral matrix will undergo physical aggregation due to charged surfaces that can be described and modeled with well developed geochemical principles. On the other hand, SOM fractions that will parameterize the SOM sub-model will partition to clay particles and clay aggregates due to their hydrophobic nature. Microbial decomposition will initiate the aggregate formation and breakdown mechanism as described earlier. Plant roots and soil biota will contribute in the formation of the aggregates and the quality of processed plant litter will determine the rate of aggregation and the strength of the aggregates. The aggregate fractionation should then be evaluated in terms of its stability using empirical meta-models derived from water stable aggregate studies and the physical changes to soil structure including changes in bulk density, porosity and change of volume.

5. Conclusions

In this review, a conceptual modeling framework is proposed, developed along the three axes: incorporate emerging ecosystem state variables, account for the ecology of life in soils, and model processes from first principles. In particular, the following are proposed:

- the dynamics of the carbon and nitrogen cycles to be interlinked,

- soil ecosystem models should be developed with state variables that link carbon and nitrogen dynamics with soil structure and the biological community,

- principles from the ecological succession theory that relate taxonomic structure with function and nutrient fluxes should be used to model plant feedback mechanisms with the physical, biochemical and biotic soil components and the symbiotic relationship between bacteria, fungi and plants, and

- a conceptual of soil structure and soil stability model is suggested that links dynamically soil organic matter to soil aggregation and structure.

The development of a new generation of soil ecosystem models is a necessary first step in order to quantify soil dynamics, understand soil tipping points, identify soils at threat and develop methods to restore soil functions.

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Table 1

Summary of feedback mechanism in the plant-soil system (Ehrenfeld et al., 2005)

Plant feedbacks with physical soil components

Soil moisture feedbacks
- Capacity of plants to alter the distribution of water in soil
- Plant adaptation to water stress
- Arbuscular mycorrhizae promote hydraulic lift, modify soil hydrophobicity, change water routing

Soil aggregates
- Roots contribute to SOM input
- Root exudates stimulate soil aggregation

Temperature
- Shading by litter and aboveground biomass
- Changes in albedo

Plant feedbacks with biochemical soil components

Soil acidity
- Plant adaptation to pH involve complex biochemical, physiological and mutualistic pathways
- Small pH changes affect plant growth
- Plants participate in the acidification of soil

Cations
- Metal hyper accumulation feedback
- Plants affect soil cation concentration through mineral weathering, uptake and redistribution
- Plants affect soil redox conditions and redox sensitive metals

Carbon and nitrogen
- Litter input affects microbial mineralization
- Feedbacks that regulate the supply of nutrients
- Plant affects carbon and nitrogen storage in soil

Plant feedbacks with biotic soil components

Microbial community structure feedback
- Sensitive to plant species
- Rhizosphere microbes respond to plant exudates due to plasmids with genes
- Quorum sensing mechanisms for regulating expressions of trait
- Plant protein can disrupt the plant-microorganism "dialogue"

Mutualistic feedback
- Communication through molecular and genetic feedbacks
- Root exudates promote the growth of disease suppressing bacteria
- Mycorrhizal mutualism operates at the level of individual plants and affects plant growth

Feedbacks with pathogens, parasites and hervivores
- Attack plant tissue
- Affect tree seedling
- Promote the invasion of exotic species

Feedbacks with Invertebrates
- Part of feedback loops linking carbon, nitrogen, microorganisms and plants
- Soil food web affects plant growth
- Invertebrate predation on soil microbial biomass affects nutrient mineralization rates

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Table 2

Factors affecting soil structure (Bronick and Lal, 2005).

Climate and exogenous factors

Climate and Terrain
- Temperature and moisture regimes (wet-dry and freeze-thaw cycles) affect biological activity
- Wet-dry cycles affect particle aggregation and stability
- Wet-dry cycles affect carbon protection
- Elevation, aspect and slope affect vegetation and erosion

Soil properties

Soil texture
- Plant adaptation to pH involve complex biochemical, physiological and mutualistic pathways
- Small pH changes affect plant growth
- Plants participate in the acidification of soil

Cation exchange capacity
- Metal hyper accumulation feedback
- Plants affect soil cation concentration through mineral weathering, uptake and redistribution
- Plants affect soil redox conditions and redox sensitive metals

Soil pH
- Litter input affects microbial mineralization
- Feedbacks that regulate the supply of nutrients
- Plant affects carbon and nitrogen storage in soil

Agents of aggregation

Organic and inorganic carbon
- Creates hot spots of aggregation
- Composition affects aggregate stability and turnover
- Increases microbial biomass
- Particulate organic carbon acts as the nuclei for aggregation
- At low organic carbon levels, carbonates decrease carbon mineralization
- High levels of carbonates in silt decreases aggregation and stability

Clays
- The degree of aggregation, stability and carbon turnover depends on the content of clay in the soil
- Clay mineralogy and surface properties affect soil development
- Affects the rate of decomposition of organic matter

Cations
- Improve soil structure through cationic bridging with clays and organic matter

Biotic influences

Plants and plant roots
- Water stable aggregation is related to the composition of plant residue
- Root exudates act as binding agents
- Roots enmesh particles and improve stability

Microorganisms (bacteria and fungi)
- Fungal and bacterial exudates (polysaccharides) act as binding agents
- Fungal hyphae enmesh particles and improve stability

Soil fauna (insects, anthropods, earthworms, nematodes and termites)
- Attack plant tissue
- Affect tree seedling

Fig. 1. Impacts of tilling and agricultural practices in a olive grove in Crete, Greece. Top soil has eroded around the roots of the tree.

Fig. 2. Abandoned agricultural terraces in Crete, Greece. Lack of terrace maintenance combined with livestock grazing have caused failure of the terraces. Soil erosion and degradation leads to desertification of the land.
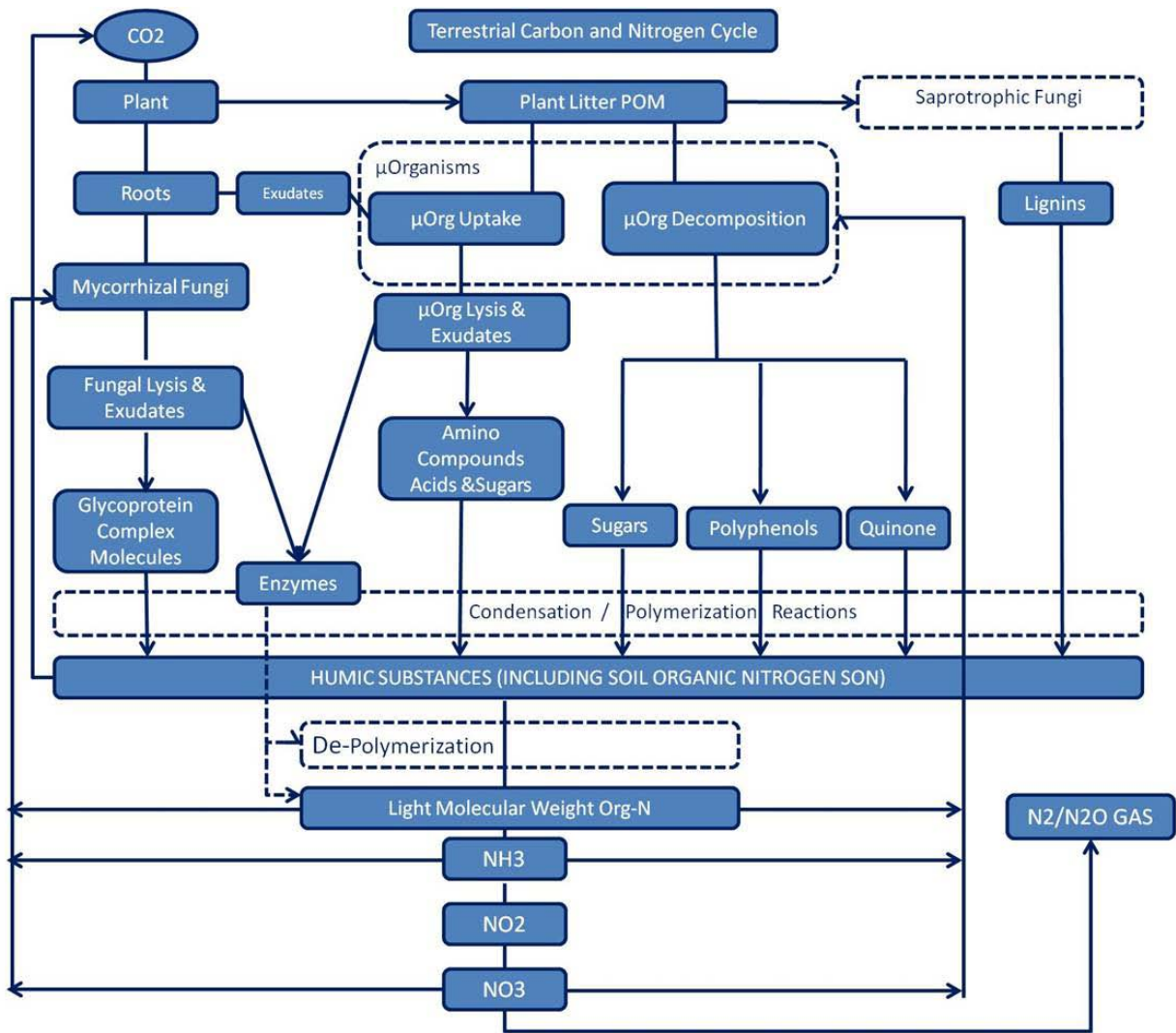
Fig. 3. Schematic representation of the combined carbon and nitrogen cycles in soils. The combined cycles were obtained by taking the point of view of terrestrial biota and follow the fate of organic matter in soil. The nitrogen cycle emerges as a separate entity after the humification process.

Fig. 4. A photograph of macroaggregates from an uncultivated olive grove in Crete, Greece. Fungal hyphae and roots are visible in the upper part of the photograph.
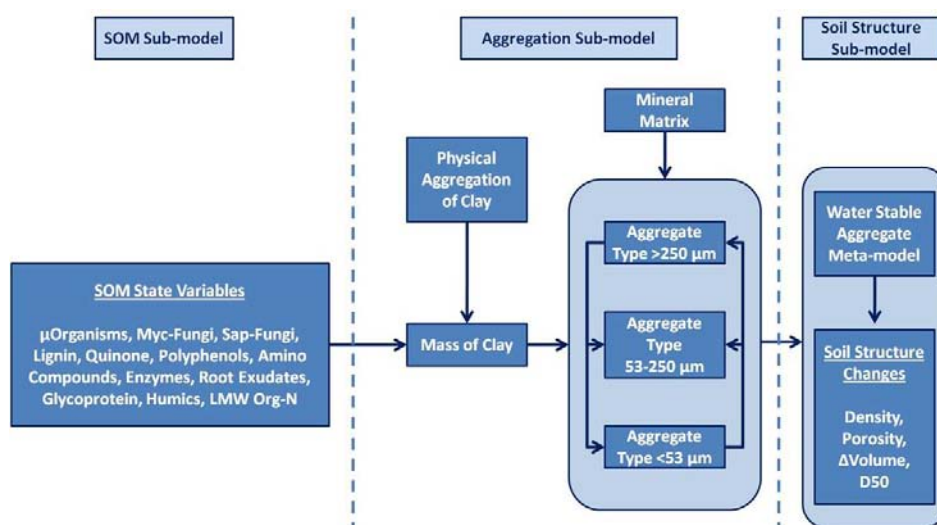

Fig. 5. Schematic representation of a soil structure conceptual model.