

Opinion

Organic Matter Degradation across
Ecosystem Boundaries: The Need for a
Unified ConceptualizationDolly N. Kothawala,^{1,*} A.M. Kellerman,² N. Catalán,^{3,4} and Lars J. Tranvik¹

The global carbon cycle connects organic matter (OM) pools in soil, freshwater, and marine ecosystems with the atmosphere, thereby regulating their size and reactivity. Due to the complexity of biogeochemical processes and historically compartmentalized disciplines, ecosystem-specific conceptualizations of OM degradation have emerged independently of developments in other ecosystems. Recent discussions regarding the relative importance of molecular composition and ecosystem properties on OM degradation have diverged in opposing directions across subdisciplines, leaving our understanding inconsistent. Ecosystem-dependent theories are problematic since properties unique to an ecosystem may change in response to anthropogenic stressors, including climate change. The next breakthrough in our understanding of OM degradation requires a shift in focus towards developing a unified theory of controls on OM across ecosystems.

What Controls Organic Matter Persistence and Reactivity?

The susceptibility of organic matter (OM) to either persist and accumulate as a long-term sink of carbon, or cycle rapidly and become **mineralized** (see [Glossary](#)) into atmospheric CO₂, is a key feature of carbon cycling across the biogeosphere. Yet, a seemingly simple question remains unresolved across soil, freshwater, and marine biogeochemistry: what controls the degradation of OM? We know that OM can be highly reactive, and is degraded within minutes in some soil and freshwater environments. Alternatively, it can also be highly persistent, lasting for millennia in soils, sediments, and the open ocean. Decades ago, the consensus would have been that OM persistence is reflected by its **molecular composition**. In time, flaws in this thinking were revealed, with the recognition that OM persists far longer than can be explained by molecular composition alone [1]. With this insight and recent technological advances [2], the relative importance of OM composition has shifted in diverging directions over time ([Box 1](#)). Most notably, the soil and freshwater lines of thinking are developing in opposing directions. The soil community came from a history of considering that soil OM could progressively become ‘refractory’ due to **humification** and selective preservation [3–5], with molecular composition (e.g., lignin:N) being important for predicting degradation rates [6,7]. The soil community now increasingly recognizes the importance of **ecosystem properties** [8], with molecular composition being less relevant [9]. By contrast, the freshwater community first proposed the river continuum concept during the 1980s [10], where shifts in the molecular composition of dissolved organic matter (DOM) with movement downstream were expected due to the preferential use of substrates. This theory continues to be validated, even with high-resolution methods [11–13]. In the marine community, there are debates about the relative importance of molecularly stable DOM [14] and environmental constraints [15–17] to understand why marine DOM has an average radiocarbon age of 6000 years [18]. In marine sediments, the wide variability in OM preservation efficiencies continues to be

Highlights

Conceptualizations of organic matter (OM) degradation are diverging within and among the soil, freshwater, and marine subdisciplines.

There is a need to step back from conceptualizations specific to certain ecosystems to holistically understand what controls the degradation of OM, regardless of the ecosystem.

Ecosystem properties are changing rapidly due to anthropogenic stressors, and we encourage the development of conceptual and earth system models to be more flexible and consider conditions that may currently seem atypical for a particular ecosystem.

We emphasize that the importance of molecular composition in regulating OM degradation should not be discarded, but rather we should understand when and why it appears more or less relevant than ecosystem properties.

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Box 1. Diverging Historical Conceptualizations of OM Degradation in Soil, Freshwater, and Marine Ecosystems over Time

The Soil Perspective: OM Persistence as a Function of Ecosystem Properties

Historically, the molecular composition of OM (e.g., lignin:N, aromatic content, solubility, molecular weight, or presence of humic substances) was thought to make soil OM persist [65–68]. Accordingly, soil OM models assumed that decay rates were linked to molecular structure [6,69]. These traditionally held viewpoints are now actively challenged [4,8,70], as reviewed elsewhere [8] (Figure 1). The long-term preservation of soil OM is increasingly recognized to be a function of its ecosystem properties, such as temperature [71,72], biological inaccessibility due to adsorption to mineral surfaces [8,60,73–75], and nutrient limitation [76], while molecular composition is considered less relevant [70]. A defining feature of soils is the presence of mineral surfaces, whereby adsorption and physical encapsulation within micropore spaces can retain OM [75,77,78], and protect it from biological degradation [3,4,70,79]. When stabilized, even 'labile' OM becomes protected from enzymatic degradation. In fact, soil OM with a radiocarbon age of several thousand years can be highly labile once destabilized back into solution phase [48], and likewise for thawing permafrost leachates [80,81]. Accordingly, it has been noted that radiocarbon age *per se* is not a good predictor of long-term persistence of soil OM [50].

The Freshwater Perspective: DOM Persistence due to Molecular Composition and Time

In stark contrast to soil ecosystems, emerging freshwater studies are reinforcing the long-held notion that molecular composition is relevant to DOM degradation. DOM in freshwaters tends to be highly reactive (mean half-life of 2.5 years) with water residence time emerging as a strong predictor of degradation rates across a range of water bodies [39]. Thus, there is an inherent assumption that labile compounds are selectively consumed first, and the remaining OM is increasingly difficult to degrade [11,82–86]. Recent high-resolution approaches have confirmed that, with time, there is a preferential loss of oxidized, aromatic compounds of high molecular weight, whereas reduced aliphatic and N-containing compounds are resistant to degradation or tightly cycled, and, thus, persistent [13]. As with soil studies, radiocarbon age is a poor predictor of long-term persistence in lakes and streams [87,88].

Emerging Marine Perspective: Molecular Composition and Ecosystem Dependence

Two main lines of thinking, which are not exclusive of each other, prevail in the marine community, as reviewed elsewhere [42]. The formation of refractory DOM during microbial and photolytic degradation, as well as thermogenesis, is supported by detailed molecular methods [14,89] (Marine 1; Figure 1). Another theory suggests that environmental conditions are relevant [17,42]. One example is the dilution theory [15,16], which suggests that highly dilute conditions of the deep sea (DOC: <42 $\mu\text{M C}$) restrict decomposition, rather than compositional recalcitrance [16] (Marine 2; Figure 1). In fact, the free energy released from highly labile substrates such as glucose can be outweighed by the high energetic costs of concentrating the substrate within the cell before metabolism [90]. Given that DOM comprises several thousand individual compounds [91], the low abundance of any individual compound under highly dilute conditions may limit specific catabolic pathways. Consequently, some DOM compounds may persist almost indefinitely in the deep ocean.

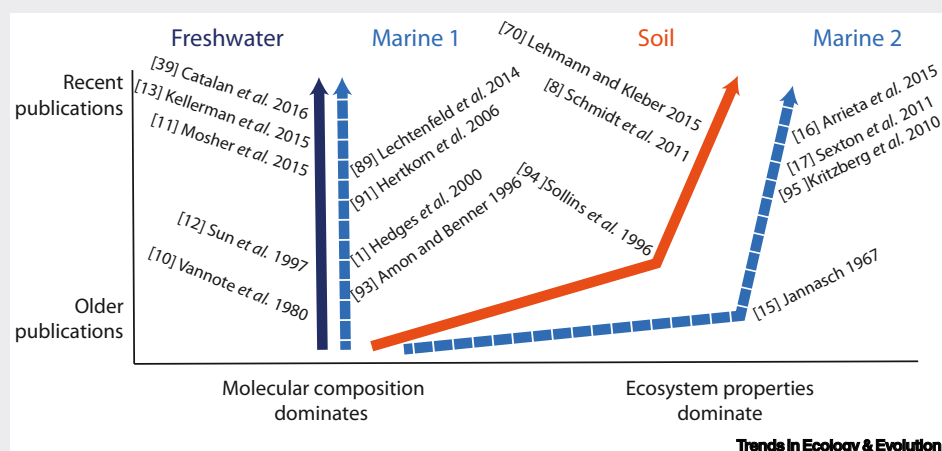


Figure 1. Illustration of the Progression in our Conceptualization of Dominant Controls on Organic Matter (OM) Degradation across Freshwater, Soil, and Marine Literature. Arrows running near the left suggest that molecular composition is highly relevant for OM degradation, while arrows running to the right suggest that environmental and biological controls dominate. The freshwater and soil literature diverge most prominently, while there are two prevailing theories in the marine literature. This shows a lack of consensus across, and within, ecosystems. Examples of literature driving the direction of arrows are indicated [1,8,10–13,15–17,39,70,89,91,93–95].

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debated, with controlling factors ranging from molecular composition and age, to environmental factors, such as association with mineral particles [19–23]. Thus, our fundamental conceptualization of controls on OM degradation is fragmented and developing in an inconsistent manner within and across ecosystems.

Why Merge Insights across Ecosystems?

Soil, freshwater, and marine ecosystems are significantly different environments. Accordingly, researchers in these areas have developed specialized terminology and experimental approaches, and have unique histories that generated current theories. Each ecosystem is unique in terms of its OM sources, decomposer communities, food-web dynamics, and ecosystem properties. These differences inherently imply that the relative importance of the factors regulating OM degradation may ‘appear’ to be unique to each ecosystem. Yet, regardless of the ecosystem, OM is fundamentally a mixture of degradation by-products originating from living biomass. In fact, aside from extreme cases [24], OM originates from cellular material, including biomolecules (e.g., carbohydrates, proteins, lipids, nucleic acids, and lignin). Accordingly, we argue here that the underlying controls of OM degradation should be universal, with the relative importance of individual controls enhanced or masked depending on local ecosystem properties. We highlight the need to question why OM degradation ‘appears’ to be regulated differently across ecosystems. Currently, the literature is full of stimulating discussions, and we have a unique opportunity to consolidate newly acquired knowledge derived from one ecosystem to help explain outliers in adjacent ecosystems. Ultimately, we encourage moving towards the development of a more holistic perspective of OM degradation that is ecosystem independent, and critical to the development of earth system models, particularly those linking terrestrial and aquatic ecosystems [25].

Ideally, our conceptual understanding of OM degradation should be robust and flexible to changing environmental conditions. Given that ecosystem properties are highly dynamic, the fate of DOM has important implications for ecosystem functioning, including whether it is a carbon source or sink. Factors such as permafrost thawing, increased primary production, shifting decomposer community composition, increased suspended sediment loads to aquatic systems [26,27], eutrophication, ocean acidification [28], land-use change [29,30], and extreme climate events [31,32] can shift OM degradation rates. These changes can traverse ecosystem boundaries. Thus, a major challenge for earth system models is the incorporation of reliable estimates of OM degradation rates across all ecosystems, particularly under changing environmental conditions. Even small shifts in biosphere OM degradation rates can have large, nonlinear consequences on the release of the greenhouse gases, CO₂ and CH₄ [33]. Thus, here we raise awareness of diverging conceptualizations of OM degradation across ecosystems, identify features of emerging theories that could be contributing to diverging viewpoints, and encourage future research efforts to develop a more unified understanding of OM degradation.

The Complex Interplay between Molecular Composition and Ecosystem Properties

In recent years, there has been a shift away from recognizing the role of OM composition in the soil sciences, with emphasis on discrediting the humification theory [9]. In fact, ‘omitting any emphasis on substrate composition’ has been suggested [9]. By contrast, the prevailing freshwater perspective and one marine perspective is that molecular composition remains highly relevant to predicting OM degradation [13,14]. However, it is important to recognize that ecosystem properties and molecular composition are not mutually exclusive and, at a given place and time, one may ‘appear’ more relevant than another. **Chemical thermodynamics** states that, under standard conditions, the molecular composition of a compound determines if **mineralization** is

Glossary

Activation energy (E_a): minimum amount of energy required for a reaction to proceed. E_a is an energy barrier that a reaction must overcome while transitioning from initial to final thermodynamic state, and regulates the rate of the reaction.

Chemical thermodynamics: field of study dedicated to defining the criteria responsible for predicting whether a reaction is feasible and will proceed spontaneously. The favorability of a reaction to proceed thermodynamically does not determine its rate.

Dilution theory: also known as the molecular diversity hypothesis; suggests that low concentrations, particularly for a complex mixture, can limit the ability of an organism to metabolize a substrate.

Ecosystem properties: include the extrinsic environmental conditions that could constrain the degradation of OM, including abiotic and biotic factors. Examples include temperature, pH, oxygen availability, nutrients, adsorption to minerals, and decomposer community composition.

Functional groups: specific groups of atoms or bonds within an organic compound that are responsible for its functional characteristics, including how it is likely to react. Carboxyl and phenolic groups are examples.

Gibbs free energy (ΔG): calculated as the difference in free energy between reactants and products for a given reaction at constant temperature and pressure. When ΔG is negative, the reaction is spontaneous; when ΔG reaches zero, the reaction has reached chemical equilibrium.

Humification: breakdown and transformation of organic material into a complex mixture of humus that is molecularly distinct from starting materials and can persist in soils.

Isomeric diversity: range of structural conformations for molecules with the same molecular formula and mass; the number of possible isomeric structures increases with molecular mass and could reflect functional diversity in terms of susceptibility to degradation.

Mineralized/mineralization: describes a set of biological and physicochemical reactions degrading OM into inorganic compounds (e.g., carbon dioxide and methane).

Molecular composition: generic term describing the chemical composition of OM, including its chemodiversity, optical

favorable. The thermodynamic favorability, or **Gibbs free energy (ΔG)**, considers bond energies, the chemical structure of OM, **functional groups**, and the oxidation state of carbon [34]. When ΔG is negative, the reaction proceeds spontaneously, and energy is released. However, in the case of DOM, ΔG is generally positive [34] and, thus, requires coupling to the reduction of a terminal electron acceptor or formation of a reduced carbon product [34]. However, thermodynamics is not concerned with the metabolic pathway or kinetics of the reaction. Rather, a kinetic energy barrier, called the **activation energy (E_a)**, must be overcome, and this regulates the rate of reactions. Thus, environmental conditions are relevant in constraining the rate of the reaction and even 'labile' OM can persist in certain scenarios. If conditions change, such that a specific enzyme becomes available for example, the activation energy is reduced allowing the reaction to proceed rapidly. Thus, in some scenarios, a reaction can be thermodynamically favorable but kinetically unfavorable. In such a scenario, even labile DOM can persist. Alternatively, a nonthermodynamically favorable reaction can occur if the activation energy is low.

characteristics, elemental composition, functional group composition, or isomeric diversity.

Since OM is a complex mixture of compounds, each with its own ΔG and E_a , it is useful to consider a continuum of thermodynamic and kinetic factors at play. Accordingly, the net effect might be that one 'appears' more relevant than another at a particular place and time. For instance, if compounds are approaching thermodynamic control rather than kinetic control, the overall reaction rate of the OM pool might reflect energy differences between reactants and products. In this case, the molecular composition can appear to be important to the 'apparent' rate of the bulk DOM reaction [scenario (i) in Figure 1]. In this case, more bioavailable and photolabile compounds might be degraded first, followed by less biolabile and photolabile compounds. When environmental constraints are imposed (such as limitations to the decomposer community), the activation energy increases, resulting in slower kinetics [scenario (ii) in Figure 1]. Within any pool of OM, there can be competing factors at play. For instance, the quality of plant litter in soils could contribute to OM pools spanning across a range of kinetics from scenario (i) to (iii) depending on how they form associations with mineral surfaces [35]. Temperature is relevant, being imbedded in the calculation of ΔG , and being relevant to kinetics, such as for enzymatic degradation [36,37]. Likewise, a range of other environmental factors, such as pH, nutrients, oxygen availability, soil moisture, the absence or presence of solar radiation, and adsorption to mineral surfaces, can shift kinetics. Under highly constrained environmental

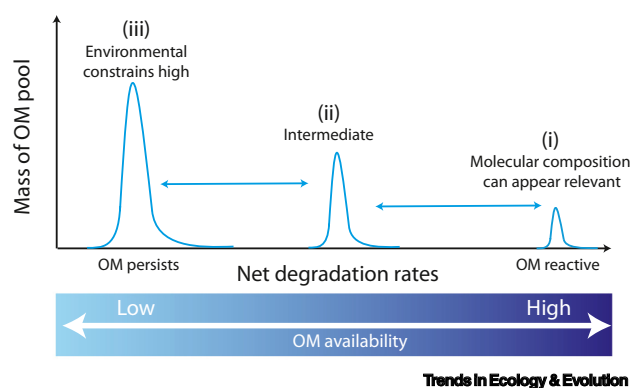


Figure 1. Title. Scenarios depicting pools of organic carbon across a continuum of degradation rates and masses under conditions that are (i) not constrained by environmental and biological conditions and highly reactive, resulting in a small mass of stored carbon, such as in freshwaters; (ii) an intermediate scenario whereby some environmental constraints slow degradation rates (such as nutrient limitation), resulting in a larger pool size; and (iii) a scenario under highly constrained conditions whereby organic matter (OM) is difficult to access and degradation rates are reduced

substantially resulting in an accumulation of organic matter (e.g., sediment, mineral soils, or peatlands). The reversible arrows indicate that conditions are fluid across a continuum of scenarios and dynamic, with the potential to be interchangeable. For instance, if environmental and biological constraints placed on scenarios (ii) and (iii) are lifted, degradation rates can shift to scenario (i) whereby the decomposer community is optimized, and degradation rates increase. In this conceptualization, we assume that production rates are constant across the continuum.

conditions, such as anoxia in peatlands or permafrost soils, the kinetic barrier increases such that OM can persist for centuries or millennia [scenario (iii) in Figure 1]. This scenario is particularly relevant where OM is physically separated or protected from enzymatic or solar photochemical degradation. As degradation rates slow, the size of the OM pool can be expected to increase [from (i) to (iii) in Figure 1]. A key point to recognize is that a single pool of OM can encounter a full range of constraints as it travels within or between ecosystems, and interchangeably appear to be regulated more, or less, by molecular composition [38] relative to ecosystem properties. For instance, OM frozen in permafrost [scenario (iii)] can become biological available upon thawing [scenario (i)], and once again be buried in lake sediment upon forming associations with particulate material [scenario (iii); Figure 1]. Likewise, DOM in a soil environment can be adsorbed to minerals and protected from decomposition [scenario (iii)] and subsequently desorbed back into solution phase [scenario (i), Figure 1].

The Relationship between Residence Time and Reactivity

In cases where the molecular composition is found to regulate degradation, as in freshwater ecosystems [13,39,40], there is a strong negative relationship between degradation rate and water residence time [39] (Figure 2A). This negative relationship between residence time and degradation rates has also been observed for marine sediments [20,41], but at far longer timescales. DOM in freshwater ecosystems is largely accessible to biological and photodegradation, lying conceptually near scenario (i) in Figure 1. However, even in freshwaters, a sizable fraction of the relationship between water residence time and degradation rates remains unexplained (59%) [39], suggesting that environmental constraints contribute to the unexplained variability in

(A) Residence time–reactivity relationship

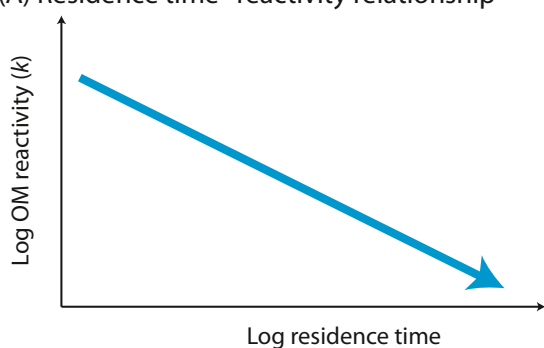
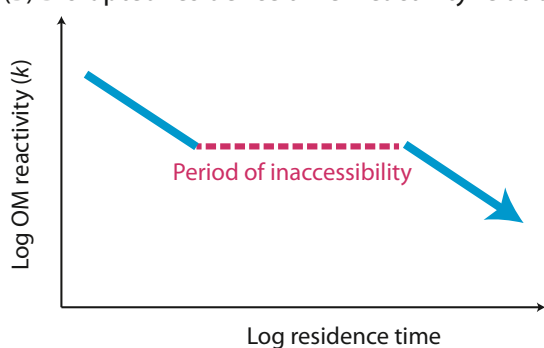


Figure 2. Title. Illustration of (A) the relationship between residence time and reactivity (e.g., [39]) with minimal environmental constraints, and (B) under a scenario where degradation is disrupted by ecosystem properties making organic matter (OM) inaccessible for biological degradation for an extended period of time (pink-broken line), before becoming accessible once again. Using radiocarbon dating to predict reactivity in scenario (B) would likely misrepresent the amount of time OM was exposed to degradation processes.

(B) Disrupted residence time–reactivity relationship



Trends In Ecology & Evolution

degradation rates. In a complimentary study of whole-lake dissolved organic carbon (DOC) budgets, reactivity was strongly related to water residence time, and nutrient status helped predict whether the lake was a carbon source or sink [40]. In the ocean, initial degradation rates of algal DOM are also rapid, with residence time likewise being inversely linked to reactivity [42]. In fact, most marine DOM is generated from primary productivity and consumed within weeks, with only $\approx 1\%$ left after a decade [42]. Only an extremely small fraction of the DOM pool accumulates, ultimately persisting for millennia. In soil environments, when the opportunity to be physically protected by mineral surfaces is removed, soil DOM can have similar degradation rates (<0.001 – 0.30 d^{-1}) [43] to its freshwater counterpart (0.001 – 0.50 d^{-1}) [44,45]. Intriguingly, the molecular composition of soil DOM can help predict how it functions; for example, whether associations with mineral surfaces will form [43,46,47]. (See Figure 3.)

When Time Stands Still: Disconnecting Chronological Time (^{14}C) from Reactivity

In the subsoil environment, soil OM with a radiocarbon age of several thousand years has been found to be highly ‘labile’ once destabilized into solution [48], as for shale degradation [49]. This observation was previously interpreted as a reason to discredit the consideration that residence time is a predictor of OM reactivity [50]. In consolidating this apparent discrepancy, it appears that, when OM is biologically inaccessible, the relationship between residence time and reactivity may be disrupted (Figure 2B). When the opportunity for enzymatic degradation, for example, is eliminated, the time–reactivity clock is effectively paused. Yet, chronological time continues, and the time–reactivity relationship resumes once the constraint is lifted. The chronological age of OM is reflected by radiocarbon dating of ^{14}C ; a proxy for the time since the original plant tissue fixed atmospheric CO_2 , and continues irrespective of degradation. Thus, when OM is biologically inaccessible due to physical and chemical factors, such as occlusion in mineral pore spaces [51], extremely dilute conditions [15,16], being frozen in permafrost [52], or anoxia [53], the radiocarbon date is irrelevant to its reactivity or degradation rate.

Recognition that a residence time–reactivity clock operates independently from chronological time is a relevant consideration and helps consolidate the fact that OM can persist in some environments for a long time. We emphasize that it would be erroneous to disregard the role of time in predicting OM reactivity and stress that effort should rather be placed on understanding when and why the residence time–reactivity clock is paused.

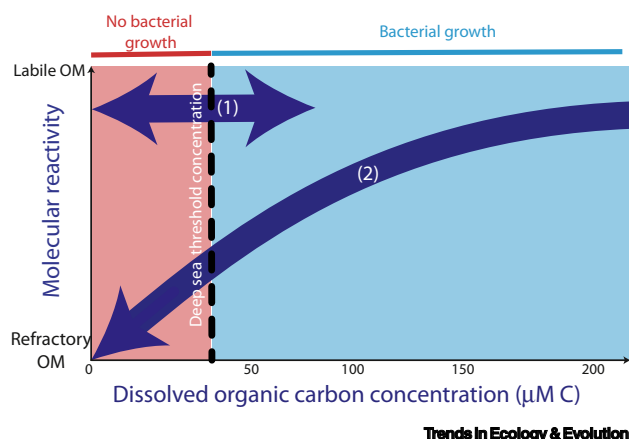


Figure 3. Title. The current conceptualization of the dilution theory (arrow 1) suggests that bacterial growth is limited below a threshold dissolved organic carbon concentration found in the deep sea (black-broken line, $42\text{ }\mu\text{M C}$ [16]), even if the molecular composition of the organic matter (OM) remains labile with progressive decomposition. An alternative theory in freshwater is that the molecular composition of OM becomes progressively less reactive with degradation (arrow 2). It remains unclear whether the dilution theory holds in ecosystems outside of the deep sea and where the minimum threshold

concentration for effective bacterial growth lies for freshwater ecosystems, such as glacial meltwaters. Figure inspired by [92].

The Need to Test Theories across Ecosystem Boundaries

As our understanding of OM degradation dynamics progresses, it becomes clear that some concepts are inconsistent across subdisciplines, and carefully designed cross-ecosystem studies are required. Ideally, emerging studies would include OM from several sources and different environmental conditions and challenge previously proposed hypotheses by testing their strengths and limitations across ecosystem boundaries. The **dilution theory** is one example of a theory that could benefit from being tested outside the marine environment. The dilution hypothesis expresses that, at concentrations typical of the deep sea (42 μM C), DOM compounds are in fact labile, but individual substrate concentrations lie below the threshold of energetic requirements of prokaryotes [16]. When DOM from the deep sea was concentrated up to a factor of 10, Arrieta *et al.* [35] found enhanced bacterial activity. This led to the conclusion that concentration was limiting bacterial utilization of DOM. However, comparable freshwater studies found that, under increasingly dilute conditions (down to 40 μM C), prokaryotic activity was not constrained [38,54]. In addition, highly reactive OM has been found in glacial meltwaters at concentrations similar to, or far lower than, the deep sea (11 μM C) [55,56]. Thus, it is possible that the threshold concentration relevant for the deep sea (42 μM C) does not apply across ecosystems and is composition dependent.

One cross-ecosystem study testing the dilution theory found that DOM from deep ocean waters exhibits higher **isomeric diversity** than lake DOM. High isomeric diversity greatly reduces the concentration of any individual compound down to picomolar concentrations, and thereby *a priori* supports the dilution theory. However, the freshwater lake sample had a higher number of chemical formulas assigned, suggesting a wider diversity of molecules but at higher concentrations individually [57,58]. Thus, it is vital to recognize that the threshold concentration may be variable in other environments. Whether this is due to DOM composition or environmental constraints needs to be answered through a common effort. Likewise, it would be useful to develop a better understanding of how effective a particular enzyme, or set of enzymes, might be at cleaving the numerous structural isomers represented within a single mass to charge peak in a mass spectrum.

Concluding Remarks

Resolving discrepancies, such as when and why a particular theory holds, is relevant for predicting future global carbon fluxes. This is particularly important where slight shifts in the reactivity of large pools of organic carbon can have substantial consequences to the flux of the greenhouse gases, CO_2 and CH_4 . For instance, it is useful to understand when and why residence time and reactivity are connected and disconnected, and when and why molecular composition appears to be more relevant than ecosystem properties. Cross-ecosystem studies are critical to making the next set of important breakthroughs in our understanding of controls on OM degradation [39,59,60]. Cross-ecosystem studies may be experimentally challenging at times [61], yet, have previously proven to give a deeper and more holistic understanding in the fields of nutrient limitation and understanding of the role of extracellular enzymes [62,63]. Eventually, these more robust theories can be incorporated into earth system models.

Although we acknowledge that ecosystem properties vary widely across ecosystems, we argue that fundamental controls on OM degradation are universal. This boundless property [64], whereby carbon exchanges across ecosystems indiscriminately, forces us to more rigorously challenge the validity of concepts that have diverged in adjacent ecosystems. To unify this fragmented understanding, we should recognize that the importance of molecular composition can appear to be 'masked', because ecosystem properties are possibly limiting degradation, and alternatively, where molecular composition appears to regulate degradation, ecosystem

Outstanding Questions

For those working, or planning on working, across ecosystem boundaries, how do we overcome the set of experimental challenges of working with OM across highly contrasting ecosystems, such as matrix effects?

What is the best measure of OM reactivity that can be used in a consistent manner across soil, freshwater, and marine subdisciplines? Since the reactivity of OM is highly variable and can be measured as radiocarbon age, turnover time, half-lives, and degradation rates, a common descriptor of OM reactivity is required to effectively compare reactivity across ecosystems.

How can we accurately measure the distribution of OM degradation rates across soil, freshwater, and marine ecosystems?

How do earth system models accommodate a flexible conceptualization of controls on OM degradation and include a universal measure of molecular composition?

How can we most effectively reduce the uncertainty associated with degradation rates entered into earth system models?

In moving forward, how do we best design empirical studies focused on unifying controls on OM reactivity that cross ecosystem boundaries?

properties could be providing the opportunity for more rapid degradation. Since the same pool of OM might be exposed to either extreme (fast or slow kinetics), our conceptualization should be flexible enough to include both molecular composition and ecosystem properties as relevant controls, and switch back and forth as needed.

Rather than complacently accepting diverging ‘ecosystem specific’ viewpoints, we suggest challenging and testing existing theories across ecosystem boundaries to reveal more universal mechanisms behind OM preservation and reactivity. We give several examples of questions that remain to be addressed (see Outstanding Questions). To address these, we encourage collaborative research from scientists across ecosystems, interactions between experimentalists and modelers and efforts to use more accessible terminology. Ultimately, we propose striving towards a conceptualization of OM degradation that is independent of the ecosystem and flexible to changing ecosystem properties.

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