

Opinion

Global Carbon Cycling on a Heterogeneous Seafloor

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Diverse biological communities mediate the transformation, transport, and storage of elements fundamental to life on Earth, including carbon, nitrogen, and oxygen. However, global biogeochemical model outcomes can vary by orders of magnitude, compromising capacity to project realistic ecosystem responses to planetary changes, including ocean productivity and climate. Here, we compare global carbon turnover rates estimated using models grounded in biological versus geochemical theory and argue that the turnover estimates based on each perspective yield divergent outcomes. Importantly, empirical studies that include sedimentary biological activity vary less than those that ignore it. Improving the relevance of model projections and reducing uncertainty associated with the anticipated consequences of global change requires reconciliation of these perspectives, enabling better societal decisions on mitigation and adaptation.

Where Has All the Carbon Gone?

Rapid and well-documented environmental change over the past century has accelerated interest in quantifying the critical role of the ocean in global carbon and nutrient cycling [1]. As human pressures [e.g., climate change and **biodiversity** (see [Glossary](#)) loss] alter physical and biological processes, we must improve our capacity to predict the consequences of these alterations and their links to global cycles [2]. Divergent thinking in evaluating global cycles [3,4] and the role of biodiversity [5] has led most marine studies to compartmentalize biogeochemical versus biological approaches, with little effort to integrate alternative perspectives [6]. The functioning of most of the global seafloor depends largely upon the addition of oxygen and organic matter to the sediment–water interface [7] ([Figure 1](#)). Biogeochemical and ecological approaches both have value in assessing these processes, but remain poorly reconciled [8], an issue also noted in geological [9] and paleobiological [10] studies. Previous authors have highlighted the need for all types of model to improve how they represent sedimentary processes [8,11,12]. Here, we illustrate how different biases and/or perspectives associated with different world views ([Figure 1](#)) can lead to both different model projections and differential abilities to interrogate model outcomes to understand better the cumulative effects of drivers of change. The nature of the questions a model is expected to inform should influence the complexity of the model. However, the application of models to broad-global scale projections often requires simplification and averaging [13], which can lose key complexity or heterogeneity [14] essential in detecting all but the coarsest change. Biogeochemical modelers focus on the physical and chemical processes [15] that affect microbial activity in a way highly suited to developing global models [16], whereas ecologists focus on developing overarching themes governing ecosystems by studying different groups of organisms and how their activities

Trends

Climate-change models hinge upon understanding how living ecosystems influence carbon cycling, but global models of oceanic systems produce carbon turnover estimates with a high degree of uncertainty.

Environmental conditions, and temperature in particular, strongly influence rates of carbon and nutrient cycling in the global ocean

Recent studies demonstrate a link between seafloor biodiversity and organic matter processing and nutrient efflux, suggesting that the functional group composition of biota is the most critical aspect of biodiversity for ecosystem functioning in the context of global biogeochemical cycles.

Strong spatial variability in carbon burial and recycling rates of organic material may relate to recognized variation in seafloor functional group composition.

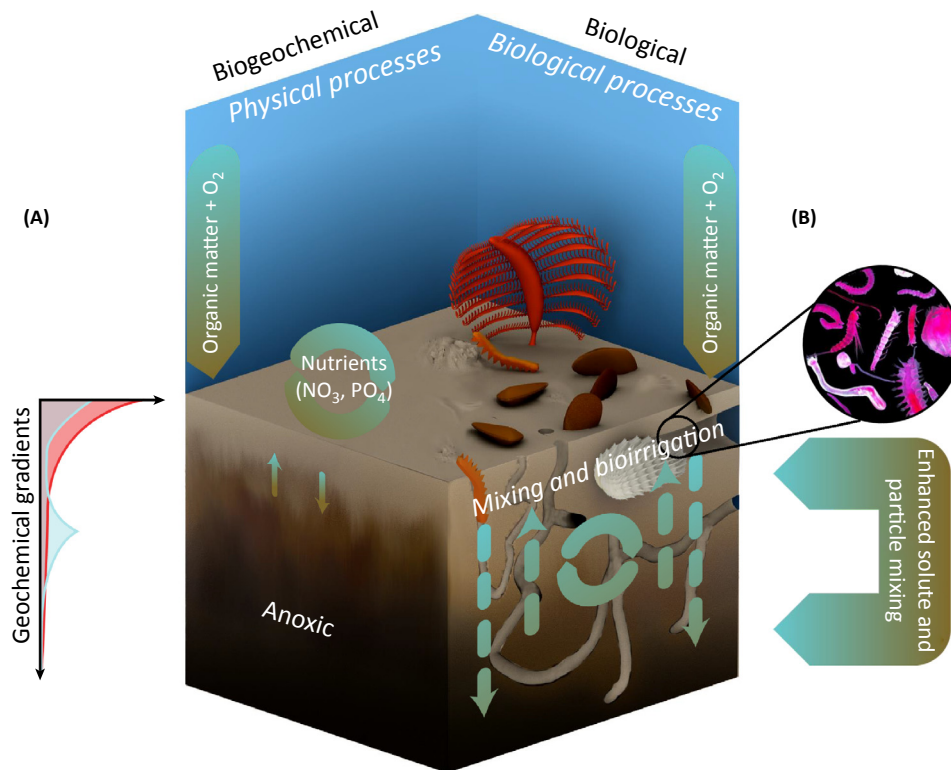
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Figure 1. Summary of the Contrasting Geochemical (A) and Biological Views (B) of Organic Matter Decomposition, Illustrating Differences in Emphasis on the Predominant Processes and in the Relative Complexities of the Two Perspectives

For a Figure360 author presentation of Figure 1, see the figure legend at <https://doi.org/10.1016/j.tree.2017.11.004>

The fundamentally different roles of the functional groups, and the key elements that most models do not accommodate (i.e., feedbacks, habitat modification, horizontal bioturbation, large bioturbators, and different process rates) all contribute to major contrasts between the two approaches.

influence their environment [17] and, thus, processing of organic matter. Ecological studies tend to emphasize heterogeneity and variability as a functional component of the system, whereas many biogeochemists, despite emphasizing strong gradients in the sediment column, tend to ‘average’ seafloor rates and processes spatially [13]. Nevertheless, both approaches have advanced our understanding of how marine sediments influence global process. Highly productive coastal, shelf, and slope sedimentary seafloor ecosystems that cycle organic material rapidly contribute disproportionately to organic **mineralization** and nutrient processing [18]. In contrast in the deep ocean, regenerated nutrients can remain unused for many hundreds of years before transport into the photic zone and uptake by photosynthetic organisms occurs [19]. Despite low rates of carbon remineralization or sequestration and nutrient regeneration, integrating across the vast area of the deep ocean makes it a major contributor to global biogeochemical budgets and cycles. These deep-ocean contributions often have long lag times (up to hundreds of years) in how they influence the cycling of materials, which the short-time scales (e.g. hours–days) of many studies fail to capture [20]. Hence,

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constraining **carbon sequestration** and mineralization globally remains a major challenge, perhaps because of the difficulty in reconciling such marked differences in biological complexity [8]. Few studies have reasonably constrained the contribution of **continental shelf** sediments as a net source or sink for nutrients and carbon, or indeed for other elements, over regions of shelf habitat [21] and some deep-sea environments [22]. However, the underlying processes and players that lead to changes in the internal pool of dissolved and particulate nutrients are not well understood [23].

The Role of Seafloor Biota

Substantial evidence accumulated over the past few decades strongly links carbon remineralization, nutrient efflux, and the activities of the diverse seabed fauna [24–26]. The active redistribution of particles, water, and solutes by **bioturbation** [27] directly contributes to the spatial and temporal heterogeneity of oxic, anoxic, and oscillatory **redox zones** [28], as well as to the distribution of other electron acceptors [29]. These physical and chemical changes in sediments generated by faunal activity have important implications for microbial assemblages [14], and the ecosystem processes they affect (e.g., organic matter mineralization and burial [30], and nutrient transformation pathways [31,32]). Whereas **infaunal** activity inherently contributes to increased solute exchange between the sediment and the overlying water, the contribution of the underlying drivers varies among **functional groups** through increased diffusional fluxes, bioadvection, and animal excretion [29]. Seafloor heterogeneity itself can influence biodiversity–function relationships [33,34] (e.g., sedentary components of the seafloor fauna, including bivalves, corals, sponges, and cnidarians) and can add significant habitat complexity by providing **emergent structures**. Additionally, the rate and extent of filtering and suspension feeding can moderate local levels of **benthic–pelagic coupling** [35]. Most biogeochemical models simplify processes and average or approximate the substantial variability in biologically mediated processes that transform food (organic matter) into living tissue, respire oxygen, and release carbon dioxide [36]. However, evidence suggests that variation in the functional attributes of communities [37–39] can affect carbon- and nutrient-cycling processes more than species diversity can [40]. Anticipated changes in the abundance, distribution, and behavior of functionally important species in response to global environmental change [2,41,42] raise concerns about significant alteration of **ecosystem function** and services, given the strong interlinkages among seabed functioning [43] and ocean productivity.

Local–regional-level studies that consider faunal mediation of carbon cycling from shallow to deep seafloor ecosystems highlight the potential importance of including organisms in global carbon models and considering the contributions of different seabed environments [44]. Correlative studies across large-scale gradients in dissolved oxygen tend to use multivariate analyses to demonstrate strong linkages between seafloor biota, nutrient recycling, and remineralization. In the Baltic Sea, for example, the density of several macrofaunal functional groups that are important in affecting rates of bioturbation explain close to 70% of the variability in nutrient fluxes, including under hypoxic conditions [45]. Similarly, comparisons of oxygen and nutrient efflux in different coastal sedimentary regions of western Canada exhibit strong spatial variation, driven equally by environmental characteristics and macrofaunal functional group diversity [46]. Species contributions can vary between different populations and functionally important aspects of the behavior of individuals within a population can be context dependent [34]. Furthermore, short-term experimental addition of organic matter [40] reveals that higher species richness can explain most of the intersite differences in nutrient flux rates, even under high levels of environmental forcing [47] (acknowledging that chronic enrichment typically creates feedbacks that differentially depress diversity and function [48]). A nutrient budget based on long-term observations [22] and *in situ* measurements [49] in Sagami Bay, Japan

Glossary

Benthic: living in or on the aquatic seafloor. An operational classification based on sieve sizes used when sampling sediments subdivides benthos into megabenthos, visible in bottom photographs or video (e.g., crabs or fish), macrobenthos >300 μm (e.g., polychaete worms or small clams), and meiobenthos, which pass through a 250–500- μm sieve but are retained on a 20–30- μm sieve (e.g., nematodes or copepods).

Biodiversity: the extent of genetic, taxonomic, and ecological diversity over all spatial and temporal scales.

Bioturbation: the dispersal of particles by organisms reworking the sediment, typically by burrowing or feeding.

Carbon sequestration: the process of capture and long-term storage of atmospheric carbon.

Carbon turnover: the transformation of organic carbon to an inorganic form.

Continental shelf: the extended perimeter of the continents and associated coastal plain.

Continental slope: the slope extending from ~100 m to 3200 m bottom depth between the outer edge of the continental shelf and the deep ocean floor.

Denitrification: the microbial reduction of NO_3^- to N_2 and O, and of NO_2^- to N_2 or other N oxide.

Diagenesis: physical and chemical changes occurring during the conversion of sediment to sedimentary rock.

Ecosystem function: changes in energy and matter over time and space through biological activity.

Ecosystem service: the benefits people obtain from ecosystems.

Emergent structures: structures that protrude above the seabed, often produced by living organisms and providing habitat for other species.

Functional group: organisms with similar trophic, morphological, physiological, behavioral, biochemical, or environmental responses.

Infaunal: (animals) living within sediments.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES): an

resolved high inputs of organic material that were linked to key ecological and biogeochemical processes, including active sinks of carbon and nitrogen as well as regional hot spots of **denitrification**, anaerobic ammonium oxidation (anammox), and oxygen consumption (and, thus, carbon remineralization) in surficial sediment strongly linked to dense patches of infaunal polychaetes that transported chemically reduced sediments towards the sediment surface and laterally downslope via tidal and other currents [49]. Indeed, comparisons of multiple seabed ecosystems that vary in the flux of organic matter to the seafloor link exponential increases in the efficiency of carbon processing via prokaryote production and nutrient regeneration with the increasing functional diversity of small, abundant sedimentary meiofauna [37]. Thus, environments with a greater influx of organic material could support higher abundances of organisms, which, in turn, can increase remineralization when that abundance includes a greater portfolio of functional groups [46]. Nevertheless, researchers largely disregard the underlying reciprocal relationship between abiotic and biotic components that can explain much of the observed variability in ecosystem processes [50].

Bridging the Sampling Gap

Reasons why ecological information has not been prominent in ocean-based global process models relate to insufficient sampling of the seafloor [38] and the limited availability of data that describes the functional performance [51] of specific communities, particularly for deep ocean regions [52]. Moreover, sampling bias frustrates any clear resolution of the roles of different biota. For example, based on empirical measurements, many researchers assume that macrofauna have a greater role in coastal shelf and **continental slopes** than they do in the deep ocean [8], but, while comparatively robust data exist for these shallow regions, the issue remains unresolved at deeper depths. Nevertheless, these deficiencies in sampling design and data availability do not fully preclude ecological analysis of carbon remineralization on a global scale. By using estimates of biological turnover based on macrofaunal, meiofaunal, and microbial biomass for different seafloor biota, we can assess the role of ecological variation in determining the outcomes of alternative model scenarios. We hypothesize that the results of global-scale biogeochemical carbon modeling efforts that do not consider the roles of seafloor biota will diverge from those that do, resulting in key differences in predictions of the spatial locations of high and low **carbon turnover** rates.

Biogeochemical and Biological Model Estimates

Our comparison of carbon turnover utilizes two simple approaches. First, we used a widely employed geochemical model of carbon export to the deep ocean based on the equation of Lutz *et al.* [16] (Figure 2A), which considers production of organic matter near the surface of the ocean, and net remineralization during transit through the water column. We omitted the lateral transport of organic matter in our model, because other processes (e.g., declining organic carbon flux with depth, increasing carbon export with seasonality, and increasing carbon degradation with temperature) likely dominate the carbon turnover in our global-scale analysis. Nonetheless, we acknowledge the importance of lateral transport and its interaction with the biological pump that transports some 50% of organic carbon to the seafloor [53], and its particular importance in regional comparisons and downslope movement of material. Second, we developed a biologically based turnover rate, calculated as sediment oxygen consumption rate (based on ship-board or *in situ* sediment incubation) divided by seafloor standing biomass (Figure 2B). In the absence of appropriate data on the specific functional roles of organisms consuming organic matter that primarily determine its degradation, we assumed that total biomass and activity correlate strongly [54].

independent intergovernmental body established to strengthen the science-policy interface for biodiversity and ecosystem services for the conservation and sustainable use of biodiversity, long-term human well-being, and sustainable development.

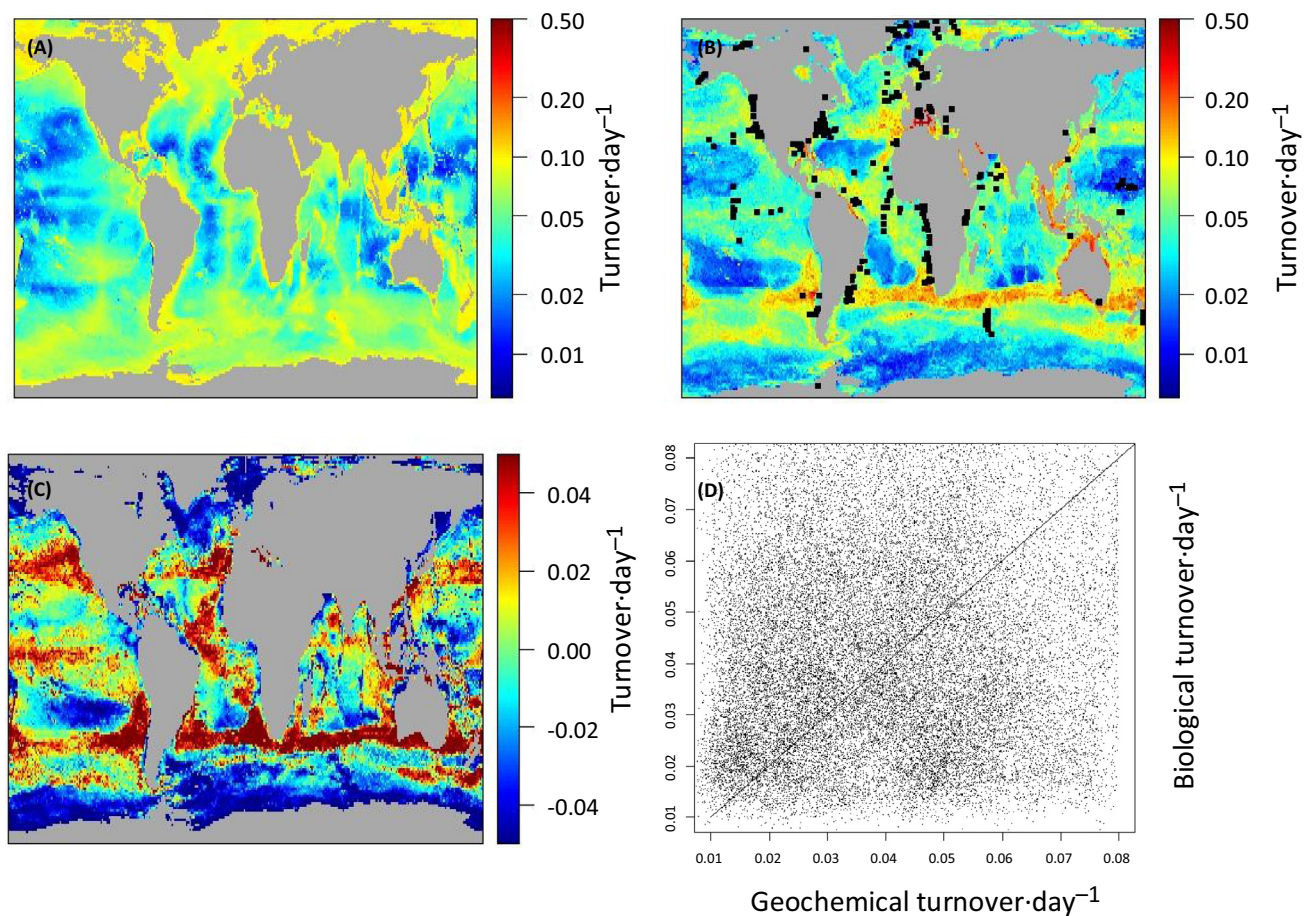
Mineralization: the process of degrading organic material.

Multifunctional: the potential for individual organisms to contribute to more than one ecosystem function.

Niche: the ecological hyperspace occupied by an organism.

Redox zone: zone in sediments where the oxidation states of atoms are changed.

Trait: any morphological, physiological, behavioral, or phenological feature measurable at the individual level.



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Figure 2. Global Map of Carbon Turnover on the Seafloor. (A) Turnover as estimated based on the equation of Lutz *et al.* [16], reproducing the aging of pelagically produced sinking organic matter. (B) Turnover of benthic organisms, estimated as the sediment community oxygen consumption (SCOC) rate divided by the infaunal biomass; dots represent SCOC data. Most of the SCOC data was estimated by whole-core sediment incubation under *in situ* temperatures. Contrasting estimates of carbon turnover based on biogeochemical and biological approaches. (C) Comparison of turnover rates based on biogeochemical and biological models where light-green colors indicate coherence between models, warm colors indicate higher estimates for the biogeochemical model, and cool colors indicate higher estimates for the biological model. (D) The density distribution of the biological and geochemical turnover estimates reflects the weak ($R^2 = 0.015$) relationship between biological and geological turnover estimates (log-log scale) and the wide scatter around the line representing a 1:1 relationship. The apparent truncation results from reactivity in shallow water that is close to the reactivity of fresh organic matter.

Geochemical versus Biological Turnover Estimates

We estimated geochemical turnover (organic matter decay) as a function of organic matter deposition flux and organic matter decay rate (see the supplemental information online for details), and biological turnover (i.e., expressed as the proportion of organic carbon remineralized by respiration per day) by dividing sediment carbon mineralization rates ($\text{C}/\text{m}^2/\text{day}$) by total benthic biomass (C/m^2). The biomass (bacteria + meiofauna + macrofauna) approximately integrated to a depth in the sediments of 15 cm, and we estimated sediment carbon mineralization rates from oxygen fluxes, assuming a respiratory quotient (RQ) of 1 mol O_2 /mol C and no burial of reduced product. Although the use of a marginally different RQ would change overall turnover rates [11], it would not alter relative values or spatial differences. Nonetheless, temporal and spatial differences in RQ add significant noise to our analysis that could eventually be refined with additional data. We integrated faunal and bacterial data over the upper 15 cm of

sediment, adjusting based on partial regression where necessary and noting that most biomass occurs within this layer (see also Figure S1 in the supplemental information online).

The Contrasting Tales of Two Models

Our two approaches to modeling carbon turnover produced very different patterns, with no clear relationship between the turnover estimates (Figure 2C,D). For example, the models predicted low biological turnover but high geochemical (flux based) turnover around Antarctica, in contrast to high biological but low geochemical turnover around 30°S. Moreover, high biomass and sedimentary community oxygen consumption in the Northern Oceans (e.g., near Alaska and Siberia) contrast low predicted biological turnover but high geochemical turnover. If seafloor biota were unimportant, then we would expect close congruence between the two types of estimate, both regionally and globally, which is not what we observed. These incongruences between approaches for key regions expected to change dramatically under many climate-change scenarios, such as those presented by the Intergovernmental Panel on Climate Change (IPCC) [55], illustrate a high degree of uncertainty when projecting the likely consequences of future change in major biogeochemical cycles. Our global estimate of sediment community oxygen consumption (SCOC) and biological turnover ranked as intermediate compared with previous comparable estimates achieved elsewhere (Table 1), adding confidence to our approach. Indeed, our analysis shows that adding even simple elements of seafloor ecology to the equation dramatically alters interpretation, potentially contributing to the five orders of magnitude variation in rate constants used in carbon models reported in the literature [34]. Importantly, researchers must evaluate the relative roles of microbial, meiofaunal, and macrofaunal contributions to carbon turnover across different habitats and seasons. Currently available data suggest similar spatial patterns in peak biomass for all size fractions, as well as similar patterns for size fractions across depth [56]. Moreover, recent correlative empirical studies confirm a clear role for sedimentary biota at larger regional scales [45,57]. Nonetheless, local manipulative process-based studies [24] offer the potential for more-detailed analysis, and to integrate meaningful data from locations (e.g. vents, seeps, upwelling regions, sponge, and coral habitat) where the rate, magnitude, or form of biogeochemical cycling differ distinctly from the surrounding habitat.

Many different types of biogeochemistry and biological models acknowledge that temporal variation in productivity and patchiness on multiple spatial scales add further complexity that complicates the prediction of rates of carbon cycling and that data availability limits our current capacity to account for this variation. Similarly, the strong gradients that living biota create in sediment vertical profiles at millimeter to centimeter scales can further influence biological

Table 1. Global Average Estimates of Sedimentary Processing of Organic Carbon in Terms of Sediment Community Oxygen Consumption (SCOC), Production of Dissolved Inorganic Carbon (DIC), and Biological Turnover^a

Source	SCOC (Tmol O ₂ -yr ⁻¹)	DIC (Gton C-yr ⁻¹)	Biological turnover (yr ⁻¹)	Biological turnover (day ⁻¹)
[63]	54.3	0.65	7.7	0.02
[64]	79.6	0.96	11.3	0.03
[65]	157	1.88	22.2	0.06
[11]	152	1.82	21.5	0.06
Our study	139.5	1.67	19.7	0.05

^aBased on a respiratory quotient (DIC:O₂ exchange ratio) of 1.0 and a total seafloor biomass of 84.9 megaton C [56].

processes and interactions. Nonetheless, biogeochemical models routinely ignore the inter-linked functions of bioturbation, trophic support, and enhanced microbial production. Yet, each of these elements includes an overlapping but distinct set of players as well as adding important complexity and heterogeneity to natural systems [58] that appropriate interdisciplinary collaboration can readily resolve [59]. These issues matter because the models we currently use to map and project changes in biogeochemical processes at global scales lack the capacity to look at unexpected outcomes and outlier data points that could link to seabed functioning, hampering our ability to predict the resiliency of systems and recovery trajectories following perturbations, and to account for natural variability.

Better Models for Future Ocean Scenarios

Rapid, ongoing transformation of global biogeochemical cycles demand improved models that produce not only more precise estimates of carbon degradation and burial, but also more accurate projections of change. Concerned by the mismatch between ecosystem processes measured at local to regional scales and the first-order approximation applied to global elemental models, we demonstrate here that the inclusion of seafloor biology in models likely changes global patterns appreciably and shifts regions of seafloor carbon processing. This conclusion is consistent with local and regional studies that link the actions of large sediment-dwelling organisms to ecosystem processes, although we recognize the potential importance of other aspects of biota (e.g., microbial biomass). This finding implies a need for particular caution in drawing inferences from current models that exclude, minimize, or oversimplify the contributions that biological communities make to ecosystem processes when projecting the effects and consequences of environmental change.

These global biogeochemical models do not fully accommodate important variables influential in determining the stocks and flows of biogeochemical cycles, or consider that changes in abiotic and biotic characteristics that are likely to produce nonadditive effects (e.g., changes in water temperature and functional group diversity produce combined effects that are less than their individual effects [46]). This gap identifies a need for case studies that specifically compare bottom-up approaches of ecologists with top-down approaches of biogeochemists, and which combine such information to generate a more-realistic evaluation of global carbon cycling [6]. Given that these biogeochemical models underpin many aspects of global climate change projections (e.g., IPCC) and **ecosystem service** assessments (e.g., **Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services**; IPBES), necessary improvements in predictive power will have important policy and socioeconomic consequences (Figure 1B). Estimates for carbon cycling in terrestrial systems would likely benefit from a similar approach that addresses ecosystem complexity and varying roles for biology.

Embracing the Complexity of Biodiversity

We urge our community to embrace ecological complexity, including the functionality and heterogeneity of seafloor biota in time and space that underpin the fate of carbon in our oceans, while also considering the 3D aspects of both the water column [4] and seafloor sediments [8]. Simultaneously, we need new concepts of **multifunctional** (e.g., sediment oxygenation, remineralization, and nutrient regeneration) ecosystems [58], where changes in carbon and nutrient cycling link to changes in the size, activity, density, and spatiotemporal arrangement of species that influence the functional performance, stability, and adaptive capacity of a system [43]. Specific arrangements of species dominance can exert greater influence than evenness in maintaining ecosystem process and function [34], and it is important to recognize that the functional role of an individual species is not static and can change with context [60]. We

suggest the following as key priorities for facilitating the next steps. First, we must generate credible maps of seafloor function that can accurately capture variation in organic matter processing in time and space. These efforts should include areas of seabed that contrast in relative performance, or where different biogeochemical pathways dominate, and eventually should consider the potential role of deep carbon wells below the redox layer [61] in global carbon models [59]. Second, we must merge models of geochemical **diagenesis** with meaningful estimates of biological turnover to reduce uncertainty in model outputs. Third, we must recognize the non-static nature of species–environment relations and account for the effects of physicochemical and biological interacting processes [40,41], including related changes in assemblage structure and adaptation capacity or alterations to geochemical cycles that accompany long-term environmental forcing [12]. Finally, the development of such combined models that couple the insights from both biogeochemistry and ecology can form the basis for realistic and defensible predictive models of global geochemical cycles and help those tasked with the management and governance of the marine environment to prepare for, or even possibly mitigate, climate-change impacts already evident in the most-remote ocean environments [26].

Concluding Remarks: A Path Forward

Massive amounts of new data on seafloor diversity and function will not appear in the foreseeable future, particularly for the deep ocean, so how can we improve estimates based primarily on available data? Our analysis illustrates how simple additions of biology can build from large-scale models, but further improvements could be achieved by working with abundance:biomass ratios, functional **trait** analysis, and spatial extrapolation of trait patterns based on environmental characteristics (e.g., grain size or bottom currents). Incorporating detailed regional data, where available, could help in this effort, particularly if oceanographic regimes (high productivity areas versus low productivity areas) are considered. Improved integration of geochemical and biological modeling approaches to refine regional and global predictions would benefit from studies that synchronize biological and geochemical measurements in time and space to examine the magnitude of difference between approaches in determining realized fluxes in and out of the seafloor. Food quantity and quality, which vary substantially over space and time in marine systems [62], add further aspects of complexity that both ecologists and biochemical modelers often ignore [8]. Biological and geochemical contributions to process rates both face the challenge of scaling measurements made at millimeter to centimeter scales upward to produce global estimates. In this respect, both aspects would benefit from stratifying data according to major habitat types with contrasting functional groups (e.g., bioturbators versus emergent structures) and environmental variables (e.g., oceanographic regimes, depth, or proximity to terrestrial input), and take advantage of natural environmental gradients to generate stronger predictive relationships [43]. Models could then build from stronger empirical data that explicitly incorporate spatial and temporal variation, improving the relevance of projections for underpinning management decisions and supporting policy options.

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Outstanding Questions

Can collaboration between biologists and geochemists reduce the uncertainty regarding projections of global carbon dioxide concentrations?

Can environmental proxies or application of basic principles regarding traits provide a means of addressing major data gaps regarding seafloor diversity?

How can we effectively incorporate the dynamic nature of ocean systems, including seasonal and cyclic signals, such as El Niño or the North Atlantic Oscillation, to evaluate the role of the oceans in biogeochemical fluxes and, thus, in climate change and global productivity?

What is the likely impact of marine biodiversity change or loss on global biogeochemical cycles?

How can we extrapolate most effectively from small-scale measurements of biological and geochemical processes to produce defensible global-scale extrapolations, and then future projections?

Supplemental Information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2017.11.004>.

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