Beyond respiration: Controls on lateral carbon fluxes across the terrestrial-aquatic interface

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Abstract

Understanding what controls the lateral flux of organic and inorganic carbon from landscapes to surface waters is key to fully understanding terrestrial ecosystem carbon balances, the biogeochemistry of freshwaters, and how the hydrologically-mediated movement of carbon between these ecosystems may be altered by global change. In this paper, we synthesize current knowledge and identify major knowledge gaps in our understanding of the mechanisms that control the magnitude and speciation of carbon that is produced and transported to freshwater ecosystems, highlight how global change may perturb these carbon fluxes, and identify major knowledge gaps and key avenues for future research.

Scientific Significance Statement

In the last decade, there has been increased recognition that lateral, land-to-water transport of carbon plays an important role in the carbon balance of terrestrial ecosystems and the biogeochemistry of freshwaters. However, lateral carbon fluxes are rarely measured in a way that includes all organic and inorganic species, and thus our understanding of how these fluxes may vary across different ecosystem types and with global change is limited. In this review, we synthesize current understanding of the mechanisms that control the magnitude and speciation of carbon that is produced and transported to freshwater ecosystems, highlight how global change may perturb these carbon fluxes, and identify major knowledge gaps and key avenues for future research.

Author Contribution Statement

SET, JBF, EH, and EK contributed equally to this work. This included working together to design the framework and scope for the manuscript, contributing equally to writing and other manuscript preparation tasks, and contributing ideas and refinements to the conceptualization and preparation of figures.

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Inland waters permeate and are strongly influenced by terrestrial environments. While soils and water bodies are distinct ecosystems, they are strongly linked by the material flows of water and carbon. The insight that inland waters are active sites for transport, transformation, and storage of considerable amounts of carbon received from the terrestrial environment (Cole et al. 2007) has spurred efforts to broaden our understanding of carbon losses from terrestrial ecosystems beyond respiration-based measures of vertical carbon flux. Previous estimates for the lateral flux of carbon from terrestrial ecosystems to inland waters suggest that it is comparable in size to the residual terrestrial CO2 sink (estimated at 3.1 Pg C yr\(^{-1}\); Le Quéré et al. 2016). The significance of this flux on the scale of the global carbon budget was recognized relatively recently and only integrated into the latest versions of climate change assessment reports.

There is large variability in the lateral transport of terrestrial carbon in both organic and inorganic forms (e.g., dissolved [DOC] and particulate [POC] organic carbon, carbon dioxide [CO\(_2\)], and bicarbonate [HCO\(_3^-\)]) across varying landscapes and over time scales ranging from days to decades. Elucidating and quantifying the controls on these fluxes is critical for refining the terrestrial carbon balance, understanding the carbon biogeochemistry of inland waters, and predicting feedbacks to climate change. Because the carbon cycle is sensitive to climate and land-use change, future perturbations to these broad-scale drivers have important and largely unquantified implications for lateral carbon flux. Notably, there are numerous reports of increasing DOC concentrations in a variety of aquatic ecosystems (e.g., Monteith et al. 2007) and also reports of long-term changes in riverine dissolved inorganic carbon (DIC) concentrations (e.g., Raymond et al. 2008). However, the drivers of these trends are under intense debate.

Here, we synthesize current knowledge and identify major gaps in our understanding of terrestrial-aquatic carbon flux. The overarching goal is to provide a mechanistic understanding of controls on the magnitude and speciation of carbon that is transported from terrestrial to aquatic ecosystems. We start by exploring the controls on soil organic carbon (SOC) stocks, which constrain the availability of carbon for dissolution, mineralization and fluvial transport. Next, we summarize the current understanding of controls on the production and removal of organic and inorganic carbon species in soils, as well as the factors that influence the movement of carbon from soils to fluvial ecosystems. We then discuss how global and regional changes in climate and biogeochemistry (e.g., N and S cycles), land-use, and wildfire regimes will alter SOC, and the flux and speciation of carbon moving across the terrestrial-aquatic interface. The review is centered on a conceptual model that frames the key processes regulating the hydrologic transport of organic and inorganic carbon from land to water (Fig. 1). We end by identifying major, cross-species knowledge gaps regarding the movement of carbon across the terrestrial-aquatic interface, and by suggesting ways forward. Our paper

**Fig. 1.** A conceptual model to illustrate the major pathways of carbon flux across the terrestrial-aquatic interface, conceptualized for forest-grassland and wetland ecosystems. The weight of arrows indicates the relative magnitude of flux.
is intended to provide aquatic and terrestrial ecosystem scientists with current knowledge about the generation and delivery of terrestrial carbon to aquatic environments, and to develop a roadmap to guide future research on terrestrial-aquatic linkages in the carbon cycle within the context of global change.

**Soil carbon stocks**

The stock of SOC within catchments benchmarks the upper limit of OC that is available for transport to aquatic systems. The spatial distribution of SOC across catchments and ecoregions, and within the soil profile, is governed by three key processes: inputs into the SOC pool, losses via mineralization and solubilization, and the presence of conditions that either enable or provide physical protection from loss (see Camino-Serrano et al. 2014). The biotic, abiotic, and environmental controls on these co-occurring processes are numerous, and vary over time and space. As a result, work to understand controls on SOC accumulation and predict its distribution over broad spatial scales is ongoing.

Temperature and moisture are well-known to be primary regulators of SOC accumulation as a result of their effect on the balance between organic matter production and degradation. However, other factors can affect this balance between production and loss. For example, variation in substrate quality can have a significant effect on SOC mineralization rates (Frey et al. 2013). Conversely, clays or the presence of Fe and Al oxides can protect against SOC mineralization through DOC adsorption in the soil profile, and thus its retention in the SOC pool (Kindler et al. 2011).

Although there are a large number of interacting factors that impact SOC accumulation, there are some broad-scale patterns in SOC distribution and its susceptibility to solubilization and consequent transport as DOC to surface waters. Across ecosystem types, wetlands, which contain approximately one-third of the world’s SOC pool, are associated with higher porewater DOC concentrations than other ecosystem types (Camino-Serrano et al. 2014). Similarly, boreal soils tend to have greater SOC per unit area than their temperate counterparts (Malhi et al. 1999), with broad surveys suggesting that coniferous forests have higher porewater DOC than deciduous forests (Camino-Serrano et al. 2014). Warmer temperatures in the tropics, which enhance both productivity and decomposition processes, cause unit-area SOC to be intermediate between boreal and temperate zones (Malhi et al. 1999). Overall, SOC content is highest in cool, wet conditions, while factors such as overlying vegetation, soil texture, and soil mineral composition explain a significant component of the remaining variation in SOC distribution (Jobbågy and Jackson 2000).

**Carbon production, export, and removal in the soil profile**

**Dissolved organic carbon**

Dissolved organic carbon is widely recognized as the most mobile and reactive fraction of soil organic matter (SOM) and it influences myriad physical and biogeochemical processes in soils. Dissolved organic carbon in soils originates from photosynthesis and is produced when precipitation is washed through vegetation, infiltrates organic soil horizons and moves downward through the soil profile. In most terrestrial ecosystems, plant litter and SOM are the dominant sources of DOC produced in the soil profile. Other soil sources of DOC include root exudates, extra-cellular enzymes produced by fungal biomass, and microbial biomass (Schmidt et al. 2011).

Rates of DOC production and removal in soils are influenced by a variety of physical and ecological factors including: vegetation type, SOC content and lability, soil temperature, moisture, redox status, and soil type. As a result, concentrations of DOC in soil pore waters are highly variable at scales ranging from the soil profile to the biome. Across soil types, average soil solution DOC concentrations range from approximately 5 mg C L⁻¹, to more than 100 mg C L⁻¹ in peatlands (Camino-Serrano et al. 2014). On seasonal scales, soil temperature has been shown to be a significant predictor of variability in soil DOC concentrations (Winterdahl et al. 2011), likely via effects on biological activity that influence the production and degradation of DOC.

The main removal processes for soil water DOC are degradation by soil microbes and chemical sorption as DOC leaches downward in the soil profile (Sanderman et al. 2008). The relative importance of degradation vs. sorption for removing DOC from soil solution varies across sites and with depth in the soil profile. The microbial degradation of the labile fraction of DOC is an important variable controlling DOC concentrations in organic carbon rich soils such as histosols and in the organic surface horizons of forested soils (Fellman et al. 2017). In mineral soils, DOC can adsorb to available mineral surfaces, rendering it physically or chemically inaccessible to soil microbes. Indeed, DOC sorption is thought to be the dominant removal mechanism for DOC in mineral soils and responsible for observed decreases in the concentration of DOC with soil depth (Sanderman et al. 2008). Ultimately, the location, rate, and specific mechanism of DOC removal in the soil profile interact to control the magnitude and chemical quality of DOC available for export from soil solution.

Soil hydrology exerts a direct control on the export of potentially mobile DOC that has been produced in the catchment. Water moving downslope acquires the chemistry of the soil profile, making the hydrological routing of water through the landscape decisive to the export of DOC to surface waters. In many forested ecosystems, low flow hydrological connectivity is mainly through deeper mineral soil
horizons, causing streamwater DOC concentrations to be low. However with increasing discharge, the flow through saturated surface soils results in high rates of DOC export to streams (Sanderman et al. 2009). Thus, organic matter-rich riparian zones and forest wetlands that have tight hydrological connections with streams are a dominant source of streamwater DOC in well-drained soils, including forests, grasslands, and soils subject to agriculture (Bishop et al. 2004). While forest organic horizons are also often high in DOC, this carbon-rich zone is generally not hydrologically connected to the stream and thus is more important as a source of DOC to subsurface mineral horizons.

The first order control that discharge exerts on DOC export from forested catchments is illustrated by seasonal variability and response to high flow events. Concentrations of DOC increase with discharge in forested watersheds and, as a result, storm events are responsible for the vast majority (typically > 80%) of DOC exported from soils to streams on seasonal and annual timescales (Raymond and Saiers 2010). In peatland-influenced watersheds, DOC concentrations may decrease during storm events due to dilution in surficial layers, however the increase in dilution volume generally outweighs this dilution effect, resulting in higher DOC export from peatlands with increasing discharge (Pastor et al. 2003). Overall, the importance of hydrological connectivity as a control on DOC export from soils increases in less humid catchments that are transport limited because of lower rainfall-runoff ratios and longer soil-stream transit times (Dawson et al. 2008). In addition to the direct hydrological control on DOC fluxes through changes in flow regime, drying and rewetting episodes can act indirectly on DOC export via changes in soil water chemistry driven by water table fluctuations. However, the overall impact of rewetting events on the production and export of DOC in peat and forested soils has been shown to be modest (Clark et al. 2012).

Particulate organic carbon

The soil production pathways for POC differ substantially from those for DOC. The bulk pool of POC in soil consists of both rock (petrogenic) organic carbon, largely in the form of insoluble kerogen, and plant-derived organic material (Blair et al. 2010). Soil kerogen is produced by the incomplete weathering of sedimentary material, which occurs most rapidly in the soils of steep, tectonically active watersheds (Leithold et al. 2006). Soil POC can also originate from the soil organic matter pool, which is dominated by plant-derived material but also includes contributions from microbial biomass. This pool of POC includes small particles (< 2 μm) that can be suspended in soil water as well as larger particles of crushed organic material that are not suspended. The production of plant-derived POC can occur via mechanical ablation of SOC, particle production by polysaccharide producing microbes, and the abiotic aggregation of DOC in soil pore waters (Fiedler et al. 2008). Concentrations of POC are rarely measured in soil pore waters, however in peat-dominated histosols, POC concentrations (15–120 mg C L⁻¹) are comparable to concentrations of DOC, particularly in cases where soils are dried and re-wetted (Fiedler et al. 2008).

The pool of POC in soil solution is less dynamic than the DOC pool because POC production is largely dependent on processes related to soil formation rather than the more rapid physical leaching and microbiologically mediated biological processes that enable DOC production. Within soils, the production of petrogenic organic carbon is dependent on tectonic and geologic factors including sediment organic matter content, while biogenic POC production is dependent on ecological factors such as vegetation type, primary production, and SOC stocks (Goni et al. 2013). Similar to DOC, however, soil hydrology is the dominant control on the export of POC from soils to streams, with the bulk of POC transport occurring through shallow soil flowpaths during high discharge events. The fact that the export of both petrogenic and biogenic POC from terrestrial ecosystems is strongly related to the movement of suspended sediment indicates that hydrologically mediated erosion of soils is the primary control on the movement of POC across the terrestrial-aquatic interface (Galy et al. 2015). The ratio of biogenic : petrogenic POC exported from soils can increase with flow intensity, particularly in catchments where there is strong connectivity between hillslope and channel such that high flow events activate the movement of biogenically derived POC from hillslope surfaces into the channel (Smith et al. 2013). In addition, the size fraction of POC mobilized from soils changes during high flow events, with export of coarse (> 1 mm) POC increasing more rapidly than that for fine POC or DOC. While erosion is the dominant mechanism of POC export from soils in many catchments, the leaching of fine, suspended POC may be substantial from undisturbed histosol-dominated landscapes such as peatlands (Fiedler et al. 2008).

Dissolved inorganic carbon

Carbon transformations in the soil also produce DIC as CO₂ and HCO₃⁻. The soil solution pool of DIC consists of carbon derived from biogenic CO₂ production and the subsequent production of HCO₃⁻ following geochemical weathering by carbonic and sulfuric acids. Soil pore waters are frequently supersaturated in CO₂ because of root respiration and organic matter decomposition (Cole et al. 2007). The enzymatic breakdown of SOC by soil microbes and subsequent solubilization to DOC appears to be the rate-limiting step controlling soil microbial respiration rates in both northern peatlands (Pastor et al. 2003) and forested ecosystems (Bengtson and Bengtsson 2007). However, as water percolates downward through the soil profile and into mineral horizons, weathering of carbonate and aluminosilicate minerals can result in a decline in biogenic CO₂ and subsequent production of HCO₃⁻. Thus, groundwater contributions to surface water contain biogenic CO₂, although
levels can be much lower than originally produced in the soil profile of unweathered soils (Skiba and Cresser 1991). In regions with carbonate-rich lithologies, carbonate rock weathering can significantly increase DIC transport to aquatic systems, through substantial production of HCO$_3^-$ (Stoddard et al. 1999).

The balance between biogenic CO$_2$ production, and geochemical processes that may either “fix” CO$_2$ as HCO$_3^-$, or release HCO$_3^-$ via rock dissolution, is an important determinant of the carbon budget across the land-water continuum. Biogenic CO$_2$ production in soils is high, with an annual global efflux to the atmosphere estimated at 91 Pg C yr$^{-1}$ (Hashimoto et al. 2015). However, these estimates are likely conservative because they do not include dissolved transport of CO$_2$ from soils to streams. In some instances, soil water DIC concentrations (largely as CO$_2$) in organic surface horizons can be as high as 280 mg C L$^{-1}$ (Fiedler et al. 2008) indicating that a considerable portion of soil respiration is dissolved in soil pore waters. Since soil carbon storage is often inferred from vertical efflux from the soil surface, failure to include the flux of dissolved CO$_2$ to surface waters in estimates of soil respiration could result in overestimates of terrestrial ecosystem carbon stocks. Similarly, a failure to include estimates of HCO$_3^-$ flux to surface water could also skew our understanding of the carbon balance of ecosystems, because chemical weathering by carbonic acid acts as a carbon sink that is effective over millennial (for carbonate rock) or geologic (for silicate rock) time scales. Conversely, when chemical weathering is initiated by sulfuric acid—derived either from acid deposition or natural processes—the resulting HCO$_3^-$ comes only from rock dissolution, and thus acts as an eventual atmospheric CO$_2$ source (over 10$^7$ yr scales).

**Lateral carbon fluxes across landscapes and time**

While the vast majority of studies exploring land-to-water carbon flux have focused on individual species, understanding the speciation of the carbon pool moving from land to water is central to determining the fate of this carbon, and its impact on the function of recipient aquatic ecosystems. For example, organic carbon that is transported as POC, rather than DOC, may be less available for microbial uptake and mineralization, and more likely to be deposited in downstream sediments. Similarly, CO$_2$ that is transformed to HCO$_3^-$ via interaction with mineral soils is protected from atmospheric evasion, and becomes available for eventual sequestration in the world’s oceans. This same speciation—along a possible continuum from POC, to DOC, to CO$_2$, to HCO$_3^-$—has critical effects on downstream ecosystem function via impacts on pH and buffering capacity, light attenuation, toxin and metal sequestration, and the availability of organic carbon for incorporation into microbial food webs.

Global estimates of the emissions and storage of carbon species in inland waters and riverine discharge to the ocean can be used to constrain the magnitude of the global flux of C from terrestrial to aquatic ecosystems (Fig. 2). As our
understanding of C burial in aquatic sediments and CO₂ evasion from aquatic surface waters improves (e.g., Tranvik et al. 2009; Drake et al. 2018; Sawakuchi et al. 2017), estimates of C flux across the land-water interface continue to be revised upward. The most recent assessments indicate a land-to-water C flux of 5.1Pg yr⁻¹ (Drake et al. 2018), which is nearly triple the 1.9 Pg estimate presented a decade ago by Cole et al. (2007). These broad-scale, global estimates obscure the fact that the speciation of C traveling to aquatic ecosystems varies markedly across landscape types, however (Figs. 1, 2; Tranvik et al. 2009), with subsequent regional variation in aquatic ecosystem function. While perturbations caused by climate change, broad-scale changes in biogeochemical cycles, and land-use change may also fundamentally alter the flux and speciation of land to water carbon flux, our understanding of these processes is typically modest at best. Below, we discuss our current knowledge of the effects of global change on SOC stocks and land-to-water carbon transfer, highlighting regional variations and levels of certainty where possible.

Effects of global change on carbon stocks, export, and removal

Climate and biogeochemical change

The broad influence of temperature and moisture on the balance between primary production and SOC decomposition suggests that climate change-induced shifts in temperature, precipitation, and soil hydrologic regime will fundamentally affect SOC at the local scale. Decomposition appears to be more sensitive to increasing temperatures than photosynthesis, with the sensitivity of soil respiration rates to temperature increases being much greater when ambient soil temperatures are low than when they are high (Plante and Conant 2014). Plot-scale warming experiments show that increasing temperatures decrease SOC, particularly in regions where standing C stocks are relatively high (Crowther et al. 2016). This suggests that regions such as the Arctic and sub-Arctic may be particularly susceptible to SOC loss, particularly when permafrost C is exposed to active biogeochemical cycling (Schuur et al. 2015; Crowther et al. 2016). Laboratory warming experiments with wetland soils in Alaska demonstrate substantial temperature-induced losses of SOC over relatively short (< 1 yr) time scales, via both DOC leaching and soil respiration (Fallman et al. 2017).

Climate-induced changes in precipitation, evapotranspiration, and thus soil moisture and hydrologic regimes, will also affect SOC stocks. However, the distribution of this effect has been much less studied than the direct effects of temperature (Falloon et al. 2011). Given that SOM decomposition tends to peak when soils are 50–60% saturated, it seems likely that the effects of changing moisture regimes will vary across regions (Plante and Conant 2014). From a broader perspective, greening (i.e., increased primary production)—which is driven by changes in both temperature and moisture—is expected to augment SOC stocks as a result of increasing terrestrial production and northward shifts in vegetation at the treeline (Finstad et al. 2016; Kritzberg 2017). Further south, the migration of temperate forests northward into boreal regions will also likely alter SOC stocks (Jobbágy and Jackson 2000). Finally, increases in vegetation and thus inputs to the SOC pool are expected to be greatest in regions experiencing increases in N deposition; where this is not occurring, N may become limiting to SOC increases that would otherwise be driven by CO₂ fertilization or increasing temperature and moisture (Norby et al. 2010).

Future changes in precipitation and runoff regimes will also have important implications for the export of all forms of terrestrial derived carbon because of the strong climatic control on the mobilization and transport of carbon via rainfall-driven high-flow events. For instance, increasing precipitation is predicted to increase mobilization of DOC from soils to surface waters resulting in the widespread increase in surface water DOC concentrations, particularly in dry regions (de Wit et al. 2016). Theoretical turnover times of riparian carbon pools are estimated to be on the order of hundreds of years, suggesting that there is potential for a long-lasting supply of DOC (Ledesma et al. 2016). Increasing soil saturation associated with greater precipitation also affects the dominant soil flowpaths and promotes reducing conditions and reductive dissolution of Fe hydroxides, which results in release of adsorbed DOC (Knorr 2013). Furthermore, the export of terrestrial carbon, particularly biogenic POC, from soils to streams should be enhanced in regions where there is an increase in the ratio of rain to snow-dominated storm events (Hilton et al. 2012). Climatic enhancement of biogenic POC export to aquatic ecosystems appears to be sustainable over long timescales because only a small fraction of terrestrial NPP is exported as POC, even at very high erosion rates (Galy et al. 2015).

The increase in extreme weather events predicted under a warming climate may also have important implications for the mobilization of terrestrial carbon as POC relative to DOC. In particular, large, low frequency rainfall events such as hurricanes have been shown to dramatically increase POC export from catchment soils in comparison to DOC export (Dhillon and Inamdar 2014). The speciation, and thus character and bioreactivity, of POC exported from soils also changes during storm events, with an increase in biogenic POC export associated with sheetwash and landslide events and an increase in less degradable petrogenic DOC associated with rainfall-induced gullying events (Blair et al. 2010). Ultimately, the strong role of precipitation intensity in mobilizing terrestrial POC suggests that climate-driven changes in rainfall intensity are more likely than cumulative changes in runoff to explain changes in the source and character of POC exported from soils to streams (Jeong et al. 2012).
While there seem to be no direct temperature effect on DOC solubility in soils (Jones and Willett 2006), rising temperatures are likely to exert various indirect effects on DOC production and mobilization. Increasing temperatures and longer growing seasons are promoting greening, which has been shown to correspond to an increase in DOC export (Finstad et al. 2016). A positive effect of warming on the fluvial transport of terrestrial DOC is expected particularly in colder regions, where export is to a large extent transport limited due to frozen conditions over extended periods. However, in warmer regions increasing production of DOC may potentially offset by increasing carbon mineralization (Laudon et al. 2012). In some permafrost-affected regions, significant increases in the riverine transport of DOC have been observed over broad spatial and temporal scales (Tank et al. 2016). However, it is unclear whether this increase is caused by changes in organic matter production, permafrost thaw, or both. As permafrost degrades with increasing temperatures, there is a general expectation that DOC mobilization to aquatic networks will increase (e.g., Vonk et al. 2015). In some regions, however, deepening active layers will increase DOC mineralization and sorption via longer transit times and flow through deeper, mineral soils. As a result, the effect of permafrost thaw on DOC delivery to freshwater systems is likely to be region-specific.

In other regions, the combination of increasing temperatures and changing precipitation patterns yield projections of increasing drought. Episodes of low water levels reduce DOC export from peatlands not only by reducing lateral flux, but also by drought-induced acidification and thereby reduced DOC solubility (Clark et al. 2012). Drought-induced acidification is to a large extent driven by S redox reactions, where oxidizing conditions lead to sulfate production. Atmospheric S deposition influences the presence of reactive S in soils, and has therefore been proposed to be an important control on long-term variability in DOC export (Monteith et al. 2007). The role of declining S deposition and the reversal of acidification as a driver of increasing DOC concentrations is supported by field experiments that show effects on soil water DOC concentrations (Ekstroim et al. 2011) and by the fact that DOC concentrations have increased proportionally to concurrent declines in sulfate concentrations across lakes in northern Europe and North America (Monteith et al. 2007). As the S legacy in soils is depleted, the role of S dynamics in controlling DOC mobilization appears to be declining (Ledesma et al. 2016). Notably, while declining S deposition is often described as a dominant driver of positive DOC trends, the only study that encompassed data from a period when S deposition was increasing points to a combined effect of land-use, changing climate, and atmospheric deposition (Kritzberg 2017).

Climate change is widely expected to increase soil respiration (Hashimoto et al. 2015) and thus likely the flux of CO₂ from land to water. In addition, because chemical weathering is largely driven by reactions with carbonic acid, increases in pore water CO₂ (as a result of either increases in soil respiration or atmospheric dissolution) are expected to increase HCO₃⁻ generation, and thus the flow of DIC from land to water. Modeling efforts have predicted (Beaulieu et al. 2012) and in-situ observations have shown (Gislason et al. 2009) significant increases in HCO₃⁻ production with climate change over contemporary time scales. In permafrost-affected regions, there has also been some evidence that permafrost thaw may enable greater HCO₃⁻ production in soils, presumably through processes such as deepening flow paths and the exposure of previously-frozen mineral soils (Vonk et al. 2015). This change—and whether it is instigated by carbonic, or sulfuric acid—has implications for the terrestrial-aquatic carbon balance that are on the same order of magnitude as changes in DOC flux (e.g., Tank et al. 2016). Recovery from acid deposition has also caused increasing HCO₃⁻ flux from land to water, following the decline of buffering reactions in catchment soils (Stoddard et al. 1999).

**Land use change**

While current trends in forest cover are neutral to increasing in boreal, temperate, and sub-tropical regions, significant amounts of forested land are being lost annually in the tropics. Meta-analyses across temperate to tropical biomes (Guo and Gifford 2002; Don et al. 2011) show that the conversion of native or secondary forest to cropland is universally accompanied by substantial (as much as 42%) decreases in SOC stocks, but that reforestation can largely reverse this process. In tropical regions, the conversion of grassland to cropland appears to cause a smaller, but still negative, change in SOC (Don et al. 2011). Soil mixing via agricultural tillage practices may also increase SOC decomposition rates (Yoo et al. 2011).

Despite the clear effect of agricultural conversion on SOC, the conversion of forested, grassland or wetland areas to agricultural or urban areas has a range of impacts on soil DOC production and export to aquatic ecosystems. For example, agro-urban studies have shown that DOC concentrations in agricultural soil water and streams are often lower than in forested or wetland-dominated streams (Wilson and Xenopoulos 2009; Toosi et al. 2014), while others show increased (Aitkenhead-Peterson et al. 2009) or undetectable (Vidon et al. 2008) changes in DOC. In urban settings, DOC export to streams may be enhanced by the movement of wastewater as well as the solubilization of aged SOC stocks, as supported by radiocarbon dating of DOC (Sickman et al. 2007). The drainage of peatlands has also received considerable attention over the last several decades, with research showing that drainage enhances peat decomposition thereby increasing DOC export to surface waters (Moore et al. 2013). Overall, these varying responses in DOC production and export in response to increasing agro-urbanization can be
expected because of the diverse range and extent of human activities (i.e., diversity of farming practices and time since conversion) and subsequent effects on SOC stocks, sources of DOC (i.e., wastewater), and the flowpaths that connect terrestrial carbon source pools with surface waters. In contrast, afforestation results in buildup of organic soil layers, which has been argued to be a driver behind long-term increases in aquatic DOC (Kritzberg 2017).

Land use changes that increase the availability of SOC stocks for mobilization via sheetwash and erosion have similarly important consequences for the movement of POC across the terrestrial-aquatic interface. The conversion of forest cover and grassland to cropland can have substantial impacts on surface soil erosion rates depending on the seasonality and type of crops, which influence the capacity of agricultural soils to act as a POC source. Agricultural land conversion can increase POC export rates to fluvial systems during storm events, particularly in cases where highly erodible croplands are established on steep mountain slopes (Jeong et al. 2012). The conversion of natural forest ecosystems to intensive plantations has also been shown to dramatically increase SOC erosion rates in surface soils thus facilitating the transfer of POC from terrestrial to aquatic ecosystems (Guillaume et al. 2015). The impacts on POC export are most pronounced in cases where protective layers (canopy and litter) are removed in the process of forest conversion.

In agro-urban watersheds, elevated CO₂ concentrations can result from the dissolution of CO₂ from pedogenic carbonates imbedded in old roads (Zeng and Masiello 2010). Similarly, greater rates of root and microbial respiration in pasture lands can significantly elevate CO₂ concentrations in soil waters relative to forest soils. Sewage inputs to streams or leaky septic systems in highly urbanized watersheds can elevate CO₂ values relative to pristine streams as a result of high rates of labile organic carbon mineralization (Kausal et al. 2014). The conversion of forested landscapes to cropland has also been associated with increasing HCO₃⁻ flux (Raymond et al. 2008), via mechanisms that include increased CO₂ and thus chemical weathering, in soils. In addition, increases in discharge caused by agricultural conversion, tillage methods that increase the exposure of mineral soils to weathering, and agricultural liming also appear to contribute to increased HCO₃⁻ flux in agricultural landscapes (Raymond et al. 2008). This agriculturally mediated increase in HCO₃⁻ flux has been found to be significant within the land-to-water carbon budget, and a CO₂ sink at present-day time scales (Regnier et al. 2013).

In contrast to agriculture, logging appears to have relatively modest effects on SOC. A meta-analysis across various North American forest types has shown logging-related declines in SOC to be relatively small (typically <10–15%), and limited to whole-tree harvest activities (Johnson and Curtis 2001). In contrast, logging that removes only commercially useful materials tends to result in an increase in SOC, particularly in boreal forests (Johnson and Curtis 2001). Several studies have also indicated that soil disturbance associated with logging may act to protect SOC through the mixing of surface organic soil layers with deeper mineral soils (Yanai et al. 2003). Both agricultural activity and industrial logging can also include drainage by ditching, which has been shown to promote decomposition of SOC (Moore et al. 2013).

Similarly, the limited information available regarding logging effects on C mobilization is somewhat contradictory: while some studies have detected a clear effect on DOC concentrations, others have not (reviewed by Stanley et al. 2012). For example, in regions where logging increases water table levels via reduced evapotranspiration, a tighter hydrological connection between organic carbon-rich surface horizons and streams enables short term increases in DOC production and export (Schelker et al. 2014). Leaching from logging slash and/or harvest residues and increased decomposition of SOM due to elevated soil temperature can also increase DOC export. In contrast, where logging causes lower groundwater inputs of DOC due to enhanced sorption of DOC on to minerals soils (Piirainen et al. 2002) or dilution via increased runoff (Palviainen et al. 2014), studies show decreased or minimal change in DOC export relative to non-logged reference streams. Finally, the impacts of logging on POC and DIC export are not well understood. Observed changes in SOC stocks are not thought to be influenced by POC export (e.g., Petenko and Friedland 2015), however, increased erosion from steeply logged slopes and logging roads could facilitate increased POC losses to streams. These results point to the importance of the interactive effects of hydrology, soil composition, and land use change for determining the production and transport of C species from logging-affected landscapes.

**Wildfire**

The incidence of wildfire has increased significantly across much of the globe over the last several decades (Jolly et al. 2015). Although wildfire can directly mineralize near-surface SOC to CO₂ and CH₄, the degree to which this mineralization occurs depends on burn severity and factors such as soil moisture and soil porosity (Gonzalez-Perez et al. 2004). SOC erosion can also increase significantly following wildfire, as a result of the increased hydrophobicity of soils (Santin et al. 2015), the deposition of soot, and the loss of below ground root structures (Gonzalez-Perez et al. 2004). Wildfire can cause significant changes in SOC composition, with sequential loss of fulvic and humic acids, and a transformation toward insoluble humins (Gonzalez-Perez et al. 2004). The pyrogenic carbon that results is generally resistant to degradation, and thus wildfire can significantly affect the persistence of organic carbon in soils, and its susceptibility to degradation in recipient aquatic ecosystems (Santin et al. 2015).
Wildfire also has the potential to substantially impact carbon production in soil waters and its export to aquatic ecosystems. Research following a prescribed burn in central Alaska showed that soil water (Shibata et al. 2003) and stream DOC concentrations (Betts and Jones 2009) decrease post-fire relative to control sites, once conditions were wet enough for an effect to be observed. Combustion of soil carbon stocks was thought to be the main driver in reduced DOC export, although transformation of soil carbon to less soluble carbon compounds, and reduced SOC mineralization due to a post-fire reduction in microbial biomass, could also reduce DOC production in soil waters. On the other hand, soil water collected from peatlands of the Boreal Plains in Canada following a natural fire showed no change in DOC concentration, suggesting that SOC needs to be removed by wildfire at the soil depth of the dominant flow path to alter DOC production and export (Olefeldt et al. 2013). These findings indicate that regions with thin organic soils or permafrost that protects mineral rather than organic deposits are more likely to exhibit altered DOC production and export following wildfire. Similar to logging, the magnitude and duration of any post-fire change in DOC export will depend on interactive effects of burn severity, soil properties and post-fire precipitation regimes.

Wildfire activity appears to affect POC export mostly via its impacts on soil erosion. Fire-derived OM in soils can be highly condensed and resistant to biological degradation. However, this protective mechanism does not compensate for increased erosion of POC from soil surface layers resulting from changes in soil hydrophobicity and the loss of erosion-controlling belowground root structures (Gonzalez-Perez et al. 2004). Wildfires can also increase the soil surface pool of POC available for export through the deposition of charred plant material. Finally, wildfire can impact DIC production and export to streams through an increase in pH due to the addition of basic ions in the ash. Streamwater DIC concentrations can increase post fire as a result of enhanced microbial respiration of SOC, although the proportion of CO₂ to DIC concentration may decrease as a result of the greater HCO₃⁻ flux associated with elevated pH (Gu et al. 2008).

**Conclusions and future research needs**

The transport of organic and inorganic carbon across the terrestrial-aquatic interface represents a key but often times poorly constrained loss in the net terrestrial ecosystem carbon balance. Improving our knowledge of the processes that control this flux across time, space, and ecoregion is thus critical to our understanding of the carbon cycle from regional to global scales, and the biogeochemistry and ecology of terrestrial and aquatic ecosystems. Much of the past research on lateral carbon fluxes has focused on understanding the production of, and mechanisms for the transport of individual species (e.g. DOC) to fluvial ecosystems, rather than examining how biotic and abiotic processes interact to control the production and loss of multiple carbon species simultaneously. Here, we argue for a more holistic examination of lateral carbon transfers. Such an approach will enable a more complete understanding of the carbon balance of terrestrial ecosystems, while also advancing our understanding of the effect of lateral carbon fluxes on the ecological and biogeochemical functioning of recipient aquatic ecosystems. Building on the synthesis presented in our review, we suggest the following priorities for future research:

1. **Quantifying lateral carbon fluxes in the context of vertical fluxes on land and in water**: The lateral C fluxes that we describe here are rarely studied in concert with and in the context of the vertical flux of carbon (i.e., CO₂ evasion from both land and water). In order to better understand the relative importance of land-water carbon fluxes, we must move toward research that fully integrates the carbon budget across terrestrial and freshwater ecosystems. Incorporating less commonly studied carbon species—such as POC and HCO₃⁻—into measurements of lateral carbon transfer is critical to our goal of moving “beyond respiration,” and taking a more holistic approach to quantifying the carbon balance of watersheds, and the effects of carbon transfers on aquatic ecosystem function.

2. **Exploring the interactive effects of key climatic and physical parameters on SOC stocks and subsequent DOC export**: We increasingly recognize that predictions of warming-induced changes in SOC stocks must also consider the concurrent effects of changing hydrology (moisture, flow paths, and connectivity), landcover, length of the growing season, and CO₂ and nitrogen fertilization. Coupled with this is the understanding that changes in the SOC pool that result from these perturbations may not be mimicked by changes in DOC export. Field and laboratory experiments to explore how some, or many of these factors interact to affect SOC and the movement of DOC across the terrestrial-aquatic interface are a clear priority for future research. Similarly, paleolimnology, remote sensing, and long-term records of C stocks and fluxes should be employed to explore how these co-occurring factors have affected land-to-water carbon flux over decadal time scales.

3. **Determining the balance between SOC mineralization and solubilization with warming**: Temperature-driven increases in microbial activity can be expected to increase both SOC solubilization, and SOC and DOC mineralization to CO₂. Given that DOC production and CO₂ loss to the atmosphere are hypothesized to be connected, neither pathway for carbon loss should be used individually as an indicator of SOC turnover. Therefore, the balance between these processes, and how they vary across ecoregions, represents a critical research gap in our understanding of future change in organic carbon cycling at the terrestrial-aquatic interface. 

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*Tank et al.* Controls on lateral carbon fluxes

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84
interface. Measurements of vertical CO₂ flux made in concert with estimates of lateral DOC and DIC production and flux will greatly enhance our understanding of this issue.

4. *Quantifying the divergent effect of landscape modification (e.g., agriculture, forestry, and wildfire) on SOC stocks and the lateral flux of all carbon species:* The short- and long-term effects of landscape modification on SOC may not be directly mirrored by changes in the amount of C available for downslope transport. For example, SOC may decline immediately following disturbance partially as a result of a transient increase in mobilization of dissolved and particulate OC. The balance between SOC stocks and OC mobilization to aquatic systems, and how this balance varies across disturbance type, ecoregion, and time since disturbance, has been poorly quantified to date. Long-term records of catchments with known land-use history, or long-term monitoring efforts may advance our understanding of how landscape modifications affect both SOC pools and lateral transport.

5. *Determining how changes in carbon transport are affected by shifts in hydrologic regimes:* The proportion of water flow that occurs during storm periods and the relative balance between precipitation as snow and rain in northern regions will have a critical effect on the proportion of OC that is exported in the particulate vs. dissolved phase, particularly given that changes in discharge across the terrestrial-aquatic interface appear to have dramatically different impacts on POC vs. DOC export. The flux of POC along the aquatic continuum is perhaps the most poorly understood of all the carbon species we document in this review, but there is also much to learn about the response of CO₂ and HCO₃⁻ flux to changing hydrology. Monitoring that appropriately captures the lateral flux dynamics of all carbon species over temporal and spatial scales that incorporate hydrologic regime shifts is a clear priority for future research.

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