CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Carbon dynamics of river corridors and the effects of human alterations

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Abstract. Research in stream metabolism, gas exchange, and sediment dynamics indicates that rivers are an active component of the global carbon cycle and that river form and process can influence partitioning of terrestrially derived carbon among the atmosphere, geosphere, and ocean. Here we develop a conceptual model of carbon dynamics (inputs, outputs, and storage of organic carbon) within a river corridor, which includes the active channel and the riparian zone. The exchange of carbon from the channel to the riparian zone represents potential for storage of transported carbon not included in the "active pipe" model of organic carbon (OC) dynamics in freshwater systems. The active pipe model recognizes that river processes influence carbon dynamics, but focuses on CO2 emissions from the channel and eventual delivery to the ocean. We also review how human activities directly and indirectly alter carbon dynamics within river corridors. We propose that dams create the most significant alteration of carbon dynamics within a channel, but that alteration of riparian zones, including the reduction of lateral connectivity between the channel and riparian zone, constitutes the most substantial change of carbon dynamics in river corridors. We argue that the morphology and processes of a river corridor regulate the ability to store, transform, and transport OC, and that people are pervasive modifiers of river morphology and processes. The net effect of most human activities, with the notable exception of reservoir construction, appears to be that of reducing the ability of river corridors to store OC within biota and sediment, which effectively converts river corridors to OC sources rather than OC sinks. We conclude by summarizing knowledge gaps in OC dynamics and the implications of our findings for managing OC dynamics within river corridors.

Key words: active channel; carbon; dam; land use; riparian zone; river.

Introduction

We propose a conceptual framework that integrates the active channel and riparian zone and use this framework to examine organic carbon inputs, outputs, and storage within river networks. We believe that this framework most effectively illuminates the important influences that river process and form exert on organic carbon fluxes.

As recently as 2001, the Intergovernmental Panel on Climate Change (IPCC) report included a conceptual model of the global carbon cycle with only two

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biologically active boxes, the land and the oceans, connected through freshwater transport of carbon from the land to the oceans and through gas exchanges with the atmosphere (IPCC 2001). Research during the 1970s and 1980s demonstrated that rivers deliver significant amounts of terrestrial carbon derived from soils and vegetation to the ocean (e.g., Schlesinger and Melack 1981), but rivers were only included in early conceptual models of the carbon cycle as neutral or passive pipes for carbon transport (Cole et al. 2007). In the past decade, we have learned that much more terrestrial carbon enters rivers than is transferred to the ocean, indicating that rivers are active pipes for carbon transport (Cole et al. 2007). However, research into rivers as active pipes in the carbon cycle has focused primarily on losses of carbon via gas exchange in all freshwater habitats (Raymond et al. 2013) and via storage of carbon in lakes and reservoirs

(Tranvik et al. 2009). Carbon exchanges in riparian wetlands and floodplains are commonly treated separately. Much less known is the role of carbon storage in river channels and floodplains. Rivers can store organic-rich sediment within the active channel in bars, beneath the active channel, particularly in an aggrading river segment, and in floodplains, deltas, alluvial fans, and other portions of the river network typically dominated by deposition and storage over time spans of 10¹–10³ yr (Walter and Merritts 2008, Hoffmann et al. 2009, Cierjacks et al. 2010, Wohl et al. 2012b, Sutfin et al. 2016). Together, research in stream metabolism, gas exchange (e.g., Raymond et al. 2013, Hotchkiss et al. 2015), and sediment dynamics (Wohl et al. 2015) indicates that rivers are an active component of the global carbon cycle, rather than neutral pipes, and that river form and process can significantly influence partitioning of terrestrially derived carbon among the atmosphere, geosphere, and oceans (Aufdenkampe et al. 2011). However, most conceptual expressions of the global carbon cycle have not yet integrated such a view.

The lack of appropriate integration of rivers into global carbon models may partly reflect differing definitions of what constitutes a river. Here, discussion of carbon dynamics in river contexts includes inputs, outputs, and storage of diverse forms of organic carbon (OC) that occur within a river corridor. We define a river corridor as including the active channel, hyporheic zone, floodplain, riparian zone, and river depositional landforms such as deltas and alluvial fans (Ward 1989, Ward and Tockner 2001, Harvey and Gooseff 2015, Fig. 1). For simplicity, we distinguish the active channel and the riparian zone as primary components of the river corridor in discussing carbon dynamics. The active channel is

a primarily erosional feature that routes water through the landscape at least episodically within defined banks: this is the portion of a river corridor that stream ecologists are most likely to think of as a river. The riparian zone includes the hyporheic zone, floodplain, delta, and alluvial fan, where these features are present. The riparian zone can be subject to erosion and deposition over differing time periods and spatial scales, but if an alluvial floodplain created and maintained by river processes is present, the riparian zone is a depositional environment over time spans of at least 10^1 – 10^2 yr, and potentially 10^3 yr (Mertes et al. 1996, Wohl 2015).

The second State of the Carbon Cycle Report (SOCCR-2) will differentiate inland waters, types of wetlands, and types of terrestrial ecosystems into separate accounting units (USCCSP 2016). The conceptual model we present here takes a more holistic view of rivers and integrates into the river corridor the inland water, wetlands, and terrestrial components of the land-scape that are directly influenced by river processes.

Although we are in the early stages of understanding the details of how river form and process influence carbon dynamics, human activities clearly have altered and continue to alter most aspects of sediment and carbon dynamics within river corridors (Hoffmann et al. 2010, Regnier et al. 2013, Wohl et al. 2015). People indirectly alter carbon dynamics within river corridors by changing inputs of OC to river networks from the uplands through changes in land cover and topography. People also directly alter the ability of river corridors to process, store, and release (downstream and to the atmosphere) OC. Direct anthropogenic modifications of river corridors that influence carbon dynamics include flow regulation, channelization, artificial levees, floodplain agriculture

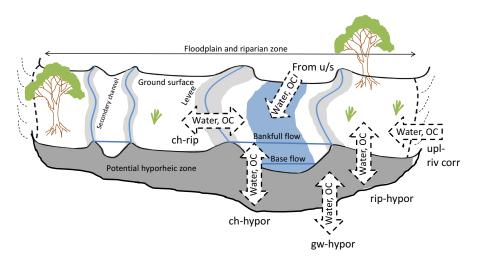


Fig. 1. Schematic illustration of the components of a river corridor referred to in this paper. The active channel includes the bankfull area of the main channel and any secondary channels present. The riparian zone includes the entire hyporheic zone, and the floodplain and riparian area. Gray shading indicates the potential extent of the hyporheic zone, only a portion of which would likely be active at any given time. Groundwater, which is not shown in this view, lies below and laterally beyond the hyporheic zone. Arrows with dashed outlines indicate primary flux directions: from upstream (from u/s), upland-river corridor (upl-riv corr), riparian-hyporheic (rip-hypor), groundwater-hyporheic (gw-hypor), channel-hyporheic (ch-hypor), and channel-riparian (ch-rip). Flux to downstream is not shown but also exists. OC, organic carbon.

and urbanization, and many other activities. Although these human-induced alterations are ubiquitous throughout river networks in temperate latitudes, they have received very little attention in the context of carbon dynamics. However, human alterations of river networks create a context in which to understand how rivers transport and store C at varying timescales.

The effects of humans on OC dynamics in river corridors are numerous and varied, and the net effect of human activities differs between channel and riparian areas. We contend that most syntheses of river carbon dynamics fail to account for (1) bi-directional fluxes between the channel and riparian zone, (2) how the processes underlying these bi-directional fluxes influence OC dynamics, and (3) how human activities have altered these processes and the resulting carbon fluxes. Severing or disrupting the linkages between the channel and riparian zone may provide a key mechanism for altering carbon storage in rivers.

Our primary objectives in this paper are to review the existing knowledge of carbon dynamics in river corridors, to develop a conceptual model of how river form and process influence carbon dynamics, and to draw on this model to infer how human activities alter carbon dynamics within river corridors. An important aspect of our review is to integrate the disparate views of river corridors and of carbon dynamics held by diverse river scientists. For example, ecologists are more likely to view rivers as active channels and to investigate OC dynamics over relatively small temporal and spatial scales (e.g., annual efflux of CO2 from a stream reach). River biogeochemists and hydrologists view rivers as continuous reactors with defined water and inorganic and organic carbon inputs and outputs, as well as biogeochemical transformations along surface and subsurface flow paths. Geomorphologists are likely to view rivers as coupled channel-floodplain systems and to investigate processes affecting OC dynamics (e.g., flux and storage of OC associated with sediment dynamics) over much larger temporal and spatial scales.

Our conceptual model of carbon dynamics within a river corridor takes the form of an OC budget that links OC pools and fluxes (Fisher and Likens 1973); shows how human activities have altered pools and fluxes; and estimates the relative magnitude of each pool, flux, and alteration. We start by briefly reviewing knowledge of the inputs, outputs, and storage terms in the OC budget. We then identify the pools, fluxes, and alterations that have been quantified and those for which relatively little is known. We show that the morphology and processes of a river corridor drive to a large extent the ability to store, transform, and transport OC, and that people are a pervasive changer of river morphology and processes that regulate these dynamics. We propose that dams create the most significant alteration of carbon dynamics within the active channel, but that alteration of riparian zones, including the lateral connectivity between the channel and riparian zone, constitutes the most significant and most highly altered aspect of carbon dynamics in river corridors. Finally, we use these assessments to discuss implications for management of river corridors in the context of carbon dynamics.

CARBON DYNAMICS IN NATURAL RIVER CORRIDORS

We conceptualize carbon dynamics in a river corridor as a carbon budget in the form of

$$\frac{dC_{S}}{dt} = C_{I} - (C_{Ogas} + C_{Oriver})$$
 (1)

in which C_S is carbon storage, t is time, C_I represents carbon inputs, C_{Ogas} represents gaseous carbon outputs, and C_{Oriver} represents fluvial outputs to downstream portions of the river corridor and the ocean (Fisher and Likens 1973).

The forms of inputs, outputs, and storage differ between channel and riparian components of the river corridor. In the active channel, inputs include OC in dissolved and particulate form (C_{IOC} in Eq. 2) from upstream, upland, groundwater, and riparian sources; CO_2 ; and net primary productivity within the channel. Outputs include emissions (C_{Ogas} in Eq. 2) and dissolved and particulate organic carbon fluxes (C_{Oriver}) downstream. Storage takes the form of downed, dead wood, particulate and dissolved organic carbon within the channel, and aquatic biomass (Fig. 2)

$$\frac{dC_{S}}{dt} = (C_{IOC} + C_{ICO_2} + C_{INPP}) - (C_{Ogas} + C_{Oriver}) \quad (2)$$

In the riparian zone, inputs include dissolved and particulate OC from upland, groundwater, and channel sources and net primary productivity within the riparian zone (Eq. 3). Outputs include plant respiration and soil respiration and OC decomposition, as well as OC and CO_2 entering the channel via surface and subsurface pathways (Eq. 3). Storage takes the form of large wood (pieces ≥ 10 cm diameter and 1 m length), smaller wood pieces, plant organic matter (litter), decomposing organic matter (duff), soil organic carbon, and aboveground biomass. Numerous exchanges occur between the channel and riparian zone (Fig. 2).

$$\frac{dC_{S}}{dt} = (C_{Iupl} + C_{Iriver} + C_{Igw} + C_{INPP}) - (C_{Ogas} + C_{Oriver})$$
(3)

In the following sections, we summarize existing knowledge of inputs, outputs, and storage, and then summarize variations in OC dynamics across space and time. We focus on organic carbon.

Inputs

Fluvial carbon inputs to river corridors reflect terrestrial sources from adjacent uplands and upstream

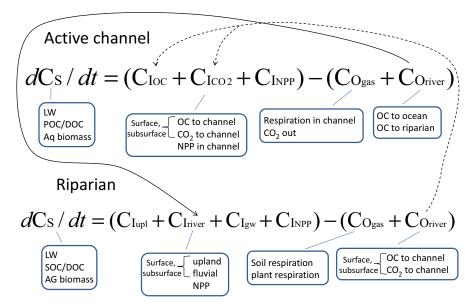


Fig. 2. Schematic illustration of the forms of carbon storage (C_S) , inputs (C_I) , and outputs (C_O) as gas or river fluxes within the active channel and riparian areas (fluxes between the two compartments indicated as dashed or solid arrows). LW, large wood; POC, particulate organic carbon; OC, organic carbon; NPP, net primary productivity; SOC, soil organic carbon; Aq, aquatic; AG, aboveground vegetation biomass; upl, upland; gw, groundwater.

portions of the river corridor, as well as longitudinal and lateral sources within the river corridor (Fig. 2). Upland carbon inputs to river corridors originate from bedrock, soils, and vegetation (Regnier et al. 2013). Fossil carbon eroded from bedrock via processes such as deep-seated landslides can be a significant source of dissolved inorganic carbon (DIC) and OC inputs to some river networks (Alin et al. 2008, Galy et al. 2008a). Soils, however, appear to be the major source of terrestrially derived OC in most river networks (Lal 2004, Fischlin et al. 2007, Hilton et al. 2008a, Bouillon et al. 2009, Gomez et al. 2010). The importance of soils as a terrestrial carbon source to river corridors is reflected in correlations across diverse river networks between fluxes of POC and suspended sediment eroded from upland soils (Galy et al. 2015), as well as progressively older POC in ecosystems carrying higher sediment loads (Marwick et al. 2015). Progressively older POC with rising discharge in Arctic rivers reflects a shift from aquatic (in situ productivity) to terrestrial sources (McClelland et al. 2016), although terrestrial in this context includes erosion of river banks, which we define as being within the river corridor. Much of the literature on POC and DOC sources to flowing water considers active channels as aquatic and all other sources as terrestrial.

Soil-derived OC can reach rivers as dissolved organic carbon (DOC), particulate organic carbon (POC), and free dissolved CO₂ from soil respiration (Sarmiento and Sundquist 1992). Episodic inputs of soil and trees associated with extreme storms that induce widespread shallow landslides can be important (Hilton et al. 2008*b*, 2011*b*, West et al. 2011, Ramos Scharrón et al. 2012,

Wohl and Ogden 2013), but remain a poorly quantified component of terrestrial carbon inputs. Significant amounts of soil-derived OC can also enter rivers each time rain falls, even in the absence of landsliding (Smith et al. 2013). Carbon inputs via groundwater can be particularly important in headwater streams (Johnson et al. 2008).

Carbon inputs also originate within river corridors as a result of in situ net primary productivity and photosynthetic carbon fixation by aquatic and riparian biota. The river continuum concept (RCC) posits that the ratio of gross primary productivity (P) to respiration (R) in shaded headwater streams is <1, where OC inputs from riparian biota are particularly important. The P:R ratio as autochthonous primary production increases downstream, but then again declines farther downstream as turbidity and depth limit primary production (Vannote et al. 1980). Data for this pattern show much higher variability than suggested by this simple model, and the continuum can be disrupted by tributary confluences (Ward and Stanford 1983). Low-order streams, however, can have much lower P:R than midsized rivers (Hall et al. 2016). In very large rivers, lateral OC inputs from riparian forests can exceed those from upstream sources (Sedell et al. 1989), particularly during the waning stages of the seasonal flood pulse (e.g., the flood-pulse concept; Junk et al. 1989) but also during other portions of the year (e.g., the river productivity model; Thorp and Delong 1994). Recent investigation of OC dynamics within large tropical rivers indicates that inputs of carbon from floodplain wetlands are major contributors to channels (Borges et al. 2015).

Isotopic signatures of DOC and POC show strong seasonal variations and indicate that the origins of these forms of OC can vary throughout a year and are largely uncoupled (Bouillon et al. 2012). On a large tropical river tributary to Africa's Congo River, for example, POC comes primarily from in situ phytoplankton production during the low-flow season, whereas topsoil and forest litter are primary POC contributors during high flows, and DOC isotopic signatures suggest at least three distinct sources that vary in importance seasonally (Bouillon et al. 2012). DOC composition in large Arctic rivers suggests substantial contributions of aged DOC from mosses and peat bogs during low flow and greater inputs of more recently produced DOC during high flow (Amon et al. 2012).

Whatever the source of the external inputs to a river, microbial processing within the river can alter the balance of externally and internally sourced OC within the river. Thawing of permafrost along Arctic rivers mobilizes ancient DOC into headwater streams, for example, but the DOC exported from the mouth of large Arctic rivers is predominantly modern because this ancient DOC is rapidly mineralized by microbes (Mann et al. 2015, Spencer et al. 2015).

Outputs

Organic carbon can leave a river corridor via gaseous emissions, losses to groundwater, or downstream transport as DOC or POC (Fig. 2). Most rivers are heterotrophic, indicating that they respire more OC than they produce. This flux can be globally significant; in the conterminous United States, about 30% of the total CO₂ emissions from rivers result from respiration of OC (Hotchkiss et al. 2015). Recent estimates of global annual fluxes of carbon suggest that gaseous emissions (1.8 Pg C/yr) from active river channels are approximately double those of downstream transport to the ocean (0.9 Pg C/yr; Battin et al. 2009, Aufdenkampe et al. 2011, Raymond et al. 2013). Estimated gaseous emissions are from active channels and lakes (Battin et al. 2008, Tranvik et al. 2009, Butman and Raymond 2011, Hotchkiss et al. 2015), however, and do not account for emissions from riverine wetlands (Abril et al. 2014) or from terrestrial components in riparian zones and floodplains. Although a substantial portion of OC produced within river corridors appears to be returned to the atmosphere via decomposition within inland waters (Cole et al. 1994), recent quantification of carbon sinks within Amazonian floodplain lakes suggests that accumulation rates may exceed rates of evasion and degassing from channels and floodplain wetlands (Sanders et al. 2017).

Remobilization of stored sediment within the river corridor can also result in loss of mineral-associated OC from mineralization during transport (Bouillon et al. 2009). Mineralization of OC during river transport elevates concentrations of dissolved CO₂, facilitating outgassing to the atmosphere (Handique 2015). Increased

supply of OC from dissolved or particulate constituents may increase the rate of mineralization through priming of previously carbon-limited sediments (Fontaine et al. 2007).

Nutrients, particularly N and P, also influence OC dynamics within rivers. Excess nutrients stimulate the production of algal biomass and associated OC sequestration, thus allowing lakes to be sinks and not sources for CO₂ (Pacheco et al. 2013). Conversely, excess nutrients can also stimulate OC loss through increased microbial processing of POC that releases CO₂ to the atmosphere and to downstream transport of OC (Rosemond et al. 2015).

Estimates of global rates of CO₂ evasion from inland waters are a function of three variables: the relative concentrations of CO₂ in the water and the atmosphere; the global surface area of inland waters; and the gas transfer velocity, which varies as a function of turbulence in the surface water and water temperature (Aufdenkampe et al. 2011). The source of inland water CO2 is still not known with certainty (Raymond et al. 2013), but appears to be mostly CO₂ from groundwater and a smaller fraction of CO₂ derived from instream metabolism (Hotchkiss et al. 2015). The concentration of CO₂ in water does not correlate strongly with climate or landscape variables, but Raymond et al. (2013) note that estimates include substantial uncertainty because of lack of understanding of factors such as how gas transfer velocity changes with increasing discharge, in steep catchments, and in higher latitudes.

Organic carbon outputs to oceans are partitioned between DOC and POC. Global and regional syntheses differ on the relative magnitude of DOC and POC fluxes, for which limited measurements are available. Meybeck (2003) estimated a global river DOC flux of 0.2 Pg/yr, roughly double the estimated POC flux of 0.1 Pg/yr, whereas Gordeev and Kravchishina (2009) estimate that annual fluxes of DOC (0.02 Pg) are five times higher than POC (0.004 Pg) in Eurasian Arctic rivers. In contrast, Zhang et al. (2009) estimate similar global proportions at 55% DOC and 45% POC. Quantitative estimates of POC export focus almost entirely on finer POC and neglect large wood, which likely constitutes an important contemporary component of OC outputs from some drainages such as the Mackenzie River (Kindle 1921; Kramer et al., in press), and was probably a greater output from most forested river drainages prior to widespread deforestation. Both DOC and POC fluxes reflect the magnitude of upland and riparian inputs vs. gaseous emissions, biotic uptake, and OC storage along river corridors. All of these factors can vary substantially through time, making it difficult to accurately quantify OC outputs.

Storage

Organic carbon is stored within river corridors in six forms: downed, dead wood in the channel and riparian

zone (LW); POC within the channel; biomass of aquatic biota; soil organic carbon (SOC), including litter and duff layers in the riparian zone; above- and belowground biomass of riparian vegetation; and DOC in water temporarily stored in the channel and riparian zone. Remarkably little is known of the sources (upland vs. riverine) or quantities of OC stored in these diverse forms or of how these quantities vary within a river network or among networks (Raymond and Bauer 2001, Downing et al. 2008). Instream obstructions such as logjams (Beckman and Wohl 2014) and beaver dams (Naiman et al. 1986, Johnston 2014) can promote storage of locally significant quantities of POC within the channel. Carbon storage within the river corridor, however, appears to occur predominantly in riparian SOC and LW in smaller rivers (Naiman et al. 1987, Wohl et al. 2012b), and the importance of SOC storage is likely to be true for larger rivers with extensive floodplains as well (e.g., Robertson et al. 1999, Hoffmann et al. 2009, Hanberry et al. 2015). Quantities of OC per unit area stored in riparian soils are disproportionately large relative to upland soils in temperate latitudes (Ricker et al. 2013, 2014). Although the details of where most OC is stored (small vs. large rivers, floodplains vs. deltas, high latitudes vs. temperate or low latitudes) remain poorly constrained (Sutfin et al. 2016), recent work suggests that floodplain lakes and wetlands are likely to store disproportionately large stocks of OC (Sanders et al. 2017).

The fate of terrestrially derived carbon in river corridor sediment depends in part on exchanges between sediment and the atmosphere via chemical weathering of inorganic substances, OC composition, riverine fluxes of sediment and OC, and decomposition by biota. Seemingly labile forms of SOC can be protected from decomposition by speciation and adsorption to mineral facies or protection within soil aggregates (Doetterl et al. 2015, 2016). An analogous process occurs in freshwater ecosystems where organo-mineral complexes can lower mineralization rates of carbon (Hunter et al. 2016). Sediment inputs and burial in floodplains remove carbon from oxygen and from greater microbial activity at the surface. However, mixing and introduction of fresh OC can facilitate the metabolism of more recalcitrant carbon at depth via the priming effect (Fontaine et al. 2007, Doetterl et al. 2015, 2016), in which labile DOC can stimulate decomposition of more refractory OC (Guenet et al. 2010).

Relatively little is also known of the influence of gross primary production (GPP) on large-scale OC cycling and transport. The implicit assumption is that riverine GPP is mineralized in place, and relatively quickly, so that there is no net effect on the OC cycle. That assumption may be mostly correct, but existing syntheses have not considered, for example, that some of the OC storage may be from algal-derived OC in rivers and lakes, and that there can be substantial export of algal-derived OC to oceans. In addition, GPP represents a labile OC source to rivers, and this labile C source may stimulate

the mineralization of OC via the priming effect (Sampere et al. 2011; Hotchkiss et al. 2014), although this finding is not universal (Catalán et al. 2015).

Battin et al. (2009) estimated that 0.6 Pg C/yr are buried in sediments associated with inland waters, but this estimate is based primarily on quantification of reservoir storage because channel-riparian linkages and the potential for riparian OC storage were not considered in this calculation. Other estimates of burial rate in freshwater sediments (lakes, reservoirs, rivers) vary between 0.2 and 1.6 Pg C/yr, with the large range in estimated values reflecting the limited field data available to constrain this process at the global scale (Regnier et al. 2013). In particular, knowledge of OC storage in the form of riparian SOC is limited, although regionally focused studies (e.g., Wohl et al. 2012b, Ricker et al. 2013, Hanberry et al. 2015, Ricker and Lockaby 2015, Omengo et al. 2016) suggest that cumulative storage of SOC in river corridors could be a significant component of global carbon dynamics. Working in an 83 km² forested watershed in Rocky Mountain National Park, Colorado, for example, Wohl et al. (2012b) estimated that the riparian portion of river corridors stored ~25% of the total OC within the watershed, despite occupying less than 1% of watershed area.

Variation in OC dynamics across space and time

The absolute and relative magnitudes of the diverse forms of inputs, outputs, and storage of OC appear to vary substantially across space and through time. Although relatively little is known of these variations, we summarize that understanding here as a means of informing our conceptualization of variations in OC dynamics within and among river networks.

Variations in OC dynamics can reflect differences in geology. Geology includes bedrock lithology and tectonic regime, as these influence topography and hillslope stability, thickness, and OC content of soils, and rates of soil erosion and delivery to river corridors (Galy et al. 2008a, b). Small, mountainous river networks, for example, typically deliver fossil POC derived from bedrock and POC from soils relatively efficiently via downstream transport to the ocean (Leithold et al. 2006, 2015, Hilton et al. 2011a, Hovius et al. 2011), and the rate of POC transport increases rapidly with discharge (Hilton et al. 2008b, 2012, Hatten et al. 2012, Jeung et al. 2012, Goñi et al. 2013, Lloret et al. 2013, Jung et al. 2014). Steep catchments have fewer storage zones for sediment and associated SOC in both uplands and river corridors (Schumm 1977, Montgomery and Buffington 1997). Organic carbon produced within river corridors is more likely to dominate carbon exports to the ocean in large, lowland rivers with extensive floodplains (Leithold et al. 2006, Galy et al. 2008b). Large, lowland floodplains both promote deposition of POC derived from upland terrestrial sources and enhance net primary productivity within the river corridor relative to steep, narrow rivers in mountainous terrain. In addition to originating predominantly

from different sources between river catchments, POC exports vary over several orders of magnitude between river catchments. High-standing oceanic islands in the southwest Pacific, for example, contribute disproportionately more to river exports relative to their proportion of global land mass (Lyons et al. 2002).

Analogous to POC, the primary controls on variation in DOC fluxes are runoff, slope, land cover, and SOC content (Lauerwald et al. 2012). DOC annual yields, however, vary over less than three orders of magnitude among diverse river catchments, whereas POC exhibits greater variability.

Location within a river network can also strongly influence several aspects of OC dynamics, such as primary productivity or residence time of water, which influences DOC supply and removal (Casas-Ruiz et al. 2017). For example, the percentage of CO₂ emissions from aquatic metabolism increases with river size; terrestrially derived CO₂ is most important in small streams (e.g., Hotchkiss et al. 2015).

Variations within a river network can also reflect reach-scale channel and river corridor geometry as this variation in morphology influences storage and residence time of sediment and organic matter. Portions of mountainous river networks with relatively wide, lowgradient river corridor geometry store much greater volumes of SOC per unit length of river than steep, narrow river corridor segments, for example, and the wide river corridor segments may account for the majority of total OC storage within the network (e.g., Wohl et al. 2012b, Sutfin 2015). Floodplains also have a greater overall community respiration than confined river segments (Bellmore and Baxter 2014). These downstream variations in relation to river corridor geometry are better approximated by conceptual models such as geomorphic process domains (Montgomery 1999) or the riverine ecosystem synthesis (Thorp et al. 2006), which emphasize patch mosaics rather than the continuous longitudinal gradients of the RCC.

There are likely also differences in the magnitudes of OC fluxes among climates. Climate influences precipitation and temperature regimes that govern primary productivity of uplands and river corridors. Precipitation influences river flow and groundwater that influence fluxes of OC to and within river corridors, including water temperature and CO₂ emissions from rivers (Raymond et al. 2013). Climate also influences precipitation-induced landslides and associated delivery of fossil OC, SOC, and upland biomass to river corridors.

Regional studies indicate strong correlations between CO₂ evasion and annual precipitation. Measured concentrations of pCO₂ in rivers typically range from 1000 to >12,000 ppm and are typically higher in tropical waters than in temperate waters (Aufdenkampe et al. 2011). The greatest CO₂ efflux occurs in Southeast Asia, Amazonia, and the eastern edge of East Asia (Rasera et al. 2013, Raymond et al. 2013). Mechanistic understanding of why river networks in these tropical regions might contribute

disproportionately to global fluxes is limited. The high values, however, likely reflect high terrestrial productivity, rapid decomposition rates linked to high moisture content and temperatures, and subsequent respiration in floodplains and wetlands and substantial hydrologic fluxes from uplands to river corridors in tropical regions (Butman and Raymond 2011).

Conversely, river corridors of the high latitudes and high altitudes are likely to dominate OC storage (Sutfin et al. 2016) and to have very long residence times of POC (Hilton et al. 2015, Marwick et al. 2015), not least because the largest of these rivers have extensive floodplain lowlands with enormous quantities of SOC stored in permafrost (Schuur et al. 2015). Although these rivers contribute substantial POC fluxes to the Arctic Ocean (McClelland et al. 2016), tropical rivers dominate global OC fluxes to oceans. Meybeck (1993) estimated that rivers in the humid tropics account for 66% of the total mass of riverine DOC and 49% of POC transport to oceans. The specific estimates have changed with time, but subsequent studies support the dominant role of rivers in the humid tropics. Tropical rivers commonly have high rates of CO₂ efflux (Aufdenkampe et al. 2011, Rasera et al. 2013, Raymond et al. 2013), as well as DOC and POC transport (Meybeck 1993, Jahnke 1996). Although floodplains along tropical rivers can store substantial quantities of OC in soil and wetland or lake sediment (Sanders et al. 2017), the residence time of this OC appears to be shorter than in floodplains of the temperate latitudes (Omengo et al. 2016).

Variations in OC storage and flux in river networks through time can be driven by processes operating at vastly different time scales. Short-term disturbances such as severe storms (Hilton et al. 2008b, West et al. 2011, Wohl and Ogden 2013), floods (Sutfin 2015), or wildfires influence inputs of OC to the river corridor, storage of OC within the river corridor, or transport downstream over periods of days to a few years. Storms and floods, in particular, typically result in greater DOC, POC, and LW inputs to rivers, which can be stored in depositional areas within the river corridor, or exported downstream to a reservoir or the ocean (Rathburn et al., in press). More sustained changes such as droughts or land use can influence OC dynamics over periods of 10^1 – 10^2 yr (e.g., Worrall and Burt 2004). Anthropogenically enhanced fluxes of OC from the Mississippi River basin, for example, which is heavily agricultural and urbanized, now dominate the OC balance within the river basin (Raymond et al. 2008). Longer-term changes in OC dynamics are associated with processes operating over 10^2 – 10^4 yr, such as continuing tectonic uplift (Galy et al. 2008a, 2015) or changing climate (Trumbore 1993, Smittenberg et al. 2006).

Finally, drainage area can influence outputs of OC, but does not appear to have consistent effects on storage. Measured fluxes of DOC, POC, and TOC (total OC, represented by the sum of DOC and POC for a river) strongly relate to drainage area simply because larger

drainage areas have higher water flux (Fig. 3A–C). More interesting is that the standardized major axis regression (Warton et al. 2006) slopes of the relationships for DOC and total export are ~0.95, showing allometric scaling in which export increases slightly more slowly than drainage area (Fig. 3A, C). This finding is evidence for lower

fluxes of DOC in big rivers, possibly due to removal along the river network, although with a sample size of approximately 100, this finding is preliminary. Sedimentation flux loosely relates to drainage area, with the slope insignificantly different than 1 (Fig. 3D). The smaller number of published values of riparian OC stocks in soil

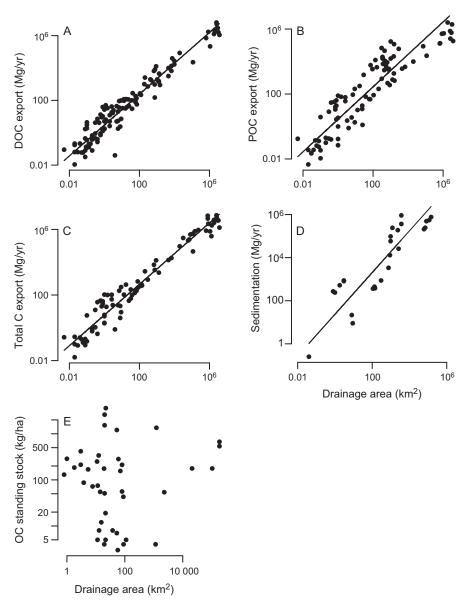


Fig. 3. Scaling of organic carbon fluxes and stock with river drainage area (see Appendix S1: Table S2 for relevant data). Lines are shown for standardized major axis regression (SMA) where the confidence interval did not exceed 1 (Warton et al. 2006). If slope is significantly less than 1, flux or stock decreases more slowly than increasing drainage area. If slope is significantly greater than 1, flux or stock decrease at a faster rate than drainage area. A slope of 0 indicates no relationship between flux or stock and drainage area. (A) The regression between dissolved organic carbon (DOC) flux and drainage area exhibits a slope < 1 (slope = 0.95, 0.91 < CI < 1.00, sample size = 123, P = 0.053, $r^2 = 0.93$). (B) The regression between particulate organic carbon (POC) flux and drainage area exhibits a slope not significantly different than 1 (slope = 1.00, 0.93 < CI < 1.10, sample size = 91, P = 0.83, $r^2 = 0.83$). (C) The regression between total organic carbon (TOC = DOC + POC) and drainage area exhibits a slope < 1 (slope = 0.94, 0.89 < CI < 0.98, sample size = 85, P = 0.009, $r^2 = 0.95$). (D) The regression between sedimentation rate of OC within the riparian zone and drainage area exhibits a slope not significantly different than 1 (slope = 0.98, 0.78 < CI < 1.18, P = 0.75, $r^2 = 0.78$). (E) Stock of OC in the form of SOC and large wood within the riparian zone for diverse rivers has no significant relationship to drainage area and is highly variable (OLS regression, P = 0.54 ($r^2 = 0.01$)).

and downed dead wood yield highly variable values and do not relate to drainage area (Fig. 3E). The lack of relationships between riparian storage and drainage area is not surprising, given the site-specific controls on river corridor geometry and sedimentation rate. These controls can vary substantially and non-systematically downstream within a river network and among river networks.

VARIATIONS IN OC DYNAMICS AMONG RIVER SEGMENTS

We posit strong differences in the relative importance of different forms of inputs, outputs, and storage for natural (or relatively undisturbed) rivers in the temperate, tropical, and high latitudes (Table 1). Because Table 1 is organized largely around expected, rather than demonstrated, patterns of OC dynamics in river corridors, we evaluated only very broad categories of river size, river corridor geometry, and climate. Headwater rivers in Table 1 are first- to third-order rivers (Strahler 1952), whereas large rivers are fourth order or higher. We categorize river corridor geometry with respect to lateral confinement. Confined river corridors have a floodplain and riparian corridor less than twice as wide as the active channel (Livers and Wohl 2015). Unconfined river corridors are

Table 1. Most important components of OC storage, inputs, and outputs (A) within a river corridor type or at the reach scale and (B) among river corridor types or at the network scale.

River corridor geometry	dC_S/dt temperate	dC _S /dt tropical	dC_S/dt high latitude	$C_{\rm I}$	$C_{ m Ogas}$	C_{Oriver}
(A)						
Active channel						
Headwater _{con} †	POC	POC	POC	OC to channel		POC/DOC‡ downstream
				CO2 to channel		
Headwater _{uncon}	LW	POC	LW	OC to channel		POC/DOC to floodplain
	POC			CO2 to channel		POC/DOC downstream
Large rivercon	POC	POC	POC	OC to channel		POC/DOC downstream
				CO2 to channel		
Large river _{uncon}	LW	POC	LW	OC to channel		POC/DOC to floodplain
	POC					POC/DOC downstream
Riparian						
Headwatercon	LW	LW	LW	Upland	Soil respiration	OC to channel
					Plant respiration	CO ₂ to channel
Headwater _{uncon}	SOC	SOC	SOC	NPP	Soil respiration	OC to channel
		AGB§		Fluvial	Plant respiration	CO ₂ to channel
Large river _{con}	SOC	SOC	SOC	Upland	Soil respiration	OC to channel
	LW	LW		•	Plant respiration	CO ₂ to channel
Large river _{uncon}	SOC	SOC	SOC	NPP	Soil respiration	OC to channel
		AGB		Fluvial	Plant respiration	CO ₂ to channel
(B)						
Active channel						
Headwater _{con}				OC to channel	CO2 from channel	
Headwater _{unco}	LW POC	POC		OC to channel	CO ₂ from channel	POC/DOC to floodplain
Large river _{con}						
Large river _{uncon}	POC	POC	LW	OC to channel		POC/DOC to floodplain
C ancon	Ag bio	Aq bio				•
Riparian	•	•				
Headwatercon						
Headwater _{uncon}	SOC	SOC	SOC	NPP		OC to channel
2.10011		AGB		Fluvial		
Large river _{con}						
Large river _{uncon}	SOC	SOC	SOC	NPP	Soil respiration	OC to channel
S uncon		AGB		Fluvial	Plant respiration	

Notes: For the active channel, variables considered are storage (LW, POC, aquatic biota), inputs (OC to channel, CO₂ to channel, NPP in channel), outputs (CO₂ from channel, POC to floodplain, POC downstream). For the riparian zone, variables considered are storage (SOC, LW, AGB), inputs (NPP, upland, fluvial), and outputs (soil respiration, plant respiration, OC to channel, CO₂ to channel).

[†] Subscript con refers to confined, subscript uncon refers to unconfined.

[†] The relative magnitude of POC to DOC is uncertain based on existing studies

[§] AGB is aboveground biomass

more than twice as wide as the active channel. Channel gradient typically correlates with lateral confinement, such that confined river corridors are steeper than unconfined river corridors (Livers and Wohl 2015). These differences in river form and associated processes can profoundly affect primary productivity, CO₂ emissions, lateral fluxes from uplands and riparian zones, and storage of OC in river corridors (e.g., Thorp et al. 2006, Wohl et al. 2012*b*, Bellmore and Baxter 2014, Sutfin 2015).

We categorize climate as temperate, tropical, and high latitude (60° N or S and higher). Although we recognize the substantial diversity within each of these broad categories, we assume that tropical climates have warm temperatures, large average annual rainfall, high rates of biological productivity and organic matter decay, high rates of river transport for OC and river emissions of CO₂, and minimal OC storage in soils outside of wetlands (Donato et al. 2011, Wohl et al. 2012a, Raymond et al. 2013, Dommain et al. 2014). We assume that climate in temperate latitudes is typically associated with cooler temperatures, moderate average annual precipitation, lower rates of biological productivity and organic matter decay, moderate rates of river OC transport and emissions, and greater OC storage in soils (Meybeck 1993, Raymond et al. 2013, Hanberry et al. 2015). (Our assumptions about tropical and temperate latitudes ignore the existence of drylands and the seasonal tropics, which we acknowledge can function quite differently than rivers in wetter regions, but we exclude drylands and the seasonal tropics here for the sake of brevity and simplicity.) We assume that high-latitude climates correspond to cold temperatures, low average annual precipitation, low rates of biological productivity and very slow organic matter decay, moderate rates of river transport and emissions, and substantial OC storage in soils (Raymond et al. 2013, Hugelius et al. 2014).

The relative importance assigned to different forms of OC inputs, outputs, and storage in Table 1 represents our interpretation of the existing literature and our personal observations of river corridors in diverse environments. These rankings reflect relative magnitude of the OC pool or flux, rather than magnitude per area. Table 1A lists the most important OC pool or flux within a river corridor type and represents a reach-scale emphasis. Within confined headwater river segments, for example, we assume that POC dominates OC storage in the active channel compared to LW or aquatic biomass. Table 1B lists the most important OC pools or fluxes among river corridor types and represents a networkscale emphasis showing which types of river segments or reaches contribute most to different components of the OC budget for the entire river network. In temperate latitudes, for example, we assume that OC pools will be greatest in LW and POC in unconfined headwaters and POM and aquatic biomass in unconfined large river segments. We cannot identify a single dominant OC pool or flux within or among river corridor types for many of the cells in Table 1 because of either variation among

individual river networks that limits generalization or because of lack of place-based data from which to generalize. Thus, these blank cells emphasize some of the more glaring data gaps that limit our ability to predict riverine OC dynamics at the global scale.

Among the trends apparent in Table 1 is that laterally confined river corridor segments, whether in the upper or lower part of a drainage network, have minimal potential for OC storage. Confined river corridor segments commonly have a steep channel with high transport capacity, as well as minimal development of an alluvial floodplain and associated storage of SOC and riparian biomass (Wohl et al. 2012b, Bellmore and Baxter 2014, Sutfin 2015, Sutfin et al. 2016).

Storage across regions, in terms of relative storage within different river segments within a network, among river networks within a region, and among river networks in different regions, is very poorly constrained by existing research. However, we expect differences in the relative importance of various forms of OC storage among regions, as reflected in the three columns for OC storage in Table 1. We expect LW to be more important in temperate and high latitudes than in the tropics, for example, because of the extremely high decay rates for downed wood in the tropics (Harmon et al. 1986; Lininger et al., *in press*). Conversely, we expect aboveground biomass to be a particularly important OC pool in tropical riparian zones as a result of high terrestrial net primary productivity (Ruesch and Gibbs 2008).

Carbon inputs to the active channel come primarily from uplands in headwater river segments and from upstream river segments and the riparian zone in large rivers. Relative contributions between upstream and riparian sources depend on the position of the river segment in the network and on the length of the river. In confined large river segments, for example, most OC enters the active channel from upstream, whereas at the cumulative, network scale, lateral or riparian OC sources are likely the most important input in large river segments (e.g., Meyer et al. 1997).

Carbon outputs from the active channel occur as CO₂ emissions and as DOC and POC fluxes downstream and to the riparian zone. We expect CO₂ emissions to be particularly important in headwater portions of a river network relative to emissions from downstream portions (Butman and Raymond 2011, Crawford et al. 2015). Downstream DOC and POC fluxes dominate river outputs in confined river segments, whereas we expect lateral fluxes to the riparian zone to be more important where floodplains are present. Carbon outputs from the riparian zone include soil and plant respiration and lateral fluxes of CO₂ and OC to the active channel. We expect soil and plant respiration to be equally important in most riparian zones, with the greatest output from the floodplain of large rivers. We expect lateral fluxes of OC to be particularly important in river segments with floodplains.

In populating Table 1, we concluded that there is no evidence to suggest differences in the relative importance

of various forms of OC inputs and outputs among and within river corridor types among tropical, temperate, and high-latitude rivers. Consequently, the three right-hand columns of Table 1 are the same for all regions. The values of fluxes likely vary in magnitudes among regions, but we have no basis for assuming that the relative magnitudes among river corridor types differ between regions. Table 1 does not address where in a river network each term is most important (e.g., OC to channel in unconfined headwaters vs. unconfined large rivers), because information from river-segment studies is not yet sufficient to support scaling to entire river networks.

We conceptualize our tabular model graphically in Fig. 4A and B, which correspond to Table 1A and B, respectively. Fig. 4 illustrates, in terms of the OC budget, those components that we consider to be most important at the reach scale within different types of river corridor segments (Fig. 4A) and those components and river corridor segments that we consider to be most important at the network scale (Fig. 4B). In particular, Fig. 4B emphasizes the relative importance of low gradient, laterally unconfined river segments within river networks.

SOURCE-SINK DYNAMICS OF OC IN RIVER CORRIDORS

Within a watershed's carbon budget, river corridors can be either net sources of OC to the atmosphere or ocean, or sinks of OC that enters sediments in the active channel or riparian zone. For the entire river corridor to be a sink, two criteria need to be met: net ecosystem productivity (NEP) plus import must be positive and exceed export such that dC_S/dt is positive. This scenario is unlikely for the active channel component of a river corridor, but is more likely in the riparian component given positive NEP in the terrestrial portion of the riparian zone and storage of upland or river-transported sediment that is likely to be at or close to saturation with respect to soil moisture.

The balance between source and sink terms varies through space and time in a manner that reflects the terms in Eq. 1. Fluxes of OC become particularly important in this context as does the manner in which a river is defined (i.e., active channel vs. river corridor). Fluxes are controlled by numerous factors, including decomposition, rates of sediment deposition vs. erosion, and conversion of POC and DOC to CO₂ (Fig. 5).

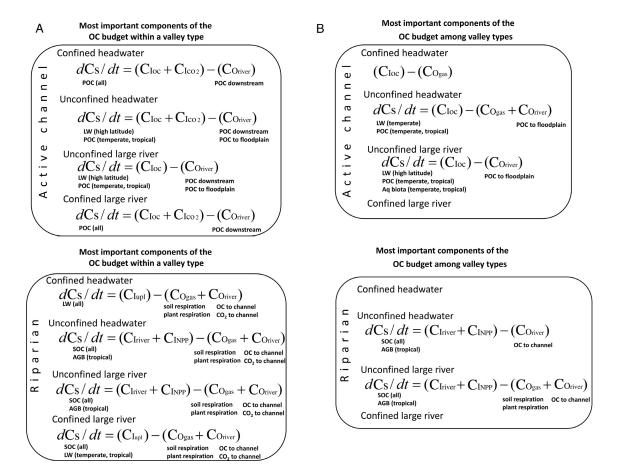


Fig. 4. Summary of Table 1 in terms of the OC budget equation from Fig. 2. (A) The OC budget equation is modified to include only the most important components of OC storage, inputs, and outputs within a valley type or at the reach scale. (B) The OC budget equation is modified to include only the most important components of OC storage, inputs, and outputs among valley types or at the network scale.

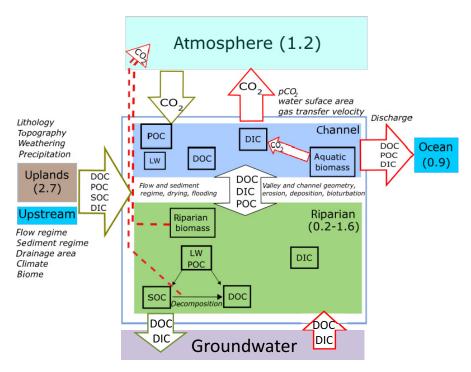


Fig. 5. Schematic illustration of carbon dynamics in river corridors. Boxes are C reservoirs; arrows are C exchanges or fluxes (red indicates C outputs, green indicates C inputs); text in italic typeface lists factors that mediate fluxes. We have quantified fluxes where possible, using estimates from existing syntheses, but the large number of unquantified fluxes in this figure reflects data gaps. The numbers in parentheses are fluxes in Pg C/yr from uplands, into the atmosphere, into the ocean, and into the geosphere, as estimated by Aufdenkampe et al. (2011: Fig. 3).

Consequently, the relative magnitude of the pools and fluxes illustrated in Fig. 5 can vary within a river network (e.g., from headwaters to large floodplain rivers, or from confined to unconfined river corridor segments; Table 1; e.g., Thorp et al. 2006, Wohl et al. 2012*a*, *b*, Bellmore and Baxter 2014) and among river networks.

At a fundamental level, river segments in which most of the OC received from terrestrial sources is released as CO₂ to the atmosphere or efficiently transported to the ocean as DOC and POC are primarily OC sources. River segments that retain substantial amounts of OC in some pool (e.g., riparian sediment or biomass) along the river corridor are primarily OC sinks.

CO₂ emissions and OC transport are high within the active channel (Butman et al. 2016). CO₂ emissions and DOC and POC export are particularly high in the tropics, likely in association with high rates of terrestrial productivity and rapid erosion (e.g., Hilton et al. 2008b, 2012). The inferred mechanisms underlying observed high emissions and river fluxes of OC emphasize the strong influence of climate on upland biomass, SOC, and transfer of OC to river corridors. In this sense, the neutral pipe model of rivers has some basis in that factors external to the river corridor exert a primary influence on both terrestrial OC inputs and riverine OC outputs. OC storage, however, occurs primarily within riparian areas of unconfined river segments, and as such depends on fluxes of water and sediment between the

channel and riparian area, as well as NPP and soil development within the riparian area. Riparian areas retain OC and function as biogeochemical reactors that facilitate the speciation, transformation, and opportunities for both long-term storage of carbon and mineralization to the atmosphere. Consequently, it is with respect to riparian storage and biogeochemical processing of OC in aboveground biomass, LW, and SOC that river corridors are least likely to be adequately conceptualized as neutral pipes.

Examples from small, headwater streams in bedrock canyons and large alluvial rivers illustrate the importance of channel-riparian fluxes on OC storage. Relatively small (third order) rivers of the Colorado Front Range in unconfined river corridor segments with oldgrowth conifer forest, numerous logjams, and multiple secondary channels store ~250 Mg C/ha in SOC as measured down to the bedrock contact. Otherwise analogous unconfined river corridor segments with wet meadows and a single channel store ~500 Mg C/ha in SOC (Sutfin 2015). The higher values of SOC storage in single-channel river corridor segments may reflect continuously saturated soils (which retard mineralization) as a result of groundwater inputs, but also longer residence time of riparian sediment as a result of different magnitude and frequency of fluxes between the channel and riparian area. An example from a very large floodplain river illustrates how changes in the characteristics of the riparian zone influence OC storage. Working in the alluvial river corridor of the lower Mississippi River valley in the United States, Hanberry et al. (2015) estimated that under contemporary agriculture the river corridor currently stores only about 2% of the inferred historical OC stock of 234 Tg associated with natural bottomland riparian forests.

A key point is that channels are connected to riparian zones and the exchange of OC from the channel to the riparian zone represents potential for storage of transported OC not included in either the neutral or active pipe model of OC dynamics in freshwater. Although changes in channel geometry and flow regime can alter carbon dynamics and especially short-term storage within a channel, as reviewed in the next section in the context of human activities, we conceptualize channels as primarily sources of OC to the atmosphere and ocean. In contrast, we conceptualize riparian areas as primarily sinks of OC over varying timescales and varying proportions of terrestrial and fluvial OC inputs.

Integrating channels and riparian areas, Yue et al. (2012) developed a framework for using sediment delivery ratio (ratio of sediment yield to the total eroded mass) and soil humin content in SOC to delineate river basins as CO2 sources or sinks. Soil exchanges CO2 with the atmosphere via chemical weathering of inorganic substances, OC formation, and decomposition by biota, all of which occur during soil erosion, re-deposition, and transport. Yue et al. (2012) propose that a river basin acts as an erosion-induced CO₂ sink with respect to the atmosphere when soil humin content is large relative to sediment delivery ratio, and as a source when sediment delivery ratio is large relative to soil humin content. Based on world average levels of these values, Yue et al. (2012) suggest that rivers cumulatively act as a global carbon sink. Again, this finding highlights shortcomings of the neutral and active pipe models of rivers, and illustrates the utility of both conceptualizing OC dynamics within river corridors in which active channels and riparian zones are coupled entities and conceptualizing river basins in source-sink terms.

HUMAN ALTERATIONS OF CARBON DYNAMICS IN RIVER CORRIDORS

Human activities affect every aspect of the carbon cycle. Although human alterations of the nitrogen cycle in freshwater environments have received more attention in the scientific literature (e.g., Rockström et al. 2009, Steffen et al. 2011) and it is widely acknowledged that human activities dominate global nitrogen fluxes (Howarth et al. 2002, Fenn et al. 2003), alterations of the carbon cycle in freshwater environments may be of similar magnitude.

Literature examining planetary sustainability with respect to the global carbon cycle focuses on fluxes of CO₂ into the atmosphere, equilibrium between the atmosphere and ocean and resulting effects such as ocean

acidification, and terrestrial carbon sequestration in biomass and soils (e.g., Berhe et al. 2007, Battin et al. 2009, Aufdenkampe et al. 2011, Raymond et al. 2013). Studies examining altered OC fluxes from freshwaters at the regional to global scale either focus on carbon dioxide emissions (e.g., Butman and Raymond 2011, Raymond et al. 2013, Butman et al. 2016) or, when examining downstream fluxes to the ocean, ignore OC storage along river corridors except in lakes and reservoirs (e.g., Regnier et al. 2013). We contend that consideration of global carbon dynamics in the context of human alterations and sustainability should also include channelriparian fluxes and storage of OC in riparian areas. Here, we discuss the multiple facets of human alterations that affect regional to global scale carbon dynamics within river corridors and consequently OC fluxes to the atmosphere, the oceans, and the geosphere.

Table 2 lists the primary human alterations of organic carbon dynamics, which we subdivide into upland alterations occurring outside of the river corridor and river alterations that involve modifications of flow regime, channel geometry, riparian areas, and riparian—channel connectivity within the river.

Indirect effects: upland alterations of carbon dynamics

Upland alterations affect carbon inputs to river corridors (the C_I term in Eq. 1). Pervasive examples include: changing sediment yield to river corridors by changing topography and land use; altered fire regimes; and climate change (Fig. 6A).

Changing topography and land use.—Alteration of topography can either increase or decrease OC inputs to river corridors. Topography is altered to facilitate construction of transportation corridors and to make the land surface more suitable for agriculture and urbanization. Humans now move more sediment than all geologic processes combined (Hooke 2000), and alterations of topography and land cover have caused an estimated additional 2.3 billion MT sediment input to rivers worldwide (Syvitski et al. 2005). An extreme example is wholesale changes to upland topography via mining (Ross et al. 2016). Reconfiguration of the land surface can increase POC fluxes to river corridors via bedrock and soil erosion if the reconfiguration results in decreased hillslope stability (e.g., roads increasing landslides; Larsen and Parks 1997). Increased terrestrial POC inputs to rivers can increase downstream transport of POC, increase burial within floodplain and delta sediments, or increase aquatic respiration and CO2 emissions. Reconfiguration of the land surface can also decrease POC fluxes to river corridors if the alteration of topography results in highly stabilized, urban environments with minimal bedrock and soil erosion and reduced terrestrial vegetation biomass.

Increased sediment yield to river corridors increases SOC inputs, whereas decreased sediment yield decreases

TABLE 2. Human alterations of organic carbon dynamics in river corridors.

Human activity	Likely effect on OC in river corridors	Sample references	
Upland alterations			
Changing topography	(+) OC inputs unless land surface is urbanized	Larsen and Parks (1997), Madej et al. (2013)	
Clearing native land cover	(±) OC inputs; (–) inputs from reduced terrestrial C pools, but (+) inputs from exacerbated upland erosion	Madej (2010)	
Crops	(±) OC inputs; (+) from enhanced soil erosion, (-) from lower NPP and depleted SOC; (+) N, P inputs and (+) CO ₂ emissions	Davidson and Ackerman (1993), Robertson et al. (1999), Quinton et al. (2010)	
Grazing	(+) OC inputs; Δ SOC is context-dependent (grazing tends to increase in SOC in C ₄ - dominated grasslands, but decrease SOC in C ₃ -dominated grasslands); intense grazing increases erosion	Trimble and Mendel (1995), Reeder et al. (2004), McSherry and Ritchie (2013)	
Timber harvest and associated roads	(-) OC wood inputs, (+) OC sediment inputs	Madej (2010), Madej et al. (2013)	
Urbanization	(+) DOC and DIC inputs from soil erosion and wastewater	Daniel et al. (2002), Sickman et al. (2007)	
Groundwater withdrawal	(–) DOC inputs	Barlow and Leake (2012)	
Fire	(±) OC inputs; (+) from increased upland erosion of SOC and charcoal; (-) from decreased LW and POM inputs, and from emission of CO ₂	Pierce et al. (2004), Hicke et al. (2012)	
Climate change	(±) OC inputs; (+) from greater upland productivity or greater soil erosion, (-) from greater oxidation of soil organic matter in uplands: (±) OC storage in river corridors; (+) from increased flooding and saturated riparian soils, (-) from decreased flooding and riparian productivity	Davidson and Janssens (2006)	
River corridor alterations			
Burial of river segments	(-) OC inputs and storage	Elmore and Kaushal (2008)	
Floodplain drainage	(-) OC storage on floodplain, increases oxidation and CO₂ emissions	Armentano (1980), Duffkova et al. (2005), Hanberry et al. (2015), Knox et al. (2015)	
Construction of levees	(±) OC storage on floodplain; (–) fluvial inputs, can (+) NPP and SOC by reducing fluvial erosion and deposition	Bullinger-Weber et al. (2014), Hatten et al. (2014), Rieger et al. (2014); Sutfin (2015)	
Channelization (dredging, straightening, bank stabilization)	 (-) OC storage in channel and floodplain because of decreased channel-floodplain connectivity and river inputs of organic matter 	Samaritani et al. (2011)	
Log floating	(–) OC storage in channel and floodplain	Schama (1996), Comiti (2012), Wohl (2014), Nilsson et al. (2005 <i>a</i>)	
Removal of instream wood	(-) OC storage in channel and floodplain	Beckman and Wohl (2014), Wohl (2014)	
Removal of native riparian vegetation	(±) OC inputs from floodplain and storage on floodplain in SOC and aboveground biomass, depending on what replaces native vegetation	DeLong and Brusven (1994), Giese (2001), Roberts and Bilby (2009), Hanberry et al. (2015)	
Removal of beaver	(-) OC inputs and storage	Wohl (2013)	
Mining within the river corridor	(±) OC storage; (–) at mining site as riparian vegetation and sediment are removed, (+) at downstream sites as sedimentation increases	Hilmes and Wohl (1995), James (1999)	
Flow regulation (dams, diversions)	(-) OC storage on floodplain; (+) OC storage in reservoir sediment; (+) CO ₂ + CH ₄ emissions from some reservoirs, (-) CO ₂ emissions from pools at low-head dams	Tranvik et al. (2009), Raymond et al. (2013), Regnier et al. (2013), Crawford et al. (2016)	
Changes in aquatic biota	uncertain and likely highly variable between sites	Schmitz et al. (2014)	
Changes in water chemistry (excess N, P)	(+) CO ₂ emissions	Rosemond et al. (2015)	
Delta engineering and indirect effects of flow regulation	(–) OC storage in channel and floodplain	Syvitski and Kettner (2011), Canuel et al. (2012)	

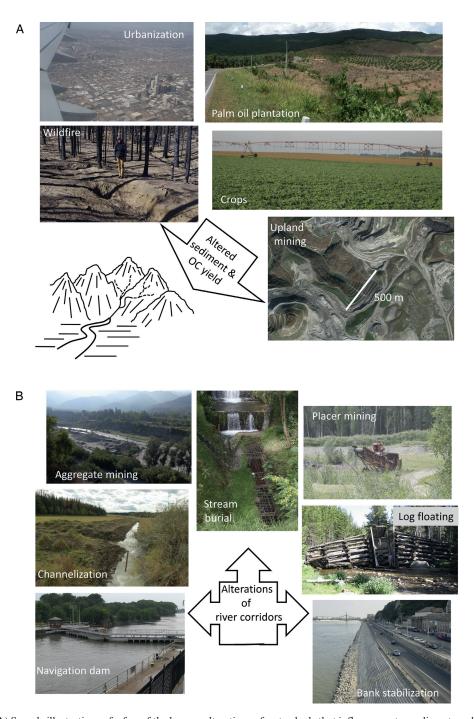


Fig. 6. (A) Sample illustrations of a few of the human alterations of watersheds that influence water, sediment, and organic carbon yields to river corridors. Illustrated here (clockwise, starting at upper left) is urbanization in Arizona, USA; a palm oil plantation in Borneo; mountaintop mining in West Virginia, USA; and burned forest in Colorado, USA. (B) Sample illustrations of human alterations within river corridors. Illustrated here (clockwise, from upper left) are aggregate mining within a channel in Chile; burial of a headwater stream entering an urban area in Colombia; placer mining in Alaska, USA; historical splash dam used in log floating in Wyoming, USA; bank stabilization along the Danube at Budapest, Hungary; a navigation lock and dam along the Mississippi River in Iowa, USA; and channelization of a small stream in Canada.

these inputs. Increases in sediment yield to river corridors resulting from changes in upland topography and land cover are particularly important because the flux of

OC mobilized into river corridors is greater than the ability of most river corridors to stabilize the OC via mechanisms such as organo-mineral complexation or burial in anoxic environments (Aufdenkampe et al. 2011). Rates of erosion, delivery, mixing of fresh mineral surfaces with organic matter, and storage within river corridors likely control watershed- to global-scale OC fluxes (Aufdenkampe et al. 2011). Whether humaninduced soil erosion creates a net source or sink of OC in river corridors remains an open question (e.g., Hoffmann et al. 2013), the answer to which partly depends on the characteristics of the river corridors into which the eroded soil is transported. If the eroded soil is transported to the ocean or deposited in a riparian zone in which the SOC is oxidized and released to the atmosphere, human-induced soil erosion can create a net source of OC within river corridors. If the eroded soil is deposited in a reservoir or in saturated or rapidly aggrading floodplain soils that limit oxidation and respiration, the OC may be stored within the river corridor (Van Oost et al. 2012).

Replacement of native vegetation with forest plantations, crops, or grazing lands can reduce or increase OC fluxes to river corridors, but generally has the overall effect of increasing net OC flux to river corridors. Reduction of OC fluxes to river corridors due to clearing of native vegetation can occur via at least three mechanisms. First, comparisons of diverse forests subject only to natural disturbances vs. managed forests or other human-managed land cover indicate lower soil OC and total ecosystem OC pools in human-altered vegetation communities (e.g., Jaramillo et al. 2003). Similarly, tilled soils are typically depleted in SOC relative to untilled soils (Davidson and Ackerman 1993). Second, removal of OC in harvested products such as timber represents a decreased upland pool available for transport into river corridors. If the harvested products are mature trees, OC is lost directly via removal of the tree and indirectly via loss of large wood that could be recruited to the river corridor, where large wood can effectively trap finer organic matter in transport and facilitate overbank deposition of organic matter (Madej 2010, Beckman and Wohl 2014). Third, replacement of native vegetation with fertilized crops and grazing animals can result in greater nitrogen and phosphorus fluxes into river corridors. Excess nutrients can stimulate production of algae and increase mineralization of terrestrially derived OC (Rosemond et al. 2015). The magnitude of each of these effects can vary through time, particularly if land use extent or intensity within a watershed varies through time. However, we propose that the increased soil erosion and flux of SOC associated with removal of native upland vegetation communities is likely to be more important than reduced terrestrial OC pools, so that removal of native vegetation is likely to increase net OC flux to river corridors.

Replacement of native vegetation with urban areas likely reduces OC fluxes to river corridors by substantially decreasing organic matter inputs and sediment yield. For example, capping the land with impervious surfaces can greatly reduce water infiltration, disrupting the linkage between surface water and groundwater recharge and thus reducing fluxes of SOC into stream networks. Urban areas can also contribute substantial quantities of N and P to river corridors (Green et al. 2004, Divers et al. 2013), with effects similar to those described above for agricultural lands. DIC inputs from urban areas can be much higher than those from a naturally vegetated landscape (Barnes and Raymond 2009). OC inputs from urban areas via wastewater are likely to be relatively low in high-income countries, but could be greater in areas with minimal sewage treatment. Urban areas also represent a concentration of food, water, and other resources from a much larger area than lies within the urban boundary (Wackernagel et al. 2006, Sabo et al. 2010) and runoff and infiltration from this concentration can influence river corridors.

Upland mining, by disrupting surface vegetation and creating point sources in the form of tailings piles, can substantially increase sediment yield (e.g., Marcus et al. 2001), and associated fluxes of fossil OC and SOC, to river corridors. As with other forms of increased sediment yield to river corridors, whether this creates a net OC flux from, or storage within, the river corridor depends on whether the sediment is exported from or stored within the river corridor. Mountain top removal, in particular, creates such enormous increases in sediment yield to rivers that low-order streams are either buried under mine spoil or can experience substantial aggradation (Bernhardt and Palmer 2011, Jaeger 2015). Mining can also substantially alter the chemistry of surface water (Palmer et al. 2010). Mining and the resulting presence of heavy metals can influence complex speciation, pH, redox state, adsorption of organic matter to mineral facies, and the decomposition of OC (Brezonik and Arnold 2011).

Human-induced alterations of the chemistry of surface and subsurface runoff entering river corridors is diverse and difficult to generalize. Alterations include enhanced concentrations of N that indirectly influence OC dynamics within river corridors (Hill 1996, Devito et al. 2000, Hill et al. 2000). A more direct alteration of OC comes from increased C loading in sewage water from humans and domestic animals (Borges et al. 2005, Regnier et al. 2013).

Lowering regional water tables may decrease OC storage in uplands and inputs to river corridors. Groundwater withdrawal for agricultural irrigation, industrial manufacturing, and municipal consumption has lowered water tables in diverse regions of the world. Groundwater can contain substantial quantities of DOC and DIC (Hem 1985, Cai 2003), so lowered water tables that result in reduced groundwater fluxes into channels and floodplains can also reduce OC inputs to river corridors. In addition, reducing the spatial extent and depth of saturated soils in uplands can result in oxidation of organic matter in the soil and lower SOC content (Armentano 1980, Duffkova et al. 2005, Trumbore and Czimczik 2008).

Altered fire regimes.—Altered fire regimes influence OC dynamics in several ways that differ through time, making it difficult to generalize their net effect. Alterations of natural fire regime in uplands, either through fire suppression or enhanced fires during initial clearing of native vegetation, can significantly change terrestrial inputs of OC to river corridors, as well as inputs of large wood. The occurrence of a fire is commonly followed by an increase in water and sediment inputs to the river corridor because of decreased infiltration capacity and slope stability (Moody and Martin 2001, Shakesby and Doerr 2006). Inputs of charcoal to river corridors also typically increase for at least a year or two (Meyer et al. 1992), but inputs of organic matter may decrease for many years following a fire as litter and duff layers gradually reform (Kane et al. 2007). Inputs of large wood can decline for several decades following a fire (Bragg 2000), but this pattern largely depends on fire severity. Research from diverse environments suggests that at least some portion of the increased sediment mobilized from burned uplands can be deposited in floodplains and alluvial fans for periods of 10^2-10^3 yr (e.g., Oguchi 1997, Pierce et al. 2004), which can bury and store charcoal moving with the sediment. Fires also release substantial quantities of upland OC as CO2 to the atmosphere (Hicke et al. 2012), which would otherwise eventually enter river networks.

Climate change.—The potential effects of climate change on OC dynamics within any river network will depend on the specific scenario of climate change likely to occur in the river network, as well as the existing characteristics of the network. Changes in temperature and precipitation will influence OC dynamics through changes in upland sediment yields, vegetation, land use, and human consumptive demand for water, especially for regions in which climate change will create warmer and/or drier conditions. The most immediate effects of changes in temperature and precipitation are likely to occur within the dynamics of soil OM and metabolism.

The net effect of climate warming on soil carbon remains uncertain due to complex interactions between soil burial, soil warming, and soil moisture content (Davidson and Janssens 2006). Organic matter persists in soil if it is physically isolated from decomposition by microbes via incorporation into soil aggregates or sorption into mineral (or other organic) surfaces (Trumbore and Czimczik 2008). Similarly, buried soil horizons and organic-rich lenses at depth are removed from the biologically active surface layer (Gurwick et al. 2008). Resistance to metabolism as a result of depth within the profile can be largely influenced by changes in temperature and soil moisture regime.

Carbon stored belowground could be transferred to the atmosphere by a warming-induced acceleration of its decomposition. On the other hand, increases of plantderived carbon inputs to soils could exceed increases in decomposition. Part of the uncertainty arises from the complexity of soil OC, which includes thousands of different compounds, each with its own kinetic properties (Davidson and Janssens 2006). Uncertainty also arises from environmental constraints that affect temperature sensitivity of decomposition. Temperature also affects OC by influencing the rates and mechanisms of POC production (Canuel et al. 2012) and the occurrence of freezing that can reduce POC decomposition (Trumbore and Czimczik 2008) or thawing of frozen ground that can release aged OC from riparian and upland soils to rivers for microbial processing (Spencer et al. 2015).

Soil moisture regime constitutes an environmental constraint on SOC that is subject to changes in climate. Flooding reduces oxygen diffusion to decomposition reaction sites, causing fewer degradative enzymatic pathways (Davidson and Janssens 2006). Anticipated decrease in annual average snowpack and earlier timing of snowmelt (Bates et al. 2008) are likely to result in drier conditions in riparian ecosystems, which could influence metabolism of SOC. Drying of otherwise saturated soils could increase decomposition. Poorly understood feedbacks are likely to occur among the numerous variables and processes influencing C dynamics. Rates of OC burial in northern lakes, for example, have increased significantly during the past century as a result of the combined effects of increased temperature, atmospheric nitrogen deposition, and other factors (Heathcote et al. 2015).

In summary, alterations of portions of a drainage basin outside of the river corridor may either increase or decrease OC inputs to river networks and the magnitude of these effects may be greater in smaller watersheds (Stackpoole et al. 2016). However, model simulations suggest that river transport of carbon has increased by approximately 20% since 1750 (Regnier et al. 2013) and measured data support this estimate (e.g., Meybeck 1982, Milliman and Meade 1983, Richey 2004). This increase is attributed primarily to deforestation and intensive agriculture that have increased sediment yield and OC inputs to rivers (Raymond et al. 2008), but it is worth noting that little attention has been given to how alterations of river corridors influence the ability of rivers to outgas or bury these increased OC inputs. For example, Regnier et al. (2013) assume that CO2 outgassing and OC burial in river corridors scale linearly with the estimated increase in soil-derived carbon exported to oceans, but note that, although this assumption may be reasonable for the air-water flux, the change in carbon burial is likely to be more complex. Most of the attention to carbon burial thus far has focused on natural lakes and reservoirs (e.g., Mulholland and Elwood 1982, Cole et al. 2007), rather than on riparian zones. Limited studies indicate that SOC storage in riparian corridors of very small channels increased substantially following regional changes in land cover (e.g., Ricker et al. 2012), whereas SOC storage decreased substantially in the corridor of large alluvial rivers that have been affected by direct alterations in the form of floodplain drainage, flow regulation, and riparian deforestation (e.g., Hanberry et al. 2015).

Direct effects: alterations of river corridors

River alterations by humans involve changing channel and floodplain process and form in ways that can influence the terms C_S, C_{Ogas}, and C_{Oriver} in Eq. 1. Basic alterations in channel and river corridor geometry include alteration of channel form via burial of river segments, mining in the river corridor, channelization (dredging, straightening, bank stabilization), log floating, and removal of instream wood; alteration of hydrologic conditions, including floodplain drainage, construction of levees, and flow regulation; alteration of aquatic and riparian biota, including removal of beaver (Castor canadensis in North America and Castor fiber in Eurasia) and removal of native riparian vegetation; alterations of water chemistry; and alterations of delta form and process, all of which can substantially influence OC dynamics (Fig. 6B). The remainder of this section briefly reviews the effects of each category of alteration.

Altered channel form.—Burial of river segments reduces OC inputs and storage. Burial occurs when channels are placed into pipes or otherwise completely covered and disconnected from floodplains and adjacent uplands. Burial primarily occurs in relatively small channels and has been undertaken in rural and urban environments (Elmore and Kaushal 2008, Roy et al. 2009). Channel burial lowers rates of ecosystem processes such as nitrogen cycling (Beaulieu et al. 2015) and metabolism (Pennino et al. 2014). The first- and second-order channels that constitute most total channel length within most river networks (Downing et al. 2012) are important for processing and uptake of nutrients (Alexander et al. 2007), as well as CO₂ emissions of terrestrially derived OC and CO₂ (Hotchkiss et al. 2015).

An extreme example of channel burial occurs during mountain top mining for coal in the Central Appalachian Mountains, USA. Here, waste rock from surface mines is deposited in river valleys, directly burying thousands of kilometers of headwater streams (Lindberg et al. 2011), along with associated indirect effects of vegetation removal, loss of carbon-rich topsoil, increased erosion, and altered hydrologic flow paths between uplands, river corridors, and river channels (Palmer et al. 2010). All of these effects have myriad consequences (reviewed above) for OC dynamics within river corridors.

Other mining activities within the river corridor also alter OC dynamics by changing sediment flux and riparian vegetation, with a net effect that varies between different portions of an affected river. Mining within channels and riparian areas can be focused on metals disseminated among alluvial sediment (placer mining) or on alluvial sediment to be used for construction aggregate. Either type of mining can remove riparian vegetation and mobilize channel and riparian sediment (Hilmes and Wohl 1995, James 1999), thus decreasing OC storage at the mining site. Increased sediment deposition downstream, however, can result in increased OC storage.

Channelization, undertaken to increase the downstream conveyance of a channel, also reduces OC inputs and storage. Among the secondary effects of channelization are decreased overbank flows, which reduces the OC content of floodplains (Noe and Hupp 2005) by drying floodplain soils and increasing organic matter oxidation; and reduced physical complexity of the active channel. Physical complexity in the form of channelmargin irregularities (bank embayments, pools and riffles, bars) and secondary channels creates areas of flow separation and at least temporary retention of fine sediment and organic matter (Livers and Wohl 2015). Organic matter that is retained in areas of flow separation is more available for uptake by stream biota (Battin et al. 2008) and is more likely to be buried within river sediments and stored for periods of up to thousands of years.

Log floating, which primarily reduces OC storage in the channel and floodplain, is the floating of timber to downstream locations for milling. In commercial operations, hundreds of thousands of logs were floated down a river each year, and even the smallest headwater channels in a network have been used for log floating. Historical records of commercial log floating in Europe date to the Middle Ages (Schama 1996), and commercial log floating continued into the 20th century in much of Europe and North America (Comiti 2012, Wohl 2014). Like channelization, log floating simplifies and homogenizes channel geometry. Direct modifications undertaken to facilitate the downstream movement of logs include blocking off secondary channels and removing obstructions such as natural logjams. Channel geometry is also simplified through the erosion of channel boundaries associated with building and then dynamiting temporary splash dams or the abrasive action of enormous quantities of wood moving downstream (Young et al. 1994, Miller 2010, Ruffing et al. 2015). The net effect of simplifying and homogenizing channel geometry is to reduce OC storage in the channel and floodplain, although some logs that were commercially floated became saturated and were buried in the streambed.

Wood removal has decreased OC storage in channels and riparian zones. Removal of naturally occurring downed wood in channels and riparian areas has been undertaken for centuries to improve navigation, reduce overbank flooding, enhance fish passage, and remove obstacles during log floating. Large wood can be recruited to a river corridor from uplands or from riparian forests. Channels from headwater streams to major rivers such as the Mississippi have been altered through the removal of hundreds of millions of logs (Wohl 2014). Where large wood is present as dispersed individual pieces or as logiams, the wood increases hydraulic roughness (Shields and Smith 1992, Wilcox et al. 2011) and creates zones of flow separation and backwaters that retain sediment and particulate organic matter (Bilby and Likens 1980, Brooks et al. 2006, Beckman and Wohl 2014). Large wood creates diverse habitat for

organisms that can process organic matter, and the wood enhances hyporheic exchange (Hester and Doyle 2008, Sawyer et al. 2011), transient storage (Day 2015), and associated biological processing of carbon. Logiams, in particular, can enhance overbank flooding, channel avulsion, and formation of secondary channels (O'Connor et al. 2003, Sear et al. 2010, Wohl 2011, Collins et al. 2012) and promote channel-riparian connectivity. Wood thus both enhances retention of POC in channel and riparian areas, and itself serves as a source of POC and DOC as it decays (Ward and Aumen 1986). Wood that reaches the ocean also serves a vital function in nearshore and even offshore marine ecosystems by providing nutrients and habitat for diverse invertebrates and vertebrates (Gonor et al. 1988). Removal of large wood from the channel and riparian zone results in loss of channel floodplain connectivity, channel complexity, and retention of OC in the form of POC and large wood (Beckman and Wohl 2014).

Altered hydrologic conditions.—Floodplain drainage reduces the OC content of floodplain sediments by decreasing soil moisture levels and facilitating oxidation of organic matter in the soil (Armentano 1980, Duffkova et al. 2005, Trumbore and Czimczik 2008). Floodplain drainage is commonly undertaken to facilitate agriculture or urbanization in the floodplain. Construction of levees reduces the OC content of floodplain sediments by laterally disconnecting the floodplain from the active channel (Bullinger-Weber et al. 2014), causing the river corridor to behave more like a confined river corridor segment. Levees limit overbank flows and the associated inputs of river-transported organic matter as well as causing drying and oxidation of floodplain sediments. Reduced overbank flows can also alter riparian vegetation, lowering inputs of organic matter from riparian vegetation. However, where precipitation or groundwater inputs are sufficient to support riparian forests or wet meadows, litterfall and downed wood may result in higher concentrations of riparian SOC from net primary production in leveed floodplains than SOC concentrations in portions of the floodplain subject to fluvial erosion and deposition (Rieger et al. 2014, Sutfin 2015). Finally, floodplain drainage can reduce or eliminate riparian groundwater fluxes into channels. Groundwater contains DOC, so reduced groundwater inputs represent another loss of OC fluxes within river corridors.

Flow regulation alters OC dynamics within river corridors in a variety of ways that remain poorly understood. These include (1) reduction of peak flows and associated reduction of lateral connectivity between channel and floodplain, (2) storage of particulate organic matter in reservoirs (Tranvik et al. 2009), (3) outgassing of CO₂ and, to a lesser extent, CH₄ (Tranvik et al. 2009, Bastviken et al. 2011, Fearnside and Pueyo 2012, Deemer et al. 2016) from reservoirs, which have a higher partial pressure of CO₂ during approximately the initial 15 yr after impoundment, but are then comparable to natural

lakes (Raymond et al. 2013), (4) generation and export of OC in tailwater reaches downstream from dams (Ulseth and Hall 2015), and (5) downstream alteration of water chemistry and temperature, thus affecting internal carbon cycling. With regard to reduced lateral connectivity, Hatten et al. (2014) found that sources of organic matter in the riparian zone changed in relation to lateral connectivity. In hydrologically connected sites, sediment OC from eroded upland soils accumulated in riparian areas in a pattern correlated with distance to and discharge of the channel. Hydrologically disconnected sites had lower rates of C deposition and transfers of C within the riparian zone, and groundwater dynamics were more important than proximity to the channel.

Construction of dams and reservoirs has strong direct effects on OC dynamics in river corridors at the global scale. For example, even though OC river fluxes to the ocean show a net increase, much of the SOC eroded from uplands is buried in reservoir sediments (Smith et al. 2001). OC retention within reservoirs correlates strongly with water retention time. The net effect of reservoirs is to reduce transport and oxidation rates of allochthonous river OC and to increase removal of atmospheric CO₂ by primary producers such as algae and macrophytes: both of these processes cause reservoir sediments to serve as an OC sink (Mulholland and Elwood 1982). For example, Butman et al. (2016) estimate that total CO2 efflux from U.S. lake and reservoir surfaces is 16 Tg C/yr, whereas total OC burial is 20.6 Tg C/yr (relative to an estimated total flux to oceans of 41.5 Tg C/yr). However, they note that the high level of uncertainty associated with burial of OC and emissions of CO2 from lakes and reservoirs highlights a gap in our understanding of the processes involved.

Altered aquatic and riparian biota.—Alteration of aquatic and riparian animal assemblages can also influence OC dynamics, although these activities are not usually considered in large-scale carbon budgets (Schmitz et al. 2014). The net effect of these alterations on OC budgets depends on the specific scenario. Animals can directly alter C cycling via calcification and bioturbation and indirectly through food web effects and engineering. Calcifiers such as mollusks release a mole of CO₂ for each mole of carbonate fixed into their shells. This physiological process can release large amounts of CO2 (Chauvaud et al. 2003), although these CO₂ fluxes are likely small relative to daily variation in gross metabolic fluxes (Hotchkiss and Hall 2010). Variation in food web structure via a trophic cascade can alter CO₂ emissions from lakes by controlling rates of CO₂ fixation (Schindler et al. 1997). Animal bioturbation of benthic sediments can also influence the amount of sediment OC released to the water column to be decomposed and released to the atmosphere (Schmitz et al. 2014). Bioturbation by fish can increase organic sediment transport and the spatial scale of carbon cycling in streams (Taylor et al. 2006). Emerging aquatic insects can return OC to terrestrial environments (Scharnweber et al. 2014) and migrating fish can import marine-derived OC to river ecosystems (Bilby et al. 1995). In riparian environments, herbivores such as moose can indirectly control rates of primary productivity and heterotrophic respiration through browsing. Moose can also influence soil microbial decomposition via their dung and by altering the nutrient content of plant litter (Pastor et al. 1988). Studies in boreal forests indicate that high densities of moose can cause declines in CO₂ uptake by vegetation and storage in plants and soil, as well as influencing humidity, soil temperature and moisture, and fire regime (Schmitz et al. 2003). Within aquatic habitats, moose can stimulate nutrient fluxes through bioturbation of sediments, with potential effects on OC cycling (Bump et al. 2016). The net effect on OC dynamics of altering aquatic and riparian animal assemblages thus depends on the species affected and the intensity of the alteration, but such alterations have received relatively little attention in terms of their potential net effects on OC dynamics within river corridors.

Of all vertebrates, beaver have the largest effects on riverine C cycling. Removal of beaver from river corridors, undertaken as part of commercial harvest of beaver fur and to reduce flooding associated with beaver dams, has the net effect of decreasing OC inputs and storage by diminishing the floodplain wetlands associated with beaver ponds and the wet meadow complexes known as beaver meadows (Naiman et al. 1988). Numerous studies have shown that removal of beaver decreases attenuation of downstream fluxes of water, fine sediment, organic matter, and nutrients, and associated decreases in storage of OC in floodplain sediment and riparian vegetation (e.g., Naiman et al. 1988, Wohl 2013, Johnston 2014).

Removal of native riparian vegetation can influence OC dynamics in diverse ways. Biomass, rates of NPP, litterfall, and SOC typically correlate with type and age of riparian vegetation (DeLong and Brusven 1994, Giese 2001, Roberts and Bilby 2009). Removal of native vegetation can reduce inputs of POC in the form of downed wood and finer organic matter, analogous to the effect described for removal of native upland vegetation, although the magnitude of this effect depends on what type of land cover replaces the native vegetation. Removal of native riparian vegetation can also reduce hydraulic roughness of the floodplain and its ability to trap and store POC transported by overbank flows (e.g., Burkham 1976). Again, the magnitude of this effect depends on what replaces the native vegetation. In some cases, exotic riparian vegetation can create greater hydraulic roughness (e.g., Griffin et al. 2005) and sediment storage (e.g., Graf 1978). Replacement of native riparian vegetation by exotic species can also result in alterations of the composition and function of the soil microbial community (Wolfe and Klironomos 2005), and

presumably in associated soil carbon dynamics, although such alterations do not yet appear to have been explored in scientific literature.

Altered water chemistry.—Alteration of water chemistry in the form of increased levels of nitrogen and phosphorus can alter fixation of DIC and mineralization of OC, with varying effects on OC fluxes. Excess nutrients have the well-known effect of stimulating gross primary production of C-rich algal biomass (Schindler et al. 1997, Conley et al. 2009). Most research focuses on the water quality problems associated with algal blooms; only recently have ecologists studied the effect on OC cycling. Findings are that eutrophication can increase burial of OC in lakes (Heathcote and Downing 2012, Anderson et al. 2014) and cause lakes to be OC sinks rather than sources of CO₂ (Pacheco et al. 2013). Excess nutrients will have the opposite effect on ecosystems that receive mainly terrestrial inputs. Recent work shows enhanced OC loss via increased POC mineralization through microbial processing, with increased CO₂ emissions and lowered standing stocks of OC in headwater streams (Rosemond et al. 2015). At the watershed scale, it is possible that increased nitrogen deposition has increased DOC yield in the Hudson River, USA (Findlay 2005).

Altered delta form and process.—Alteration of delta form and process likely has the net effect of reducing OC storage in delta sediments. Alterations of deltas include construction of levees, channelization, and removal of native vegetation on the delta, as well as the downstream effects of flow regulation (e.g., reduced sediment inputs, altered magnitude and timing of flow, altered nutrient inputs; Canuel et al. 2012). Deltas are naturally dynamic environments subject to regular inputs of sediment and organic matter from distributary channels on the delta, and to reworking of sediment via waves on the lake or ocean in which the delta is formed. Deltas form a potentially enormous but poorly quantified reservoir of OC in the form of sediment and, to a lesser extent, vegetation. Flow regulation has reduced regular inputs of sediment and organic matter from upstream, while processes such as compaction, subsidence, and wave erosion continue, resulting in accelerated erosion of deltas around the world (Syvitski et al. 2009, Syvitski and Kettner 2011).

In summary, although enhanced hillslope instability and soil erosion add OC to river corridors, the net effect of most human activities, with the exception of reservoir construction, appears to be that of reducing the ability of river corridors to store OC within biota and sediment (Fig. 7). This increase in inputs and decrease in storage is reflected in increased OC fluxes to oceans (Regnier et al. 2013). Human-induced soil erosion has increased sediment transport by rivers by an estimated 2.3 ± 0.6 Pg/yr, but reduced the flux of sediment to coastlines by $\sim 1.4 \pm 0.3$ Pg/yr because of sediment storage within reservoirs (Syvitski et al. 2005). These numbers suggest that POC fluxes to the ocean have decreased. Estimates

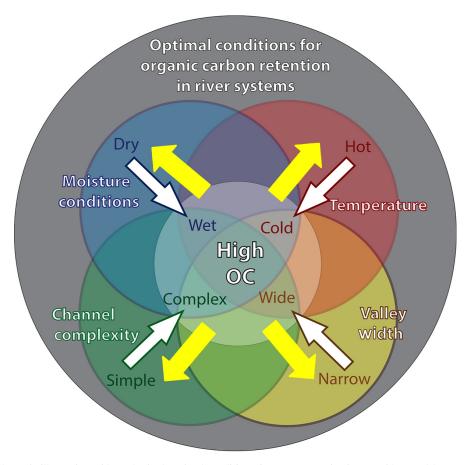


Fig. 7. Schematic illustration of hypothesized optimal conditions for OC storage in river corridors and human alterations of optimal conditions. White arrows indicate the gradient toward optimal conditions. Each component illustrated here can be influenced by numerous variables: soil moisture, for example, can be influenced by climate, flow regime, channel–floodplain connectivity, valley geometry, and so forth. Yellow arrows indicate the net effect of human activities, which tend to decrease the width and physical complexity of river corridors, reduce soil moisture and, indirectly, increase soil temperature via reduced shading and climate warming. Modified from Sutfin et al. (2016: Fig. 5).

of increased OC fluxes to oceans therefore likely represent primarily increased DOC fluxes. The net effect of human activities is therefore to effectively convert river corridors from sinks for OC in riparian soils and biomass to OC sources to the atmosphere and ocean. Engineering of river corridor and channel geometry and flow regulation reduce storage capacity in channels and, most importantly, in floodplains and deltas. Riparian sediment storage is a particularly critical component of OC dynamics. Only 5-25% of eroded sediment reaches the ocean. The great majority of sediment is stored in uplands, along river corridors, and in other inland freshwaters (lakes, reservoirs; Aufdenkampe et al. 2011), so that the cumulative global effect of reduced storage capacity along river corridors outside of reservoirs is likely to substantially influence global C dynamics. Human alterations of river corridors are also changing the spatial arrangement of OC storage within river networks, by increasing storage capacity within reservoirs but reducing the potentially much larger riparian storage outside of reservoirs.

Another way to consider human alterations of C dynamics in river corridors is to recognize that, as with global N dynamics, human activities now likely constitute the dominant influence on inputs, storage, and outputs of OC within river corridors. Although limited studies appear to have specifically evaluated historical changes in OC content of nearshore marine sediments in the context of land use, for example, there is evidence that land uses associated with soil erosion and the presence of reservoirs can dominate OC delivered to and preserved in continental margin sediment (Sampere et al. 2011).

Net effects of human activities on source–sink dynamics of OC in river corridors

The net effects of human activities are to increase OC inputs to rivers and decrease OC storage along the riparian portion of river corridors outside of reservoirs. The result of increased inputs and decreased storage is increased DOC fluxes to the ocean and CO₂ emissions to

the atmosphere (Fig. 8). Regnier et al. (2013) estimate that, of the 1.0 Pg C/yr entering inland waters as a result of human activities, ~0.4 Pg C/yr is emitted back to the atmosphere as CO₂ and ~0.5 Pg C/yr is sequestered in sediments of river corridors (including reservoirs), estuaries, and coastal waters. Regnier et al. (2013) note that the latter number is poorly constrained, and other syntheses have proposed different numbers: Raymond et al. (2013), for example, estimate a global evasion rate of 2.1 Pg C/ yr. The details of where these human-induced changes in OC fluxes are greatest remain relatively poorly known, but we can infer likely trends based on available compilations of relevant human activities. For example, changes in land use/land cover associated with agriculture and urbanization have been greatest within the temperate latitudes and the tropics outside of sub-Saharan Africa and parts of the Amazon and Congo basins (Ramankutty and Foley 1999, Pielke et al. 2011). Elsewhere, only Antarctica and boreal/tundra areas in Siberia and North America have avoided extensive changes.

The most recent global syntheses of dams (Nilsson et al. 2005b, Lehner et al. 2011, Grill et al. 2015) indicate that most of the world's major river basins have at least some degree of flow regulation. Only a few basins, predominantly at high latitudes, are minimally impacted by dams. This synthesis does not include flow diversions,

which would increase the extent of river basins in which flow has been directly altered. Within the United States, for example, only about 2% of the 5.6 million kilometers of rivers is unaffected by dams, and these dams impound a volume of water approximately equal to the annual continental runoff (Graf 2001). Globally, impounded waters cover approximately 337,000 km² (Downing et al. 2006). In addition to altering downstream flow regime and channel-riparian connectivity, dams create reservoirs that can store OC in sediment and release CO₂ and CH₄ to the atmosphere. Although OC burial in reservoir sediments has increased by 300% whereas CO2 emissions from inland waters have increased by 180%, CO₂ emissions are still estimated to represent a flux nearly twice that of OC burial (Regnier et al. 2013). The combined effects of increased sediment storage within reservoirs (Syvitski et al. 2005) and removal of LW likely have resulted in reduced POC fluxes to the ocean, although DOC fluxes may have increased (Regnier et al. 2013).

An important question in relation to OC storage in reservoir sediment is how human-induced changes in water bodies within river networks have changed the magnitude and distribution of stored OC. Annual burial rates of OC and IC tend to be highest in small, eutrophic lakes and impoundments and the concentration of OC in sediment is greatest in lakes with a low ratio of

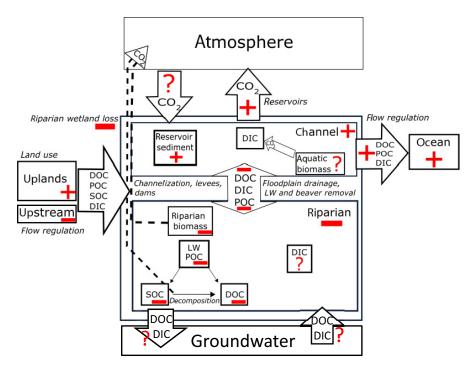


Fig. 8. A modified version of Fig. 5, highlighting the hypothesized net effects of human alterations as red plus (positive) or minus (negative) symbols or, where unknown, as red question marks. Human alteration of aquatic biomass, for example, includes increases in biomass associated with eutrophication and decreases associated with overfishing and alteration of channels in ways that minimize biomass (e.g., dredging). Consequently, the net global effect of human activities on aquatic biomass is unknown. Text in italic typeface lists the primary human activities resulting in the changes in carbon dynamics. The net effect of human activities is likely to be an increase in OC stored within reservoirs in channels and inundated riparian areas, and a decrease in OC stored in unimpounded riparian zones.

watershed to impoundment area (Downing et al. 2008). This finding suggests that small water bodies may be disproportionately important with respect to OC storage relative to their size. Severe reductions of beaver populations throughout Eurasia and North America have significantly reduced OC storage in beaver ponds, which have the potential for substantial OC concentrations in pond sediments and adjacent wet riparian areas (Naiman et al. 1986, 1988, Wohl 2013, Johnston 2014). On the other hand, the loss of beaver has been somewhat offset by construction of numerous small agricultural impoundments. These have greater sedimentation rates than natural lakes (Downing et al. 2008) and have presumably increased sediment storage of OC in river networks. Comparisons of natural and artificial impoundments indicate that reservoirs accumulate OC faster than natural lakes, although natural lakes cumulatively store a much greater volume of OC than reservoirs because the lakes are much older (Cole et al. 2007). The magnitude of OC once stored in small, natural beaver ponds and riparian wetlands vs. the magnitude of OC currently stored in small, agricultural impoundments and large reservoirs remains unknown.

Unlike impoundments, no global or even continental-scale analysis has quantified the geographic distribution or proportional or total values of channelization, levee construction, or alteration of riparian areas. Gleick et al. (2001) estimate that more than 500,000 km of inland waterways were altered for navigation globally during 1981–1990. They also estimate 50% wetland loss globally during 1900–1998, with regional values exceeding 50% in western Europe and the United States, although extensive wetland loss also occurred prior to 1900. These values are for all types of wetlands, including riparian or floodplain wetlands. We consider it reasonable to assume at least 50% floodplain wetland loss and alteration of native riparian vegetation along river corridors throughout high-income countries.

We originally proposed that dams create the most significant alteration of carbon dynamics within a channel, but alteration of riparian zones constitutes the most significant and altered aspect of carbon dynamics in river corridors. We use existing estimates of natural lake area (Verpoorter et al. 2014), reservoir area (St. Louis et al. 2000, Downing et al. 2006, Tranvik et al. 2009), and active channel area (Downing et al. 2012, Raymond et al. 2013) to roughly estimate the total global area of altered river corridors. Such estimates include substantial uncertainty because existing estimates of global channel area vary by a factor of 1.4 and estimates of reservoir area vary by a factor of 5.8 (Appendix S1: Table S1). Additional uncertainty comes from relatively limited measurements of riparian width. As a first approximation, we estimate global area in river corridors (active channel plus riparian zone) at somewhere between 2.6 and 6.2 million km². Using the existing upper and lower estimates of reservoir area and our upper and lower estimates of river corridor area indicates that reservoirs have altered anywhere from 4% to 70% of river corridors globally: we suggest that $\sim 10\%$ is a reasonably conservative estimate.

The assumptions of 10% river corridor alteration by dams and 50% river corridor alteration through other human activities underlie our inferences regarding the primary direct human effects on carbon dynamics in river corridors. Estimates of increased OC flux from rivers to oceans (e.g., Regnier et al. 2013) also support our inferences that reduced riparian OC storage outside of reservoirs has, at a minimum, a slightly greater net effect on OC balances in river corridors than increased OC storage in reservoir sediments. We submit that alteration of land cover and consequent changes in soil erosion and OC influxes to river corridors are likely the largest indirect human effect on carbon dynamics in river corridors.

Returning to Eq. 1, we add upward and downward arrows to indicate an increase or reduction, respectively, in the magnitude of the terms in the equation as a result of the cumulative effects of human activities:

$$\frac{\downarrow dC_{S}}{dt} = \uparrow C_{I} - \uparrow C_{Ogas} + \uparrow C_{Oriver}$$
 (4)

Despite substantial uncertainties in the magnitude of individual human alterations and the interacting effects of multiple forms of alteration, the synthesis presented here suggests the shortcomings of the existing active and neutral pipe models of river channels in the global carbon cycle.

Conclusions

Diverse lines of evidence indicate the most likely scenario for cumulative effects of human activities on OC dynamics in river corridors. Widespread removal of native land cover and alteration of topography dramatically increase OC inputs to river corridors, primarily through increased soil erosion. Where these inputs affect small rivers without dams, levees, or continuing agricultural use of the riparian zone, the net effect may be increased OC storage in riparian soils (e.g., Ricker et al. 2012). Where increased upland inputs enter larger rivers, however, the net effect may be different. Channelized, physically simpler and more uniform channels provide fewer opportunities for temporary storage and biological processing of OC inputs (Battin et al. 2008, Aufdenkampe et al. 2011), and laterally disconnected riparian areas store far less OC in riparian soil and biomass (e.g., Bullinger-Weber et al. 2014, Hanberry et al. 2015). These changes in channels and riparian areas lead to increased downstream fluxes of POC and DOC and increased CO2 fluxes to the atmosphere. However, POC is trapped within the numerous artificial reservoirs now present along most channels and stored in reservoir sediments. Model simulations suggest that the net effect of these changes within uplands and river networks is increased DOC flux to the ocean, increased CO₂ flux to the atmosphere, and a likely decrease in POC flux to the ocean.

At least four fundamental knowledge gaps exist in our understanding of OC dynamics in river corridors. First, we lack quantitative estimates of how OC inputs to river corridors have varied over timescales of 10¹–10³ yr as a result of human activities. This uncertainty applies to individual watersheds and regions, as well as globally. Although many studies have estimated changes in global sediment fluxes (Hooke 2000, Syvitski et al. 2005, Syvitski and Kettner 2011), these estimates have not been effectively coupled with knowledge of SOC levels and terrestrial biomass to quantify changes in OC fluxes to river corridors.

Second, we have only limited quantitative estimates of OC riparian storage, resulting from either OC fixed in the riparian zone or transported to the riparian zone from the channel, in relation to biome and position within a river network, as well as how such storage has changed under human modification of riparian areas. One might reasonably assume based on knowledge of SOC content by biome (Tarnocai et al. 2009, Schuur et al. 2015), for example, that large floodplain rivers at high latitudes would store most riparian OC. However, relatively small riparian areas within temperate latitudes can contain very high levels of SOC (Walter and Merritts 2008, Appling 2012, Wohl et al. 2012b), and 70–80% of total river (and riparian) length in most river networks is in lower order channels (Downing et al. 2012).

A third fundamental knowledge gap is our ignorance of the magnitude and geographic distribution of alterations in riparian areas at regional to global scales. A few studies estimate the spatial extent and magnitude of changes in riparian SOC content and biomass for a particular region (e.g., Hanberry et al. 2015), but no comprehensive, global synthesis has been undertaken to identify regions with extensive historical or ongoing riparian modification, or the implications of these modifications for carbon dynamics. Further, our admittedly coarse, first approximation of the effects of altering river corridors and disconnecting them from their channels for OC influxes illustrates the limitations of the existing active pipe and neutral pipe models of OC dynamics in rivers.

Finally, we lack adequate understanding of how diverse environmental variables might interact to influence the net effect of climate or land use change on Eq. 1 for diverse river segments and entire watersheds. Given the strong likelihood of nonlinear interactions among water and sediment yield to a river corridor, flow regime, soil moisture, primary productivity, CO₂ emissions, and SOC content in response to climate warming of 2°C, for example, we need many more studies focused on the mechanics of OC fluxes and transformations within river corridors.

The primary management implication to emerge from our study is the critical need to protect and restore the physical complexity of river corridors, including the lateral connectivity between channels and riparian areas. The importance of lateral connectivity and ecosystem integrity in riparian areas has previously been emphasized in many contexts, including enhanced flood controls (Opperman et al. 2010), reduced nutrient loading to channels (Zhang and Mitsch 2007), protecting fish stocks (Ogston et al. 2015), and reducing fine sediment concentrations in rivers (Fitzpatrick et al. 2009). To these we can now add OC storage in riparian soil and biomass. Current emphases on upland afforestation as a means of carbon sequestration (Van der Gaast et al. 2016) should be expanded to explicitly include riparian areas.

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