Soil and Freshwater and Marine Sediment Food Webs: Their Structure and Function

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The food webs of terrestrial soils and of freshwater and marine sediments depend on adjacent aboveground or pelagic ecosystems for organic matter input that provides nutrients and energy. There are important similarities in the flow of organic matter through these food webs and how this flow feeds back to primary production. In both soils and sediments, trophic interactions occur in a cycle in which consumers stimulate nutrient cycling such that mineralized resources are made available to the primary producers. However, aquatic sediments and terrestrial soils differ greatly in the connectivity between the production and the consumption of organic matter. Terrestrial soils and shallow aquatic sediments can receive organic matter within hours of photosynthesis when roots leak carbon, whereas deep oceanic sediments receive organic matter possibly months after carbon assimilation by phytoplankton. This comparison has implications for the capacity of soils and sediments to affect the global carbon balance.

Keywords: soil, sediment, organic matter, food web and trophic control, stoichiometry

Soils, freshwater sediments, and marine sediments harbor high levels of biodiversity and support biogeochemical processes that are pivotal to life on Earth (Wall et al. 2010). The soil and sediment biota function within food webs. The structure of these soil and sedimentary food webs, as well as their role in transforming carbon and nutrients, are often studied separately (Wall 2004) because of the habitat-centered organization of the research. However, soil and sediment food webs share many characteristics. For example, both types depend on external organic matter resources produced in adjacent (aboveground or pelagic) ecosystem compartments, and they feed back to those compartments in a variety of direct and indirect ways (Moore et al. 2004). Here, we compare the structure and function of soil and sediment food webs and their coupling with primary producers. This comparison will help identify key differences and similarities in soil and sediment food web properties and will offer perspectives on their roles in the global carbon cycle.

The soil or sediment food web of any ecosystem is the place where organic and inorganic particles are eventually trapped, mineralized, or stored, and this has important consequences for the global carbon balance (Falkowski et al. 2000, Wall 2004, Cole et al. 2007). The organisms in both soils and sediments interact in dynamic food webs, and the regulation of organisms by their consumers within the food web controls the fate of organic matter at local and global scales (de Ruiter et al. 1995, Rooney et al. 2006). Terrestrial, freshwater, and marine environments contrast in abiotic conditions such as oxygen availability and temperature fluctuation. However, indirect interactions, such as *bioturbation* (the biological reworking of soils and sediments by organisms including microbes, rooting plants, and burrowing animals; Meysman et al. 2006) and diseases caused by pathogens, or direct interactions, such as trophic effects caused by grazers, result in flows of organic matter through subsurface food webs that are remarkably similar in soils and sediments (de Ruiter et al. 1995, Rooney et al. 2006).

There are also important differences in the organic matter that fuels these food webs. This is particularly the case with respect to the temporal and spatial scale of interactions between the aboveground or pelagic primary producers and the rest of the food web, as well as in the ecosystem-scale

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feedback interactions with carbon cycling and climate (Ruhl et al. 2008, Bardgett and Wardle 2010, Marcarelli et al. 2011). In both terrestrial and aquatic ecosystems, soil- and sediment-dwelling biota interact directly or indirectly with primary producers, which are in the sunlit portion of the environment, and the scale of separation varies depending on the biome. In terrestrial ecosystems, such interactions are called *aboveground–belowground interactions* (Hooper et al. 2000), whereas in aquatic systems, the analogous process is called *benthic–pelagic coupling* (Palmer et al. 2000). We will discuss these two-way interactions and use the term *coupling* to further define the temporal and spatial scales of the interactions. Coupling is defined as *short* when the transit time of mineral nutrients or organic matter is less than a year or as *long* when transit takes decades or more. Furthermore, coupling is defined as *tight* when all material will be recycled locally, such as in micrometer or millimeter interactions in the rhizosphere of soil. In the case of the import of distant external material, such as the transport of terrestrial organic matter through rivers and streams to the ocean, coupling is defined as *loose*.

Organic matter enters soil or sediment food webs as living or dead material. We make a distinction between the living (*green*) and detrital (*brown*) material and discuss the interaction pathways between green and brown material for each ecosystem and the organic matter quality associated with them (*sensu* Moore et al. 2004). We further discuss how the food webs that process the inputs of organic matter are structured. This is done through a schematic comparison of trophic interactions among the main compartments in the green and brown pathways of soil and sediment food webs (figure 1a–1c). We then address the importance, tightness, and time scales associated with the interactions within each food web. Finally, we briefly discuss the need for integrated research across habitats, studying how soils and sediments may feed back on the global carbon cycle and their interactions with climate change. The goal of this work is to describe the similarities and differences in interactions and coupling (short versus long and tight versus loose) in soil and sediment food webs with respect to the quality, quantity, and origin of the organic matter inputs. We make a cross-system comparison of soils and sediments to highlight their importance as a distinct biome with critical global functions. By synthesizing our knowledge of the subsurface biome in a simplified way, we hope to stimulate cross-habitat research that leads to an improved understanding and a cross-ecosystem theory.

Organic matter inputs to ecosystems: Quality and coupling

The quality and quantity of organic resources affect the rate of feeding and, therefore, the rate of nutrient recycling in food webs (Cebrian et al. 2009). The growth of primary producers is generally limited to a similar degree by nitrogen and phosphorus in terrestrial, freshwater, and marine ecosystems (Elser et al. 2007). However, there are large differences among these three habitats in the quality of primary producer biomass. Many land plants need structural tissues, such as woody stems, that are rich in lignin and have a very high carbon:nitrogen ratio (Sterner and Elser 2002). Lignin can be degraded only by a limited number of microorganism species. Land plants are therefore frequently less nutritious for herbivores and other subsurface food web components than are aquatic primary producers (Sterner and Elser 2002). The difference in plant tissue quality has implications when the degree and scale of coupling between soil and sediment food webs and primary producers are considered. Although aquatic sediments tend to be supplied by plant biomass that is of higher quality than that received by terrestrial soils, the temporal and spatial scale of coupling can be larger because of the physical separation between the photic zone and deep sediments. However, in shallow aquatic systems, this physical separation is not present most of the year, and in these systems, there is a more direct coupling between sediment food webs and primary producers (e.g., macrophytes or benthic algae; Scheffer 1998).

Differences in resource supply to soil and sediment food webs affect the state in which these resources arrive. The designation of a pathway as brown or green is subject to interpretation, and the line between the two is subject to reasonable debate (Moore and de Ruiter 1997, Allison 2006). Carbon may enter soil and sediment food webs as living plants or algae, which can be directly consumed by root herbivores, root pathogens, mutualistic root symbionts, or by algal feeders and algal pathogens. This is called the *green pathway* and is typically characterized by a rapid exchange of carbon and nutrients between the photosynthetic zone and the subsurface food web. It involves mostly herbivory, feeding on living roots in soils, microalgae living on the surface of aquatic sediments, or suspension feeders living at or in the sediments consuming phytoplankton. In contrast, in the *brown pathway*, the majority of the carbon enters the soil and sediment food webs through decomposition (Cebrian 1999). In terrestrial soil and sediments of shallow aquatic systems, decomposers eat organic matter such as dead plants and animals or root exudates. In the aquatic sediments of deep lakes and oceans, they eat dead phytoplankton and dead consumers that sink to the floor. The brown pathway supports detrital food webs (see figure 1 for a schematic of trophic control in the green and brown pathways within three different biomes).

The designation of a pathway as brown or green provides a coarse description of organic matter quality. However, a designation based on the chemical composition of organic matter is more precise. The relative amounts of carbon, nitrogen, and phosphorus can determine the quality of resources but also their chemical structure (Sterner and Elser 2002). For instance, lignin has a very complex molecular structure, whereas cellulose has a relatively simple structure. The quality of a substrate is important, because it can affect its path through a food web (Cebrian 1999). Again using lignin as an example, its decomposition is limited to very specialized groups of fungi (Kirk and Farrell 1987) and possibly their consumers. Organic matter entering through both the green and the brown pathways supports large interacting

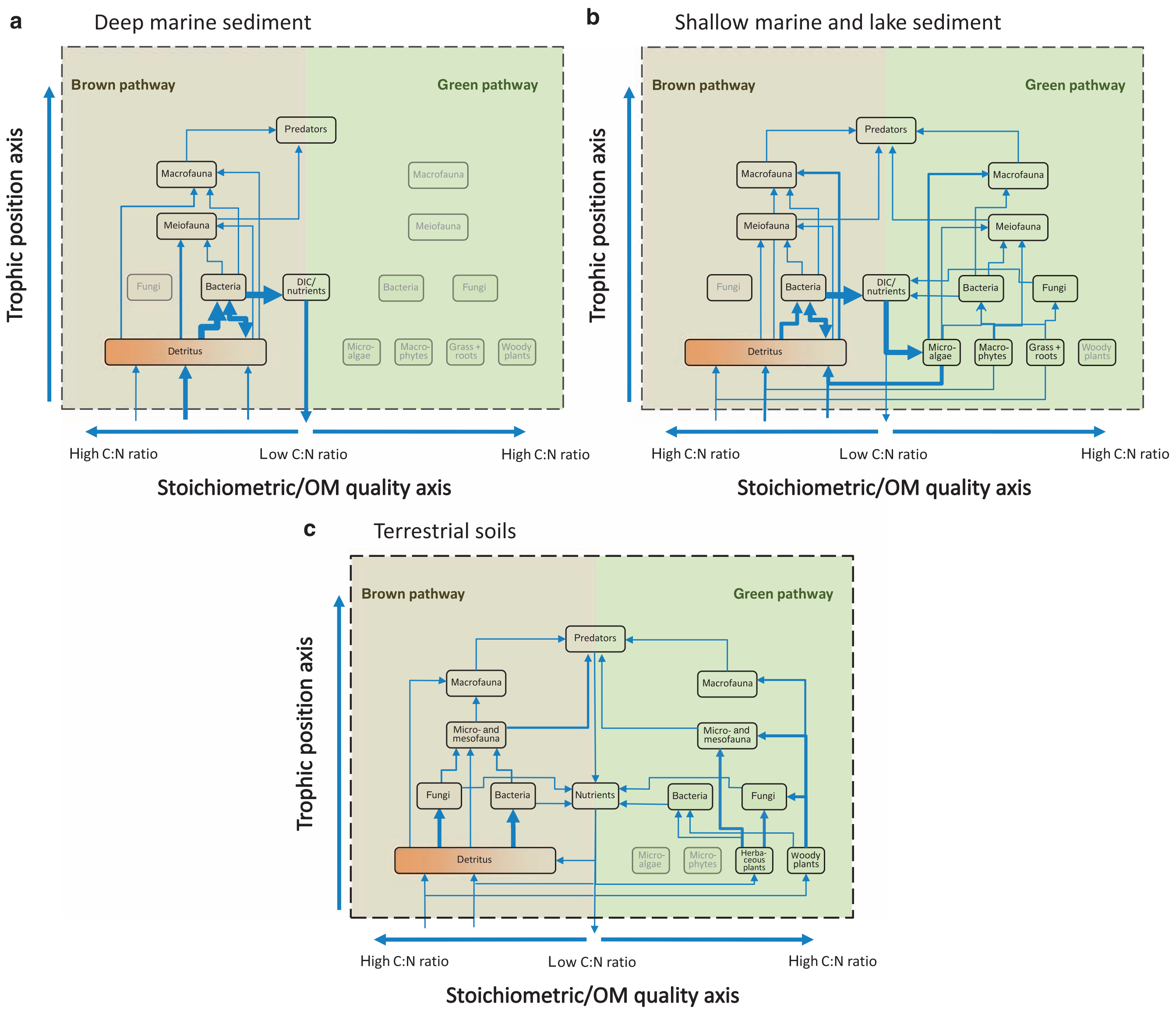

Figure 1. Trophic structure in subsurface food webs as a function of organic matter (OM) quality, including material and interaction flows through both green (right side) and brown (left side) pathways. The arrow weight in the figure indicates the relative importance of material flow and interaction in (a) the deep marine sediment habitats, (b) shallow marine or lake sediment habitats, and (c) terrestrial soil habitats. The arrows entering and leaving detritus reflect their relative position along the stoichiometric quality scale. Although they are depicted as separate boxes, the brown and the green pathways are not separate; there is a high degree of linkage between the two, and they are drawn separately only to convey the concept visually. Furthermore, we show arrows from dead photosynthetic production to the detrital pool, because this is the primary source of biomass flux there. Although the arrows connecting higher trophic levels with detritus were excluded, we do not want to ignore their contributions, but we leave them out for clarity of presentation. Abbreviations: C, carbon; DIC, dissolved inorganic carbon; N, nitrogen.

food webs (Moore and Hunt 1988), and these food webs exist simultaneously. Recent theory states that the feeding pathways supported by brown and green organic matter ultimately converge on omnivores and predators, which stabilize the structure and function of the food web (McCann and Rooney 2009).

Terrestrial and aquatic couplings provide a two-way connection between subsurface food webs, where organic matter is decomposed and nutrients are mineralized, and the sunlit zone, where nutrients are assimilated in primary production. Nutrients released from deep-water sediments become available again for primary producers after upwelling, but the centennial replacement times of deep-water masses (Ruhl et al. 2008) result in loose and long coupling. In lakes, seasonal turnover makes coupling relatively more tight and short. Whether a system is coupled loosely or tightly does not reflect the importance of the organic matter subsidy. For instance, even distant terrestrial inputs of carbon can be basal resources of a significant part of aquatic food webs. Cole and colleagues (2011), for example, found that zooplankton in lakes receive up to 50% of their carbon from terrestrial sources. In the aquatic subsurface food webs, the tightest coupling probably occurs in intertidal shallow areas, where the benthic community is tightly coupled with local production from diatoms (Middelburg et al. 2000). Short and tight coupling exist, for example, in the case of the micrometer scale of bacteria consuming exudates from microphytobenthos (Middelburg et al. 2000) or bacteria and fungi (mycorrhizal or saprotrophic) absorbing carbon from within living roots and from root exudates in the rhizosphere (De Deyn et al. 2011). Coupling can be extremely long—for example, in the cases of the decadal scale of lignin degradation in soils (Benner et al. 1986) or refractory detritus in the deep sea (Henrichs and Doyle 1986). In summary, coupling in terrestrial soils and shallow aquatic systems varies mostly with respect to time (short to long), whereas coupling in deep aquatic systems can vary both spatially and temporally (short versus long and tight versus loose, respectively).

The fate of the organic matter

Organic matter is cycled in numerous ways, which we outline below.

The role of microbes in trophic interactions. With respect to microbial decomposition, bacteria dominate the degradation of refractory detritus in marine (figure 1a; van Oevelen et al. 2011) and freshwater (figure 1a, 1b; Tranvik et al. 2009) biomes. In contrast, bacteria and fungi are the main decomposers of detritus in terrestrial biomes (figure 1c; Bardgett and Wardle 2010). One way for fauna to exploit refractory detritus is through *microbivory*, which is consumer grazing on bacteria and fungi (Osler and Sommerkorn 2007). Theoretical arguments led Jumars and colleagues (1990) to suggest that bacterivory is important in deep-sea food webs through a *flash-cook* strategy, in which fauna, through their own metabolism and sediment mixing, provide an enhanced supply of labile organic matter, oxygen, and ammonium to the detritus layers, which stimulates bacterial degradation of detritus (van Nugteren et al. 2009). This flash-cook strategy stimulates bacterial growth, which can, in turn, be used by fauna as a carbon and nitrogen source. This preprocessing of detritus by microbes is also important in terrestrial food webs in which microbes metabolize detritus. Subsequently, microbial decomposition followed by microbivory by protozoans and bacterivorous nematodes forms the basis of the detritivorous food web in soil (figure 1c; Bonkowski 2004).

The movement of organic matter through microbes to fauna has variable importance, depending on the biome. Guilini and colleagues (2010), using an isotope-labeling approach, found that bacteria are of only limited importance for nematodes in deep Arctic Ocean sediment. However, few empirical tests of the importance of microbivory in deep-sea food webs currently exist because of the difficulty with experimentation in this environment. The importance of transfer from bacteria to fauna also seems to be of limited importance in lake sediments (figure 1b; Cotner and Biddanda 2002); it represents less than 15% of faunal diets in intertidal sediments (van Oevelen et al. 2006) and less than 1% in deeper sediments (figure 1a; Guilini et al. 2010). In shallow aquatic sediments, the transfer from bacteria to fauna may be more important, depending on the vegetation (e.g., benthic algae or macrophytes) present (Wetzel 2001). Likewise, in terrestrial systems in which rooted vegetation plays a critical role in carbon transfer (figure 1c), fauna depend to a great extent on microbes to fulfill their carbon demands, since the energy transfer through the detritus pathway is typically channeled by bacteria and fungi to the soil fauna (Coleman et al. 2004, Moore et al. 2004). One may speculate that the additional microbial transfer and its associated respiration losses in terrestrial food webs render the detritivorous pathway less efficient, such that less faunal biomass can be supported by the same detritus input. However, terrestrial and shallow-water food webs may compensate for a lower efficiency, because primary consumers can feed directly on roots and root exudates (Moore et al. 2004), whereas consumers in deep-water sediments cannot because of the absence of rooted primary producers.

The primary consumer's role in trophic interactions. Primary consumers operate in the green pathway when they graze fresh plant material and in the brown pathway when decomposers feed on dead organic matter (figure 1a–1c). On land, belowground herbivory in the green pathway is mostly limited to root-feeding nematodes, some microarthropods, and insect larvae that feed on the roots of herbaceous and woody plants (figure 1c). This root feeding can reduce primary production but also results in soil nutrient enrichment when damaged roots leak carbon to the surrounding soil, where it fuels microbial activity and further mineralization of organic matter and nutrient release (Yeates et al. 1998).

The degree to which primary producers are grazed by herbivores, the efficiency with which consumers acquire nutrients from their resources after ingestion, and the way in which they redistribute these resources through metabolic waste strongly influence the fate of carbon in the subsurface. In terrestrial soils, carbon is consumed by root herbivores and decomposers in excess so that they can acquire sufficient nutrients for growth. Therefore, if it is not released as carbon dioxide (CO_2), carbon remains in the soil as feces or unconsumed living or dead producer biomass (Hessen et al. 2004). The degree to which this occurs may support carbon sequestration in undisturbed terrestrial soils and has implications for global carbon cycling—whether carbon is ultimately stored in the subsurface, assimilated as biomass, or respired as CO_2. Because primary consumers ingest relatively more plant biomass to scavenge scarce nutrients (nitrogen and phosphorus), carbon is left in excess (Cebrian 1999). The mismatch in stoichiometric signature between producer and consumer biomass directly affects the activities of the primary consumer trophic level. In both terrestrial and aquatic ecosystems, there is a positive relationship between an individual's rate of herbivory and stoichiometric mismatch such that the more different the elemental ratios of primary producer and consumer are, the higher the rates of herbivory will be, and at the level of an individual herbivore, the rate of herbivory may be affected by the presence of lignin or chemical defenses in the primary producers (Hillebrand et al. 2009). In shallow marine and lake sediments, the stoichiometric quality of the primary producers (microalgae) is high. Therefore, consumption is high and biomass turnover is rapid (Cebrian 1999), which leads to short and tight coupling. In terrestrial soils, the balance between production and storage of soil organic matter and nutrient mineralization is controlled by the stoichiometric quality of both the consumer and the resource (Osler and Sommerkorn 2007). In that case, coupling between primary producers (e.g., roots) and consumers is tight, but the temporal separation varies with quality.

In deep marine sediments in which primary production is almost nonexistent, the activity of viruses dominates in a role similar to that of consumer-driven nutrient cycling. Danovaro and colleagues (2008) reported that lysis following viral infection is the dominant fate of prokaryote production in shallow and especially in deep marine sediments. Danovaro and colleagues (2008) concluded that viral infection exerts an important top-down control on prokaryotic biomass. The released labile organic matter following viral lysis, in turn, seemed to stimulate prokaryote production, as is evident from a positive correlation between viral production and prokaryotic production. These findings support theoretical models (e.g., the viral shunt) describing viral impacts on microbial carbon cycling and community composition (Miki et al. 2008).

The secondary consumer's role in trophic interactions. The highest trophic levels in the food web are occupied by secondary consumers and top predators. These groups exert a top-down control that limits the population sizes of their prey and that can cycle nutrients back to the basal level. Osler and Sommerkorn (2007) argued that the feeding activity of top consumers can stimulate nutrient cycling and can therefore affect plant community composition and growth. The degree to which the feeding activity of predators positively affects nutrient release and primary production depends on the degree to which the system is coupled and, likewise, on the habitat. On land and in shallow water, indirect interactions between predators and plants are often tightly coupled. For example, on land, predatory mites and nematodes prey on herbivores in the rhizosphere and thereby release nutrients that are available to plants (Moore et al. 2003). In shallow water, macrofauna, benthivorous fish, and birds prey on herbivores and release nutrients available to plants (Scheffer 1998). Although predator–prey interactions are present in deep-water sediments, the absence of primary producers dictates that the total biomass and composition of the sediment community is primarily determined by the quality and quantity of the detritus inputs from the photic zone and not by nutrient release from predators (Smith et al. 2008, Wei et al. 2010).

Table 1. Estimates of carbon storage and flux in four soil or sediment biomes.

Subsurface biome	Carbon storage (in petagrams)	Carbon storage reference	Carbon flux (petagrams per year)	Carbon flux reference
Terrestrial soil	2.1×10^3	Lal 2003	68	Woodwell and Mackenzie 1995
Peatland soil	455	Gorham 1991	0.076	Gorham 1991
Inland freshwater sediments	0.23	Cole et al. 2007	0.23	Cole et al. 2007
Oceanic sediments	7.78×10^7	Mackenzie et al. 2004	2.5	Sarmiento and Gruber 2006

Conclusions

Cross-ecosystem understanding of soils and sediments in the subsurface is increasing. Food web theorists are developing models of structure and function that can be generalized to a wide range of habitats (Olff et al. 2009). Furthermore, purely theoretical models describing trophic interactions and their role in terrestrial soil food web stability (Neutel et al. 2007) have been tested successfully in shallow marine food webs (O'Gorman and Emmerson 2009). More such work needs to be done to improve general theory (Wall et al. 2010). Once it is achieved, this generalized theory can be used to predict interactions between the subsurface and global carbon cycling and their effects on climate change. There are various estimates of the source–sink capacity of terrestrial and aquatic or marine systems in relation to buffering increasing global atmospheric carbon levels (table 1). Existing carbon storage in soils may be up to 2.1×10^3 petagrams (Lal 2003), whereas aquatic (marine and freshwater together) carbon storage in sediments may be up to 1.0×10^7 petagrams (Cole et al. 2007, Mackenzie et al. 2004).

The capacity of soils and sediments to store carbon will inevitably interact with climate change and atmospheric CO_2 concentration (Coleman and Whitman 2005, Ruhl et al. 2008, Wall et al. 2010). Much of this feedback between the subsurface and the atmosphere is primarily mediated by microbial metabolism (Allison et al. 2010). Microbial decomposition in soils is a metabolic process that is very sensitive to changing environmental conditions, such as moisture and temperature (Davidson and Janssens 2006), as well as to the stoichiometric quality of organic matter consumed (Osler and Sommerkorn 2007). As global temperatures increase, decomposition may increase, which would result in released carbon as CO_2 that would otherwise be stored in the subsurface. Bellamy and colleagues (2005) showed that over a 25-year sampling period, organic carbon was lost from soils across England and Wales in proportion to what was previously stored. This result was seen across diverse terrestrial habitats and land-use patterns. For the oceans, increased sea surface temperatures are expected to narrow the mixed layer of the ocean's photic zone and to increase the strength of water column stratification. This may shift pelagic ecosystems from export food webs, such as those dominated by diatoms and large zooplankton that give high export fluxes to the seafloor, to retention food webs, such as those dominated by small phyto- and zooplankton with low export to the deep sea (Smith et al. 2008) and less organic matter input to sediments. Moreover, elevated temperatures stimulate microbial consumers more than primary producers, which results in reduced production of organic matter (Wohlers et al. 2009). Temperature increases would thus reduce food inputs to an ecosystem that is strongly regulated by food limitation, which would result in negative feedback to carbon storage capacity (Wei et al. 2010).

Climate change is likely to be far more complex than shifts in temperature alone. For example, seasonal variation and shifts in rainfall patterns are expected. Changing patterns will not manifest in the same way in terrestrial and aquatic environments (Lal 2003). Drying and wetting patterns will have a direct effect on terrestrial soil communities but only an indirect effect on aquatic sediment communities through land-to-water coupling (*sensu* Cole et al. 2011). Coupling has thus far been underappreciated in the consideration of climatic feedbacks. Relatively little is known about how coupled systems will respond to changes in the global carbon balance and how that might interact with a changing climate. Feedbacks between the photosynthetic zone and the subsurface in aquatic or terrestrial environments may not respond in predictable ways. Depending on abiotic conditions, soils and sediments may become a source or a sink for atmospheric CO_2. The net response cannot be predicted easily because of the complexity and dynamics of the organic matter being decomposed and the feedbacks to primary production (Davidson and Janssens 2006). For instance, elevated CO_2 may enhance microbial carbon cycling, leading to interactions between atmospheric CO_2 concentration and available soil nitrogen (McKinley et al. 2009). The challenges of understanding these feedbacks grow as one considers the added layers of nutrient availability—an important area of future research.

This article is a next step following studies compiled by Wall (2004) in an effort to synthesize subsurface food web structure and function in freshwater, marine, and terrestrial biomes in order to enhance attention to their roles in the changing global carbon cycle. However, a greater understanding of feedback interactions, coupling, and the role of organic matter quality from local to global scales is required in order to fully understand the balance of global carbon, how it can be influenced by management and policy options, and how it will affect our future climate. To do this, a concerted effort is needed so that ecosystem-specific researchers collaborate and share ideas. Organic matter—the base of all soil and sediment food webs—can be transported between systems. It moves through rivers and streams to the ocean, where it ultimately settles (Cole et al. 2011), or organic matter cycling through pelagic food webs can be transported to land through the feeding and nesting activities of sea birds (Fukami et al. 2006). The quality of organic matter moving from terrestrial soils into streams affects microbial metabolism and, ultimately, carbon storage (Lennon and Pfaff 2005). Research tracking carbon as it moves through habitats, ecosystems, and greater biomes will provide information on system balance that can guide long-term predictions and the modeling of future climate scenarios.

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