Climate Change Ecology 2 (2021) 100025

Contents lists available at ScienceDirect

Climate Change Ecology

journal homepage: www.elsevier.com/locate/ecochg

Patterns and trends of organic matter processing and transport: Insights from the US long-term ecological research network

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ARTICLE INFO

Keywords:
Organic matter storage
Coupled biogeochemical cycles
Transport
Organic matter composition
Stabilization
Cross-site synthesis

ABSTRACT

Organic matter (OM) dynamics determine how much carbon is stored in ecosystems, a service that modulates climate. We synthesized research from across the US Long-Term Ecological Research (LTER) Network to assemble a conceptual model of OM dynamics that is consistent with inter-disciplinary perspectives and emphasizes vulnerability of OM pools to disturbance. Guided by this conceptual model, we identified unanticipated patterns and long-term trends in processing and transport of OM emerging from terrestrial, freshwater, wetland, and marine ecosystems. Cross-ecosystem synthesis combined with a survey of researchers revealed several themes: 1) strong effects of climate change on OM dynamics, 2) surprising patterns in OM storage and dynamics resulting from coupling with nutrients, 3) characteristic and often complex legacies of land use and disturbance, 4) a significant role of OM transport that is often overlooked in terrestrial ecosystems, and 5) prospects for reducing uncertainty in forecasting OM dynamics by incorporating the chemical composition of OM. Cross-fertilization of perspectives and approaches across LTER sites and other research networks can stimulate the comprehensive understanding required to support large-scale characterizations of OM budgets and the role of ecosystems in regulating global climate.

1. Introduction

Organic matter (OM) dynamics in ecosystems are among the most complex phenomena in environmental science, and the outcomes of OM dynamics have value to society. Vast transfers of carbon (C) from fossil, detrital, and soil pools to the atmosphere have warmed the climate and shaped ecosystem productivity [7,8,65,76,123,131]. Storage of C within ecosystems in turn provides the valued service of climate regulation [83,86,125]. However, significant uncertainties in broad-scale patterns and trends of OM pools in soil, water, and primary producers (e.g., [46,143]) limit projections of OM storage and application of management strategies, particularly regarding changes in large global

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Supplemental Information

https://doi.org/10.1016/j.ecochg.2021.100025
Received 18 December 2020; Received in revised form 5 August 2021; Accepted 9 August 2021
Available online 11 September 2021

pools, rates of processes that stabilize OM within ecosystems, and the role of transport within and between ecosystems [14,149]. Resolving these uncertainties requires integrating approaches across disciplines and ecosystem types.

We synthesized insights from the US Long-Term Ecological Research (LTER) network to highlight emerging understanding and critical uncertainties about patterns, trends, stabilization processes, and transport of OM within and between ecosystems. The LTER network consists of 28 sites including forest, grassland, dryland, lake, stream, wetland, coastal, oceanic, polar, agricultural, and urban ecosystems (Supplemental Table 1) that study primary production, disturbance, fluxes of inorganic nutrients, populations and communities, and dynamics of OM [22]. Long-term observations and experiments maintained by the LTER network therefore represent a rich resource for analysis of the complex global dynamics of OM.

Our analysis is anchored by a conceptual model of OM dynamics developed to facilitate cross-ecosystem comparisons and stimulate integrated approaches (Box 1). This conceptual model integrates geochemical, ecosystem, and earth system perspectives and emphasizes the role of disturbances that potentially destabilize OM stocks. The conceptual model seeks to identify patterns and processes that are shared across terrestrial, aquatic, and marine ecosystems. Anchored by the conceptual model, we synthesized OM dynamics across the LTER network, including a survey of LTER scientists, vignettes describing OM dynamics at each site, and publications selected by researchers. These diverse approaches to qualitative synthesis complement efforts to quantitatively model OM dynamics by highlighting critical interactions and complexity that may be lacking in models or current large-scale assessments. Specific objectives of the synthesis were to: 1) describe temporally dynamic patterns in OM *storage*, 2) highlight key *processes* that stabilize or destabilize these storage pools, 3) characterize the nature and extent of OM *transport* within and between ecosystems, and 4) summarize *long-term trends* in OM pools that have emerged from long-term monitoring.

2. Factors influencing OM pools and transport

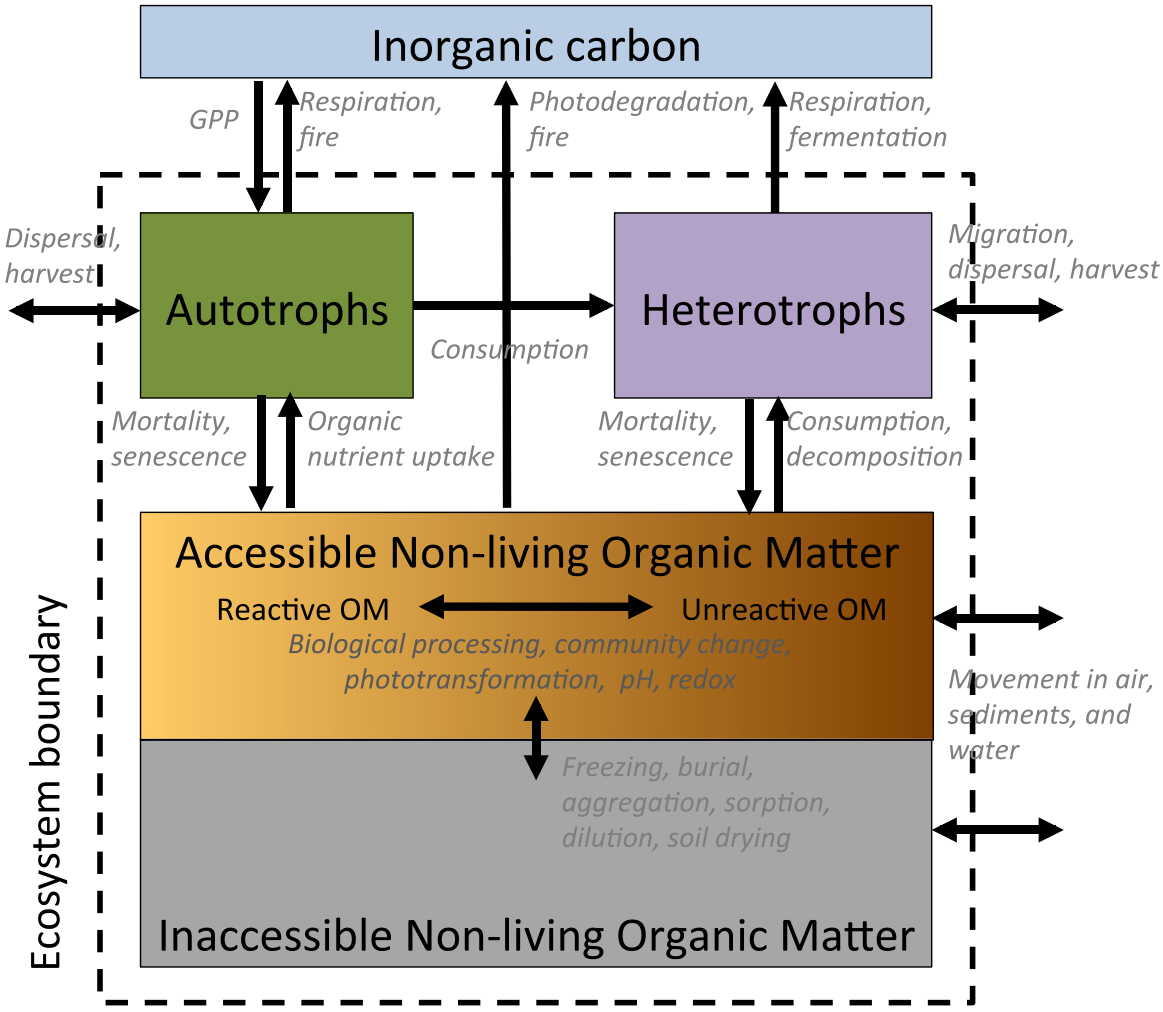
We administered a survey to gather qualitative assessments of the factors governing the vulnerability of OM to transformation, loss, and transport within and across ecosystem boundaries. The survey contained queries about the relative importance of factors contributing to preservation of OM in ecosystems that recent conceptual models and experiments have identified as influential, including physical protection or isolation, dilution, freezing, sorption, decomposer communities, chemical composition of OM, nutrients, and redox [87,121,134,145]. The survey also addressed potential vectors that transport OM within ecosystems and across boundaries. Though studies of aquatic ecosystems routinely address transport, conceptual and quantitative models have not yet captured the roles of multiple potential vectors transporting OM within ecosystems and across ecosystem boundaries. Potential mechanisms influencing OM storage and transport were assessed on a 5-point Likert scale, and respondents optionally contributed additional mechanisms thought to influence preservation of OM at their LTER site that were not captured by the survey (Supplemental Table 2). Finally, the survey included open-ended queries assessing the most significant press and pulse disturbances influencing OM dynamics at each LTER site. Of 28 total LTER sites, 24 responded, three of which (BNZ, MCM, PIE) provided separate responses on freshwater, terrestrial, and/or marine ecosystems. At each site, the survey was completed by a single investigator or by small-group consensus. Disciplinary expertise of respondents included oceanography, decomposition, geochemistry, microbial ecology, vegetation, and modeling.

Most LTER sites rated decomposer communities, nutrient limitation, and substrate chemistry of high importance in influencing accessibility of OM to loss, whereas relevance of photodegradation and redox was heterogeneous across sites (Supplemental Fig. 1). Conceptual models and experiments focused on OM storage in terrestrial or marine ecosystems have similarly emphasized the roles of microbial communities and substrate chemistry, highlighting their interactive effects [3,71,89,118]. Survey responses generally concurred with emerging conceptual models that emphasize preservation of OM due to physical disconnection of OM from microbial communities or environmental conditions that are conducive to decomposition, such as aggregation, burial, and sorption (Fig. 1; [47,87,119,121,152]). However, the perceived relative importance of some factors influencing preservation varied among freshwater, marine, and terrestrial ecosystems. First, burial was rated as less important to OM decomposition in terrestrial compared to marine ecosystems (Fig. 1). We note that persistence of OM via burial in marine systems may be similar to the effect of soil depth in terrestrial ecosystems, but the mechanisms by which OM transport occurs are distinct. Second, drying was rated of greater importance in terrestrial than freshwater ecosystems (Fig. 1). Such contrasts likely reflect the environmental conditions of different ecosystems, but also suggest that synthesis of conceptual models across ecosystem types might promote discovery of unifying principles explaining OM storage.

Vectors of OM transport were assessed as nearly identical in relative importance whether movement occurred *within* ecosystems (data not shown) or *across* ecosystem boundaries (Fig. 1). Such similarities might reflect limited studies that distinguish between internal and cross-boundary transport, and could be resolved with multi-scale studies of transport. Water was of greater perceived importance for transport in freshwater and marine than terrestrial ecosystems, whereas animals were viewed with greater importance in marine and terrestrial ecosystems (Fig. 1). Individual transport mechanisms are already recognized as integral to dynamics of some OM pools, such as hydrologic flux in river networks [114], particle sinking in oceans [13], and soil erosion [27]. The survey results indicate that multiple vectors of transport might significantly influence OM dynamics within or between ecosystems, but this diversity of vectors is not yet represented in most conceptual or predictive models of OM dynamics.

Expert assessment of the relative importance of factors influencing OM dynamics did not consistently follow gradients in temperature (mean annual temperature; MAT) or precipitation (mean annual precipitation; MAP) encompassed by the LTER network. Likert-scored survey items were analyzed by ordered logistic regression with MAT and MAP as predictors and relative rankings of factors influencing OM dynamics were largely heterogeneous with respect to MAP and MAT (Supplemental Fig. 2). Significant responses included an increased importance of freezing in drier ecosystems, and increased importance of humans as vectors of OM transport across ecosystem boundaries in warmer ecosystems (Supplemental Fig. 2). Though precipitation and temperature drive global patterns in OM storage and export (e.g., [11,21,36,41]), the survey results highlight uncertainty regarding the influences of climate on particular pathways of OM processing and storage.

Survey respondents listed the most important factors influencing vulnerability of OM to loss from ecosystems (Fig. 2), as well as the most important long-term (i.e., press) and short-term (i.e., pulse) global changes. Climate was the most-cited factor thought to strongly influence OM dynamics at each site, followed by export processes, redox, and OM composition (Fig. 2). Further, climate change was most frequently cited as the primary long-term (press) catalyst of OM loss (18/23 responses), whereas the next most-cited global change, drought, was identified by only four sites. Other long-term threats included atmospheric deposition, land use change, precipitation regime, sea-level rise, and human decision-making. Changes in storm size and dynamics were the most-cited short-term (pulse) factor influencing OM dynamics, identified by 8/14 respondents to this survey item. Other important short-term changes included fire, thaw (ice or permafrost), and drying or drought. The diversity of factors identified as threats to OM stores reflects views emerging from personnel oriented by expertise in ecosystems, microbial communities, and geochemistry and studies across a network of sites encompassing terrestrial, freshwater, and marine ecosystems. These diverse perspectives suggest opportunities for cross-fertilization among ecosystem types and disciplinary perspectives. For example, export, re-



Box 1. Pools and fluxes of organic matter in ecosystems and the processes that influence their vulnerability to environmental change. Organic matter dynamics are studied from diverse perspectives including those of ecologists, geochemists, and agronomists; in aquatic and terrestrial ecosystems; and with research foci ranging from species to ecosystems. Here we develop a general conceptual model of OM dynamics that merges these perspectives to support development of large-scale OM budgets and mechanistic models for projecting the responses and effects of ecosystems on global climate. This model encompasses patterns and processes that are shared across terrestrial, aquatic, and marine ecosystems. Arrows represent fluxes between pools (boxes). Gray text represents processes that mediate those fluxes and are subject to press and pulse disturbances.

We define non-living OM as the pool that is accessible to decomposer organisms, whose activity determines its rate of decay. The size of the non-living OM pool in an ecosystem is determined by the balance between inputs to OM from autotrophs (either directly or via consumption by heterotrophs) plus imports of OM from other ecosystems and losses of OM via decomposition, fire, photodegradation, and exports. Within the **accessible OM pool,** factors such as nutrient limitation, energetics (as influenced by substrate chemistry, redox, and the availability of electron acceptors), the community composition and physiology of decomposers (that determine degradative capabilities, C use efficiency, and stoichiometry), pH, and solar radiation determine the relative reactivity of OM. Organic matter in the accessible pool can be made **inaccessible** by processes such as sorption or complexation with minerals; physical protection within soil and sediment aggregates; burial; freezing; abiotic and biotic transformations; and impediments to diffusion, such as dilution of organisms or substrates, or soil drying. The size of the non-living OM pool is further influenced by **import and export** processes such as harvest and movement of food and waste; animal migration; and movement in air, sediments, and water as a result of wind-driven processes like erosion and dispersal; water-driven processes including advection, tides, runoff, and currents; and gravity-driven processes like settling and mass wasting. Finally, abiotic processes such as fire and photodegradation can mineralize OM and contribute to losses and transformations along the continuum from reactive to unreactive OM.

The vulnerability of the non-living OM pool to environmental **press and pulse disturbances** depends on how those disturbances alter the various processes involved in inputs to and losses from the OM pool. For instance, OM will be vulnerable to environmental changes that alter the reactivity of OM, such as changes in climate, solar radiation, atmospheric deposition, or disturbance regimes that in turn alter autotrophic and heterotrophic community composition, substrate chemistry, temperature, moisture, pH, and redox. Environmental changes that move OM from the inaccessible to the accessible pool, such as permafrost thaw, tillage, and drainage, will promote decomposition and OM loss, whereas changes that render OM inaccessible, such as burial and flooding, will promote OM accumulation. In addition, OM will be vulnerable to environmental changes that promote or diminish transport of OM across ecosystem boundaries, such as climate change effects on sea level, stratification of water bodies, ocean currents, surface runoff, landslides, and animal migration or dispersal.

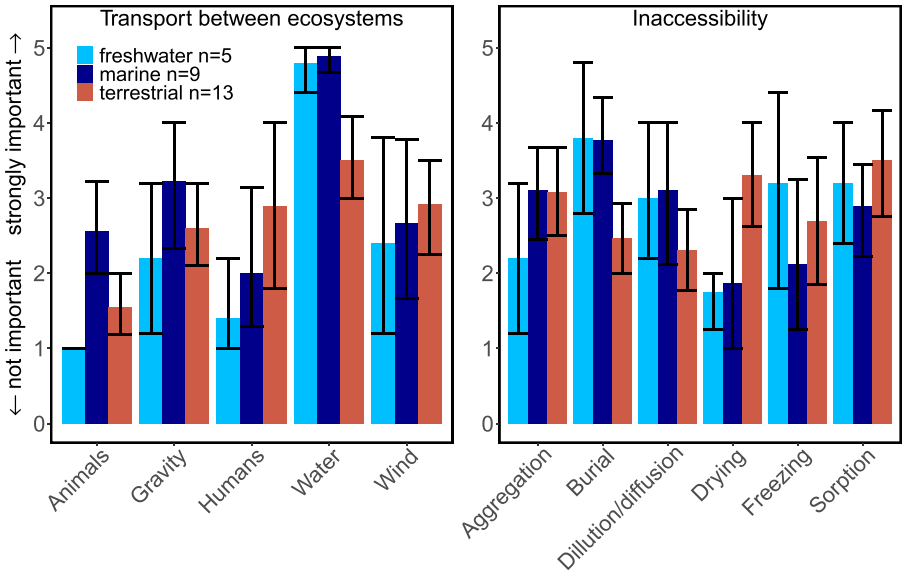


Fig. 1. Importance of vectors transporting OM across ecosystem boundaries (left) and contributing to inaccessibility of OM to transformation and loss (right) as assessed by survey respondents for freshwater, marine, and terrestrial ecosystems within the LTER network. Non-overlapping 95% confidence intervals (bootstrapped) indicate significant differences among ecosystem types.

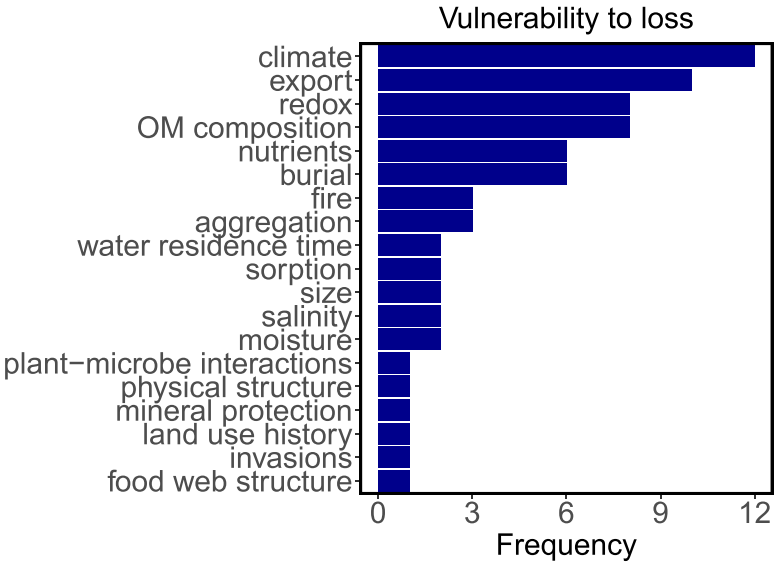


Fig. 2. Frequency of factors cited as most important in determining whether OM is vulnerable to transformation and loss. Each site's (n = 27) response is represented by up to four terms.

dox conditions, and burial processes were frequently cited as key to determining the vulnerability of OM to loss from ecosystems, yet these mechanisms are infrequently included in conceptual models of terrestrial OM storage.

3. Organic matter processing, patterns, trends, and transport

We synthesized current understanding of patterns, processing, transport, and temporal trends in OM dynamics and storage derived from the LTER network. This qualitative synthesis of experiments, monitoring, and models was facilitated by four approaches: 1) site-specific modifications and emphases added to a draft of the conceptual framework (Box 1) presented at the 2018 LTER All Scientists Meeting (n = 15 sites); 2) references submitted in support of responses to the previously described survey; 3) a vignette highlighting a key set of findings related to OM dynamics at each site (n = 17 sites), and 4) a query regarding insights into OM resulting from long-term experiments and monitoring (n = 10 sites).

3.1. Patterns

Documenting the spatial and temporal patterns of OM distribution establishes the present state and future scenarios of ecosystem OM storage, reducing uncertainty in managing this ecosystem service. L Long-standing research, including studies at LTER sites prior to inception of the network, has linked patterns in storage and processing of OM in terrestrial and wetland ecosystems to five state factors of soil and ecosystem formation [67]: climate, parent material, topography, organisms, and time (e.g., [144] [BNZ], [10] [CWT], [62] [ARC], [33] [GCE], [2] [SEV]). Research in marine and freshwater ecosystems established the roles of light regime, inundation, salinity, currents, and vertical mixing in organizing the distribution of OM (e.g., [111] [MCM], [50] [NES], [94] [FCE], [132] [CCE], [135] [CCE]). Current efforts have integrated some of these data into shared databases, but additional work is needed to leverage the breadth of OM data across ecosystems from the LTER and other research networks [147,148]. Below we highlight how the LTER network has built on these established templates to characterize non-stationary patterns in OM dynamics, which is required for forecasting.

Land use and its legacies shape spatial and temporal patterns in OM dynamics. For example, soils of urban, temperate grasslands are more organic-rich than surrounding forests (BES; [109,113]). Similarly, enhanced storage of OM in soils of urban, arid ecosystems relative to native desert occurs because relatively large stores of OM are a legacy of fertilized and irrigated agriculture that preceded urbanization, and atmospheric deposition of OM derived in part from fossil fuel combustion contributes significantly to the OM pool in urban soils (CAP; [55,74,75]). Urban land use and water management practices also re-

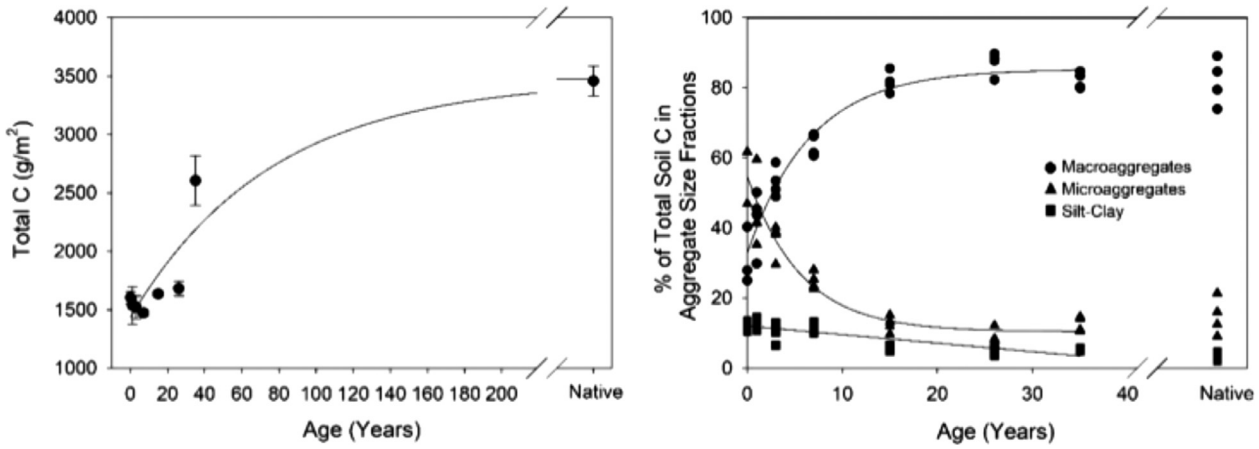


Fig. 3. Long-term consequences of land management for OM storage in grasslands (KNZ). In temperate grasslands, restoration of native prairie following long-term tillage resulted in multi-decadal accumulation of soil OM and recovery of soil aggregate C distribution across a 35-year restoration chronosequence. A model of C recovery based on observations of soil OM (0–10 cm) indicates that more than two centuries will be required to achieve 90% of soil C stock in never cultivated prairie (left; [153]), whereas the distribution of C among aggregate fractions becomes similar to never cultivated prairie within three decades (right; [154]).

sulted in increased concentration of labile dissolved OM in streams relative to undeveloped catchments and increased rates of microbial mineralization and photooxidation, suggesting enhanced potential for CO_2 evasion from streams (CAP, BES; [40,52,73]). However, structures designed to retain water in urban watersheds are effective at reducing loads of dissolved OM (CAP; [52]).

Agriculture has large, biome-specific effects on OM storage. OM storage declines when boreal forests, which are characterized by large OM stores in the forest floor, are converted to agriculture (BNZ; [49]). Cultivation practices, such as soil tillage, can influence the magnitude of OM lost during agriculture. For example, significant declines in soil OM followed 20 years of plowing, compared to smaller losses from no-till and plowed cover crops (KBS; [126]). Accumulation of OM then follows abandonment of agriculture or active restoration of temperate ecosystems to native vegetation cover. Agricultural lands restored to grassland continue to accumulate soil OM for at least a century following restoration, whereas the distribution of C among aggregate fractions becomes representative of never-cultivated prairie soil on a decadal time scale (KNZ; Fig. 3; Scott et al. 2017).

Projections of OM storage following cultivation and harvest remain uncertain due to complex trajectories and varying time scales associated with recovery of OM pools. Recovery of C pools following harvest of old-growth forest occurs on a century time scale, and depends on the amount of large wood remaining after harvest relative to the rate at which forests re-establish (AND; [58]). Reduced forest harvest combined with agriculture abandonment has led to increased OM storage in re-growing northeastern US forests on a similar timescale, and this pattern is attributed to OM in tree biomass, though the contribution of soil storage remains uncertain (HFR; [43]). OM in mineral soil, the largest pool of soil OM in temperate forests, was lost and accumulated slowly in the decade following an experimental harvest, slowing recovery of OM storage in the ecosystem despite rapidly regrowing vegetation (HBR; [53]). Subsequent intermittent disturbances to vegetation growth further delay recovery of balanced inputs and outputs of OM (HBR; [42]). Accurately projecting change in large, heterogeneous pools such as soil OM remains challenging and tracking changes in particular components of large pools might lend mechanistic understanding needed to more accurately estimate changes in total OM storage. For example, catchments clearcut forty years ago exported less total DOM, but more microbial and protein-like DOM than unharvested catchments, which could indicate that recovery of plant and humic fractions lags recovery of less reactive microbial products (HBR; [23]).

Disturbance regimes contribute to spatially heterogeneous and temporally dynamic OM stocks. Increasingly intense fire regimes and longer fire seasons significantly reduce stocks of soil OM in the boreal forest (BNZ; [141]), and along with increasing temperature, shift OM storage from the forest floor to aboveground biomass (BNZ; [1,72]). Experimentally increased fire frequencies reduced storage of biomass and soil OM in temperate savannas (CDR; [105]) and in arid grasslands (SEV; [64]). Soil OM was also enhanced by suppression of fire and removal of grazers in more mesic temperate grasslands, though the increase in soil OM storage under low fire frequencies was associated with increased woody plant cover and loss of grassland habitat (KNZ; [29]). Responses of OM pools to fire are due in part to variation in the strength of nitrogen limitation and effects of fire on N availability, highlighting the importance of OM-nutrient interactions (e.g., [104]).

Large storms and long-term patterns in the frequency of storms have long-lasting and widespread influence on OM storage. Disturbance of tropical forests by hurricanes was simulated in an experiment that enhanced organic debris deposition and removed the tree canopy. Experimental litterfall enhanced storage of OM in tropical soils at depths >50 cm 10 years after the manipulation, but canopy loss partially counteracted this effect (LUQ; [51]). Regions or time periods (e.g., El Niño) subject to more frequent or intense storms suppress giant kelp growth due to wave action (SBC; [115]), not only influencing productivity of kelp forests, but also diminishing export of kelp detritus and storage on sandy beaches (SBC; [117]).

Insect outbreaks can reshape ecosystem OM storage, particularly in combination with changing climate. For example, hemlock-dominated stands in a northeastern forest have become a net source of C to the atmosphere due to the widespread outbreak of hemlock wooly adelgid, whose spread is closely tied to climate (HFR; [43]). A girdling experiment simulating tree mortality expected due to insect outbreaks in an arid ecosystem did not enhance growth of an unmanipulated, competitor tree species because a simultaneous drought suppressed vegetation growth. This experiment suggested that insect outbreaks concurrent with drought could ultimately cause replacement of woodlands with grasslands, which store less soil OM in this region (SEV; [97,106,112]).

Dynamic hydrologic conditions, including spatial and temporal patterns in inundation, precipitation, waves, and vertical mixing also contribute to spatially and temporally variable OM storage and dynamics. Sea-level rise increases the duration of flooding on salt marshes, where inundation preserves OM in sediments due to low redox potential, but also diminishes primary production, suggesting an eventual tipping point in the capacity for accumulation of OM (PIE; [44]). Further, increasing salinity in tidal salt marshes in response to sea level rise reduces soil OM as compared to brackish and tidal freshwater marshes and forests (GCE; [34]). Water residence time constrains processing and

storage of allochthonous OM in temperate lakes, with greater opportunities for storage in lakes where stream and groundwater discharges are smaller components of the lake water budget (NTL; [56]). In both nearshore and pelagic marine ecosystems, long-term variation in net primary production and detrital OM exports are correlated with supply of nitrate and/or iron delivered by upwelling from deep waters (CCE, SBC; [19,138]). Hydrologic conditions also shape OM storage in terrestrial ecosystems. For example, soil OM content of desert grasslands is preserved under hot, dry conditions, and declines when precipitation exceeds a seasonal threshold, likely due to stimulation of water-limited decomposer activity and water loss to runoff [64,142]. However, fewer studies explicitly address hydrologic effects on OM distribution in terrestrial ecosystems, where hydrology might influence redox conditions or availability of limiting substrates. Investigation of similar hydrologic effects to those established in aquatic ecosystems might therefore reduce uncertainty in projecting changes to stocks of terrestrial OM.

Understanding the relationships of OM storage with disturbance events and regimes can guide management activities to promote OM storage in ecosystems. For example, seeding replaced seagrass beds lost to disease and hurricanes while enhancing OM stores in estuarine sediments, with greater accumulation under highest seagrass density (VCR; [48]). In contrast to many examples of OM loss following disturbance, some pools may be resistant to disturbance, and the mechanisms supporting resistance could inform restoration activities. For example, temporally stable DOM concentrations in wetlands subject to fire, drought, and hurricanes suggest that large OM pools and intact hydrologic connections maintain stable flows of OM from terrestrial to aquatic ecosystems (FCE; [79]). Overall, whereas the LTER network and other long-term studies have established the roles of disturbance regimes in structuring spatial and temporal patterns in OM storage, existing conceptual models infrequently represent disturbance or explicitly consider only a single disturbance type (e.g., [88,121,152]). Thus, merging empirical characterization of disturbance effects with models presents an opportunity to advance theoretical understanding and enhance management of OM storage.

3.2. Processing

Long-term experiments, spanning up to multiple decades, have contributed to understanding how ecosystems process OM. Decomposition experiments revealing species-specific decay rates and ubiquity of “slow” and “fast” phases of decomposition across ecosystems underscore the long-known influence of chemical composition of detritus on decomposition rate (16 LTER sites; [28,57,59]). Addition of leaf litter over decadal scales resulted in little change in pools of soil OM in forests, indicating the role of labile pools in priming decomposition of older OM (AND, HFR; [81]). In the same long-term experiment, removal of root inputs reduced storage of particulate OM, but increased mineral-associated fractions (AND; [107]). Shorter-term decomposition experiments have additionally emphasized photodegradation as a mechanism of OM transformation and loss across multiple biomes and ecosystem types, even under lower light conditions beneath forest canopies (SEV, CDR, ARC; [16,32]).

Experiments simulating aspects of global change have often caused rapid changes in inputs and losses of OM (e.g., photosynthesis and respiration). Experimental drought applied over six months that was intended to simulate projected climate change in the sub-tropics reduced potential storage of OM in freshwater wetlands due to decreased primary production and increased ecosystem respiration (FCE; [91]). In contrast, simulating drought over three years in desert grasslands caused declines in both soil respiration and primary production, but changes in storage of soil OM have not yet been observed (SEV; [80,102]), perhaps due to rapid microbial decomposition of recalcitrant C pools [129]. In tidal marshes, experimental, chronic saltwater intrusion reduced CO_2 and CH_4 emissions, but also reduced belowground biomass, leading to soil subsidence and decreased OM stocks after two to four years of treatment (GCE; [61,133]).

Multi-year experiments have revealed non-linear effects of global change, particularly warming, on OM storage and losses. Experimental, summertime warming of an arctic tundra ecosystem for 6–9 years increased OM storage, largely due to increases in total plant biomass driven by growth of particular species, and this effect was observed after several years of treatment (ARC; [25,128]). In contrast, experimental warming caused losses from sub-arctic tundra over a similar time scale when warming was sustained over winter, due to increased soil respiration in winter that exceeded gains in primary production during summer warming (BNZ; [92]). Soils from a mid-latitude hardwood forest lost OM nonlinearly over 26 years of experimental warming, with substantial C loss after initiation of warming, and diminishing losses over time, as well as periods showing little to no C loss (HFR; [95]). However, when evaluated from a whole ecosystem perspective, increases in plant biomass due to forest regrowth and climate change over this same period offset soil C losses due to experimental warming (HFR; [43]). Significant changes in C storage and fluxes in response to global change experiments portend large changes in C stocks in diverse ecosystems, but time-varying responses underscore the importance of maintaining experiments over long time periods to resolve both the mechanisms linking OM dynamics to global change and the non-linear trajectories of OM storage.

Motivated by widespread nutrient enrichment of terrestrial and aquatic ecosystems by fertilizer use and atmospheric deposition, long-term fertilization experiments have revealed the strong coupling of C with other elemental cycles. Decadal-scale fertilization of a tidal freshwater marsh with nitrogen or phosphorus alone decreased soil OM, though OM storage increased when nitrogen and phosphorus were added together because of increased belowground macrophyte biomass (GCE; [156]). Nitrogen fertilization of a tropical forest increased total OM storage in soil after five years despite more rapid decomposition of actively cycling C, due to increased turnover time of slowly cycling pools (LUQ; [35]). Similarly, 20 years of nitrogen addition to a temperate hardwood forest suppressed decomposition, resulting in increased storage of OM in soils (HRF; [45]), an effect that counterbalanced observed losses of soil OM from experimentally warmed plots in the same forest (Fig. 4). In contrast, 12 years of nitrogen addition to temperate grasslands resulted in decreased rate of OM storage relative to N inputs as plant communities shifted from a species-rich assemblage of native grasses to one composed of fewer species (CDR; [146]). In alpine tundra, nitrogen fertilization also changed species composition, but accelerated the decomposition of light-fraction soil OM, increasing relative abundance of compounds with longer turnover times, without changing total soil OM stocks (NWT; [12,99]). Experimental replacement of calcium lost due to acid rain in a temperate forest simulated the long-term trajectories of OM storage that are expected under declining acid deposition, which has resulted from changes in environmental policy. Despite increasing tree biomass, calcium addition caused large losses of OM from organic soils, though it remains unclear whether biological or chemical processes contributed to the loss (HBR; [6,68]).

Fertilization experiments have also revealed surprising consequences of coupled elemental cycles that contribute to the dynamics of ecosystems over decadal or greater timescales. Phosphorus fertilization of a tundra stream caused a 10-fold increase in OM storage as moss biomass, though this sustained effect did not occur until seven years after initiation of the experiment (ARC; [130]). Fertilization of terrestrial tundra with nitrogen and phosphorus resulted in increased plant biomass with effects that were greater after nine, compared to three years; however, after 20 years, loss of OM from deep soils resulted in net loss of OM from the ecosystem despite continued increases in aboveground biomass (ARC; [25,90,128]). In temperate salt marshes, nine years of nitrogen addition increased rates of decomposition and decreased belowground production, which collapsed tidal creekbanks, underscoring a structural role of OM in these ecosystems (PIE; [37]).

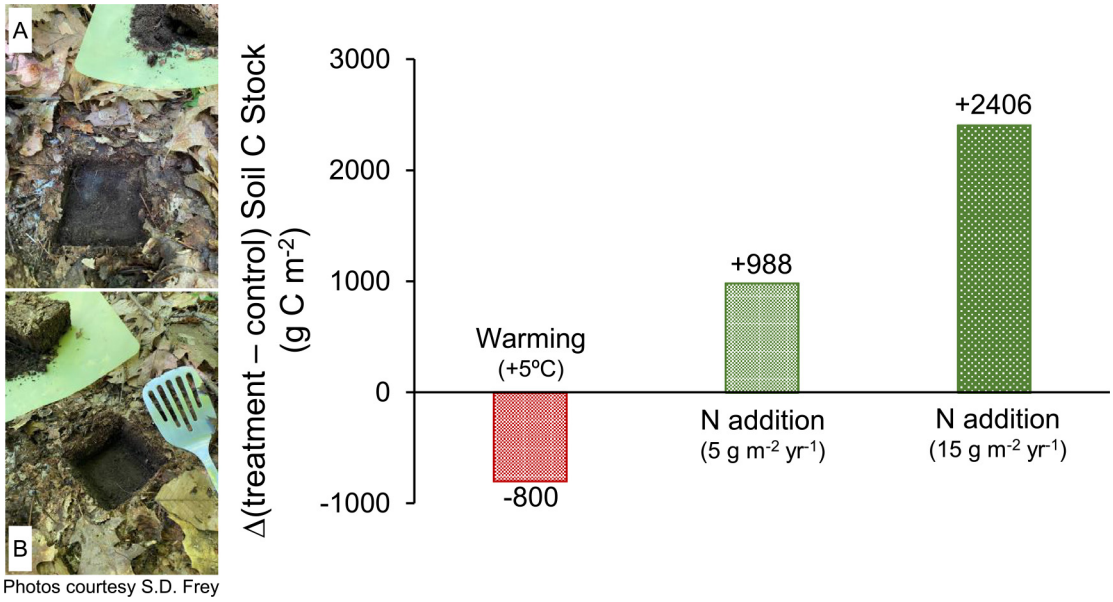


Fig. 4. Strong coupling of carbon storage with nitrogen availability overrides warming-associated losses of OM in temperate hardwood forest (HFR). Fertilization with nitrogen at a rate consistent with observed and predicted rates of atmospheric nitrogen deposition (5 g N ha^{-1} y^{-1}) and a rate expected to induce nitrogen saturation (15 g N ha^{-1} y^{-1}) stimulated storage of OM in the ecosystem, largely in the organic horizon, due to suppression of decomposition [45]. Carbon in the organic horizon of the fertilized treatments was 1.2 to 3 times greater than the C lost during a simultaneous warming experiment [95]. Photos show depth of the organic horizon in warmed (A) and fertilized plots (B).

Recent conceptual models and mechanistic studies have emphasized that interactions between microbial communities and the chemical composition of OM govern OM storage and processing in ecosystems [71,87,89,152]. Long-term studies of the LTER network have clarified how disturbance regimes and environmental change influence OM dynamics, emphasizing patterns at broad spatial scales and revealing non-linear changes that occur over multiple years. Integrating long-term studies of OM dynamics with observations of microbial communities and chemical composition of OM, particularly within an experimental context, could reveal cross-scale interactions that ultimately determine the persistence of OM within ecosystems.

3.3. Transport

Transport by wind, water, animals, and mass transfer alters patterns of OM storage, and can stimulate consumers and microbial respiration in receiving ecosystems. Transport processes have been most thoroughly studied in aquatic ecosystems or in a catchment context. For example, streams draining catchments that contain extensive wetlands or low-lying topography have higher concentration of dissolved organic C, likely due to connectivity with ecosystems supporting low rates of decomposition (PIE, BNZ, BLE; [31,60,151]). Seasonality of dissolved OM in alpine lakes is also shaped by topography, whereby elevation constrains terrestrial productivity, and therefore the potential for inputs of allochthonous dissolved OM to lakes (NWT; [96]). Export of dissolved OM from catchments also responds to land management, climate, and their interactions. For example, long-term monitoring has documented declines in DOM export during hurricanes in tropical forests, due to rerouting of hydrologic flowpaths and decreased contribution of throughfall (LUQ; [93,127]). In temperate forests, experimental logging that removed large wood diminished export of dissolved OM in streams (AND; [82]). Model projections based on long-term monitoring of a freshwater slough also suggest declining export of dissolved OM in response to water management, saltwater intrusion, and drought (FCE; [116]).

Imported OM subsidizes heterotrophs in recipient ecosystems. For example, respiration exceeds primary production in Antarctic lakes, where primary production is limited by light under thick ice cover and polar night, implying import of OM from streams and upwelling (MCM; [111]). Groundwater delivers large loads of terrestrially-derived dissolved OM to Arctic lagoons and this hydrologic flux of OM is expected to increase as permafrost thaws, potentially supporting productivity of coastal food webs (BLE; [30]). Transport processes are a primary constraint on OM dynamics in marine ecosystems, where nutrients delivered by vertical mixing and advection stimulate net primary production, and non-sinking OM is also exported from nearshore regions of high productivity to less productive ecosystems both on and offshore (CCE, SBC; Fig. 5; [38,77,135]). Large fluxes of OM from pelagic zones also subsidize nearshore marine ecosystems, including inputs of kelp wrack that support detrital food webs on sandy beaches (SBC; [85]) and stimulate bacterial production in coral reefs by delivery of dissolved OM derived offshore (MCR; [100]). Importantly, dissolved and gaseous fluxes in receiving ecosystems can be as large as net ecosystem production of the donor ecosystem (HBR; [42]) and therefore integration of C budgets across ecosystem boundaries will reduce uncertainty in estimates of C storage (e.g., [21]).

Transport processes also enhance storage by relocating OM to compartments with low capacity for processing. For example, vertical export of OM in pelagic ecosystems enhances storage of OM in sediments. Sinking rates increase with nutrient inputs due to influences on phytoplankton community composition, biomass, and grazing rates, which in turn influence the magnitude of export (CCE; Figure 5a & b; [84,98,140]). Subduction of particulate and dissolved OM at fronts, eddies, and filaments can additionally account for a quarter of C sequestration in coastal upwelling ecosystems (CCE; Figure 5c; [137]). However, these events occur less frequently during warm periods and under rising temperature (CCE; [69,70]). Climate change is also causing increased inputs of colored dissolved OM, which reduce primary production, and limit storage of OM at depth (NGA, NES; [4,5]). In contrast, diminished sea ice in Antarctica has resulted in increased rates of marine primary production and export of OM to depth where it may be stored over longer timescales (PAL; [122]).

Although studies of transport processes have focused on outcomes for aquatic ecosystems, soil OM and biomass of terrestrial ecosystems

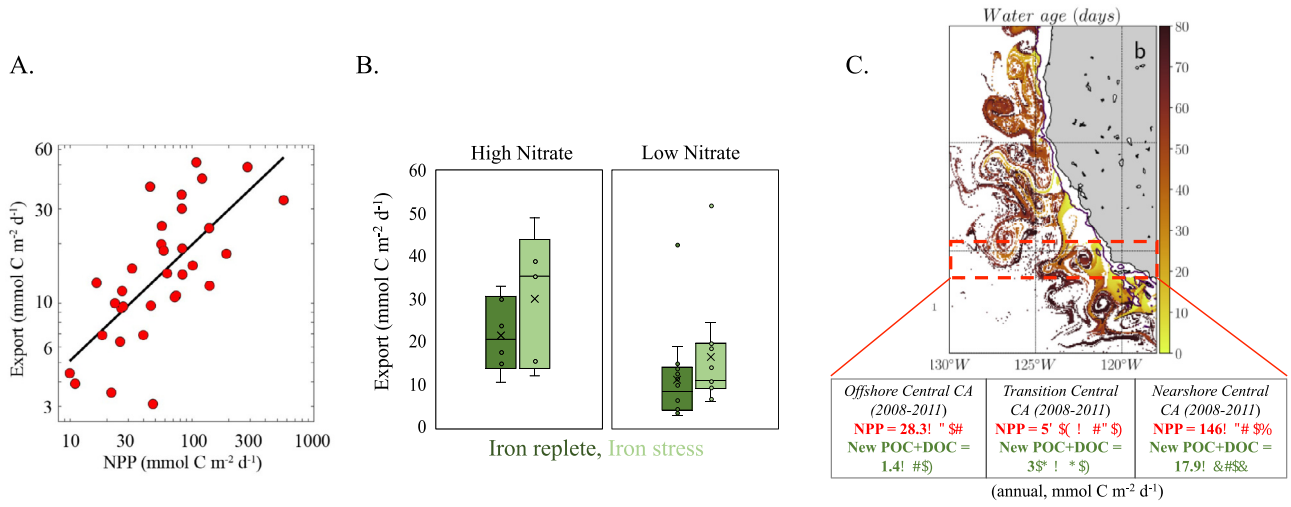


Fig. 5. Transport of OM in pelagic ecosystems occurs vertically via sinking detritus that connects the surface to deep ocean and by lateral movement of non-sinking OM (CCE). A) Sinking flux (i.e., export) of OM is strongly related to rates of net primary production in the photic zone [155]. B) The rate of OM export by sinking is further influenced by supply and differential influences of nitrate and iron on phytoplankton (y-axis scale as in A; [138]). C) Lateral transport of OM may be important for supporting offshore food webs, as evidenced by coastal-to-offshore gradients in recently produced non-sinking forms of OM (i.e., suspended particulate and dissolved OM; [135]), and water mass trajectories in the surface ocean that originate in more productive regions (0 water age days) and move toward less productive regions (>50 water age days) [24].

are often structured by contemporary and historic legacies of transport. For example, sediments transported from ancient lakebeds supply OM to valleys in Antarctica (MCM; [20]). Drylands incur significant losses of dissolved and particulate OM by wind and overland flow, with greatest losses in shrublands where inter-plant space is larger, and limited loss from grasslands or under annual plant cover (JRN, SEV; [18,103,142]). Wind-driven loss of particulate OM in aridlands is further accelerated by fire, where experimental burns demonstrated high rates of wind erosion and redistribution of OM from shrubs to bare microsites or grasslands (SEV; [39]). These examples highlight significant roles of transport in OM dynamics of terrestrial ecosystems and suggest that frameworks emphasizing connectivity, water residence time, or donor/recipient dynamics (e.g., [118,152]) might clarify spatial and temporal dynamics of OM storage and processing in terrestrial ecosystems.

3.4. Trends

Accurately describing C dynamics under continued or accelerating changes in climate, land use, and environmental policy remains a barrier to projecting ecosystem feedbacks with global change [15]. The LTER network provides complementary long-term data that document trends, modeled projections based on contemporary dynamics, and experiments that evaluate potential trajectories of OM dynamics. Maintenance of these records increasingly reveals surprises that are difficult to predict from short-term observation or retrospective analysis alone.

Rapid climate warming at high latitudes and high elevations has caused some of the clearest trends and most significant temporal changes in OM dynamics. Earlier snowmelt and ice-off are associated with increased primary production in alpine lakes and greater autochthonous dissolved OM production that alters freshwater community composition and function (NWT; [110]). A model parameterized using data from a rare fire in Arctic tundra projected a net increase in OM stored in the ecosystem over centuries despite loss of soil OM in the fire, due to positive responses of tundra vegetation to enhanced nutrient availability under climate warming (ARC; [157]). Declining discharge-normalized concentration of dissolved OM in an Arctic river over the past several decades was hypothesized to result from deepening hydrologic flowpaths that bypass organic soils as permafrost thaws (ARC; [78]). Indeed, warming experiments have predicted loss of soil OM from sub-arctic tundra due to permafrost thaw, with significant loss of old C (BNZ; [108,124]), and alpine ecosystems also show trends of sustained soil OM loss from permafrost thaw (NWT; Knowles et al. 2019).

In warmer biomes, responses of OM to recent climate change are more nuanced. For example, desert grassland has limited OM-storage potential in most years relative to shrubland (SEV; [2]). However, net ecosystem exchange of arid grassland and shrubland ecosystems was resilient to a short-term (two years) drought, though lower-than-average precipitation in winter decreased OM storage in shrublands over the last 100 years (SEV; [9]). In temperate lakes, trends in dissolved OM concentration were also variable (24 years of observation), but the composition of the dissolved OM changed in concert with drought severity, suggesting recent declines in allochthony and increased photobleaching (NTL; Figure 6; [66]). A decade of observation in coastal marshes detected declines in biomass in years with elevated temperature, but increases in years with high discharge, projecting a decline in biomass with ongoing warming and drought (GCE; [150]). In contrast, soil OM has accumulated over the past 50 years due to encroachment of native grasslands by woody shrubs on barrier islands (VCR; [17]). In pelagic marine ecosystems, primary production and the communities responsible for that production are linked to nutrient availability, which responds to changing surface ocean temperatures, resulting in variable frequency and magnitude of episodic vertical transport of particulate OM and sequestration in deep sediments over the past 20 years (CCE; Figure 5; [132]). Both macro- and micronutrient limitation can control vertical flux; for example, iron limitation in some regions could constrain production and velocity of sinking biomass (CCE; [63]).

Overall, analysis of long-term data suggests that large losses of OM have occurred from high-latitude and high-elevation ecosystems and will continue under ongoing warming. Complex trajectories of OM dynamics in warmer biomes add uncertainty to the future of OM storage there. However, relatively few studies have characterized long-term trends in OM, and accumulating long-term datasets provide an underused opportunity to project trajectories of OM dynamics and storage. Long-term datasets, including observations of both OM pools and fluxes collected by the LTER network, are critical to accurately projecting trajectories of OM storage in ecosystems, particularly because they capture non-linear dynamics less likely observed during short-term monitoring. Maintaining long-term experiments has further proven valuable in revealing surprises and drivers of OM dynamics that are difficult to detect from monitoring alone.

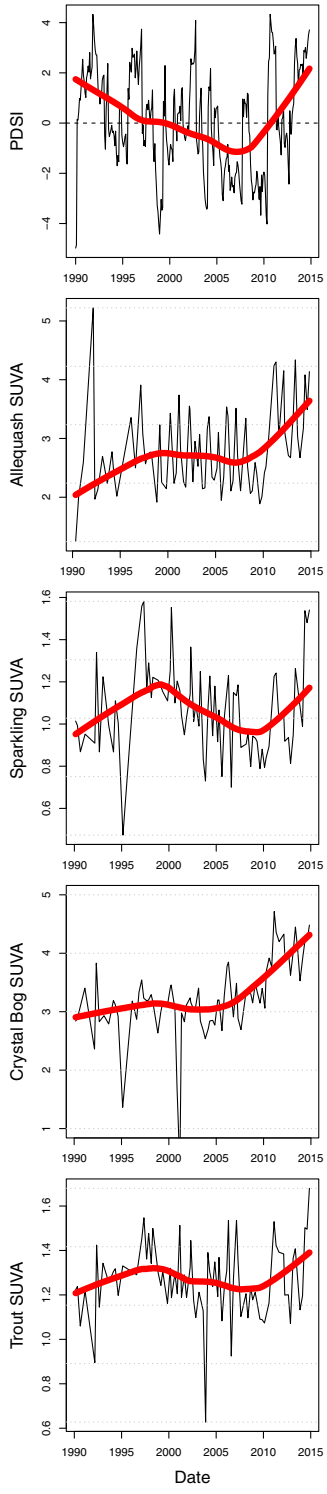


Fig. 6. Composition of dissolved OM in temperate lakes is synchronous with climate (NTL). Aromaticity of dissolved organic C, as measured by specific ultraviolet absorbance (SUVA) at 254 nm increased under wetter conditions (increasing Palmer Drought Severity Index; PDSI) over the period 2010–2014. More aromatic C is likely transported to lakes during wet periods from sources in wetlands and forest soils, while reduced water residence time in lakes curtails opportunity for in-lake processing of OM [66].

4. Summary

Integrating approaches and foci among ecosystem types and disciplines is required to unify understanding of OM dynamics across larger spatial scales and longer timescales, and to provide accurate estimates of OM storage in ecosystems. This synthesis of OM research from the US LTER Network revealed opportunities to accelerate such understanding. For example, quantifying the *chemical composition of OM pools* alongside tracking temporal dynamics in pool sizes has revealed the mechanisms of OM processing and long-term monitoring of OM composition might complement attempts to quantify changes in the size of large, heterogeneous pools. Cross-fertilization of perspectives founded in different ecosystem types also offers opportunities to expand the scope of OM budgets. For example, a transport-focused perspective that emphasizes the role of hydrologic *import and exports of OM* in aquatic ecosystems has been little applied in terrestrial ecosystems. Quantifying the role of transport in terrestrial ecosystems might decrease uncertainty in local OM budgets and contribute to holistic estimates of OM storage over larger spatial scales.

Synthesis of monitoring, experiments, and modeling revealed patterns that could be leveraged to project future trajectories of OM storage in ecosystems. Climate change, including *warming, variation in timing and amount of precipitation*, and *sea-level rise*, resulted in net loss of OM from many ecosystems. In terrestrial ecosystems, effects of warming and precipitation regime are known with greatest certainty in cold and dry climates, respectively. Though warming can enhance autotrophic biomass or primary production, increased heterotrophic activity or concurrent disturbances can offset this increase, resulting in losses of OM (Box 1). Effects of changing precipitation varied with regional climate, whereby drought reduced OM stores in mesic ecosystems, but OM was lost from drylands under increased precipitation. Long-term observations and experiments have contributed these critical insights, and maintenance of ongoing time series, coupled with additional experiments to evaluate interactions of multiple global changes, offers the empirical support needed to project OM storage under continued change.

Fertilization experiments and spatial or temporal gradients of fertility have revealed strong *coupling between C and other elemental cycles,* with emergent patterns in OM dynamics often tracking the duration of observations. The effects of fertilization on OM storage depended upon the relative strength of nutrient limitation for autotrophs and heterotrophs, wherein provision of nutrients limiting to heterotrophs typically offset OM gains resulting from nutrient stimulation of primary production. Fertilization also caused changes in species composition or dominance, which reorganized the locations of OM storage within ecosystems. The central role of nutrients in OM budgets underscores the value of continuing long-term fertilization studies.

Experiments and space-for-time substitution approaches have identified significant changes in OM storage due to changing *land use and disturbance legacies*, finding recovery over decadal to century scales. Recovery trajectories depended on the relative size of OM pools and rate of primary production before and after the disturbance. Complex responses to disturbance might be resolved by continuing long-term experiments. Ultimately, quantifying responses of the major components of net ecosystem C balance (Box 1; [26]) within a long-term context reduced uncertainty in estimates or trajectories of OM storage. Finally, this synthesis emphasized that OM storage contributes to the physical structure of ecosystems as well as to biotic composition and processes, highlighting cascading influences of loss of OM on ecosystem structure and function.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We acknowledge participants in the 2018 LTER Science Council and All-Scientists Meetings for discussions that contributed to the ideas, design, and implementation of this synthesis, both of which were supported by the US LTER Network Office (NSF-DEB 1545288). We thank Melinda Smith, Richard Bowden, and an anonymous reviewer for comments that improved the manuscript. WRW was supported by the Niwot Ridge LTER program (NSF-DEB 1637686) and TKH by the Bonanza Creek LTER (NSF-DEB 1636476 and USDA Forest Service, Pacific Northwest Research Station RJVA-PNW-01-JV-11261952-231).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2021.100025.

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