Received Date:-12-Sep-2014

Revised Date:-01-May-2015

Accepted Date:-10-May-2015

Article Type:- Research Review

Terrestrial and Marine Perspectives on Modeling Organic Matter Degradation Pathways

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Abstract

Organic matter (OM) plays a major role in both terrestrial and oceanic biogeochemical cycles. The amount of carbon stored in these systems is far greater than that of carbon dioxide (CO_2) in the atmosphere, and annual fluxes of CO_2 from these pools to the atmosphere exceed those from fossil fuel combustion. Understanding the processes that determine the fate of detrital material is important for predicting the effects that climate change will have on feedbacks to the global carbon cycle. However, Earth System Models (ESMs) typically utilize very simple formulations of processes affecting the mineralization and storage of detrital OM. Recent changes in our view of the nature of this material and the factors controlling its transformation have yet to find their way into models. In this review, we highlight the current understanding of the role and cycling of detrital OM in terrestrial and marine systems and examine how this pool of material is represented in ESMs. We include a discussion of the different mineralization pathways available as organic matter moves from soils, through inland waters to coastal systems and ultimately into open ocean environments. We argue that there is strong commonality between aspects of OM transformation in both terrestrial and marine systems, and that our respective scientific communities would benefit from closer collaboration.

Introduction

Anthropogenic release of CO_2 to the atmosphere perturbs the global carbon (C) cycle and alters feedbacks between components of the global climate system, such as the production and decomposition of organic matter (OM). Annual global production of organic carbon (OC) through photosynthesis is divided almost equally between terrestrial and oceanic ecosystems (Table 1) with about 56% of this material entering the detrital OC pool (Cebrian & Duarte, 1995). Globally, detrital OC pools are larger than (soil OC) or comparable to (oceanic OC) the atmospheric CO_2 reservoir (Table 1). Respiration of detrital OC from terrestrial soils (60 – 75 Pg C y^{-1}) is comparable to that from the world's oceans (70 – 80 Pg C y^{-1}), with both being approximately an order of magnitude larger than fossil fuel emissions (Ciais et al., 2013). The size of these detrital pools and magnitude of the fluxes makes it critical to develop a mechanistic understanding of the processes regulating them, so as to accurately predict how the large natural flux of C to the atmosphere will be altered under a changing climate.

Decomposition (mineralization) of detrital pools in both marine and terrestrial systems is regulated by a complex interplay between physical and biological mechanisms (Box 1). Accurate representation of these processes and feedbacks runs afoul of the tension between developing comprehensive models on the one hand, and the availability of computational resources and observational constraints on the other. The accuracy of Earth System Models (ESMs) used to simulate the coupling between physical and biogeochemical processes in the climate system depends partly on understanding and quantifying the mineralization processes transforming non-living OM to CO_2, and the feedbacks between these processes and the atmosphere (Ciais et al., 2013). Current ESMs provide reasonable estimates of global annual primary production, though with considerable scatter, but have difficulties accurately predicting spatial and temporal patterns of OC storage and mineralization (Duteil et al., 2012; Anav et al, 2013; Bopp et al., 2013; Moore et al., 2013; Todd-Brown et al., 2013; Cabré et al., 2014).

Recent developments in our understanding of detrital OM, as well as advances in microbiology and model development, provide the opportunity to improve the representation of mineralization processes within ESMs. Here we review the physical, chemical, and biological processes that result in the degradation and oxidation of detrital OC both in terrestrial soils and the marine environment, concentrating on how these processes are currently represented in models. We devote attention to bridging the distinct methodological and linguistic differences that separate the terrestrial and marine scientific communities. We highlight areas of similarity and difference, areas where each community can learn from the other, and we make recommendations on fruitful approaches that can be drawn from either community.

Sources & Composition of Detrital Organic Matter

Detrital C in the biosphere exists in a variety of chemical and physical forms (Table 1), with a multitude of pathways transforming material between them and atmospheric C pools (Fig. 1). Operationally, OC can be divided into dissolved (DOC) and particulate (POC) pools (Hedges, 2002), but differences in terminology and methodology make direct comparison of terrestrial and oceanic OC pools difficult (See Box 1). Consequently, the OC pools represented in models differ between the terrestrial and marine communities.

Photosynthetic organisms provide the OC inputs to both terrestrial soils and marine systems (Fig. 1). Primary production in terrestrial systems is mainly conducted by relatively long-lived, multi-cellular plants, with litter, roots, and root-zone exudates providing the main OC inputs to soils. Microbial byproducts (exudates and necromass), produced during the decomposition of plant materials represent a substantial portion of the OM stored in soils (Schmidt et al., 2011) and are an important C source for mineralization by soil microorganisms. In contrast, primary production in marine systems is dominated by single celled organisms (phytoplankton), leading to a faster turnover time of biomass than seen in terrestrial systems (~days as opposed to weeks, months or years) (Trumbore, 2009; Hansell, 2013). Organic C inputs to the marine environment mainly include cells and their exudates, and material transformed by heterotrophic organisms (e.g. zooplankton fecal pellets, discarded animal feeding structures etc. (Nagata, 2000)).

Chemically, OC in both systems ranges in size and complexity from simple monomers to mixtures of large biopolymers and humics (Hedges and Oades, 1997; Hedges et al., 2000). These compounds are found at various stages of degradation, from recently-deposited, readily available OC with fast turnover times (seconds to years) to highly processed material bearing little resemblance to the compounds from which it was derived, having turnover times of decades to millennia (Baldock et al., 2004; Trumbore, 2009; Hansell, 2013). Understanding the extent to which chemical structure determines the stability of OC is vital for calculating C storage dynamics both on land and in the oceans (Baldock et al., 2004).

The interplay between abiotic (e.g., aggregation) and biotic processes can differ in the two environments and fundamentally affect degradation and mineralization rates. Most ESMs divide OC pools based on chemical lability, even though this understanding of recalcitrance is currently being re-examined (Stockmann et al., 2013). The historical view, in terrestrial systems at least, was that the molecular structure of organic materials was a primary control on the formation and stabilization of soil OM (Marín-Spiotta, 2014). However, new observations demonstrate that physicochemical and biotic factors, rather than chemical recalcitrance, are the predominant controls on C cycling in soils (Schmidt et al., 2011). While this emerging view is starting to be incorporated into ecosystem models (Wieder et al., 2014), that is not yet the case for current Earth system models (Table 2), though it is built in to some recent ecosystem models (Wieder et al., 2014).

The chemical composition of OC is broadly classified in terms of polysaccharide, protein, lipid/aliphatic and lignin compounds (Kögel-Knabner, 2002; Whitehead et al. 2008). However, the composition of OM derived from primary production differs substantially between terrestrial and marine ecosystems, with terrestrial OM inputs containing a larger fraction of carbohydrate-rich structural components, whereas marine OM contains more protein-rich material (Nelson & Baldock, 2005; Arrigo, 2005; Whitehead et al., 2008). Primary producers in both ecosystems are enriched in labile sugars, starches and proteins, the majority of which are preferentially mineralized by microorganisms (Benner, 2002; Grandy & Neff, 2008). In marine environments, sinking OM is enriched in amino acids and polyunsaturated fatty acids relative to suspended OM and tends to be rapidly degraded in the water column (Benner, 2002; Wakeham et al., 1997).

Degradation rates of organic compounds in terrestrial and marine systems decrease with depth and time and are controlled by the interplay between the OC biochemical composition and factors such as temperature, physical accessibility, microbial community structure, and nutrient availability (Heal et al., 1997; Jobbagy & Jackson, 2000; Kujawinski, 2011, Dungait et al., 2012). The degradation pattern of detrital OC is often described in models using first order kinetics. However, the OC pool consists of many distinct molecular species, the majority of which are uncharacterized and which degrade at different rates (Boudreau and Ruddick, 1991,Vähätalo et al, 2010). Although residence times of OC vary, the average residence times, determined by radiocarbon dating, of the largest OC pools (deep soil OM, marine sediments, deep oceanic DOC) are all on the scale of thousands of years (Bauer et al., 1992; Schmidt et al., 2011), suggesting similarities in the factors controlling OC turnover on those scales, though these time scales are averages, combining compounds with residence times of minutes to those with degradation timescales of thousands of years.

Mineralization: Processes and Transformations

Radiocarbon dating of OC in soils and oceans shows that, in general, the age of OC increases with depth. The average radiocarbon age of deep ocean DOC in the Atlantic and Pacific Oceans ranges from 4000 – 6000 years (Bauer et al., 1992), suggesting that the majority of DOC in the oceans takes on a truly recalcitrant chemical nature (Kujawinski, 2011). Similarly, ages of the deep, stable component of soils varies from a few centuries in tropical soils to up to 3000 years in temperate soils (Hsieh, 1996). Microbes rapidly degrade labile OC in both soils and marine systems, altering the chemical composition of the OC and leaving a mixture of less labile material and microbial-derived compounds, the proportions of which increase with OC age and with depth (Grandy & Neff, 2008; Jiao et al, 2010). For example, microbes produce polysaccharides that, in soils can persist for decades (Kiem & Kögel-Knabner, 2003; Schmidt et al., 2011). In the oceans, the proportion of carbohydrates in DOC decreases with depth indicating that these dissolved sugars can serve as an important substrate for microbes in the deep ocean, albeit at very low rates (Kaiser & Benner, 2012). Further, studies of deep ocean DOM suggest the predominant biomolecular structure to be predominantly microbial derived carboxylic-rich alicyclic molecules (Hertkorn et al., 2006).

Whereas there is some evidence that the dominant process stabilizing DOM in the deep ocean is alteration into a chemically recalcitrant form, there is increasing evidence that chemical recalcitrance is not the primary process that stabilizes C on long time scales in soils (Marschner et al., 2008; Schmidt, et al., 2011). If chemical recalcitrance does not provide stability to OC in either system, then changes in biotic communities and climate conditions may make long-lived C pools vulnerable to degradation and thus result in climate feedbacks. This is currently hypothesized to have occurred during an Eocene global warming event where otherwise recalcitrant pools of marine DOC were mineralized, releasing CO_2 into the atmosphere and raising global temperatures (Sexton et al., 2011).

Soil OC (SOC) is more likely to be stabilized by binding to mineral complexes (Kögel-Knabner et al., 2008) or by being physically protected within aggregates, and if climatic conditions (Schmidt et al., 2011) or energy limitation of the microbial community (Ekschmitt et al., 2005; Fontaine et al., 2007) permits, even old SOC can turn over rapidly regardless of presumed chemical recalcitrance (Marín-Spiotta et al, 2014). Soil aggregates, comprised primarily of mineral particles, provide regions of physical protection for OM and areas of OM binding to mineral surfaces (Fig. 1). This has led to the suggestion that degradation of OM in soils might be better viewed as a “logistical problem” involving microbial ecology, diffusion limitations, enzyme kinetics, environmental factors, and physical protection (Kleber, 2010; Stockmann et al., 2013). Moreover, soil aggregates exert an important control on lateral OC fluxes through their role in selective transport by water erosion. The role of aggregates in marine systems is slightly different, but can also be viewed in terms of reducing the exposure of OC to heterotrophic microbial communities. In contrast to soil aggregates, marine aggregates are primarily composed of biological components (e.g. algal cells, fecal pellets etc.) brought together through physical aggregation, by the formation of fecal pellets, or through being trapped on discarded feeding structures. The effect of aggregation is to increase the settling velocity of the individual particles caught up in the aggregate, allowing it to travel deeper into the ocean without being mineralized. Calcium carbonate and biogenic silica, parts of many algal cells, may also provide physical protection (Hedges et al., 2001; Armstrong et al., 2002). As with soil systems, the mineralization of this material now becomes a logistical problem involving the rates at which organisms can find and process these sinking particles (Herndl and Reinthaler, 2013). The stability of deep ocean DOC makes the partitioning of DOM into a surface-derived semi-labile OM pool, and a deep recalcitrant OM pool of particular interest (Hansell, 2013).

Environmental drivers can affect mineralization rates by either forming physical barriers to mineralization, or by affecting physical processes that help drive mineralization. In the marine environment, seasonal water column stratification and/or horizontal and vertical transport away from regions of origin can alter mineralization times of oceanic OM (e.g. Carlson et al., 1994), as can macronutrient availability and microbial community composition (Kujawinski, 2011). In the deep ocean where OM concentrations are generally low, diffusion limitation has also been suggested to limit OM mineralization (Kattner et al, 2011). Diffusion limitation of C within soils has also been suggested as a mechanism to explain changes in SOC mineralization when dry soils are wetted (Xiang et al., 2008).

Photodegradation also contributes to OC decomposition in marine and terrestrial ecosystems, though it may be more important in the former because of the greater depth of light penetration. Sunlight alters the rate of detrital OC degradation directly by oxidizing it to inorganic forms (e.g. CO_2) and indirectly by producing free radicals and reactive oxygen species (ROS) changing degrader and primary producer communities, and altering detrital OC chemical composition (Rozema et al., 1997; Searles et al., 2001; Xue et al., 2005; King et al., 2012). The best-documented effects come from aquatic ecosystems, where there are clearly documented differences in the rates of photo-oxidation of aquatically-derived OM versus terrestrially derived OM (Obernosterer and Benner, 2004). As UV penetrates through the water column, it produces free radicals and ROS that destabilize OC and can increase decomposition rates (Sepp et al., 2011). Organic carbon compounds capable of absorbing UV wavelengths, such as chromophoric dissolved organic matter (CDOM), are bleached and degraded, providing a large influx of bioavailable OC to microbial decomposers (Sepp et al., 2011). Sunlight can also induce biological polymerization and condensation of OM into recalcitrant materials (Harvey et al., 1983, Mopper et al, 2015) and decrease microbial decomposition by competing for substrates and causing oxidative stress (Scully et al., 2003; Lesser, 2006).

In marine systems, direct photo-oxidation of OC to inorganic C produces an estimated 12-16 Gt CO_2 annually, and indirect photo-oxidation produces an additional 1 Gt C available to microbial decomposition (Moran & Zepp, 1997). No global estimates exist for terrestrial ecosystems, but recent work suggests that similar effects of UV radiation account for substantial OC losses from leaf litter (King et al., 2012) and soil (Rutledge et al., 2010).

Representing Respiration/Mineralization in Global Models

The mineralization of OM is a critical component in the exchange of CO_2 between the atmosphere, the land, and oceans. Consequently, being able to accurately model the pools of detrital OC and the processes affecting them is important for predictions of the global C cycle and Earth's climate. In general, current ESMs are able to reasonably reproduce global and, to a lesser extent, hemispheric patterns of atmosphere-land and atmosphere-ocean CO_2 exchange (Anav et al., 2013). However, the ability of these models to accurately represent the global distribution of existing OC stocks is highly variable, and this variability could influence projections of future carbon-climate feedbacks (Todd-Brown et al., 2013). For example, SOC stocks predicted by the latest Climate Model Inter-comparison Project (CMIP5) ranged from 510 to 3040 Pg C globally and from 60 to 340 Pg C in circumpolar regions. In comparison, current SOC stocks based on soil databases are estimated to be

1260 Pg C globally with an additional 500 Pg C in circumpolar permafrost soils (Todd-Brown et al., 2013).

Generally, climate models report C fluxes for the ocean realms rather than stocks. The variability in CMIP5 predictions for ocean-atmosphere CO_2 flux is smaller than for the corresponding land-atmosphere flux (Anav et al., 2013), which is due in part to the strong thermodynamic constraints of carbonate chemistry on CO_2 flux. Models diverge more in the context of simulated marine primary productivity and fluxes of OC into various detrital pools. Most CMIP5 models fail to reproduce the seasonality of ocean production (Anav et al., 2013; Jiang et al., 2014), and underestimate oceanic primary production. Primary production is usually parameterized as a multiplicative function of limiting factors, including temperature, light, and a limiting nutrient. The most advanced ecological routines include multiple nutrient limitations (nitrate, phosphate, and iron) which typically improve primary production estimates (e.g. Moore et al 2002b, Cabré et al, 2014). Some models separate phytoplankton into multiple size types, usually small and large, affecting the patterns and the magnitude of primary production and export of OM out of the euphotic layer, as large phytoplankton sink faster and are more likely to form aggregates than small phytoplankton (Cabré et al., 2014).

The differences between terrestrial and marine model results and observations can be traced in part to how OM pools and degradation processes are represented in ESMs (e.g. Moore et al., 2013; Cabré et al, 2014). Typically, only very coarse classifications of OC pools are used, with processes being parameterized using semi-empirical relationships rather than being explicitly represented.

Mineralization rates used in models are at best functions of temperature, soil moisture content (terrestrial), and oxygen content (marine), and at worst a constant. For example, two widely used soil OC models, CENTURY and RothC, partition OC into discrete pools based on soil properties and predefined turnover times (Dungait et al., 2012) (Table 2): a fast, active pool that includes live microbial biomass and rapidly (1-5 year turnover) degrading soil OC, a slow pool that is chemically or physically protected (20-40 year turnover time), and a passive OC pool that is stable on longer time scales (200-1500 years)

(Parton et al., 1987). Marine models typically divide detrital OM into dissolved and particulate pools (POC), though some consider only the particulate pool (Table 2), and some models subdivide these pools according to their lability, assigning each sub-pool a fixed mineralization rate. Most CMIP5 marine biogeochemical models use a constant POC mineralization rate combined with a POC sinking speed that is either constant or increases with depth (Table 2). In the former case, the flux of POC decreases with depth exponentially, whereas if sinking speed increases linearly with depth, POC flux decreases according to a power law (Kriest and Oschlies, 2008). Both simple exponential and power-law functions have been used to fit observed changes in POC flux with depth, though more sophisticated functions combination of these have also been used (Marsay et al., 2014). For example, CESM1(BGC) uses two classes of sinking POC based on the commonly used ballast model (Armstrong et al., 2002): a rapidly sinking class associated with mineral ballast (e.g. diatom silicate frustules) that mineralizes deeper in the water column, and non-mineral associated OC that mineralizes at shallower depths. The depth of mineralization is a key control on oceanic C sequestration, as deeper water masses tend to be out of contact with the atmosphere for longer timescales. For example, the commonly used exponential and power laws translate into different mineralization depths.

With such a limited number of detrital OM pools, it goes without saying that the chemical complexity of this material is not well represented in models. Many marine biogeochemical models follow a single element (usually nitrogen or phosphorus) and use stoichiometric ratios (atomic ratios of carbon, nitrogen, and phosphorus) to calculate corresponding changes in carbon and nitrogen. Particulate organic matter in the global ocean has an average C:N:P ratio of 106:16:1, though many use a revised ratio of 117:16:1 (Anderson & Sarmiento, 1994). A corresponding benchmark ratio is less applicable to terrestrial ecosystems because terrestrial POM has a larger component of C-rich structural compounds (e.g. lignin) and a significantly wider range of nutrient ratios (Sterner & Elser, 2002). However, DOM is similarly depleted in nitrogen and phosphorus in both terrestrial and marine systems, suggesting a greater similarity in chemical composition than for POM (Neff et al., 2000; Kaiser & Benner, 2012; Lønborg & Álvarez-Salgado, 2012). Although initial C:N:P ratios of OM can explain >80% of the variance in mineralization rates (Coleman et al., 1983; Enriquez et al., 1993), using constant stoichiometric ratios in models is problematic because the ratios change due to preferential mineralization (Paulmeier et al., 2000). In marine systems, mineralization tends to increase C:N:P ratios of POM, whereas the opposite tends to occur in terrestrial systems (Blair, 1988; Adams & Angradi, 1996; Badcock et al., 2004).

Accurately modeling how rates of OM degradation might change under future climate scenarios is crucial to making accurate predictions of the global C cycle. Models of SOC typically employ degradation rates based on temperature sensitivity (using a single temperature factor Q_{10}; the increase in a rate following a 10°C rise in temperature) and soil moisture (Todd-Brown et al., 2013). It is unclear whether using a single global Q_{10} value is realistic, although recent evidence suggests a global convergence on $Q_{10}=1.4$ for terrestrial ecosystems (Mahecha et al., 2010). Despite the potential convergence of temperature sensitivity, we have an incomplete understanding of the conditions under which temperature is the main rate-limiting factor, and how enzyme kinetics, microbial community dynamics, and SOC stabilization respond to temperature (Giardina & Ryan, 2000; Davidson et al., 2006; Isse & Moorcroft, 2006). In addition, the first order degradation functions that represent temperature responses and enzyme kinetics are only realistic when substrates are highly abundant, a condition that is rare in nature (Schimel & Weintraub, 2003).

In contrast, not all existing global ocean C cycle models incorporate temperature dependent mineralization rates (Table 2). Temperature effects have been shown to produce a 3.5-fold decrease in C-specific respiration rates when changing from average surface (15°C) to deep ocean (4°C) temperatures (Iversen & Ploug, 2013). Incorporating temperature dependent degradation rates into the Max Planck Institut Earth System Model (MPI-ESM) using $Q_{10} = 2$ produced a modest change in C export from the surface to the deep ocean, but shifted nutrient and primary production distributions (Taucher & Oschlies, 2011). Dissolved oxygen concentrations in the oceans are predicted to change under a warming climate, and this will affect heterotrophic processes mineralization regimes in low oxygen zones, as most models shift from oxic to anoxic mineralization at a given low oxygen threshold (Maier-Reimer et al., 2005) (Table 2).

For the marine components of ESMs it is important to accurately predict depth-dependent mineralization rates for sinking OC (Moore et al., 2006), which can affect atmospheric CO_2

concentrations (Kwon et al., 2009). For example, the CESM1(BGC) overestimates the amount of mineralization in the mesopelagic resulting in underestimates of OM fluxes to the deep ocean, affecting the profiles of dissolved inorganic C, and contributes to larger than observed oxygen minimum zones (Moore et al., 2013). Uncertainties in the ventilation rates of thermocline and deep waters can also alter retention of biologically sequestered C and the degree of oxygen depletion. Due to these uncertainties, the CMIP5 marine biogeochemical models show little agreement in terms of their oxygen content and biologically sequestered nutrients, even though total nutrient inventories are relatively consistent with observations (Duteil et al., 2012; Bopp et al., 2013).

Depth dependence has also been shown to be important in models of soil biogeochemistry (Koven et al., 2013). Although soil models include a vertically resolved submodel for the transport of heat and moisture in soils, soil biogeochemistry is usually dealt with using a single layer box model and a fixed profile of SOM. The assumption in this approach is that SOM in deep layers of the soils plays a negligible role in C cycling. However, this assumption might not be correct. Subsurface soils can contain large SOM pools (Baisden and Parfitt, 2007) and deep-rooting plants can input C and N deep into the soils. Results from a global model with depth-resolved soil biogeochemistry with more realistic twentieth century C dynamics compared well with site-level comparisons of soil radiocarbon profiles (Koven et al, 2013).

Mineralization from terrestrial to marine systems

Terrestrially derived OC can be mineralized within the soil where it is produced and deposited, or “downstream” within streams, rivers, lakes, and ultimately, the oceans (Figure 2). However, models and C budgets often treat the fate of this material differently. For example to calculate the land C sink, the sum of the ocean uptake and atmospheric CO_2 increase is subtracted from the sum of fossil fuel and land use emissions and combines the terrestrial and inland water C sinks (e.g. Le Quéré et al., 2014). Carbon sinks inferred from atmospheric inversion methods represent processes on continental scales (Peylin et al., 2013) and also combine terrestrial and inland water C sinks. ESMs also implicitly combine terrestrial and inland water sinks. However, global budgets that are able to include more processes use a variety of methods to explicitly separate out the terrestrial and inland water C sinks (e.g. Ciais et al., 2013).

Approximately 1.9 Pg C yr^{-1} of total soil C finds its way into inland waters where it is transformed, stored, or transported downstream such that only ~0.9 Pg C yr^{-1} is input into the coastal ocean (Battin et al., 2008; Regnier et al., 2013; Bauer et al., 2013). Riverine inputs of terrestrial OC into the coastal ocean amount to approximately half of the total C input (0.45 Pg C yr^{-1}) (Bauer et al., 2013), with approximately 60% in the form of DOC (Cowan et al., 2002). Thus, inland waters not only transport terrestrially derived OM, but also allow additional transformation and storage along the way (Battin et al., 2008; Bianchi 2011).

Several factors impact the transport of soil OC to inland waters, including basin slope and temperature (Ludwig et al, 1996), so that the amount of soil-derived OC entering inland waters is spatially and temporally variable. However exact amounts and precise mechanisms through which these transformations occur are not fully understood (Seitzinger et al., 2010; Laudon et al, 2012). A comprehensive study of boreal lakes and rivers in Sweden estimates that a minimum of 0.03–0.87% of the surface SOC pool is exported annually into Sweden's lakes and rivers (Weyhenmeyer et al, 2012). Other studies have indicated that DOC concentrations are generally increasing over time in inland waters, and whilst the mechanisms leading to this increase remain unknown, there is general consensus that catchment soils are a major contribution (Evans et al., 2005; Roulet and Moore, 2006; Monteith et al., 2007). Erosion can play a significant role, particularly during extreme precipitation events that act to physically disrupt soil aggregates and increase the bioavailability of protected OC (Hilton et al., 2008; Yoon and Raymond, 2012). Microbial communities within streams and rivers also impact the transport of soil derived OC through mineralization with input of terrestrial OC sustaining conditions of net heterotrophy and CO_2 supersaturation found in most inland waters (Raymond et al., 2013).

Lakes, ponds, and impoundments are efficient at retaining sediments, allowing for burial of OC. In this sense, lakes act more like the oceans in that the vertical dimension is important for understanding the cycling of OC. Most lakes are small and shallow (Downing et al., 2006) so that sediments are in contact with a well-mixed water column, conditions that favour mineralization of OC over burial in the sediments. Globally, CO_2 emissions from lakes could be as high as 0.53 Pg C yr^{-1} (Tranvik et al., 2009) and lake sediments store an estimated 820 Pg of OC, with estimates of global storage rates ranging from 0.03 to 0.07 Pg C yr^{-1} (Tranvik et al., 2009), which can be compared with 0.2 Pg C yr^{-1} for burial in marine sediments (Ciais et al., 2013). As in the oceans, flocculation can be important in boreal lakes where sedimentation fluxes of DOC through flocculation can be similar to the flux of outgassing CO_2 (Wachenfeldt and Tranvik, 2008). A study of 20 lakes in the English Lake District indicates that most of the CO_2 evaded from these lakes arrives from streams and rivers, with 1.2–2.2% of net primary production being lost to the atmosphere (Maberly et al., 2012). This suggests that changes in land use practices that affect the mobilization of SOM can affect regional C budgets.

Lateral transport of OC is important in streams and rivers, and can be thought of as taking on the role of vertical transport in soils and the oceans. Soil OM finds its way into inland waters in both dissolved and particulate forms and transport rates differ for these two components. Dissolved OC will be advected by the water flow and acted upon by microbial communities within these waters. Particulate OC will also be affected by the ability to gravitationally settle (Hu and Kuhn, 2014). There are several consequences of this. Firstly, large particles will be deposited close to the region where they were mobilized and this can have consequences for models. Smaller particles will also settle, but can be readily resuspended, potentially altering the residence time of OC in the system. Stream microbial communities have been observed to change as one moves downstream, adapting to the changing chemical composition of the organic material present (Winter et al, 2007; Battin et al., 2008). Similar gradients with depth are seen in the ocean, even among ecotypes of the same organism. For example, deep-water ecotypes of *Alteromonas macleodii* show greater adaptation for living on large particles and degrading more recalcitrant compounds that shallow-water ecotypes (e.g. Ivars-Martinez et al., 2008).

Estimates of global CO_2 outgassing from streams and rivers vary from 0.5 – 1.8 Pg C yr^{-1} (Cole et al., 2007; Battin et al., 2009; Aufdenkampe et al., 2011; Raymond et al, 2013), with more recent higher values arising from larger estimates of the role of temperate rivers and streams (Raymond et al., 2013). Outgassing of CO_2 from the rivers and wetlands of the Amazon river basin alone has been estimated at 0.5 Pg C yr^{-1}, an order of magnitude greater than export of OC by the Amazon to the oceans (Richey et al., 2002). The precise contribution that respiration of soil OM makes to riverine outgassing of CO_2 remains highly uncertain; however, the higher rates found in low order streams suggests that the contribution of terrestrial SOM could be significant (Raymond et al, 2013). For rivers comprising the Amazon River basin, export of DOC from soils into rivers accounts for 15% of the C outgassed by the rivers (Richey et al, 2002), and 80% of the CO_2 outgassed is of terrestrial origin.

Another change to the potential for mineralization of soil OM in inland waters is the increased propensity for photochemical oxidation which in some lakes has been shown to exceed the microbial mineralization of soil-derived OC (Cory et al. 2014). Over the last decade, it has become evident that the lateral input of soil DOC into inland waters has increased (e.g. Evans et al. 2005; Monteith.et al. 2007). In addition, the coloured component of this DOC is selectively lost as this material is transported to the coasts such that longer residence times (e.g. slower running rivers) result in a greater loss (Weyhenmeyer et al, 2012).

Inland waters transport terrestrially derived OC to coastal waters with approximately 0.45 Pg C yr^{-1} of total OC being carried by rivers into estuaries, along with an approximately equal amount of inorganic C (Bauer et al., 2013). This carbon combines with that produced by the highly productive tidal wetlands, and is respired (about 0.35 Pg C yr^{-1} from the combined tidal wetlands and estuaries). Approximately 0.5 PgC yr^{-1} is transported from estuaries onto the coastal shelf and approximately 0.3 Pg yr^{-1} of OC and 0.15 Pg yr^{-1} of inorganic C is then deposited in coastal sediments (estuaries and shelf) (Reigner et al. 2013). Part of this is the result of the increased ionic strength of seawater allowing for rapid aggregation and sinking of clays minerals and the OC associated with them (e.g. Dyer 1985). Some is the result of exchange with tidal wetlands where vegetation increases the trapping efficiency of particulate material. This re-deployment of terrestrial-derived POC means that this C sees different environments where differences in mineralization processes can affect CO_2 and methane production.

Coastal systems are dynamic and complex environments with water salinity varying from fresh, through brackish, to saline. At the high salinity end, salt marshes and mangrove swamps sequester at least 44.6 Tg C yr^{-1} globally (Chmura et al., 2003). Carbon sequestration in these systems is highly efficient; the high sedimentation rates and high soil C content of estuarine wetlands leads to a C sequestration rates that are 10-fold higher compared with other wetland ecosystem on an areal basis (Bridgham et al., 2006). Carbon sequestered in coastal vegetated system is frequently referred to as “blue carbon” (e.g. Mcleod et al., 2011).

Multiple physical and biological processes affect C mineralization in coastal marshes. In saltmarshes, oxygen is utilized quite rapidly in the surface sediments, so that most OM mineralization occurs under anoxic conditions (Howarth, 1993). Because of the high sulphate component in seawater, sulphate reduction is an important microbial process.

Bioturbation by plant roots and invertebrates (e.g. crabs) affects the pathways of OC mineralization in salt marsh sediments by stimulating iron-reducing bacteria (Kostka et al., 2002). Similarly, saltwater intrusion in tidal freshwater marshes stimulates microbial decomposition of OM, increasing rates of sulphate reduction and flux rates of CO_2 and methane out of the sediments (Weston et al., 2011). These results indicate that sea level rise will have a significant impact on coastal wetlands and their sequestration of C.

Based on limited available data, coastal wetlands are thought to be a net source of C to estuaries (Cai, 2011; Regnier et al. 2013; Bauer et al., 2013). This C either settles in the estuaries, or is exported to the coastal shelf region and the open ocean. Terrestrial-derived DOC occurs at surprisingly low concentrations in the open oceans, and the fate of this material is an area of active research. Photochemical reactions in the surface shelf waters can transform the aromatic fraction of terrestrial DOC into more stable components (Stubbins et al, 2010), and bacteria found in shelf waters are able to degrade lignins from terrestrial plants (Hernes et al., 2003). Such reaction pathways may help to explain the low terrestrial DOC concentrations and long marine DOC residence times.

Improving mineralization in ESMs.

Explicitly incorporating microbial populations and dynamics into ESMs could provide a significant improvement over current models. Traditional soil and marine models implicitly include microbial populations and use first-order kinetics to represent OM mineralization (Table 2). This assumes that the microbes are effectively not responding or adapting to changes in their environment. However, in both systems, the efficiency of microbial processes have been shown to be impacted by climate (Allison et al., 2010; Frey et al., 2013) and microbial populations and functions change with depth in both the ocean and in soils (Fierer et al., 2003; Robinson et al., 2010). At small spatial and short temporal scales, explicit representation of microbial populations has improved predictions of OC cycling, but at larger scales complex models are often no more accurate than simple models, possibly because greater mechanistic accuracy is needed, rather than more parameters (Manzoni and Porporato, 2009). Yet, initial attempts to explicitly represent soil microbial processes in ESMs using Michaelis-Menton kinetics to represent their interactions with SOC, show greater agreement with actual observations of soil C pools than models without them (Wider et al., 2013). Explicitly incorporating microbial dynamics into ESMs will increase the complexity of these models. However, developments in modeling techniques may alleviate this issue. For example, trait-based models (Follows & Dutkiewicz, 2011; Allison 2012) may provide a common platform for the terrestrial and marine modeling communities. Results from novel, more computationally intensive techniques with a more focused scope may provide insights than can inform more traditional ESMs. For example, the rapid development of “omic” techniques seen in recent years could provide detailed genomic and transcriptomic information for single-cell models, the results from which could inform ESMs through new parameterizations.

In addition to uncertainties associated with process representation, global C models suffer from uncertainties arising from two major issues: (1) scaling and model resolution, and (2) the availability of representative measurements. The scaling issue has received considerable attention within the modeling community over the last decade. Model resolution is important because crucial processes occur at the local (e.g., soil respiration in response to hot spots and/or hot moments) to regional scales (e.g. ocean upwelling), that are typically not adequately represented in global models but can substantially impact global scale processes. For example, estuarine and coastal processes such as delivery and transformation of OC to the coastal shelves are not currently included in models. High resolution eddy resolving models do allow some of these processes to be captured (e.g. Bernard et al, 2011) for shelf systems, but estuarine processes require sub-grid parameterizations and scaling. In addition, these models cannot be run at the global scale and so cannot be used to address questions related to changes in climate. The opposite problem can also arise when measurements made at the local scale, which are not representative at larger scales, are used to create global estimates. Resolving these scaling problems represents a key challenge for building accurate models for both terrestrial and marine fields.

The development, validation, and verification of models depends crucially on the availability of observational constraints. Conant et al (2011) suggested that models will be improved by focusing on mechanisms that distinguish how changes in microbial substrate use, enzyme efficiency, or adsorption-desorption dynamics underlie soil OC-temperature relationships. One of the biggest challenges for verifying the internal dynamics of soil OC models is the ability to deconstruct and test the mechanisms that produce certain model outputs (Six et al., 2002). Attempts to experimentally isolate soil OC fractions, which correspond to conceptual model fractions, have been unsuccessful, partly because the conceptual pools do not correspond to specific soil fractions (Six et al., 2002), and partly because isolation and fractionation methods are imprecise and often disrupt more than one stabilizing mechanism at once (von Lutzow et al., 2007). Similar arguments can also be made for marine biogeochemical models.

The terrestrial components of ESMs do not in general consider the lateral transport of SOM through inland waters to coastal systems. However, it is unclear at present if including such terms in ESMs would significantly affect model projections. For example, the latest IPCC report estimates the flux of OC from soils to inland water to be 1.7 Pg C yr^{-1} (Ciais et al., 2013), which is approximately 3% of terrestrial net primary production. An increase or decrease in this flux by a factor of two would still be small compared to terrestrial respiration and emissions. However, estimates of anthropogenic perturbations suggest that the flux from soils to inland waters has increased by 0.8 Pg C yr^{-1} since pre-industrial times, almost doubling the natural flux (Regnier et al., 2013).

There is also a problem involved in neglecting lateral OC fluxes between systems. Currently, ESMs mineralize OC within soil. However, the factors affecting the rates and availability of OC mineralization vary between soils and aquatic environments. Thus, OC released from soils to aquatic systems could have different turnover times, affecting the overall feedback to the atmosphere (Carvalhais et al., 2014). Further research is needed to fully understand the implications of how lateral transport of OC with ESMs is represented.

The spatial resolution of ESMs limits the processes that can be explicitly included in these models. This raises the problem of how to incorporate suitable parameterizations of these processes into global models. One possible approach might be to use parameterizations developed from more mechanistically detailed, but spatially restricted models. For example, there are many detailed models of soil OC mineralization (e.g. Manzoni and Poprorato, 2009) which could be used to develop simpler parameterizations for ESMs. Similarly, reaction-diffusion models of OM decay in marine sediments that include physical protection by aggregates (e.g. Rothman and Forney, 2007) predict simple relationships for the OM decay rate that are consistent with sediment core data. Such models could be extended to water column and terrestrial OM providing a suite of relationships that can be used in ESMs.

A lack of global datasets causes problems in constraining and validating global models. This is especially a problem for models of soil and marine OM degradation. A recent global database of soil respiration (Bond-Lamberty & Thomson, 2010, 2012) showed a correlation between total soil respiration and heterotrophic soil respiration for multiple biomes, indicating a possible approach to improving model parameterizations. For oceans, similar databases (e.g. http://www.socat.info/about.html) have started to emerge, but these primarily focus on surface waters (often < 100 m depth) making it difficult to derive general conclusions. In addition, we were unable to find sufficient data to make global estimates of POC and DOC entering inland waters from soils. Measures of total OC exist (eg Ciais et al., 2013), and some estimates for a handful of lakes (e.g. Tranvik et al, 2009). Since we expect soil derived DOC and POC to have different fates, reliable estimates of both need to be obtained.

The relative merits of various methods used in terrestrial and marine science to measure aspects of the C cycle (e.g. storage and turnover) relevant for ESMs are still vigorously debated in the literature (e.g., Wienhold, 2007; Gasol et al., 2008; Burd et al., 2010). Use of field data allows realism and complex interactions to be kept intact, but is subject to confounding effects which may be hard to discern and account for. Laboratory experiments on the other hand have the advantage of being able to isolate individual mechanisms and investigate simple cause-effect relationships, but realism may be sacrificed. Validation of ESMs requires information on two main variables derived from field and laboratory measurements: global C stocks and turnover rates, respectively. Global soil OC estimates derived from different data sources vary by a factor of two (Hiederer & Köchy, 2011) and ESM representation has proven to be highly variable (Todd-Brown et al., 2013). Similarly, reliable estimates of ocean C stocks and turnover times require accurate estimates of production and degradation, as well as the physical transport of POC and DOC from land to the sea and between the upper and deep ocean. Estimates of, for example, the amount of POC sinking out of the surface ocean vary from 4 Pg C y^{-1} to more than 12 Pg C y^{-1} (Boyd & Trull, 2007; Henson et al., 2012, Marsay et al., 2014). An increased understanding of these processes, in both terrestrial and marine systems, is essential to accurately predict the effects of future climate change.

Quantifying and understanding model performance is also a crucial area for development. In marine systems, efforts have been made to develop systematic and quantitative frameworks for assessing the skill of upper ocean biogeochemical models against field data and satellite observations (e.g. Doney et al., 2009). Similar efforts to arrive at a consistent benchmarking framework have been developed for terrestrial models (Randerson et al., 2009; Luo et al., 2012). Models can be compared not only with data values, but also with spatial and temporal patterns seen in observational data sets. However, one significant problem that arises with such efforts is the availability of sufficiently complete observational data and associated uncertainties. This means that the chosen data sets themselves have to be evaluated in the formulation of suitable benchmarks. Agreement of statistical measures suitable for benchmarking is also an ongoing problem. Commonly used metrics include model-data residuals, root-mean-square-error, time and space correlations, and Taylor diagrams; however, there is as yet no generally accepted choice of metric allowing different model performance to be compared (Luo et al. 2012). This is something that would benefit both terrestrial and marine modeling communities. Moreover, ESM results and observations show little correlation at scales of 100s of km as the models fail to capture specific mechanisms that create spatial complexity (Todd-Brown et al., 2013).

Given the uncertainties in global estimates, a major task for modelers, and observational and experimental scientists is to determine which estimates and variables are best used. This means that there needs to be an iterative dialog between communities on best-practices, determining which variables are best predicted by models for meaningful comparisons with data, and what data need to be collected for improving the models.

Conclusions & Recommendations

Organic matter degradation is a key process in both the terrestrial and marine components of ESMs. But, there is considerable concern that model projections are biased. Changing climate conditions are likely to alter multiple ecosystem components simultaneously. As primary production, nutrient inputs, ocean stratification, land management practices, etc. change, it is important that ESMs get OC dynamics right for the right reasons (Anav et al., 2013; Bopp et al., 2013; Moore et al., 2013; Todd-Brown et al., 2013). Although the physical environment differs between marine and terrestrial systems, the metabolic processes mediating OM degradation are similar. Moreover, similar challenges in modeling these processes are faced by both communities, making a dialogue between the two communities potentially fruitful. Some areas where we think dialogue would be particularly useful include: improving representations of particle aggregation (e.g. Burd, 2013) and its implications for altering OM degradation rates; understanding the sensitivity of degradation rates to environmental variables and heterotrophic community composition; better representation of heterotrophic microbial communities (perhaps through trait-based approaches) and degradation pathways; and parameterization and validation of models from scarce and highly variable data.

One key similarity between OC degradation in the marine and terrestrial systems is that decomposition is microbially mediated. A primary area of crossover, therefore, is to develop mechanistic representations of microbial physiology and ecology that determine degradation rates. Better microbial representations in models will rely on observations of metabolic processes and constraints. A robust model verification test bed should endeavor to confront model formulations with observations from field studies and experimental manipulations. In addition, there should be agreement between both terrestrial and marine modeling communities on best practices for benchmarking models. This should lead to the development of an accepted suite of quantitative metrics allowing for different models to be compared against a standard suite of data.

Acknowledgements

This article grew out of a multidisciplinary workshop “Key Uncertainties in the Global Carbon Cycle” in August 2013 organized by N. Levine, R.Q. Thomas, M. Long, G. McKinley, C. Deutsch, and A. Bracco and hosted by the National Center for Atmospheric Research, Boulder, CO, USA and sponsored by the U.S. Department of Agriculture, U.S. Climate Variability and Predictability Research Program (US-CLIVAR), the U.S. National Science Foundation, Ocean Carbon Biogeochemistry (OCB), and the Carbon Cycle Interagency Working Group (CCIWG) (Thomas et al., 2014). The work behind this article was funded in part by NSF grant OCE0645485 (ABB).

Author Contribution

ABB and SDF conceived the manuscript and prepared Fig. 1,2 and Box 1. ABB led manuscript preparation. All authors contributed to the writing and editing of the manuscript.

Conflict of Interest

None of the authors have a conflict of interest with the material in this article.

Box 1: Organic Carbon Mineralization in Oceans and Soils.

Most organic carbon (OC) entering the surface ocean or soil is rapidly (~ hours – days or months) consumed and some of it respired by heterotrophic organisms. In soils this occurs primarily in the rooting zone (top 10 – 20 cm) and in the oceans within the surface mixed layer (top 10s of m). This rapid mineralization returns CO_2 back to the atmosphere quickly and is controlled in part by the composition of the organic matter inputs and environmental factors (e.g., temperature, soil moisture, soil texture/mineralogy).

A variable fraction of the organic matter input escapes rapid mineralization and is stabilized over long (years - centuries) time-scales, with important differences between soils and oceans due to their intrinsically different physical structure. For example, soils are a complex matrix of minerals, organic materials, and pore spaces variably filled with water and air. In contrast, the oceans are mainly water with the occasional particle. Mineralization occurs more or less in place in soil systems, with deep roots, water percolation, and bioturbation (e.g., earthworm activity) moving OC deeper down the soil profile. While the soil surface (top ~20 cm) has the highest OC concentrations and is considered the zone of greatest microbial activity, the subsurface contains significant OC stocks with turnover times of 100s to 1000s of years. Organic matter formation and stabilization in soils largely depends on processes that protect OC against decomposition, particularly aggregation and organo-mineral associations (Fig. 1).

In marine systems, organic material can undergo significant vertical and horizontal excursions. Particulate material sinks to the ocean floor and DOC can be transported to the deep ocean by convection and mixing, with both DOC and POC being carried on ocean currents. Ocean sequestration of carbon is partly determined by the depth at which OC is mineralized; OC mineralized in the surface mixed layer can be exchanged with the atmosphere within hours to days; whereas, it may take centuries to millennia for OC mineralized below 1000 m to return to the atmosphere. Organic C that reaches the sediment can be consumed and respired as CO_2 by organisms on the surface and within the sediments. So, for the oceans, long-term storage of OC depends on the circulation and motion of the water, the sinking speed of particulate material, and the protection and composition of the carbon.

Organic Matter: This refers to the sum of all relevant organic compounds.

Organic Carbon: This refers to just the carbon contained within the organic matter, whether it is in dissolved or particulate form.

Mineralization: The oxidation of organic C to inorganic C through heterotrophic consumption and respiration (**often termed “remineralization” in the aquatic/marine literature)**.

Labile organic C: Organic C that is rapidly (hours to days) utilized by heterotrophic organisms.

Recalcitrant: Organic material that is resistant to consumption and mineralization, due to its chemical structure or physical/chemical protection.

Sequestration: Removal of C from exchange with the atmosphere for a predefined length of time (e.g. 100 years, 1000 years).

Soil organic matter (SOM): All organic matter in soils smaller than 2 mm, including dead plant material in various stages of decay, living microbial biomass, and microbial byproducts from decomposition.

Particulate organic matter (POM): Operationally defined in terrestrial systems as SOM retained on a 53 μm sieve after complete dispersion of the soil to disrupt aggregates and separate mineral particles. In marine systems, POM is typically considered the material retained on a filter with a pore size between 0.2 to 0.7 μm with care taken not to disrupt aggregates, and includes photosynthetic bacteria, particle attached bacteria etc.

Dissolved organic matter (DOM): In terrestrial systems, DOM is sampled either as soil solution collected by lysimeters installed in the soil profile or as a water extract of fresh soil samples. In both lysimeter-collected and extracted samples, solutions are typically passed through a filter (usually 0.7 μm) prior to analysis for DOC. In marine systems, DOM is defined as the material passing through a 0.2 to 0.7 μm pore size filter. This typically includes some bacteria and viruses, as well as colloids. In marine sediments, DOM is collected as pore water obtained from centrifugation of sediments.

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Figure 1: Schematic of the main processes affecting detrital organic matter in soils and the oceans (some symbols courtesy of Integration and Application Network, Univ. of Maryland Center for Environmental Sciences (ian.umces.edu/symbols/).

Figure 2: Schematic showing the main conduits of organic matter from soils to the open ocean along with the primary processes (in italics) affecting the mineralization of that organic matter.

Table 1

	Net uptake (Pg C y^{-1})	Stock (Pg C)
Atmosphere		
Inorganic carbon		744
Land		
Vegetation	0.75 – 1.17	550
Soil inorganic C	--	924 (?)
Soil organic matter	--	1760
Ocean		
Biota	1.73 – 2.33	3
Dissolved inorganic carbon		37800
Dissolved organic carbon		662
Particulate organic carbon		15
Surface sediment organic carbon		575

Table 1: Values of uptake and stock in various organic matter components of terrestrial and marine systems.

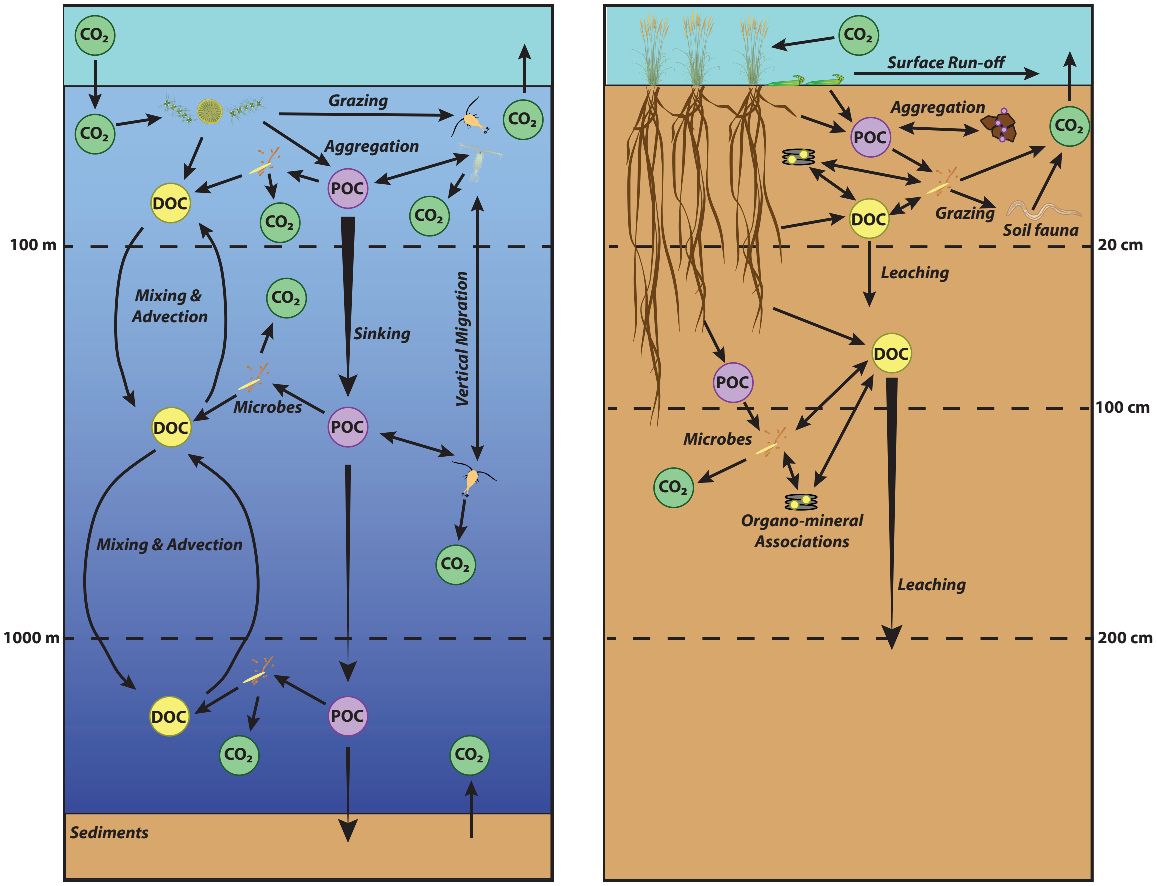
Table 2.

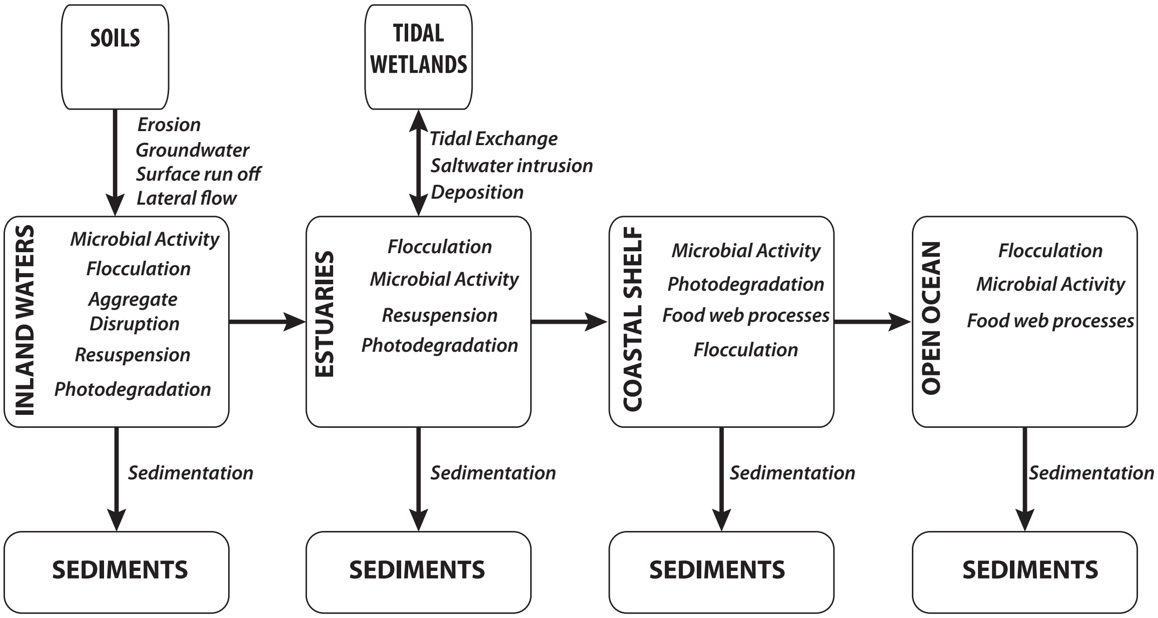
	Model	Mineralization Rate	Detrital OC pools	Physical Protection	Heterotrophic microbes/fungi	References
Ocean						
	BEC	Temperature dependent, 2 rates (ballast associated & soft) & O_2 dependent (lower rate through denitrification in anoxic zones)	DOM (labile & semi-labile) 2 POM classes (ballast associated & soft)	Implicit	Implicit	(1)
	PELAGOS	Temperature dependent (through bacterial growth) & O_2 dependent	DOM (C,N,P), POM (C,N,P,Si,Fe)	No	1 explicit	(2)
	TOPAZ2	2 rates (ballast associated & soft) & O2 dependent (lower rate through denitrification in anoxic zones)	DOM (labile & semi-labile) 2 POM classes (ballast associated & soft)	Yes	Implicit	(3)
	Had-OCC	Constant (shallow &	POM	No	Implicit	(4)

		deep)				
	Pisces	Temperature & O_2 dependent (same rate but through denitrification in anoxic zones)	Semi-labile DOM Small & large POM	No	Implicit	(5)
	HAMOCC	O_2 dependent (lower rate through denitrification in anoxic zones)	DOM POM	No	Implicit	(6)
Soil						
	CENTURY	Temperature & moisture dependent	5 litter pools 1 surface microbial pool 3 SOM pools (active, slow and passive) DOC pool	No	Implicit (assumed steady state)	(7,8)
	RothC	Temperature, soil moisture	2 litter pools 2 SOM pools 1 pool inert OM	No	1 explicit	(9)

	Biome-BGC	Temperature, moisture	4 litter, 4 SOM	No	Implicit (assumed steady state)	(10)
	DNDC	Soil texture, nitrogen, soil temperature & moisture	3 litter pools 2 microbial pools 3 SOM pools 1 DOC pool	No	Explicit	(11)
	ORCHIDEE	Temperature, humidity	4 litter 3 soil C	No	Implicit	(12)

Table 2: Comparison of different model formulations used for representing processes affecting detrital OC in terrestrial and marine systems. References: (1) Moore et al., 2002; (2) Vichi et al., 2007; (3) Dunne et al., 2010; (4) Palmer & Totterdell, 2001; (5) Aumont et al., 2003; (6) Ilyina et al., 2013; (7) Parton et al., 1993; (8) Parton et al., 1996; (9) Coleman & Jenkinson, 1999; (10) Thornton & Rodenbloom 2005; (11) Li et al., 1994; (12) Krinner et al., 2005


CO$_2$
Grazing
Aggregation
DOC
POC
100 m
Mixing & Advection
Sinking
Vertical Migration
Microbes
1000 m
Sediments
Surface Run-off
Soil fauna
20 cm
Leaching
100 cm
Organo-mineral Associations
200 cm


SOILS
Erosion
Groundwater
Surface run off
Lateral flow
TIDAL WETLANDS
Tidal Exchange
Saltwater intrusion
Deposition
INLAND WATERS
Microbial Activity
Flocculation
Aggregate Disruption
Resuspension
Photodegradation
ESTUARIES
Flocculation
Microbial Activity
Resuspension
Photodegradation
COASTAL SHELF
Microbial Activity
Photodegradation
Food web processes
Flocculation
OPEN OCEAN
Flocculation
Microbial Activity
Food web processes
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