



Muddy Waters: Unintentional Consequences of Blue Carbon Research Obscure Our Understanding of Organic Carbon Dynamics in Seagrass Ecosystems

E. Fay Belshe^{1,2*}, Miguel A. Mateo^{2,3}, Lucy Gillis⁴, Martin Zimmer^{1,4} and Mirta Teichberg⁴

¹ Department of Biology and Chemistry, University of Bremen, Bremen, Germany, ² Centro de Estudios Avanzados de Blanes, Consejo Superior de Investigaciones Científicas, Blanes, Spain, ³ Center for Marine Ecosystems Research, Edith Cowan University, Perth, WA, Australia, ⁴ Leibniz Centre for Tropical Marine Research, Bremen, Germany

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*Correspondence:

E. Fay Belshe
fbelshe@gmail.com

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The recent surge in research on organic carbon sequestration by seagrass ecosystems has begun to reveal the complexity of the carbon cycle within these ecosystems. In this prospective we discuss two areas of investigation that require further scrutiny: (1) why organic carbon is stabilized in seagrass sediments, and (2) how long organic carbon resides within these sediments. By delving into these topics, pointing out current pitfalls, and highlighting methodological advances, our motive is to focus future efforts and provide a frame work to manage the complexity found within the diverse seagrass bioregions. The high rate of seagrass degradation and loss, coupled with increasing atmospheric CO₂ concentrations gives precedence to these lines of research, which require rigorous reevaluation if we are to substantially advance our understanding of OC dynamics in seagrass ecosystems.

Keywords: organic carbon, seagrass, residence times, state-factors, stabilization mechanisms

INTRODUCTION

Seagrasses provide key ecological functions and services to coastal ecosystems, including sediment stabilization, coastline protection, nutrient cycling, support of fisheries, and enhancement of biodiversity (de la Torre-Castro and Rönnbäck, 2004; Duffy, 2006; Orth et al., 2006) due to the role they play as ecosystem engineers trapping sediment, altering hydrodynamics, and modifying biogeochemical processes in the water column and sediment (Marbá et al., 2006). From when seagrass meadows were recognized as potentially important “blue” carbon (organic carbon sequestered by vegetated coastal ecosystems) sinks, there has been a surge in efforts to determine the magnitude and variability of organic carbon (OC) storage within their sediments (Nellemann et al., 2009; Duarte et al., 2010, 2013; Fourqurean et al., 2012; Lavery et al., 2013; Campbell et al., 2014; Macreadie et al., 2014; Serrano et al., 2014, 2015, 2016b; Miyajima et al., 2015; Phang et al., 2015; Armitage and Fourqurean, 2016; Dahl et al., 2016; Jankowska et al., 2016; Röhr et al., 2016; Samper-Villarreal et al., 2016; Schile et al., 2016). Here, we point out two notable knowledge gaps, along with current methodological pitfalls, that are obscuring our ability to understand seagrass OC dynamics. First, we explore why OC is stabilized in coastal marine sediments, with emphasis on the need to look beyond a unifying mechanism governing OC storage across all seagrass ecosystems. Second,

we address the question of how long OC is stored in seagrass sediments, with focus on how current methodologies may give misleading estimates of OC accumulation rates and residence times. Both of these topics have a rich history of exploration and by pointing out common stumbling blocks our quest is to clarify the obstacles we face and propose a framework for a direction forward. We hope to open dialogue and refocus efforts, so we do not repeat the past two decades of research, but instead utilize and build upon it to understand the unique dynamics of OC cycling in coastal marine sediments. Accelerating seagrass degradation and loss (Waycott et al., 2009) and rising atmospheric CO₂ concentrations (IPCC, 2013) emphasize the relevance and timeliness of this discussion.

WHY IS OC STABILIZED IN SEAGRASS SEDIMENTS?

Although it is important to identify where high carbon storage occurs in coastal marine landscapes, it is equally important to correctly identify why. In the past 5 years there has been a concerted effort to determine which environmental or biological variables predict carbon stock location and size across the broad range of seagrass bioregions (Lavery et al., 2013; Serrano et al., 2014, 2015, 2016a; Miyajima et al., 2015; Dahl et al., 2016; Röhr et al., 2016; Samper-Villarreal et al., 2016). An unintended consequence of searching for these broad unifying predictors is the potential to narrow our understanding of OC dynamics, which creates the risk of misidentifying why OC is stabilized within seagrass sediments. Within the process of OC stabilization, there is often a mechanism (crucial step or physiochemical condition) that disproportionately affects the stabilization or destabilization of organic matter (Torn et al., 2009). In the past two decades a paradigm shift in carbon research has broadened focus to include four primary mechanisms of OC stabilization (Sollins et al., 1996; Six et al., 2004; Burdige, 2007; Marschner et al., 2008; Torn et al., 2009; Trumbore, 2009; Schmidt et al., 2011):

- Inherent molecular characteristics of organic matter (recalcitrance).
- Physical stabilization of OC on mineral surfaces.
- Inaccessibility of OC to microbes due to barriers of interaction among microbes and substrates, such as occlusion of OC within aggregates.
- Biotic suppression of microbial abundance and/or activity due to factors such as freezing temperatures, extreme pH, or low O₂ content.

However, there is still a tendency within seagrass OC research to focus on correlative attributes of the seagrass, landscape, or sediment without direct investigation into the mechanism(s) of stabilization. Many propose carbon source mechanisms (recalcitrance) when explaining OC stabilization based largely on correlative isotopic (¹³C) evidence and seagrass tissue stoichiometry (C:N ratios, (Kennedy et al., 2010; Duarte et al., 2013; Serrano et al., 2015; Röhr et al., 2016). To definitively determine when, where, and to what extent recalcitrance

controls OC stability in seagrass sediments there needs to be further research into the molecular composition of the OC (Vichkovitten and Holmer, 2005; Kaal et al., 2016), in tandem with rigorous investigation into its decomposability under the physical conditions experienced within the sediment. Several studies have shown sediment characteristics, such as grain size and type, to be important predictors for seagrass OC stocks (Dahl et al., 2016; Röhr et al., 2016; Serrano et al., 2016a), implying that biotic suppression (due to low O₂ content within fine grain sediment) or physical stabilization on certain sediment types are potentially important mechanisms. The next steps must be taken to investigate molecular composition and decomposability, along with sediment mineralogy and geochemistry, and microbial diversity and activity (Mikutta et al., 2006; Chabbi et al., 2009; Schmidt et al., 2011; Simpson and Simpson, 2012; Macreadie et al., 2015; Bracho et al., 2016), if we are to draw definitive conclusions about why OC is stabilized in seagrass sediments.

Here, we outline some of the existing methodologies that can aid in our understanding of OC stabilization (Table 1). We have grouped methods under four broad lines of investigation: (1) determining the molecular composition of OC; (2) mapping the physical and chemical structure of the sediment environment; (3) tracing pathways and timelines of OC; and (4) revealing the identity, function, and activities of the sediment community. To substantially advance our understanding of OC dynamics in coastal marine ecosystems it will require a collaborative effort across disciplines, utilizing this broad spectrum of methodologies. However, this does not negate the importance of the continued efforts and expert knowledge of seagrass ecologists, who provide valuable insights and data required to understand the complex spatial and temporal variation of OC stabilization across seagrass ecosystems.

HOW LONG IS OC STABILIZED IN SEAGRASS SEDIMENTS?

The second major knowledge gap we face is in our understanding of the timelines of OC stabilization within coastal marine sediments. This information, in addition to pool size, is critical for understanding the influence of seagrass carbon reservoirs on atmospheric CO₂ concentrations. The ability of a reservoir to act as a net sink depends on both the fluxes of carbon into the reservoir and the timescale it is stabilized within it (Trumbore, 2000). Only systems with long carbon residence times (decades or longer) act as important mitigators for climate change.

The need to quantify timelines of carbon storage within seagrass sediments was pointed out two decades ago (Mateo et al., 1997, 2006); however, carbon accumulation rates and residence times have been reported based on estimates from age-depth relationships acquired by dating material within sediment layers (Mateo et al., 1997, 2010; Serrano et al., 2012, 2014, 2015, 2016b,c; Miyajima et al., 2015; Jankowska et al., 2016; Rozaimi et al., 2016) or by simply assuming sedimentation rates equal OC accumulation rates (Duarte et al., 2004; Kennedy et al., 2010; McLeod et al., 2011; Lavery et al., 2013; Macreadie et al., 2014; Röhr et al., 2016). These methodologies lead to

TABLE 1 | Some of the existing methodologies utilized to aid in the understanding of organic carbon stabilization in soils and sediments.

Use	Methodology	Citations
Investigating the molecular structure of organic matter in soils and sediments.	Pyrolysis-Gas Chromatography/Mass Spectrometry (Py-GC/MS)	Grandy and Neff, 2008; de la Rosa Arranz et al., 2009; Tolu et al., 2015
	Nuclear magnetic resonance spectroscopy (NMR)	Hedges et al., 2000; Kogel-Knabner, 2002, 2003; Chabbi et al., 2009; Simpson and Simpson, 2012
	Near-edge X-ray Absorption Fine Structure (NEXAFS) spectroscopy	Solomon et al., 2004; Lehmann et al., 2005
	Near-Infrared Spectroscopy (NIRS) / Fourier-Transform Infrared Spectroscopy (FTIR)	Moros et al., 2008, 2010; Verchot et al., 2011; Fuentes et al., 2012; Vinduskova et al., 2015
Measuring and mapping of the physical and chemical structure of soils and sediments.	X-ray fluorescence spectrometry / X-ray computed tomography	Feeney et al., 2006; Nunan et al., 2006; van Oort et al., 2006; West et al., 2007; Sleutel et al., 2008; Boyer-Villemare et al., 2013
	Scanning Transmission X-ray or Electron Microscopy (STXM & STEM)	Brodowski et al., 2005; Maurice and Hochella, 2008; Remusat et al., 2012
	Nano-scale secondary ion mass spectrometry (NanoSIMS)	Herrmann et al., 2007; Amstalden van Hove et al., 2010; Remusat et al., 2012
	Microsensors	Werner et al., 2006; Dadi et al., 2015; Burdorf et al., 2016
Reconstructing sources, pathways and timescales organic matter in soils, including tracing microbial utilization.	Compound-specific isotopic analysis	Rethemeyer et al., 2004; Ingalls et al., 2010; McIntosh et al., 2015
	Biomarkers w/ stable- and natural-abundance radio-isotopes	Rethemeyer et al., 2004; Bouillon and Boschker, 2006; Amelung et al., 2008; Kramer et al., 2010; McIntosh et al., 2015
	Low-level ¹⁴ C pulse-chase labeling Stable isotope probing (SIP)	Carbone et al., 2007; Schuur et al., 2016 Webster et al., 2006; Neufeld et al., 2007; Ruamps et al., 2011
Assessing biodiversity and functional diversity, and elucidating potential activities and interactions among sediment communities and their environment.	Metagenomics	von Mering et al., 2007; Maron et al., 2011; Paula et al., 2014; Bracho et al., 2016; Nesme et al., 2016; Pajares et al., 2016
	Metatranscriptomics	Carvalhais et al., 2012; Jones et al., 2015; Thureborn et al., 2017
	Metabolomics	Bundy et al., 2008; Wallenstein and Weintraub, 2008; Kivlin and Hawkes, 2016

Not all methods fit cleanly into a specific category of usage and most can be used to investigate a variety of research questions.

an overestimation of OC ages and accumulation rates because they do not take into account decomposition losses (however small) from deeper sediment layers (Clymo, 1984; Korhola et al., 1995; Mateo et al., 1997). Furthermore, they ignore the addition of younger carbon (via root turnover and exudates) deeper in the sediment profile (Duarte et al., 1998, 2005). Even though many marine sediments vertically accrete, we must consider that OC does not accumulate in a static fashion, after deposition it continues to be cycled by microbes where it can be transformed and/or lost from the reservoir at rates that depend on the efficacy of the stabilization mechanisms (Torn et al., 2009). Additionally, seagrasses are vascular plants that transfer OC throughout the plant and exudate an estimated 6–17% of production via roots (Moriarty et al., 1986), which equates to various ages of carbon continuously entering the sediment pool.

Models can improve estimates of OC accumulation rates and residence times but have limitations. In an effort to account for OC decomposition, Clymo (1984) adapted a simple one-pool “box” model fit to cumulative carbon vs. age to achieve

a more reasonable accumulation estimate that decreases as the stock grows. In this model decomposition is represented as a first-order process: $dC/dt = -kC$, where C is the amount of carbon at a given time and k is the decomposition rate, and the residence time (also known as transit time) of the carbon within the pool is 1/k. To better represent sediment OC dynamics, which have continual OC inputs, this model was adapted as a multi-input system (vs. the decay of a single input; Trumbore and Harden, 1997; Manzoni et al., 2009, 2012; Hicks Pries et al., 2012), where both the decay constant and inputs can be estimated. Although these types of models have a rich history of usage for modeling OC dynamics, they are typically fit to data of mass loss through time (i.e., litter decomposition) or fluxes of CO₂ (incubations; Eriksson, 1971; Bosatta and Agren, 1985; Ågren and Bosatta, 1996; Manzoni et al., 2009, 2012; Cornwell and Weedon, 2014). To fit them to data of cumulative OC vs. time (dated depths) from a sediment core the following assumptions must be made: (a) the system is in steady state; (b) initial OC in the sediment is zero; (c) carbon is accreted vertically (no

inputs of new OC below dated depths); (d) the dated material is equal to the age of the bulk OC at the same depth in the sediment profile (see below); (e) there are no changes in OC dynamics through time, so recent OC dynamics (top of core) are representative of initial OC dynamics of the system. According to the above critique, none of these assumption holds true for the actual situation and OC dynamics in marine sediments. On top of this, it is assumed the entire core is one pool of OC, all residing for the same time period, and although multi-pool box models exist, the data from sediment cores often do not support the increased model complexity. Furthermore, the use of cumulative data, which are not independent, leads to unrealistic confidence in model estimates (due to underestimation of model uncertainty; King et al., 2015). In spite of these limitations, these models have proven to be useful for providing more realistic estimates of OC accumulation and residence time of OC within non-vascular dominated, vertically-accreting ecosystems (Clymo, 1984; Trumbore and Harden, 1997; Hicks Pries et al., 2012). However, extreme caution must be used when applying them to sediment-core data from vascular plant dominated ecosystems such as seagrass meadows.

Another factor that influences estimates of OC ages and residence times is the type of material used for dating. Previous works in seagrass ecosystems have utilized closed-system materials (assumed to be no longer exchanging carbon with the environment), such as shells or sheaths, for radiocarbon (^{14}C) dating (Mateo et al., 1997, 2010; Serrano et al., 2012, 2014, 2015, 2016b,c; Rozaimi et al., 2016). Because sediment OC consist of a spectrum of pools cycling on different time scales, choosing the oldest, most stable carbon within the sediment and ignoring all other OC (of a variety of ages) residing at the same depth in the sediment profile, leads to an overestimation of OC ages and residence times (Trumbore and Zheng, 1996; Torn et al., 2009; Trumbore, 2009; Trumbore et al., 2016). To illustrate the potential for overestimation, OC ages have been shown to vary by three orders of magnitude, from 3 years ($\Delta^{14}\text{C} = +170\text{‰}$) to $\sim 3,000$ ($\Delta^{14}\text{C} = -310\text{‰}$) years, within a 5-cm sediment layer in tropical forest soils (Trumbore and Zheng, 1996; Trumbore, 2009). Therefore, when the goal is to understand OC dynamics, and estimates of residence times of the various carbon pools are needed (as opposed to exact calendar ages), a different methodological approach is required.

Because of the limitations outlined above we suggest an alternative methodology utilized in terrestrial systems over the past two decades (Trumbore, 1993, 2000, 2009; Schuur et al., 2016). Organic matter is more appropriately thought of as a heterogeneous open-system (continuously exchanging carbon with its environment), so directly measuring ^{14}C of the bulk sediment OC pool along with manually separating and dating pools (that are relatively homogenous in terms of decomposition rates) provide more realistic estimates of the suite OC ages occurring within the sediment (Trumbore, 2009; Schuur et al., 2016; Trumbore et al., 2016). Since OC is a complex mixture of compounds that cycle along a continuum of time scales from minutes to millennia, no separation method will be perfect. However, methods exist to partition OC into various pools, which

allows for the determination of both pool size and residence time (Trumbore and Zheng, 1996; von Lützow et al., 2007; Trumbore, 2009; Trumbore et al., 2016). The same linear-system box models can be adapted to estimate the residence time of ^{14}C of each pool:

$$d^{14}\text{C}(t)/dt = I^{*14}\text{C}(t) - k^{*14}\text{C}(t) - \lambda^{*14}\text{C}(t)$$

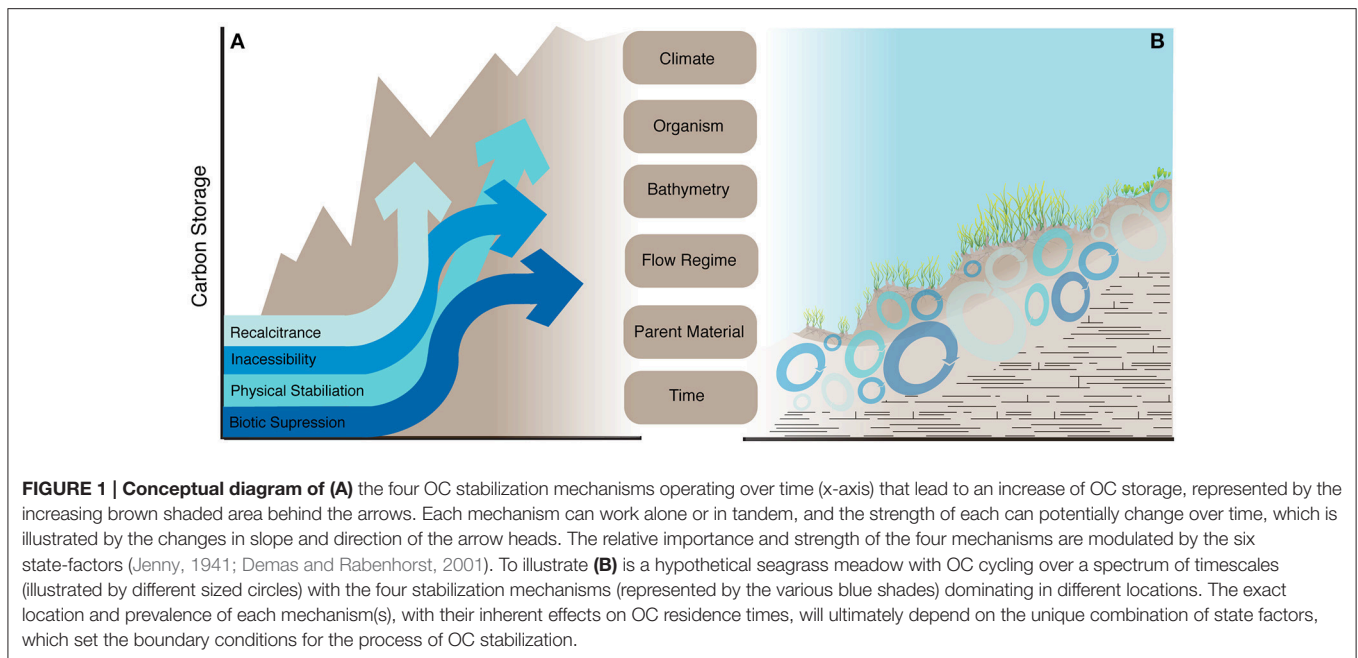
where λ is the radioactive decay constant ($1.21 \times 10^{-4} \text{ yr}^{-1}$), $I^{*14}\text{C}(t)$ are the inputs of ^{14}C based off a time series of ^{14}C from of the reservoir the plant uptakes CO_2 from, and $k^{*14}\text{C}(t)$ are the estimated outputs. These models can also be extended to multi-pool models and only requires a measurement from your desired pool of either the F (fraction modern prior to 1950) or F' (fraction modern that includes bomb ^{14}C) and a bomb carbon time series of F' of the reservoir (Manzoni et al., 2009, 2012; Trumbore et al., 2016). For terrestrial systems, the time series of the reservoir (atmosphere) F' is well known (Hua et al., 2013), but becomes more complicated in marine systems because of the reservoir effect (Mangerud, 1972; Stuiver et al., 1986). However, in many coastal systems, post-bomb ^{14}C time series exist (Weidman and Jones, 1993; Kalish et al., 2001; Mahadevan, 2001; Kilada et al., 2007; Scourse et al., 2012; Tisnérat-Laborde et al., 2013). Another potential hurdle in marine systems is the presence of terrestrial carbon (fixed from the atmospheric pool), so care must be taken to disentangle these signals (Marshall et al., 2007; Yu et al., 2007). Although there are some hurdles, this methodology avoids complications created by simplistic assumptions of carbon ages and depths, and provides direct measurements of residence times directly linked to pools of known sizes and locations. These techniques could be used in tandem with attributes of the OC pool and sediment (such as mineralogy, redox, and molecular composition), to advance our understanding of the timescales over which different stabilization mechanisms operate (Mikutta et al., 2006; Chabbi et al., 2009).

A WAY FORWARD

Here, we propose a conceptual framework to focus research efforts across the diverse environments where seagrasses occur. This framework is adapted from the Jenny (1941) state-factor system utilized in terrestrial ecosystems, to incorporate factors identified for subaqueous soils (Demas and Rabenhorst, 2001; Torn et al., 2009; Trumbore, 2009). In this model a soil property such as OC storage is described by the function:

$$\text{Soil property} = f(\text{C, O, B, F, P, T}),$$

where C = climate, O = organism (vegetation), B = bathymetry, F = flow regime, P = parent material, T = time). These factors set the boundary conditions and modulate the mechanisms that determine the magnitude and timescales of carbon stabilization (Figure 1). By selecting study sites where one state-factor varies, while the other factors are held relatively constant, we can begin to identify the role each factor plays and what mechanism(s) operate within the unique combination of state-factors that occur throughout the seagrass bioregions (Short et al., 2007). For example, within *Posidonia spp.* meadows OC storage varies



predictably with bathymetry in sheltered bays (flow regime) in both the Mediterranean and Western Australia (Serrano et al., 2014), with the difference in magnitude of OC storage between the locations potentially explained by variations between seagrass species (organism-vegetation). The usefulness of this framework can be further illustrated by the finding that across the European geographic distribution (climate) of *Zostera marina* (organism-vegetation), OC can be predicted by sediment grain size (parent material and/or flow regime; (Dahl et al., 2016). Furthermore, in two sites with contrasting sediment characteristics they found that OC did not decrease with sediment depth (indicating minimal decomposition over time), which lead to the hypothesis that different stabilization mechanisms were at play: a) biotic suppression due to low oxygen availability in the fine-grain site, and b) recalcitrance of allochthonous carbon inputs in the coarse-grain site. This framework can also potentially explain why sediment grain size does not correlate to OC storage when looking across a mixture of different parent materials, climates, seagrass species, flow regimens, and bathymetry (Serrano et al., 2016a). We believe that embracing the complexity found within seagrass ecosystems and utilizing the state-factor system to systematically identify which mechanism(s) control the spatial and temporal variations of OC is a way forward to understand carbon dynamics in coastal marine systems.

CONCLUSION

As policy makers and managers identify pathways to conserve seagrass systems embedded under a blue carbon framework (Herr et al., 2012), the potential for OC sequestration opens the door for both positive and negative consequences. On the positive side, this creates an avenue for conservation of

these valuable ecosystems, along with their well-established ecosystem services. On the negative side, CO₂ will be emitted in exchange for carbon credits, resulting in an increase in atmospheric CO₂ unless we are able to correctly estimate the magnitude and timelines of OC sequestration. The future of blue carbon research is not trivial. There are both spatial and temporal scales on which OC stabilization/destabilization mechanisms operate, with complex processes and controls working in combination. As we come to terms with this complexity, and embrace technological advances in genetic, molecular, spectrometric, and isotope-tracing techniques in tandem with gathering more data from a diversity of seagrass ecosystems, we can move forward with this important line of research.

AUTHOR CONTRIBUTIONS

EB produced the conceptual framework, wrote the first draft of the manuscript, and synthesized the inputs and revisions of the coauthors. MM contributed to the conceptual knowledge and critically revised the manuscript. LG contributed to the conceptual knowledge and critically revised the manuscript. MZ contributed to the conceptual knowledge and critically revised the manuscript. MT contributed to the conceptual knowledge and critically revised the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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