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# Biogeochemistry of wetland carbon preservation and flux

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## ABSTRACT

The recognition that wetlands play an important role in regulating global climate has led to management actions intended to maintain and enhance the globally significant amounts of carbon preserved in wetland soils while minimizing greenhouse gas emissions. Our goal in this chapter is to review the biogeochemical processes that are relevant to wetland climate regulation, which we do by discussing: 1) the concepts of radiative balance and radiative forcing, 2) the mechanisms for wetland carbon preservation, 3) factors influencing greenhouse gas emissions and other carbon losses, and 4) opportunities for wetland management actions to influence carbon preservation and flux. Wetland carbon preservation, which reflects the accumulation of undecomposed organic material, is a function of the redox environment, organic matter characteristics, and physicochemical factors that inhibit decomposition. However, the conditions that favor carbon preservation often result in increased emissions of methane and nitrous oxide such that there is a biogeochemical tradeoff between carbon preservation and greenhouse gas emissions. The losses of carbon via gaseous and dissolved pathways are sensitive to environmental disturbances and raise challenges about fully accounting for the climatic impacts of wetlands. Wetland management and disturbance intentionally or unintentionally affect biogeochemical processes, such that wise environmental management offers opportunities to enhance wetland carbon preservation, prevent the destabilization of accumulated soil carbon, and reduce greenhouse gas emissions, thus maintaining the role of wetlands as regulators of global climate.

## 1 INTRODUCTION

Climate regulation by wetlands is an important ecosystem service that is increasingly a focus of management and restoration efforts (Erwin, 2009; Moomaw et al., 2018). The basis for these efforts is the observation that wetlands have accumulated globally significant amounts of organic carbon in their soils (Mitra et al., 2005), carbon (C) that is no longer in the atmosphere as the greenhouse gas carbon dioxide ($CO_2$). It is becoming apparent that much of the organic carbon preserved in wetlands is not inherently resistant to decay but instead accumulates because its reactivity is reduced under the environmental conditions in wetland soils (e.g., Spivak et al., 2019). An important corollary of this understanding is that changes to the wetland environment (e.g., as initiated through management decisions or disturbances) could alter those conditions, thus destabilizing the large wetland carbon stores and allowing their export to adjacent aquatic systems as dissolved or particulate carbon or their return to the atmosphere as $CO_2$ and methane ($CH_4$). Further, some of the wetland conditions that promote carbon preservation also lead to the production of the greenhouse gases $CH_4$ and nitrous oxide ($N_2O$), the emissions of which can offset some or all of the climatic benefits provided by wetland carbon preservation.

Environmental management and other human actions, whether purposeful or accidental, can affect the pathways of carbon preservation and removal and therefore have the potential to alter the effects of wetlands on the global climate. In this chapter, we briefly summarize 1) the concepts of radiative balance and radiative forcing as ways of describing how ecosystems and management actions influence the climate. We then address 2) the factors that control wetland carbon preservation. The term “carbon preservation,” which we use throughout this chapter, is largely synonymous with “carbon sequestration” and “carbon storage.” We use preservation to emphasize the absence of decomposition; this framework has helped us think about the processes and mechanisms in a slightly different way. After discussing carbon preservation, we review 3) the processes leading to emissions of greenhouse gases and other losses of carbon from wetlands, before discussing 4) how wetland management can be used to manipulate those biogeochemical factors that affect wetland carbon preservation and flux. We offer this synthesis in the hopes that it will help guide wise decisions.

## 2 RADIATIVE BALANCES AND RADIATIVE FORCING

The terms “radiative balance” and “radiative forcing” are used when discussing the climatic impacts of an ecosystem or a management action. While these terms are related, they are distinct terms that are often – but mistakenly – used interchangeably. The radiative balance of a wetland or other ecosystem is a static measure of how the ecosystem affects Earth’s energy budget over a defined time period, typically 100 years. In contrast, radiative forcing is a measure of how a perturbation to the ecosystem alters Earth’s energy budget. Thus, a change in radiative balance leads to radiative forcing, which causes the planet to warm or cool. If Earth’s energy budget does not change (that is, if there is no radiative forcing), then there is no climate change.

A wide variety of perturbations can affect the radiative balance of a wetland and, therefore, cause radiative forcing. The radiative balance of an individual wetland can change with changes in biogeochemistry, which may be accidental or purposefully designed into environmental management programs in order to influence climate. For example, rates of wetland carbon sequestration are sensitive to factors including climate, hydrology, and vegetation composition (Chmura et al., 2003; Loisel et al., 2014). The production and emissions of $CH_4$ vary with soil water saturation, salinity, and acid rain inputs of sulfate ($SO_4^{2-}$) and nitrate ($NO_3^-$), among other factors (Bridgham et al., 2013). Likewise, the rate of nutrient loading to a wetland can alter rates of $N_2O$ emissions to the atmosphere (Moseman-Valtierra et al., 2011). On a broader regional or global basis, the radiative balance of wetlands can change as the area of wetlands changes. Despite some regional increases in the areal extent of wetlands (e.g., Niu et al., 2012), there has been a global loss of wetland area (Millennium Ecosystem Assessment, 2005). The direction of radiative forcing (that is, whether the net loss of wetlands has contributed to warming or cooling of the climate) is dependent on the kinds of wetlands that have been created and lost.

In order to compare the fluxes of different greenhouse gases, it is necessary to convert them to a common set of units. The global warming potential (GWP), which is the "time-integrated radiative forcing due to a pulse emission of a given component, relative to a pulse emission of an equal mass of $CO_2$" (Myhre et al., 2013), has long been used by wetland scientists to calculate radiative balances and radiative forcing (e.g., Gorham, 1991; Whiting & Chanton, 2001). For the commonly used 100-year time scale, the GWP of $CH_4$ is 30 and that of $N_2O$ is 265, meaning that a unit mass of $CH_4$ or $N_2O$ causes 30 or 265 times more warming, respectively, than the same mass of $CO_2$ when integrated over a century (Myhre et al., 2013). Recently, we argued that the use of GWPs is inappropriate when calculating radiative balances for wetlands and other ecosystems (Neubauer & Megonigal, 2015) because ecosystems exchange greenhouse gases with the atmosphere year after year, not just as a one-time pulse. To address this issue, we proposed the sustained-flux global warming potential (SGWP), which is the "time-integrated radiative forcing due to sustained emissions of a given component, relative to sustained sequestration of an equal mass of $CO_2$" (Neubauer & Megonigal, 2015; Neubauer & Verhoeven, 2019). For a gas like $CH_4$, which has a much shorter lifetime than $CO_2$, the SGWP is very different from the GWP (45 vs. 30 over 100 years). In contrast, because $CO_2$ and $N_2O$ have similar average atmospheric lifetimes of roughly 100 years, the 100-year SGWP and GWP values of $N_2O$ are similar (270 vs. 263, respectively; Neubauer & Megonigal, 2015).

The choice of GWP vs. SGWP metrics has large implications for calculating radiative balances and radiative forcing, especially when $CH_4$ fluxes are involved. Using the SGWP instead of GWP would make a wetland appear to be a stronger greenhouse gas source (or, a weaker greenhouse gas sink). Although use of the GWP might be tempting here because "the numbers look better," one should be careful to use the most appropriate metric when calculating how wetland management and restoration activities will influence radiative forcing. Because the SGWP is based on continuous fluxes between ecosystems and the atmosphere, it is the better metric to use when looking at radiative balances in wetlands (Neubauer & Megonigal, 2015).

We have used the SGWP to calculate the radiative balance and radiative forcing for two hypothetical wetlands (Table 1). At Time 1, Wetlands 1 and 2 had a positive radiative balance over a 100-year period, indicating that the warming due to $CH_4$ emissions was greater than the cooling due to long-term carbon preservation in each wetland. For Wetland 1, the radiative balance was exactly the same in the two time periods because carbon sequestration and $CH_4$ emission rates did not change. Thus, the radiative forcing of Wetland 1 was zero (Table 1) and its contribution to Earth's energy budget had not changed over time. In contrast, the radiative balance in Wetland 2 was lower in Time 2 than in Time 1 due to a management action. This means that radiative forcing was negative, such that the perturbation (that is, the management action) applied to Wetland 2 had offset some of the climatic warming from fossil fuel combustion and land use changes. In this example, Times 1 and 2 correspond to any pair of years. In the context of the attribution of current climate change, the Intergovernmental Panel on Climate Change (IPCC) reports radiative forcing relative to the year 1750 (i.e., the pre-Industrial era; Myhre et al., 2013). Determining what the radiative balance of a wetland was more than 250 years ago presents considerable challenges.

Finally, please note that the GWP and SGWP are properties of greenhouse gases, not of an ecosystem. We sometimes see them incorrectly used as a synonym for radiative balance, as in the "global warming potential (GWP) was calculated in $CO_2$ equivalents" or "we observed a significant difference in GWP between aerobic and anaerobic treatments." We do not wish to single out specific authors, so we have purposely not provided citations for these quotes. Instead, our goal is to illustrate how these terms have been misused in the scientific community.

# 3 FACTORS CONTROLLING CARBON PRESERVATION

Wetlands are global hotspots for the preservation of organic carbon in terms of the total amount of preserved carbon (Sabine et al., 2004), the annual rate of carbon preservation (Mcleod et al., 2011), and the efficiency of carbon preservation (e.g., >5% of ecosystem net primary production stored in peatlands vs. <<1% in ocean sediments; Frolking et al., 2010; Hedges & Keil, 1995). From a climate perspective, organic carbon preserved in a wetland represents $CO_2$ that was fixed by primary producers in the wetland (or elsewhere) and therefore is no longer in the atmosphere acting as a greenhouse gas. The long-term preservation of organic carbon in wetland soils is the major reason why wetlands can have beneficial climatic effects (Frolking & Roulet, 2007). Below, we discuss factors that contribute to carbon preservation in wetland soils.

## 3.1 Carbon inputs

The magnitude of carbon inputs to a wetland determines the maximum rate of carbon preservation in that wetland, although the actual rate will be considerably lower due to decomposition of organic carbon and losses of gaseous, dissolved, and particulate carbon from the wetland (Figure 1). Carbon inputs can be autochthonous (originating within the system, e.g., $CO_2$ fixation by wetland plants) or allochthonous (originating from outside the system, e.g., inputs of sediment-associated carbon and terrestrial detritus). The importance of autochthonous vs. allochthonous inputs varies from one wetland to the next. For example, carbon inputs to ombrotrophic bogs are dominated by autochthonous production by *Sphagnum* mosses and other plants. In contrast, the ratio of autochthonous to allochthonous carbon inputs can be very different in tidal marshes and other wetlands that are regularly flooded by sediment-laden waters (e.g., Megonigal & Neubauer, 2019). In order to increase the rate of carbon preservation in a wetland, one could increase the inputs of poorly reactive organic matter to the wetland and/or change the environment to increase the carbon preservation efficiency. Note that changing the inputs of highly reactive organic matter or altering its rate of turnover does not directly affect the long-term rate of carbon preservation because highly reactive organic matter, by definition, is not preserved. However, inputs of highly reactive organic matter can enhance the decomposition of poorly reactive organic matter through priming effects (Bernal et al., 2017; Mueller, Jensen et al., 2016) and the decomposition process itself can change highly reactive organic matter into compounds with lower reactivity (Baldock et al., 2004; Jiao et al., 2010). Finally, spatiotemporal changes to the wetland environment can alter the reactivity of organic matter (Section 3.2).

### *3.1.1 Autochthonous production*

Primary production in wetlands can rival that in other highly productive systems such as tropical rain forests and agricultural systems (Millennium Ecosystem Assessment, 2005). Despite this generalization, there is considerable spatial and temporal variability in rates of primary productivity – both between and within wetlands – that is driven by factors including vegetation type, hydrology, climate, soil properties, and water quality. We focus here on production by higher plants but recognize that algal production can be substantial in some systems (e.g., Tobias & Neubauer, 2019 and references therein). Across a wetland landscape, spatial patchiness in vegetation assemblages can lead to greater temporal evenness in ecosystem carbon inputs compared to a system with more homogeneous vegetation (Korrensalo et al., 2020). Spatial variations in vegetation type can also influence carbon preservation since the chemistry of organic matter added to the soil varies with plant species (Belyea, 1996; Dunn et al., 2016; Kögel-Knabner, 2002). Regular hydrologic pulsing (e.g., tidal rhythms, seasonal river flooding) enhances productivity versus wetlands with stagnant water or continuous deep flooding (Brinson et al., 1981; Odum et al., 1995). Interannual variations in sea level cause corresponding changes in salt marsh plant productivity (Morris et al., 2002). Vegetation productivity and species composition responds to climate over both short and long periods (e.g., Cavanaugh et al., 2014; Feurdean et al., 2019; Johnson et al., 2005; Mendelssohn & Morris, 2000). Rising atmospheric $CO_2$ levels increases production rates of C3 wetland plants but not C4 plants (Caplan et al., 2015; Curtis et al., 1989; Fenner et al., 2007). This generalization is supported by wetland studies, but it is worth noting that C4 plants can show positive growth responses, albeit smaller responses than are seen in C3 plants (Ainsworth & Long, 2005; B. G. Drake, 2014; Wand et al., 1999). Increasing salinity reduces plant productivity (Sutter et al., 2014), even in plants that are adapted to growing in saline conditions (Mendelssohn & Morris, 2000), although this may be a transient response at the ecosystem scale if the plant assemblage shifts to become dominated by salt-tolerant plants (Herbert et al., 2015). Although wetlands are efficient at recycling inorganic nutrients (Hopkinson, 1992; Neubauer, Anderson et al., 2005), primary production often increases with allochthonous nutrient inputs (Brantley et al., 2008; Morris et al., 2002; Thormann & Bayley, 1997). Soil pH can influence plant productivity and community composition, especially in highly acidic conditions (Chapin et al., 2004; P. H. Glaser et al., 1990; MacCarthy & Davey, 1976). Interactions between these factors are common (e.g., Erickson et al., 2007; Langley & Megonigal, 2010), but discussing them is beyond the scope of this chapter.

### *3.1.2 Allochthonous inputs*

Wetlands can be sinks for a variety of allochthonous materials including sediment-associated carbon (discussed below), organic detritus, and atmospheric inputs of dust, ash, and pollen. Organic detritus can take the form of plant material (e.g., leaves, wood) from terrestrial systems (Fetherston et al., 1995; Holgerson et al., 2016) as well as phytoplankton, macroalgae, and seagrass detritus from aquatic environments (Hanley et al., 2017; Kon et al., 2012). Treatment wetlands receive allochthonous carbon inputs in sewage (Nag et al., 2019). Carbon inputs associated with dust, ash, and precipitation are not often measured and probably are not important carbon sources in most wetlands.

Allochthonous sediment-associated carbon can represent a major carbon input to wetlands that experience (semi)regular overbank flooding (González et al., 2014; Hupp et al., 2019; Neubauer et al., 2002). The deposition of allochthonous sediments varies as a function of suspended sediment availability in the water column; the degree of connectivity between the wetland and channel; the frequency, depth, and duration of tidal flooding; and the biomass and physical structure of vegetation (Friedrichs & Perry, 2001; Hupp, 2000). The erosion of sediments from terrestrial landscapes (Wilkinson & McElroy, 2007) has caused increased deposition of allochthonous sediment (and carbon) to some riverine and estuarine wetlands (Khan & Brush, 1994), but others have seen reduced sediment inputs due to reservoirs and levees that restrict sediment movement (Blum & Roberts, 2009; Cabezas et al., 2009). Because wetlands occupy local topographic low spots, they can be sinks for sediment that is eroded from surrounding upland ecosystems (Gleason & Euliss, 1998; McCarty & Ritchie, 2002; S. M. Smith et al., 2001), even in the absence of overbank flooding.

## 3.2 Mechanisms for carbon preservation

The preservation of organic carbon occurs because the multi-stage process of decomposition does not always proceed to completion. The emerging understanding of organic matter decomposition is that the chemical composition of organic matter is important during the early stages of decay but ecosystem properties drive the overall rates of decomposition (Conant et al., 2011; Lehmann & Kleber, 2015; Schmidt et al., 2011; Spivak et al., 2019). Organic carbon that might be highly resistant to decomposition under one set of environmental conditions may be quickly decomposed under a different set of conditions. By altering the wetland environment, management activities and disturbances have the potential to alter carbon preservation rates and (potentially) destabilize organic carbon that has accumulated over centuries to millennia (e.g., Dorrepaal et al., 2009; Hopple et al., 2020).

Below, we discuss the factors that contribute to efficient preservation of carbon in wetland soils. As an organizational framework, we have classified the controls on wetland carbon preservation into three categories: 1) the redox environment; 2) organic matter characteristics, and 3) physicochemical inhibition of decomposition. Many of these mechanisms are interlinked and could fall into multiple categories.

### ***3.2.1 Redox environment***

The presence of anoxic soils is a characteristic feature of wetlands and one that plays a key role in enhancing carbon preservation by affecting the efficiency of carbon metabolism, the composition of the decomposer community, and the activity of extracellular enzymes (Section 3.2.3.1). The diffusion of $O_2$ slows as soils become water-saturated, leading to typical $O_2$ penetration depths of millimeters to centimeters at the wetland soil surface and around the roots of vascular plants, where $O_2$ can leak into the soil through the process of root $O_2$ loss (Reddy & DeLaune, 2008). The importance of redox status for carbon preservation is visually apparent in wetlands where the drainage of organic soils causes noticeable declines in surface elevation from the degradation and loss of soil carbon (Figure 2). Rates of soil carbon mineralization are typically higher under aerobic vs. anaerobic conditions (Table 2; Chapman et al., 2019), although the initial decay of the most-reactive organic compounds may proceed at similar rates regardless of whether $O_2$ or an alternate terminal electron acceptor is used (Kristensen & Holmer, 2001). Bioturbation by crabs and other infauna mixes $O_2$ into the soil, increasing rates of soil carbon mineralization (Guimond et al., 2020). Litter decomposition can be higher in oxygenated hummocks than in low-oxygen hollows (Courtwright & Findlay, 2011).

#### *3.2.1.1 Anaerobic metabolism*

Where $O_2$ is depleted, a suite of anaerobic pathways can be used by microbes to mineralize organic carbon to $CO_2$ and/or $CH_4$. Thermodynamics dictates that the energy yield from the use of alternate electron acceptors proceeds in the order $NO_3^-$ (denitrification), Mn(III, IV) (manganese reduction), Fe(III) (iron reduction), humic acids (humic acid reduction), $SO_4^{2-}$ (sulfate reduction), and $CO_2$ (methanogenesis). In an idealized wetland soil, aerobic respiration would occur in surface soils to the depth where $O_2$ becomes depleted, whereupon denitrification would occur in deeper soils where $NO_3^-$ was available, followed next by the reduction of Mn oxides, and so on, following the thermodynamic order presented above. The same sequence of processes would be expected as one moves laterally away from a wetland plant root. In reality, multiple respiratory pathways can co-exist within the same volume of soil due to microscale variations in the availability of electron acceptors and electron donors (Angle et al., 2017; Oremland et al., 1982).

The availability of electron acceptors is important in determining which metabolic pathways are most important in any given wetland. Regardless of the thermodynamics at standard conditions, a reaction will not proceed at appreciable rates if its electron acceptor is present at low concentrations. Thus, low concentrations of $NO_3^-$ mean that denitrification often accounts for ≤1% of anaerobic carbon mineralization in wetland soils (e.g., Keller & Bridgham, 2007; Kristensen et al., 2011; Tobias & Neubauer, 2019). Similarly, differences in the abundance of Fe(III) explain why rates of Fe(III) reduction are trivial in peatland soils (Keller & Bridgham, 2007) but can account for the majority of anaerobic carbon turnover in soils with more mineral matter (Kostka et al., 2002; Neubauer, Givler et al., 2005; Roden & Wetzel, 1996; Yao et al., 1999). Likewise, $SO_4^{2-}$ limitation causes methanogenesis to be more important than $SO_4^{2-}$ reduction in freshwater wetlands (Neubauer, Givler et al., 2005; Weston et al., 2014), with the relative importance of these processes switching in brackish and saline wetlands as $SO_4^{2-}$ availability increases (Poffenbarger et al., 2011).

The resupply and regeneration of electron acceptors is necessary to maintain rates of soil metabolism. Soluble electron acceptors such as $NO_3^-$ and $SO_4^{2-}$ can diffuse into the anaerobic zone or be resupplied by the advective movement of water through the soil. In contrast, solid-phase electron acceptors such as Mn(III, IV) oxides and Fe(III) (oxyhydr)oxides are effectively regenerated *in situ* at aerobic–anaerobic interfaces, including the rhizosphere and walls of infaunal burrows (Gribsholt et al., 2003; Luo et al., 2018; Neubauer, Givler et al., 2005) or where moving water delivers $O_2$ to subsurface soils (Roychoudhury et al., 2003). Lastly, electron acceptors including Fe(III) and $SO_4^{2-}$ can be regenerated in wetlands through anaerobic chemoautotrophic reactions where the oxidation of $Fe^{2+}$ is coupled with the reduction of $NO_3^-$ (Straub et al., 2001) and the oxidation of reduced sulfur compounds proceeds with $NO_3^-$, $MnO_2$, or Fe(III) serving as the oxidant (Schippers & Jørgensen, 2002). The contribution of these chemoautotrophic reactions to anaerobic carbon cycling is largely unknown (Burgin & Hamilton, 2008; Carey & Taillefert, 2005; but see Schippers & Jørgensen, 2002).

The supply of electron donors is as important as the resupply/regeneration of electron acceptors in regulating anaerobic metabolism. The energetic potential of an electron donor (that is, its ability to give up electrons to an electron acceptor) can be summarized in thermodynamic concepts such as the nominal oxidation state of carbon (NOSC: LaRowe & Van Cappellen, 2011) and the oxidation state of organic carbon ($C_{ox}$; Masiello et al., 2008). For uncharged molecules, the difference between NOSC and $C_{ox}$ values is negligible (Hockaday et al., 2009) and we treat these terms as synonymous. Thermodynamic calculations and experimental culture work indicate that aerobic microbes can use a wide range of organic carbon molecules as electron donors, but anaerobic decomposers can use fewer substrates due to thermodynamic limitations (Keiluweit et al., 2016; LaRowe & Van Cappellen, 2011). As a group, $NO_3^-$ and metal reducers can use many organic molecules as electron donors, including amino acids, short- and long-chain fatty acids, some aromatic compounds, the monomers (e.g., glucose) resulting from extracellular enzymatic hydrolysis of polymers, and products of fermentation such as $H_2$, acetate, lactate, and pyruvate (Küsel et al., 1999; Megonigal et al., 2004; Reddy & DeLaune, 2008). Sulfate reducers are able to use many of the same electron donors (Christensen, 1984; Parkes et al., 1989; Sørensen et al., 1981), but some cannot use glucose and other monomers and thus are largely dependent on the activities of fermenters for electron donors (Reddy & DeLaune, 2008). The denitrifiers, metal reducers, and $SO_4^{2-}$ reducers can oxidize electron donors all the way to $CO_2$ (or to $H_2O$, when $H_2$ is the electron donor) or they can ferment larger molecules to acetate (Megonigal et al., 2004; Reddy & DeLaune, 2008). The thermodynamics of using $CO_2$ as an electron acceptor means that methanogens can use the smallest number of electron donors. Hydrogenotrophic methanogens use $H_2$ (and sometimes formate) as the electron donor while acetoclastic methanogens use acetate as both electron acceptor and electron donor, with some also able to use methanol, methylated amines, and methylated sulfur compounds (Bridgham et al., 2013).

#### *3.2.1.2 Decomposer communities*

The redox environment affects the community of bacterial and fungal decomposers, with fungal activity being greatly reduced under anaerobic conditions. Because fungi are capable of degrading poorly reactive molecules such as lignin and cellulose (Thormann, 2006), the suppression of fungal activity in anaerobic soils likely enhances carbon preservation. Fungi are often more important than bacteria in the initial decomposition of litter from wetland and riparian plants (Hieber & Gessner, 2002; Kuehn et al., 2000; Verma et al., 2003). Fungal abundances decline with depth from surface litter layers to wetland soil horizons, reflecting the lower $O_2$ availability in the soil (Ipsilantis & Sylvia, 2007). Fungal abundances in bulk anaerobic soil can be orders of magnitude lower than those of bacteria and archaea (Dang et al., 2019). Given their redox sensitivity, it is perhaps not surprising that fungal community composition, extracellular enzyme activities, and soil respiration rates respond to water level changes (Jassey et al., 2018). However, fungi may be able to transport $O_2$ into anaerobic soils, facilitating their own aerobic metabolism (Padgett & Celio, 1990), and obligately anaerobic fungi have been found in the deep biosphere and the guts of ruminants (H. Drake & Ivarsson, 2018 and references therein), raising questions about the true role of fungi as decomposers in anaerobic wetland soils.

### ***3.2.2 Organic matter characteristics***

The chemical composition and structure of organic molecules influences their reactivity and ultimate fate (mineralization vs. preservation) in wetlands. Organic matter has often been referred to as recalcitrant, meaning highly resistant to degradation, or labile, meaning highly susceptible to degradation. However, the reactivity of organic matter depends on the chemical composition of the organic molecule itself and the physicochemical environment. Therefore, we will avoid using the terms recalcitrant and labile and will instead talk about the reactivity of molecules, with the recognition that reactivity can vary between different environments (after LaRowe et al., 2020).

The chemistry of wetland organic matter depends, in part, on its source. For example, lignin makes up ~15-30% of woody tissue biomass, <10% of the biomass of vascular plants, and is absent in mosses (Benner et al., 1987; van Breemen, 1995). The concentration of the phenol sphagnum acid, which is only found in *Sphagnum* mosses, varies by an order of magnitude between different species (Rudolph & Samland, 1985). Phytoplankton and benthic microalgae have lower concentrations of structural carbohydrates (e.g., cellulose) than herbaceous or woody plants and, therefore, have lower ratios of carbon to nitrogen (N) (Sterner & Elser, 2002). Differences such as these can influence the preservation of various autochthonous and allochthonous carbon inputs.

#### *3.2.2.1 Carbon quality*

Major classes of organic matter include carbohydrates, proteins and amino acids, lipids, lignin, and tannins. The reactivity (or “quality”) of organic carbon varies as a function of factors including its elemental stoichiometry, bond structure, and the degree of oxidation (e.g., NOSC or $C_{ox}$). For example, lignin and tannins are phenolic compounds that contain aromatic ring structures that are difficult to cleave. Proteins and amino acids are rich in nitrogen whereas carbohydrates lack nitrogen entirely. Carbohydrates range from simple sugars (e.g., glucose) to large polysaccharides (e.g., cellulose, hemicellulose). Lipids are partially or completely hydrophobic and can have linear, branching, and ring structures.

These compound classes differ in their potential thermodynamic energy yield, as indicated by their nominal oxidation state of carbon (NOSC) (Table 3). The degree of organic matter oxidation and the physicochemical environment control which molecules are energetically available for microbial degradation and which are preserved (Boye et al., 2017; Pracht et al., 2018). Even molecules with a high potential energy yield can be preserved if they contain bonds that are difficult to cleave (e.g., those in phenolic rings) or if environmental conditions inhibit the activities of extracellular enzymes of the microbial decomposer consortium. This helps explain why, for example, there can be high concentrations of tannins in wetlands and surrounding "blackwater" aquatic systems, even though tannins have the highest NOSC of the major compound classes (Table 3). Similarly, the persistence of tropical peats despite warm temperatures is related to high concentrations of aromatic compounds (including phenolics) in low latitude peatlands (Hodgkins et al., 2018).

As organic carbon undergoes decomposition in wetlands, different molecules are preferentially mineralized or preserved, leading to changes in the composition of soil organic matter. The carbon in leaves, stems, and roots of herbaceous plants is more oxidized (higher NOSC) than that in woody plants, which is consistent with higher rates of decay of non-woody biomass (Randerson et al., 2006). Leaves with higher lignin concentrations decay more slowly than those with less lignin (Day, 1982; J. Hines et al., 2014). During decomposition, cellulose and hemicellulose decay faster than does lignin, as would be predicted by their NOSC values, and leads to changes in organic matter chemistry over time in both litter and soil (Baldock et al., 2004; Benner et al., 1987; Worrall et al., 2017).

The transformation of organic compounds during the decomposition process creates a large pool of soil organic matter of altered reactivity in a process called humification. There is debate as to whether humification generates an amalgamation of small, poorly characterized compounds (Sutton & Sposito, 2005), the synthesis of complex macromolecules with a higher molecular weight than the starting compounds (De Nobili et al., 2020), or if the entire idea of humification should be abandoned entirely (Lehmann & Kleber, 2015). Regardless, it is clear that the chemistry of soil organic matter does change during decomposition. For example, organic matter in deeper peats from bogs, fens, and swamps was more decomposed and less oxidized (lower NOSC) than surface peat, with most of the change happening within the top 50 cm (roughly the last 200 years) (T. R. Moore et al., 2018).

#### *3.2.2.2 Nutrient availability*

The carbon:nutrient ratio of plants is generally larger than that of soil bacteria and fungi, indicating an imbalance between the supply and demand for nutrients during decomposition (Hessen et al., 2004; Sterner & Elser, 2002). Indeed, litter decomposition studies often show an increase in nutrient concentrations over time, reflecting microbial immobilization of nutrients from the environment (e.g., Conner & Day, 1991). Litter decomposition is sensitive to nutrient availability in plant litter (Enríquez et al., 1993; Webster & Benfield, 1986) and/or the environment (Rejmánková & Houdková, 2006; Song et al., 2011). The degradation of plant litter can be limited by nitrogen availability, as indicated by negative correlations between litter C:N ratios and rates of decomposition (Keuskamp et al., 2015; Lee & Bukaveckas, 2002; Neely & Davis, 1985; Song et al., 2011). A similar pattern is seen with phosphorus (P), where higher litter phosphorus levels can lead to higher decomposition rates (J. Hines et al., 2014). The decomposition of leaf litter is generally limited by phosphorus when leaf N:P ratios are high and by nitrogen when leaf N:P ratios are low. Although there is not a universal N:P ratio that determines when the limiting nutrient changes (Güsewell & Freeman, 2005; Güsewell & Verhoeven, 2006), plants growing in organic wetland soils are more likely to be limited by phosphorus whereas plants in mineral substrates often are limited by nitrogen availability (Bedford et al., 1999). There can be interactions between nutrient availability and carbon quality, with higher nutrient levels stimulating decomposition to a greater degree when leaf litter is of higher quality (i.e., lower lignin content) (Hobbie, 2000). Alternately, the effects of low carbon quality may limit decomposition regardless of nutrient availability (Bridgham & Richardson, 2003).

### ***3.2.3 Physicochemical inhibition of decomposition***

Physicochemical inhibition preserves carbon through physical or chemical interferences with microbial decomposition processes. We define inhibitory factors as those that prevent mineralization from proceeding at the potential rate set by the free energy yield of the dominant redox couples. We treat inhibition as a distinct category but acknowledge that it interacts strongly with mechanisms that operate through the redox environment (i.e., $O_2$ availability) and the chemical composition of organic matter.

#### *3.2.3.1 Phenolic inhibition*

Phenolic compounds can accumulate and inhibit decomposition under conditions that limit the activity of phenol oxidase, the enzyme that degrades phenolics. Because phenol oxidase requires $O_2$ to function, its activity generally is low in fully anaerobic soils, increases in surface soils, and is greatest in aerobic surface litter (Wright & Reddy, 2001). Although other extracellular enzymes involved in carbon mineralization exhibit low activities at lower $O_2$ concentrations (Freeman, Ostle et al., 2004; McLatchey & Reddy, 1998), this is probably not a direct effect of $O_2$ since hydrolytic enzymes do not require $O_2$ to function. Instead, low $O_2$ concentrations result in low phenol oxidase activity, allowing phenolic compounds to accumulate and inhibit hydrolytic enzymes (Figure 3) (Fenner & Freeman, 2011; Freeman, Ostle et al., 2001). So, the $O_2$-related inhibition of phenol oxidase activity does not just affect the decomposition of lignin and other phenolic compounds, it inhibits the breakdown of multiple classes of organic carbon and acts as an "enzymic latch" that preserves large quantities of carbon in organic wetland soils (Freeman, Ostle et al., 2001). The activity of phenol oxidase is also inhibited by moisture limitation, which may help limit carbon mineralization during droughts when soil $O_2$ concentrations increase (H. Wang et al., 2015).

The enzymic latch mechanism may be most important in wetlands with lignin-poor vegetation (e.g., those dominated by *Sphagnum* mosses) and/or those with low soil iron contents (Y. Wang et al., 2017). Although phenol oxidase activity increases in some wetlands with water table drawdown (that is, increased $O_2$ penetration into the soil), this is not a universal response. Instead of being restricted by low soil $O_2$, the activities of phenol oxidase and hydrolytic enzymes can be enhanced in the presence of $Fe^{2+}$ (Van Bodegom et al., 2005; Hall & Silver, 2013; Liu et al., 2014) and, therefore, may decline following a sustained water table drawdown (Y. Wang et al., 2017). This “iron gate” mechanism differs from the enzymic latch and suggests that increasing soil oxidation in mineral soil wetlands may help protect against the decomposition of lignin (Y. Wang et al., 2017).

#### *3.2.3.2 Physical protection*

Organic matter can be physically protected from decomposition through chemical associations with mineral surfaces, by being physically inaccessible in soil pores, or as a result of encapsulation by humic materials. The importance of these mechanisms has been well-illustrated by studies in terrestrial soils and marine sediments, where organic matter associated with mineral particles can be preserved for thousands of years yet is rapidly mineralized once desorbed (Keil et al., 1994; Nelson et al., 1994). For wetlands, more than half of the soil carbon pool could be protected by minerals at low soil carbon concentrations, but the mineral-protected fraction necessarily drops as soil carbon concentrations increase (Needelman, Emmer, Emmett-Mattox et al., 2018).

Evidence from soils and sedimentary systems indicates that interactions between organic carbon and mineral particles play a role in carbon preservation (Hedges & Keil, 1995; Hemingway et al., 2019; Mayer, 1994a; Torn et al., 1997). In this respect, aluminosilicate clays are especially important due to ionic surface charges and the high surface area to mass ratio of these smallest sediment particles. Early research suggested that organic carbon uniformly coated aluminosilicate minerals in a monolayer (Keil et al., 1994; Mayer, 1994b), but it now seems that distribution of organic matter is discontinuous across the mineral surface. Some areas of the aluminosilicate minerals are carbon-free, whereas other regions contain organic carbon that is strongly adsorbed to the mineral plus an outer zone characterized by hydrophobic interactions between sorbed molecules and those in solution (Kleber et al., 2007). Physical sorption appears to be especially important in protecting organic molecules with low C:N ratios (e.g., amino acids, proteins) through electrostatic bonds between negatively charged portions of the clay and positively charged organic side chains (Aufdenkampe et al., 2001). Hydrophobic organic molecules in solution can interact with the hydrophobic end of molecules sorbed directly to the mineral surface, creating a membrane-like layer that provides a degree of protection to the outermost layer of organic molecules (Kleber et al., 2007). Further, the surface of aluminosilicate minerals contains a multitude of pores of various sizes that 1) increase surface area versus a (theoretical) pore-free mineral and 2) exclude microbial and/or enzymatic access to sorbed organic molecules (Jastrow et al., 2007). In sandy subtropical marsh soils, the organic matter found in pores of 6 μm diameter (versus those of ~200 μm) had a greater thermodynamic potential (i.e., higher NOSC), a larger level of chemical complexity, and a higher degree of microbial reactivity (Bailey et al., 2017). Similarly, ~20% of the amino acid nitrogen in an Arctic tussock soil was physically isolated in pores (Darrouzet-Nardi & Weintraub, 2014). At the nanoscale, even the smallest extracellular enzymes are largely excluded from pores with diameters ≤ 8 nm (Mayer, 1994a; Zimmerman et al., 2004). Typical pore sizes vary with mineralogy (Dalal & Bridge, 1996), but pore diameters are often < 8 nm (Mayer, 1994a), implying that organic carbon preservation in pores is a widespread mechanism.

Organic matter can be chemically stabilized through sorption and coprecipitation with Fe(III) (oxyhydr)oxides (Kaiser & Guggenberger, 2000; Lalonde et al., 2012) or by forming a noncrystalline floc with $Fe^{2+}$ (Henneberry et al., 2012). For example, the aeration of porewater from a fen removed 27% of the dissolved organic carbon (DOC) due to coagulation with newly formed Fe(III) hydroxides (Riedel et al., 2013) and salt marsh soils had up to 50% of their soil organic carbon stabilized due to associations with Fe(III) (oxyhydr)oxides (Cui et al., 2014). Protection by iron helps explain why lignin is preferentially preserved in wetland soils. Iron minerals strongly sorb phenolic molecules (Riedel et al., 2013) and inhibit the mineralization of lignin but not that of bulk soil organic matter (Hall et al., 2016). At redox interfaces like the wetland plant rhizosphere, there is dynamic redox cycling of Fe (e.g., Weiss et al., 2004) where the microbial and chemical dissolution of Fe(III) can release sorbed carbon into solution (Chin et al., 1998; Knorr, 2013). However, many wetlands contain solid-phase Fe(III) as a coating on vascular plant roots, in shallow soils where atmospheric $O_2$ penetration occurs, and as Fe-rich concretions (R. M. Chambers & Odum, 1990; Duan et al., 1996; Emerson et al., 1999; Mendelssohn et al., 1995). While there is an overall decline in Fe(III) with increasing soil depth (Cutter & Velinsky, 1988; Griffin et al., 1989), oxidized iron can persist under anaerobic conditions over geologically relevant time scales (Haese et al., 1997). We have focused here on the preservation of organic carbon, but wetlands can contain measurable amounts of inorganic carbon in the form of siderite ($FeCO_3$) (Duan et al., 1996; Hansel et al., 2001; T. Wang & Peverly, 1999).

Lastly, proteins and amino acids can become encapsulated in humic acids and protected from hydrolysis. In soils and sediments, humic acid fractions can be hundreds or thousands of years old yet have high concentrations of amide and amino nitrogen, forms of organic matter which often are highly reactive (e.g., Hedges & Keil, 1995; Knicker et al., 1996; Mahieu et al., 2002; Zang et al., 2000). The humic acids may be forming a micelle-like structure that traps reactive organic molecules within the hydrophobic interior of the structure (Zang et al., 2000), which is consistent with observations that hydrophobic organic contaminants also have a high affinity for humic acids (De Paolis & Kukkonen, 1997). This protective mechanism may be most important at low pH where humic acids form structures with a lower surface–volume ratio (versus a chainlike structure at higher pH), which enhances the ability of the humic materials to physically trap organic matter (Myneni et al., 1999). Given the low pH of many peatlands and their general paucity of mineral matter, the encapsulation of organic matter by humic acids in peat is likely to be more important than interactions with aluminosilicate clays or iron minerals.

#### *3.2.3.3 pH*

Wetland soils span a wide range of pH values, from bogs and pocosins with pH values of ~4 or less to riparian floodplains and other wetlands where the pH can exceed 7.5 (e.g., Jacob et al., 2013; Richardson, 2003). We focus here on low pH wetlands since that is where pH has the largest inhibitory effect on carbon mineralization. Rates of $CH_4$ production and emission are low in acidic wetlands and increase when pH is experimentally increased (Dunfield et al., 1993; Ye et al., 2012). The suppression of $CH_4$ emissions by low pH occurs through direct inhibitory effects on the hydrogenotrophic and acetoclastic methanogenic pathways as well as interference with the fermentative processes that generate the substrates used by methanogens (Ye et al., 2012). Atmospheric acid deposition also depresses $CH_4$ emission rates, although this effect is mediated by the competitive suppression of methanogenesis by $NO_3^-$ and/or $SO_4^{2-}$ rather than a direct pH effect (Gauci et al., 2004; Watson & Nedwell, 1998). Rates of soil carbon mineralization to $CO_2$ are also limited by low pH due to the inhibitory effects of pH on fermentation (Ye et al., 2012), the suppression of phenol oxidase activity (Williams et al., 2000; Xiang et al., 2013), a microbial community characterized by slow-growing bacteria (Hartman et al., 2008), and/or the encapsulation of reactive organic matter by humic acids (Section 3.2.3.2). Experimental increases of soil pH in the lab often lead to higher rates of $CO_2$ production (e.g., Ye et al., 2012) although a multi-year field experiment found a decrease in soil $CO_2$ production rates in response to increased pH, perhaps because the native microbial community was well-adapted to the original low pH environment (Keller et al., 2005).

#### *3.2.3.4 Temperature*

Temperature affects the efficiency of carbon preservation through several related mechanisms. Firstly, biological processes such as decomposition generally slow down at cooler temperatures, as demonstrated for multiple indices of decomposition including litter decay, soil enzyme activities, biological oxygen demand, $CO_2$ and $CH_4$ production and emissions to the atmosphere, and the hydrologic export of dissolved organic and inorganic carbon (Freeman et al., 2001; Kadlec & Reddy, 2001; Miller et al., 2001; Neubauer & Anderson, 2003; Segers, 1998; Treat et al., 2014). Rates of peat decomposition are negligible at temperatures below 0°C and increase sharply as the liquid water content increases in warmed permafrost soils (Dioumaeva et al., 2003). Secondly, temperature sensitivities can vary within the consortium of decomposers, with subsequent effects on the efficiency of carbon mineralization. Terminal metabolizers (e.g., $SO_4^{2-}$ reducers) can be more sensitive to temperature than are fermenters, thus leading to the accumulation of fermentation products (e.g., acetate) at lower temperatures and the limitation of terminal metabolism by the (low) abundance of these compounds at higher temperatures (e.g., Fey & Conrad, 2003; Weston & Joye, 2005). Indeed, in some high latitude wetlands, acetate is the terminal end product of anaerobic decomposition (Duddleston et al., 2002; M. E. Hines et al., 2001). Thirdly, changing temperatures can result in vegetation shifts that change the nature of organic matter inputs to the soil. Along a 40-year progression of permafrost thaw, rates of potential $CO_2$ and $CH_4$ production were highest in the sites that had been thawed the longest, a difference mediated by indirect role of temperature in changing vegetation assemblages and, therefore, the chemistry of organic matter inputs to the soil (Hodgkins et al., 2014). While cold temperatures contribute to wetland carbon preservation, the existence of tropical peatlands is strong evidence that temperature is not the only driver (Hodgkins et al., 2018).

# 4 GREENHOUSE GAS EMISSIONS AND OTHER LOSSES

Wetlands are fundamentally open ecosystems that exchange gases, dissolved compounds, and particulate matter with the atmosphere, surrounding terrestrial ecosystems, and aquatic environments. A simple mass balance perspective illustrates that whatever autochthonous and allochthonous carbon is exported from a wetland is, necessarily, not preserved within the wetland (Figure 1). Management actions can manipulate the factors that cause carbon loss in order to reduce carbon export or change the form of exported carbon to a more climatically benign form.

## 4.1 Greenhouse gas emissions

### *4.1.1 Carbon dioxide ($CO_2$)*

On a mass basis, $CO_2$ almost always accounts for the majority of wetland greenhouse gas emissions. Growth and maintenance respiration by autotrophs produce $CO_2$, with rates of autotrophic respiration typically returning ~40–50% of gross primary production to the atmosphere (Dai & Wiegert, 1996). The mineralization of dissolved and particulate organic carbon within wetland soils also produces $CO_2$ that is emitted directly to the atmosphere or dissolved into wetland porewaters. Because $CO_2$ is an end product of most terminal metabolic pathways, the same factors that enhance carbon preservation (Section 3.2) will tend to reduce rates of $CO_2$ production, emission, and export.

Wetland $CO_2$ emissions are affected by a variety of climate-related disturbances. Drought increases soil $O_2$ levels and can remove the enzymic latch that inhibits extracellular enzyme activities in moss-dominated peatlands (Freeman, Ostle et al., 2001) but not necessarily in tree/shrub-dominated wetlands due to differences in the quantity and types of phenolic compounds produced by the different vegetation types (H. Wang et al., 2015). The drying and warming of wetland soils can stimulate root productivity, especially in shrubs (Malhotra et al., 2020). With increasing atmospheric $CO_2$ levels, enhanced plant productivity and shifts in species composition (Caplan et al., 2015; Erickson et al., 2007) have the potential to prime the decomposition of soil carbon through inputs to the soil of $O_2$ and/or highly reactive organic matter from enhanced root growth, inclusive of root exudates (Bernal et al., 2017; A. A. Wolf et al., 2007). In some peatlands exposed to elevated $CO_2$, the activity of the extracellular enzymes β-glucosidase and phenol oxidase decreased (Fenner et al., 2007) or did not change (Kang et al., 2005), perhaps because reactive carbon was not limiting at those sites. Using elevation change as a proxy, elevated $CO_2$ enhanced belowground productivity and increased soil carbon storage in a brackish tidal marsh (Langley et al., 2009).

The intrusion of saline water into freshwater systems can affect wetland–atmosphere $CO_2$ exchanges. Net ecosystem production is often depressed by saltwater intrusion (Herbert et al., 2018; Neubauer, 2013) but can be unchanged in some years or in response to transient salinity increases (Herbert et al., 2018). The changes in net ecosystem production reflect salinity-related declines in plant $CO_2$ fixation (Neubauer, 2013; Sutter et al., 2014) and variable heterotrophic respiration responses to increased salinity (Herbert et al., 2015). Changes in heterotrophic respiration could reflect a shift from methanogenesis to energetically-favorable $SO_4^{2-}$ reduction (Weston et al., 2011), reduced activity of extracellular enzymes (Jackson & Vallaire, 2009; Neubauer et al., 2013), or indirect effects that are mediated through soil organic matter availability and composition, microbial community structure, soil $O_2$ availability, and/or nutrient availability (Herbert et al., 2015; Tully et al., 2019).

Fire is an increasingly common feature in many wetlands, especially during drought or periods of seasonal water drawdown (Hope et al., 2005; Turetsky, Kane et al., 2011) and intentional land clearing activities (Marlier et al., 2015). Fire represents a pathway for the abiotic oxidation of wetland biomass and soil organic matter, generating emissions of $CO_2$ (and much smaller amounts of $CH_4$; Kuwata et al., 2016). Surface fires cause a short-term burst of $CO_2$ emissions as surface vegetation and litter are burned but may promote a decrease in long-term $CO_2$ emissions if thermally altered organic matter becomes more resistant to microbial decomposition (Flanagan et al., 2020). Smoldering fires can burn tens of centimeters of soil organic matter, converting hundreds to thousands of years of accumulated carbon back to $CO_2$ and significantly increasing global $CO_2$ emissions (Page et al., 2002; Turetsky et al., 2015; Turetsky, Donahue et al., 2011).

#### *4.1.2 Methane ($CH_4$)*

Under anaerobic conditions, the final step of the mineralization of organic carbon results in the production of $CH_4$, which is carried out by a subset of the Archaea called methanogens (Bridgham et al., 2013; Megonigal et al., 2004). Methane emissions to the atmosphere reflect the balance between rates of $CH_4$ production (methanogenesis) and $CH_4$ oxidation (methanotrophy). Methane also can be produced abiotically by the burning of vegetation and peat, which can be especially important in years when large peatland fires occur (Kuwata et al., 2016). The last fifteen years have seen reports of aerobic $CH_4$ production by plants (Bruhn et al., 2012; Keppler et al., 2006), fungi (Lenhart et al., 2012), soil macrofauna (Kammann et al., 2009), and in the water column (Damm et al., 2010; Grossart et al., 2011); the importance of these pathways in wetlands is unknown. Globally, wetlands are the largest source of $CH_4$ to the atmosphere, with natural wetlands accounting for 30% of all $CH_4$ emissions (natural + anthropogenic) and paddies associated with rice cultivation adding another 5% to the total (Saunois et al., 2016). Although $CH_4$ is a powerful greenhouse gas, wetland $CH_4$ emissions are not contributing to recent climate change, except to the extent that these emissions have changed in the last ~250 years (Section 2).

Methanogenesis has the lowest yield of the terminal metabolic pathways so it tends to be most important when other terminal metabolic pathways are limited by low rates of electron acceptor resupply/regeneration and/or when supply rates of acetate, $H_2$, and other suitable electron donors are high enough to relieve competition with other anaerobic decomposers. The production of $CH_4$ typically requires anaerobic conditions, such that rates of $CH_4$ emissions are inversely related to soil $O_2$ levels (Smyth et al., 2019) and rates of methanogenesis drop sharply in response to decreases in wetland water levels (MacDonald et al., 1998; T. R. Moore & Knowles, 1989). Oxygen inputs can stimulate aerobic respiration (Mueller, Jensen et al., 2016; A. A. Wolf et al., 2007) and/or reoxidize alternate terminal electron acceptors (Laanbroek, 2010; Neubauer, Givler et al., 2005), such that methanogens may be unable to successfully compete for electron donors. Rates of methanogenesis also can be suppressed by the delivery of alternate terminal electron acceptors – largely $NO_3^-$, Fe(III), and/or $SO_4^{2-}$ – from saltwater intrusion (L. G. Chambers et al., 2013; Kroeger et al., 2017; Neubauer et al., 2013), fertilizer runoff (Bodelier, 2011; Kim et al., 2015), atmospheric deposition (Gauci et al., 2004; Watson & Nedwell, 1998), and river flooding (Luo et al., 2020).

There is tight coupling between plant activity and $CH_4$ emissions (Whiting & Chanton, 1993), in part because plants produce low molecular weight organic molecules that can be used by methanogens (Dorodnikov et al., 2011; Megonigal et al., 1999). Plants can also prime the decomposition of soil organic matter (Basiliko et al., 2012; Bernal et al., 2017), thus providing substrates that fuel methanogenesis. Plant species composition affects $CH_4$ cycling (Kao-Kniffin et al., 2010) due to differences in the reactivity of carbon supplied by each vegetation type (e.g., Chanton et al., 2008). Humic substances inhibit the production of $CH_4$, either through direct competition between microbial humic reducers and methanogens or, alternately, by abiotically reoxidizing reduced sulfur compounds and therefore supporting sulfate reducers that outcompete the methanogens (Heitmann et al., 2007; Keller, Weisenhorn et al., 2009). The polyphenol sphagnum acid and the polysaccharide sphagnan, both of which are produced by *Sphagnum* mosses, can interfere with methanogenic activity (van Breemen, 1995; Bridgham et al., 2013) and help explain why some peatlands have low rates of methanogenesis despite low concentrations of inorganic terminal electron acceptors such as Fe(III) and $SO_4^{2-}$ (Galand et al., 2010; Keller & Bridgham, 2007; Vile et al., 2003).

Methanotrophy, which oxidizes $CH_4$ to $CO_2$, can proceed aerobically using $O_2$ as the electron acceptor or anaerobically using the entire suite of alternate terminal electron acceptors (Bridgham et al., 2013). Whether a wetland emits gas as $CH_4$ or $CO_2$ is unimportant in the context of a wetland's carbon budget but has large implications for the radiative balance of the wetland. On a global basis, the aerobic oxidation of $CH_4$ can prevent 40–70% of the $CH_4$ produced in wetlands from reaching the atmosphere (Megonigal et al., 2004), but it is rare that annual wetland $CH_4$ oxidation exceeds methanogenesis (that is, very few wetlands are net sinks for CH4; Bridgham et al., 2006; Harriss et al., 1982; Petrescu et al., 2015). Beyond the first-order control that the aerobic oxidation of $CH_4$ requires $O_2$, the availability of $O_2$ can regulate methanotrophy when there is a narrow aerobic zone, when $CH_4$ spends little time in the aerobic zone before being emitted to atmosphere (as would happen when most $CH_4$ emissions are via ebullition and/or transport through plants), and/or when rates of $CH_4$ production are high (Megonigal et al., 2004). Conversely, methanotrophy can be limited by the availability of $CH_4$ when rates of $CH_4$ production are low and/or there is a large diffusive aerobic zone (Megonigal & Schlesinger, 2002). High concentrations of ammonium ($NH_4^+$) inhibit methane oxidation because both $CH_4$ and $NH_4^+$ compete for the same sites on the enzyme methane monooxygenase (Bodelier & Frenzel, 1999; Crill et al., 1994). However, it is also possible that methanotrophs can be nitrogen limited, such that fertilization increases rates of $CH_4$ oxidation (Bodelier et al., 2000). Like all biological processes, rates of aerobic methanotrophy increase with increasing temperatures, although methanotrophy is less sensitive to temperature than is methanogenesis (Segers, 1998).

Rates of the anaerobic oxidation of $CH_4$ can be of the same magnitude as aerobic oxidation (Smemo & Yavitt, 2007) and, globally, may be comparable to the total $CH_4$ emissions from freshwater wetlands (Segarra et al., 2015). Rates of anaerobic oxidation of $CH_4$ in wetlands and wet soils are correlated with rates of $CH_4$ production (Blazewicz et al., 2012; Segarra et al., 2015). The anaerobic oxidation of $CH_4$ can be coupled with the reduction of $NO_3^-$ or nitrite ($NO_2^-$)

(Hu et al., 2014; Raghoebarsing et al., 2006), Mn(III, IV) and Fe(III) (Beal et al., 2009; Egger et al., 2015), humic acids (Smemo & Yavitt, 2011; Valenzuela et al., 2017), or $SO_4^{2-}$ (Egger et al., 2015; Knittel & Boetius, 2009). It is not always straightforward to identify which electron acceptors drive the oxidation of $CH_4$ (Gupta et al., 2013; Segarra et al., 2013), but the electron acceptor likely varies in freshwater vs. saline wetlands, organic vs. mineral soils, and oligotrophic vs. eutrophic sites, as is the case for terminal metabolism (Section 3.2.1.1 above).

#### *4.1.3 Nitrous oxide ($N_2O$)*

Although this chapter is focused on carbon, we will briefly discuss the emissions of $N_2O$. Recent global wetland emissions of $N_2O$ are “negligible” (Anderson et al., 2010), but management activities and environmental changes have the potential to increase emissions of this powerful greenhouse gas. The production of $N_2O$, which is a byproduct of both denitrification and nitrification, is largely controlled by nitrogen availability and soil redox status (Davidson et al., 2000). Nitrous oxide emissions are greatly enhanced in wetlands exposed to high nutrient loading (Hefting et al., 2003; Moseman-Valtierra et al., 2011) and inversely related to soil C:N ratios (Klemedtsson et al., 2005). Further, peatlands that experience drought or anthropogenic lowering of the water table have higher $N_2O$ emissions than those with a high water table (Pärn et al., 2018; Prananto et al., 2020). The production of $N_2O$ is also affected by the availability of electron acceptors and electron donors, concentrations of hydrogen sulfide, temperature, and pH (Cornwell et al., 1999; Joye & Hollibaugh, 1995; Megonigal et al., 2004; Pärn et al., 2018; Parton et al., 1996).

#### *4.1.4 Emission pathways*

There are three major pathways by which gases produced in wetland soils can be emitted to the atmosphere: diffusion, transport through plants, and ebullition. The rate of diffusion of gases out of a wetland soil is a function of the concentration gradient between soil pore spaces and the overlying water column or atmosphere, the wetness of the soil, and the amount of atmospheric/water column turbulence (Lai, 2009; Le Mer & Roger, 2001). Because molecular diffusion is a relatively slow process, rates of $CH_4$ oxidation can be more important when diffusion is the major route of export from the wetland (Bridgham et al., 2013). However, while a low water table increases the distance $CH_4$ has to diffuse through oxidized soils and therefore provides more opportunities for the aerobic oxidation of $CH_4$ (Roslev & King, 1996), this can occur at the radiative expense of higher rates of $N_2O$ production (Pärn et al., 2018).

The aerenchyma tissues that allow vascular wetland plants to transport $O_2$ to their roots permits gases produced in soils to be efficiently vented through plants by passive diffusion or (faster) convective gas flows (Colmer, 2003). Gas transport through both herbaceous and woody plants can account for a substantial portion of total wetland $CH_4$ emissions (Covey & Megonigal, 2019; Gauci et al., 2010; Neubauer et al., 2000; Pangala et al., 2017; Whiting & Chanton, 1992). Methane that is transported through plants spends less time in oxidized surface soils and therefore is less susceptible to being oxidized to $CO_2$ (Joabsson et al., 1999), although $CH_4$ oxidation can be enhanced in the rhizosphere due to root $O_2$ loss (van Bodegom et al., 2001). There is a temporal coupling between $CH_4$ production and emission in vegetated wetlands but this relationship breaks down in unvegetated sediments because the lack of vegetation reduces $CH_4$ emissions and promotes transient $CH_4$ storage (Reid et al., 2013) that leads to enhanced ebullition.

Ebullition (bubbling) occurs when the local hydrostatic pressure decreases due to changes in temperature, air pressure, and water levels (Chanton et al., 1989; Männistö et al., 2019; Tokida et al., 2007), allowing gas bubbles to rise. As with plant-mediated gas transport, the rapid vertical movement of gas bubbles allows $CH_4$ to quickly transit active $CH_4$ oxidation regions (Lai, 2009). Rates of ebullition are spatially patchy and temporally variable but can be the major route of $CH_4$ transport from some wetlands (Devol et al., 1988; Goodrich et al., 2011; Walter et al., 2006). The importance of ebullition can be substantially lower for $CO_2$ and $N_2O$ due to their higher solubility (McNicol et al., 2017). Because gas transport through plants helps prevent the accumulation of gases in soil pore spaces (Reid et al., 2013), ebullition is likely to be most important in unvegetated wetlands or those with few vascular plants (Stanley et al., 2019).

## 4.2 Export of dissolved organic and inorganic carbon

Wetland soils contain high concentrations of dissolved organic and inorganic carbon that can be exported to adjacent surface water and groundwater systems. Quantifying the export of dissolved forms of carbon requires accurate measures of water flow, which is especially challenging where flows are bidirectional (e.g., in tidal wetlands) or diffuse (that is, not in defined channels). The issue is further complicated by the fact that some – but not all – of the carbon exported from wetlands will end up in the atmosphere as $CO_2$ or $CH_4$. Therefore, accurately describing the climatic impacts of a wetland requires the accurate quantification of how much dissolved carbon is exported from the wetland and the ultimate fate of that carbon (that is, emissions to atmosphere vs. long-term preservation) in downstream aquatic systems.

### *4.2.1 Dissolved organic carbon*

Wetlands are a major source of DOC to streams, lakes, rivers, and estuaries (Childers et al., 2000; Kristensen et al., 2008; Mulholland & Kuenzler, 1979). DOC export rates depend on DOC concentrations in soil pore spaces, leaching that occurs directly into the water column (e.g., of plant litter), and flows of water through the wetland (Dinsmore et al., 2013; Jager et al., 2009; K. C. Petrone et al., 2007). The DOC concentrations in streams draining peat-dominated catchments have been increasing (Freeman, Evans et al., 2001) as have DOC concentrations in many rivers and lakes (Evans et al., 2005; Monteith et al., 2007; Skjelkvåle et al., 2005). The DOC exported from tidal wetlands has distinctive optical properties such as high DOC-specific absorption, low spectral slope, and high fluorescence that reflect its relatively high molecular weight and aromatic-rich structure compared to estuarine-derived DOC (Tzortziou et al., 2008), a property that can be used to observe DOC sourced from tidal wetlands using remote sensing (Cao et al., 2018).

Climate change and alterations in atmospheric chemistry have the potential to increase rates of wetland DOC export. Rising air temperatures increase wetland DOC concentrations and cause DOC to become enriched in phenolic compounds (Freeman, Evans et al., 2001), thereby inhibiting DOC degradation in receiving systems (Freeman et al. 1990). Similarly, there is generally greater DOC export from tropical vs. boreal peatlands (Drösler et al., 2014). In boreal and alpine regions, melting permafrost is leading to higher DOC export from wetlands to aquatic systems (Frey & Smith, 2005), with evidence that this DOC is rapidly consumed by heterotrophic bacteria or degraded through photochemical mechanisms (T. W. Drake et al., 2015; Selvam et al., 2017). Rising atmospheric $CO_2$ concentrations increase plant productivity in peatlands and enhance DOC exudation from plants, contributing to increased rates of DOC export (Freeman, Fenner et al., 2004). Similarly, salt marshes respond to elevated $CO_2$ with higher porewater DOC concentrations, but only in the plant communities that exhibit $CO_2$-related increases in growth (C3 but not C4 plants; Keller, Wolf et al., 2009; Marsh et al., 2005). There can be synergies between elevated $CO_2$ and warming that further increase DOC export (Fenner et al., 2007). The observed increases in DOC export can also be related to the recovery from acidification due to atmospheric deposition (Monteith et al., 2007), driven by the increased solubility of organic matter at higher pH (Evans et al., 2012; Pschenyckyj et al., 2020).

The export of DOC from peatlands is sensitive to water discharge (Dinsmore et al., 2013; Pastor et al., 2003), which can vary due to changes in precipitation, storage within the wetland, and/or losses to evapotranspiration. Since climate change is altering the frequency and severity of precipitation events (Hartmann et al., 2013), this could affect DOC export by changing the water balance or making export more flashy (Holden, 2005). Following large rain events, there are increased inputs of DOC to aquatic systems (Jager et al., 2009; Paerl et al., 2018) that can cause hypoxia and anoxia in downstream aquatic systems (Paerl et al., 1998). In colder climates, changes in the balance between snow and rain, plus earlier melting of the snowpack, can change the timing of DOC export (Billett et al., 2012).

The DOC exported from wetlands is generally “modern” in age (that is, post-1950), which is consistent with shallow flow paths of water through surface soils (Billett et al., 2012; Evans et al., 2007; S. Moore et al., 2013; Raymond & Hopkinson, 2003). However, the recent origin of exported bulk DOC can mask inputs of smaller amounts of millennial-aged DOC, which can be mineralized upon entry to the aquatic system (Dean et al., 2019). In aquatic systems, DOC from wetland and terrestrial systems is subject to microbial mineralization, photochemical oxidation, and flocculation in lakes, streams, rivers, and estuaries (Cole et al., 2007). Much of this processing occurs in freshwater lentic and lotic systems. The relatively short transit time from estuaries to the coastal ocean suggests that DOC exported from estuarine wetlands (e.g., salt marshes) is likely not metabolized within estuaries (Cai, 2011). Although the chemical structure of terrestrial DOC should make it resistant to decay – certainly in comparison to phytoplankton-derived DOC – very little terrestrial DOC is found in the ocean (Blair & Aller, 2012; Cai, 2011; Hedges & Keil, 1995).

### *4.2.2 Dissolved inorganic carbon and methane*

Wetlands can export inorganic carbon as dissolved $CH_4$, dissolved $CO_2$ (plus small amounts of carbonic acid, $H_2CO_3$), bicarbonate ($HCO_3^-$), and carbonate ($CO_3^{2-}$). For consistency with the literature, we use the term dissolved inorganic carbon (DIC) to refer to the sum of dissolved $CO_2$, $HCO_3^-$, and $CO_3^{2-}$; dissolved $CH_4$ will be mentioned specifically when we are talking about that molecule. Wetland porewaters are often supersaturated with inorganic carbon that can diffuse into overlying water when a wetland is flooded or can be advectively transported out of the wetland into adjacent water bodies. The observed supersaturation of $CO_2$ in both freshwaters (Butman & Raymond, 2011; Regnier et al., 2013) and estuaries (Cai, 2011; Chen et al., 2013) is partially due to DIC exports from wetlands (Cai & Wang, 1998; Neubauer & Anderson, 2003; Richey et al., 2002; Tzortziou et al., 2011).

The export of DIC is a function of porewater DIC concentrations and hydrology. The DIC concentrations are sensitive to the factors that affect rates of soil respiration and the emission of $CO_2$ to the atmosphere (Section 4.1.1). In regularly inundated tidal marsh soils, the DIC export to the estuary parallels seasonal patterns in marsh productivity and respiration (Neubauer & Anderson, 2003; Z. A. Wang & Cai, 2004). In contrast, when hydrology is less consistent, water flow has a controlling role on DIC export. For example, precipitation events serve to transfer porewater DIC into adjacent aquatic systems (Butman & Raymond, 2011). Similarly, dissolved gases that accumulate in soil during winter can be flushed out during the spring thaw (Billett & Moore, 2007).

Below, we use DIC flux studies from two wetlands – an acid peat bog in the Central Valley of Scotland and a tidal freshwater marsh in Virginia, U.S.A. – to illustrate the importance of water chemistry on $CO_2$ evasion. The hydrologic export of DIC represented a sizeable route of carbon loss from each system (Dinsmore et al., 2010; Neubauer & Anderson, 2003). In the stream draining the peat bog, roughly 90% of the exported DIC was emitted to the atmosphere as $CO_2$ within the local catchment (Dinsmore et al., 2010). In contrast, as water drained from the marsh, only ~2-6% of the exported DIC was emitted to the atmosphere during a single ebb tide (Neubauer & Anderson, 2003). In both sites, $CO_2$ evasion to the atmosphere would continue with additional downstream transport until equilibrium with the atmosphere was achieved. The lower atmospheric evasion of wetland-derived DIC in the marsh compared to the peatland reflects the effects of pH on DIC partitioning. The low pH of stream water at the peatland (annual pH means of 4.5–4.8; Billett et al., 2004) means that the vast majority of the DIC was exported as dissolved $CO_2$. In contrast, the pH of the marsh tidal creek was 6.4–7.2, such that 19% of the DIC was exported as dissolved $CO_2$ and the remainder as $HCO_3^-$ and $CO_3^{2-}$ (Neubauer & Anderson, 2003). Because carbonate alkalinity does not change due to $CO_2$ evasion (Frankignoulle, 1994), the 81% of the DIC exported as $HCO_3^-$ and $CO_3^{2-}$ acts as a longer carbon sink and may be exported through the estuary to the ocean. The exported alkalinity also plays a role in buffering pH changes in aquatic systems (Sippo et al., 2016). It is worth noting that high turbulence, as occurs in shallow, fast-moving streams like the one draining the Scottish peat bog (Dinsmore et al., 2010), can speed the rate of gas evasion but would not change the amount of wetland-produced $CO_2$ that would ultimately be emitted from the aquatic system to the atmosphere.

Methane can be exported from wetland soils to adjacent water bodies where, because of its low solubility, it will quickly equilibrate with the atmosphere. This can be a substantial pathway of $CH_4$ loss. In a tidal salt marsh, the export of $CH_4$-supersaturated porewater to a tidal creek, followed by degassing, was as important as $CH_4$ diffusion across the marsh–atmosphere interface (Bartlett et al., 1985). In a temperate freshwater wetland, nearly a third of the annual $CH_4$ emissions were released from the water (Poindexter et al., 2016). In peatlands, the emissions of $CH_4$ from the surface of streams and ponds is on the order of 2-5% of the diffusive soil–atmosphere fluxes (Billett & Moore, 2007; Dinsmore et al., 2010).

## 4.3 Erosion and losses of particulate carbon

Wetlands can export particulate organic carbon (POC) through erosion, hydrologic transport, feeding activities, and direct anthropogenic activities including peat extraction and timber harvesting. Once POC is mobilized, its fate depends on the chemistry of the exported carbon and the environment to which it is transported. In some cases, POC can be redistributed and stored in aquatic sediments or even redeposited back onto the wetland (Hopkinson et al., 2018). However, when POC is solubilized or mineralized to $CO_2$ or $CH_4$, a large fraction is likely to be returned to the atmosphere (e.g., Brown et al., 2019) and the wetland could change from a net carbon sink to a source (Pawson et al., 2012). A related question concerns the fate of soil carbon in coastal wetlands that are drowned by rising sea levels: Will the soil and its preserved carbon stay intact after the vegetation is lost or will it be eroded and dispersed? This is an area of much uncertainty (e.g., DeLaune & White, 2012; Needelman, Emmer, Emmett-Mattox et al., 2018; Pendleton et al., 2012).

Erosion of tidal marshes, peatlands, and other wetlands can represent an important vector for the transport of soil carbon into adjacent aquatic systems. The potential importance of POC exports via erosion can be inferred from metrics like the drainage density (that is, km of channel per km$^2$ of wetland) or the extent of wetland edge (Pawson et al., 2012). There is abundant evidence that aboveground plant biomass can reduce erosion by dissipating turbulence and wave energy, even under storm surge conditions (Duarte et al., 2013; Gedan et al., 2011; Möller et al., 2014). Belowground, the network of intact roots and rhizomes helps bind soils, increasing their shear strength and resistance to erosion (Micheli & Kirchner, 2002). Thus, reductions in plant biomass – aboveground or belowground – can make the wetland more susceptible to erosion and losses of particulate organic carbon (Deegan et al., 2012; Shuttleworth et al., 2015; Silliman et al., 2012; Walter et al., 2006). Surface soils in wetlands can be mobilized by rain events (Mwamba & Torres, 2002; Tolhurst et al., 2006). Marsh biota can also facilitate erosion, either directly through activities like bioturbation (S. M. Smith & Green, 2013) or indirectly through grazing that removes the stabilizing influence of wetland vegetation (T. J. Smith & Odum, 1981; Visser et al., 1999).

Particulate organic carbon can be exported as water moves across wetland surface or as the biomass of consumers that feed in the wetland. In tidal wetlands, for example, large accumulations of dead plant material (“wrack”) can be redistributed within a wetland or exported to the estuary, especially during spring tides and large storms (Hackney & Bishop, 1981; Hemminga et al., 1990). Aquatic, terrestrial, and avian consumers are able to forage on the wetland surface, consuming organic matter and removing it when they leave the wetland (Fritz & Whiles, 2018; Gurney et al., 2017; Kitti et al., 2009; Klopatek, 1988; Wantzen et al., 2002), but this likely does not impact long-term carbon preservation.

Lastly, POC can be lost from wetlands through directed anthropogenic activities. The extraction of peat for fuel and horticultural purposes removes the preserved soil carbon and results in the emission of $CO_2$ back to the atmosphere through combustion or decomposition (Cleary et al., 2005). Further, peat extraction typically destroys the living vegetation, resulting in the loss of the wetland carbon sink (Waddington et al., 2010). The logging of forested wetlands can be specifically for harvesting timber (Hutchens et al., 2004) or may be incidental to preparing a site for agriculture or aquaculture (Page et al., 2009; Richards & Friess, 2016). Some wetlands are used directly for grazing of livestock or the plants are harvested for off-site use (Harrison et al., 2017; Morris & Jensen, 1998; D. C. Smith et al., 1989). Whenever significant amounts of primary production are removed, wetland soil carbon pools and long-term preservation rates can be affected (Morris & Jensen, 1998).

# 5 MANAGEMENT OF WETLAND CARBON PRESERVATION AND FLUX

Carbon capture, preservation, and flux are foundational processes that govern all facets of wetland ecosystem function, and are thus both the target of, and a response to, management activity. Wetland management and disturbance intentionally or unintentionally affect the biogeochemical mechanisms that preserve organic matter, with consequences for coupled element cycles such as nitrogen mineralization. Here we consider how biogeochemical processes can be manipulated to increase carbon preservation, decrease greenhouse gas emissions, or improve water quality. Our goal is to highlight some common management actions rather than provide a thorough overview of this topic; we leave that to the collective efforts of the other authors in this volume.

## 5.1 Managing the redox environment

The redox environment, organic matter characteristics, and physicochemical inhibition are biogeochemical mechanisms that can be manipulated to enhance wetland carbon preservation. From a management perspective, the most important of these is redox, which leverages the large difference in free energy yield of microbial respiration in the presence versus absence of $O_2$. Redox manipulation is the goal of the age-old technique of raising or lowering water table depth through structures that drain or impound water (McCorvie & Lant, 1993; Rozsa, 1995), and a largely unintended consequence of other activities such as tree thinning in forested wetlands (Jutras et al., 2006) and road construction (Winter, 1988). Draining removes water from soil pore spaces, dramatically increasing the rate of $O_2$ diffusion into the rooting zone. As the rate of $O_2$ flux rises to exceed $O_2$ demand, aerobic respiration becomes the dominant microbial respiration pathway, leading to faster decomposition rates and a decline in soil carbon stocks (Armentano & Menges, 1986).

Subsidence of the soil surface is a nearly universal consequence of prolonged drainage because many wetland soils are carbon-rich and carbon loss translates into a loss of soil mass and volume (Figure 2). As such, subsidence is a useful metric of soil organic matter stock change in peatlands and other wetlands with organic-rich soils. The relative contributions of microbial respiration, compaction, fire, and wind erosion to soil elevation change can be modeled to infer that accelerated microbial respiration is a primary driver of elevation loss (Deverel et al., 2016; Ewing & Vepraskas, 2006). As expected of redox-driven organic matter preservation, subsidence is positively related to water table depth below the soil surface, and rates are higher at sites where the water table is drawn down continuously rather than where it fluctuates seasonally (Carlson et al., 2015; Stephens et al., 1984). Rates of subsidence are fastest during the years immediately following the drawdown of the water table and slow as the soil surface approaches the lowered water table (Figure 2). This is related to multiple factors including a decline in the volume of soil located in the aerobic zone, decreases in organic matter quality as the most reactive compounds are preferentially lost, and enrichment in soil mineral content as the organic fraction is decomposed (Bhadha et al., 2009).

The global impact of drainage on soil carbon stocks was originally estimated by Armentano and Menges (1986) at 239–319 Mt $CO_2$ $yr^{-1}$ in 1980. Subsequent estimates are larger by a factor of 4 or more with rates of 1,298 Mt $CO_2$ $yr^{-1}$ in 2008 (Joosten, 2010). The increase reflects continuing carbon losses from historical drainage (Drexler et al., 2009; Hooijer et al., 2012) and extensive new drainage activity in tropical peatlands, where peat loss to microbial respiration can be comparable to $CO_2$ emissions from instantaneous oxidation due to fire (Couwenberg et al., 2010; Hergoualc'h & Verchot, 2014). Vast areas of tidal marshes have been drained and "reclaimed" for agriculture in China (Ma et al., 2014) and mangrove forests are excavated for shrimp and salt ponds, releasing large amounts of soil carbon (Kauffman et al., 2014). The global impact of land use/land cover change on coastal wetlands, riparian wetlands, and peatlands is to decrease net $CO_2$ uptake by 70–457% compared to their natural state (Tan et al., 2020). The sole exception to this pattern is the creation of relatively fresh wetlands from saline coastal wetlands, which perhaps increases NPP by relieving salt stress, although (from a radiative forcing perspective) this may be offset by increased $CH_4$ emissions.

Hydrologic restoration to wetland vegetation (Knox et al., 2015) or rice agriculture (Deverel et al., 2016) can dramatically slow the rate of soil organic carbon loss but recovery of soil carbon stocks requires decades to centuries (Craft et al., 2003; O'Connor et al., 2020; Sasmito et al., 2019). Rewetting tends to reduce $CO_2$ emissions (Wilson et al., 2016; Xu et al., 2019) with the magnitude of change varying with factors such as climate, site nutrient status, antecedent water table depth, and chemical composition of soil organic matter.

Counterintuitively, rewetting can increase $CO_2$ emissions in some circumstances (R. M. Petrone et al., 2003; Waddington et al., 2010). There are instances where wetland responses to drainage or drought do not follow the expected pattern of increased $CO_2$ emissions and soil carbon loss (Laiho, 2006; H. Wang et al., 2015), results that run counter to expectations based solely on redox control of decomposition rates and reflect regulation by other factors. For example, poor substrate quality prevented an increase in soil respiration in response to three years of experimentally imposed drought in a minerotrophic fen (Muhr et al., 2011); rewetting increased decomposition in a peatland because a preceding drought triggered an increase in enzyme activity (Bonnett et al., 2017); and drought or drainage can suppress decomposition rates indirectly through plant community composition changes that favor species with phenolic-rich tissue (H. Wang et al., 2015).

### 5.2 Managing organic matter characteristics

Chemical composition and the structure of chemical bonds strongly influence the preservation of organic matter. The wide variety of methods used to quantify chemical composition reflects the chemical complexity of organic matter including the content of specific classes of organic compounds (Section 3.2.2.1); ratios involving specific elements such as C:N ratio or lignin:N ratio; and quantification of functional organic matter moieties such as the O-alkyl carbon content or syringyl-to-vanillyl ratio. Chemical composition is applied to wetland management primarily for understanding decomposition responses to disturbance or manipulation. For example, aerobic microbial respiration rates across a depth sequence of soils from a drained peatland was well explained by the abundance of O-alkyl carbon (Figure 4), suggesting that soil carbon quality data can be used to improve models of soil carbon loss in response to drainage or drought (Leifeld et al., 2012).

Organic matter composition is rarely the direct target of wetland ecosystem management activities. Perhaps the most common management application for plant chemical composition control of decomposition is in the design of wetlands for wastewater treatment, in which C:N ratios are manipulated to maximize nitrogen removal while minimizing greenhouse gas emissions. A review of constructed wetland designs concluded that a ratio of chemical oxygen demand to nitrogen of 5:1 optimizes nitrogen removal versus $N_2O$ in free-flowing systems, and a C:N ratio of 5:1 minimizes $CH_4$ emissions in vertical subsurface systems (Maucieri et al., 2017). Such ratios can be manipulated through selection of plant species that vary in C:N ratio, lignin content, or other relevant traits (Moor et al., 2017). Similarly, there may be opportunities during wetland restoration projects to select plant species that will promote carbon preservation, while also balancing other project objectives.

Wood has chemical and physical properties that can be leveraged for management of restoration of herb-dominated wetlands. For example, Fenner and Freeman (2020) proposed that wood amendments preserve soil carbon during drought, a technique that is untested in the field but founded on a well-developed understanding of the physicochemical inhibition of decomposition by phenolic compounds. Similar considerations suggest that sequestration rates can be improved by encouraging higher woody plant species cover, a process that is occurring unintentionally through climate-driven invasion of herbaceous-dominated tidal marshes by woody mangrove species (Doughty et al., 2016). The high lignin content of wood is the basis of adding wood chips to restored wetland soils in order to reduce compaction and therefore the negative effects of restoration construction on plant growth (E. C. Wolf et al., 2019).

Plant chemical composition is one of several interacting factors that set the molecular structure of soil organic matter (Kögel-Knabner, 2002; Schmidt et al., 2011), which is an important control on the soil carbon pool response to disturbance. A history of $O_2$ exposure results in compounds that are resistant to decomposition under aerobic conditions, making the ecosystem less responsive to periodic drought or drainage (Muhr et al., 2011). Carbon mineralization rates in drained wetlands generally decline over time as surficial, labile carbon pools are lost, a pattern due in part to the increasing age and declining carbon quality of soil organic matter with increasing soil depth (Evans et al., 2014; Leifeld et al., 2012). Lab incubations designed to isolate factors such as chemical composition suggest that the sensitivity of soil organic matter decomposition to $O_2$ availability varies widely among wetland ecosystem types (Table 2), as does the potential to produce $CH_4$ under anaerobic conditions (Chapman et al., 2019). Thus, the potential for rewetting to reduce both $CO_2$ emissions and $CO_2$-equivalent $CH_4$ emissions varies considerably and for reasons that are not well understood.

### 5.3 Managing physicochemical Inhibition

The availability of $O_2$ regulates carbon preservation through mechanisms other than the often-cited high free energy yield of aerobic respiration, a thermodynamic constraint on decomposition rates. By contrast, kinetic constraints are imposed by the activity of extracellular enzymes required to break chemical bonds. As discussed earlier (Section 3.2.3.1), the enzymic latch hypothesis states that the absence of $O_2$ triggers a series of events leading to the accumulation of phenolic compounds, which inhibit the hydrolase enzymes that cleave organic bonds (Figure 3; Freeman, Ostle et al., 2001). The hypothesis has been invoked to explain slow decomposition rates in peatlands and to speculate that the concentration of inhibitory phenolics could be manipulated to suppress decomposition rates in peatlands (Freeman et al., 2012). Raising the water table depth achieves this by limiting $O_2$ availability, but it may be possible to achieve similar results by altering pH, adding reductants, or manipulating plant traits through genetic engineering or plant species composition (Freeman et al., 2012).

The response of extracellular enzymes such as phenol oxidase to management can be complex and generate a wide range of carbon responses ranging from increased carbon preservation to increased carbon mineralization. In an elaboration of the enzymic latch hypothesis, the increase in enzyme activity and decomposition rate triggered by $O_2$ exposure leads to higher nutrient availability and soil pH, which in turn increases decomposition in a positive feedback loop that persists for months to years after the soil has been rewetted (Bonnett et al., 2017; Fenner & Freeman, 2011). Another nuance of the enzymic latch hypothesis is that drainage or drought may inhibit phenol oxidase activity due to low soil water content. Under such conditions, rewetting will increase the activity of the enzyme and stimulate decomposition rates (H. Wang et al., 2015). Management activities based on assumptions about water level controlling decomposition rate should also consider the response of inhibitory phenolic compounds.

Microbial access to organic matter can be physically inhibited by mineral-carbon interactions that operate in intact wetlands via sorption onto surfaces and co-precipitation of DOC (Hedges & Keil, 1995; Lalonde et al., 2012). Mineral soils tend to be rich in Fe- and Al-oxides that preserve organic matter by forming bonds and physical structures that interfere with microbial degradation (LaCroix et al., 2018), so increasing the availability of minerals could enhance carbon preservation. Dredged sediments from navigation channels are sometimes used to create new wetland islands or are added to tidal marshes to increase elevation (Cornwell et al., 2020; Streever, 2000). The ability of dredge spoils to enhance the preservation of wetland carbon through physical inhibition of decomposition depends on whether their mineral surfaces are already saturated with organic carbon, which is likely to be site specific. Some deltaic sediments tend to have less than a monolayer-equivalent coating of organic carbon due to enhanced mineralization resulting from $O_2$ exposure during periodic reworking events (Blair et al., 2004), but we do not know the extent to which this applies to river and harbor sediments. Organic-mineral interactions are promoted in the wetland plant rhizosphere by root $O_2$ loss driving deposition of poorly crystalline iron oxides (Weiss et al., 2005), some of which are stable under anaerobic conditions (Henneberry et al., 2012; Shields et al., 2016). Drainage triggers ferrous iron oxidation and increases mineral protection of organic matter, provided there is sufficient iron in the soil to support this carbon-stabilizing process (LaCroix et al., 2018). The possibility that iron amendments could be used to stabilize carbon in drained soils has not been investigated to our knowledge. Biochar amendments may enhance wetland carbon preservation by altering microbial assemblages and stabilizing existing organic-mineral complexes (Zheng et al., 2018); the same mechanism helps explains the high-organic *terra preta* soils in the Amazon basin (B. Glaser & Birk, 2012).

Soil pH also exerts strong control on decomposition rates and is negatively correlated with soil carbon preservation. Regulation of extracellular enzyme activity is one mechanism by which pH interferes with decomposition and has been cited as a reason why soil carbon pools sometimes increase in response to drainage or decrease in response to rewetting (Fenner & Freeman, 2011). In northern peatlands, pH exerts indirect control on soil carbon stocks by favoring *Sphagnum* species that decompose slowly (low pH) or vascular species that decompose relatively quickly (high pH). Thus, pH manipulation to favor one functional plant group over another is one option for altering carbon preservation (e.g., Beltman et al., 2001).

Temperature regulates the rates of all biological, physical, and chemical processes that control organic matter decomposition, and is another physicochemical factor that may cause unexpected soil carbon responses to drainage. For example, short-term lab and field drainage in wet tussock tundra tends to increase soil organic matter decomposition rates, as expected, but feedbacks operating at larger spatiotemporal scales involving plant community shifts and their effects on snow cover, albedo, and thermal balance have the potential to slow permafrost degradation and preserve soil carbon (Göckede et al., 2019). Feedbacks involving wetland responses to a warming planet include shifting plant distributions, changing estuarine salinity distributions, and altered wetland hydrology, all of which can directly or indirectly impact the preservation of wetland carbon. Incorporating large-scale feedbacks into wetland management activities is a contemporary challenge.

### 5.4 Managing greenhouse gas emissions

The emission of greenhouse gases is one of several ecosystem processes to consider when managing, restoring, or conserving wetlands. Greenhouse gas management is challenging because wetlands tend to simultaneously act as $CO_2$ sinks and $CH_4$ or $N_2O$ sources. Management decisions based solely on greenhouse gas emissions have the potential to create perverse incentives leading to degraded ecosystem function. However, there are many opportunities to reduce greenhouse gas emissions as one goal of overall ecosystem management because wetland greenhouse gas emissions typically increase in response to land use/land cover change (Figure 5; Tan et al., 2020).

Tan et al. (2020) performed a meta-analysis of the greenhouse gas consequences of land use/land cover change (LULCC) on coastal wetlands, riparian wetlands, and peatlands and found that anthropogenic disturbances increase radiative forcing by 65–2,949% compared to their natural state (Figure 5), amounting to 0.96 ± 0.22 Gt $CO_2$-eq $yr^{-1}$, which is equivalent to ~8–10% of annual global emissions due to LULCC. Changing emissions of $CO_2$ contributed to radiative forcing because ecosystem respiration increased more than did gross primary production, reflecting the fact that wetland LULCC frequently involves drainage. The direction of LULCC on $CH_4$ emissions is typically opposite that of $CO_2$, with systems changing from net sources of $CH_4$ to smaller net sources (or sinks) due to increased $O_2$ flux (Knox et al., 2015). Radiative forcing from $N_2O$ occurs when LULCC activities are accompanied by nitrogen loading from fertilizer or manure. Reducing fertilizer applications and managing runoff from agricultural fields that drain to wetlands is one option for managing $N_2O$ emissions (Verhoeven et al., 2006)

Coastal wetlands have the potential to sequester carbon at relatively high rates while emitting $CH_4$ at low rates (Poffenbarger et al., 2011), making them attractive for ecosystem management and carbon financing projects (Needelman et al. 2018, Moomaw et al. 2018). Hydrologic restoration and management of degraded sites tends to increase soil carbon sequestration, achieving rates similar to natural sites after two decades in many cases (Craft et al., 2003; O'Connor et al., 2020). However, the increase in carbon sequestration can be accompanied by an increase in $CH_4$ emissions resulting in net radiative forcing (O'Connor et al., 2020). Uncertainty in spatiotemporal variation in $CH_4$ emissions and the factors that regulate this variation are a significant barrier to wetland management for greenhouse gas reduction (Holmquist et al., 2018).

The global potential to manage wetlands for greenhouse gas reductions is limited by their area and the biogeochemically imposed trade-off between $CO_2$ preservation and $CH_4$ emissions. Yet, wetland management can make a significant contribution to nature-based climate solutions (Fargione et al., 2018). For example, at least 27% of U.S. coastal marshes have been freshened due to tidal restrictions, so the restoration of (saline) tidal rhythms could reduce radiative forcing by 12 Tg $CO_2$-eq $yr^{-1}$ by reducing $CH_4$ emissions (Fargione et al., 2018; Kroeger et al., 2017). Reconnecting wetlands to (freshwater) rivers through the construction of large-scale river diversions could also suppress $CH_4$ emissions by supplying $NO_3^-$, Fe(III) oxides, and $SO_4^{2-}$, although these effects may be limited to the immediate vicinity of the diversions (Holm et al., 2016). In the U.S., the radiative balance of $CO_2$ and $CH_4$ fluxes is favorable for restoring peatlands and seagrass meadows (9 and 6 Mg $CO_2$-eq $ha^{-1}$ $yr^{-1}$, respectively), and for avoided losses of seagrass (7 Mg $CO_2$-eq $ha^{-1}$ $yr^{-1}$; Fargione et al., 2018). In cases where wetland restoration or creation would cause greenhouse gas emissions to increase (O'Connor et al., 2020), techniques such as transplanting intact soils and plants can minimize these impacts by avoiding soil disturbances that otherwise favor greenhouse gas emissions (Moomaw et al., 2018 and references therein). Methane emissions often vary between patches of different vegetation types (Kao-Kniffin et al., 2010; Mueller, Hager et al., 2016; Villa et al., 2020) due to a variety of plant traits that affect the production, oxidation, and transport of $CH_4$ (Moor et al., 2017; Section 4.1.4). This suggests that greenhouse gas emissions could be managed in restoration projects through careful selection of plant species composition. To do so, it is important to realize that the influence of different plant traits on $CH_4$ emissions cannot be entirely understood from short-term flux measurements because they fail to capture ebullition and hydrologic export. For example, Bansal et al. (2020) reported that short-term $CH_4$ fluxes were 5-times higher from planted vs. plant-free sediments, but when they accounted for pulses of $CH_4$ release, total emissions were equal between sites. Thus, the influence of plant species must account for the full $CH_4$ budget and not rely entirely on inferences based on diffusive flux rates. One challenge to implementing wetland activities in carbon financing systems is projecting how the greenhouse gas balance will change over a century time scale (Needelman, Emmer, Oreska et al., 2018).

## 5.5 Managing dissolved organic carbon export

Wetland management can alter rates of wetland DOC export, with implications for both climate and water quality. Wetland-derived DOC affects the color of aquatic systems, which can be seen by the casual observer as the tea-colored water draining from swamps and organic-rich soils. This colored DOC reduces the penetration of visible and ultraviolet light through the water column, can alter temperature gradients and vertical stratification, and affects primary production and food web structure (Schindler et al., 1996; Wetzel, 1992; Williamson et al., 1999, 2015). In aquatic systems, DOC also alters acid-base interactions, often by reducing the acid-neutralizing capacity (Driscoll et al., 1994), and can alter the bioavailability of metals including aluminum, copper, and lead (Brooks et al., 2007; Landre et al., 2009; McAvoy, 1988).

Anthropogenic disturbances including drainage, deforestation, and fire can substantially change DOC dynamics and the chemical composition of the exported DOC (S. Moore et al., 2013; Rixen et al., 2016; Strack et al., 2008; Urbanová et al., 2011). The drainage of wetlands increases DOC export (Drösler et al., 2014; Kreutzweiser et al., 2008; S. Moore et al., 2013; Rixen et al., 2016). The rewetting of wetlands can return DOC export rates to pre-drainage levels, although there may be a short-term DOC pulse during the initial stages of rewetting (Blain et al., 2014). Further, disturbances such as drainage and deforestation cause an increasing fraction of the DOC to be derived from preserved soil carbon rather than recent plant production (Gandois et al., 2013; S. Moore et al., 2013). Over time, the depletion of soil carbon due to disturbance can reduce the export of DOC (Sippo et al., 2019). Fires in peatlands can cause a short-term increase in DOC concentrations and export (Clay et al., 2009; Olivares et al., 2019; Zhao et al., 2012) but a decrease over the longer-term (1-10 years post-fire; Shibata et al., 2003; Worrall et al., 2007). The effects of fire on DOC export may be less important than the effects of climate change in northern peat-dominated catchments (Burd et al., 2018). Lastly, wetlands export substantially more DOC per unit area to aquatic systems than do other land use types (Raymond & Hopkinson, 2003) so where wetlands have been lost, there likely has been a substantial reduction in the amount of DOC export (Kristensen et al., 2008; Raymond et al., 2004).

## 6 CONCLUSIONS

The redox environment, organic matter characteristics, and physicochemical factors are well understood to be the fundamental attributes that determine the capacity of wetlands to capture, preserve, and release carbon. Just one of these – the redox environment – has been the focus of most management-informed research and management activities. Yet, even this relatively rich body of knowledge has proven insufficient to accurately predict counter-intuitive responses that have been observed in response to drainage or impoundment. Developing a more robust predictive capacity for carbon-focused management activities in wetlands requires a nuanced application of the biogeochemical processes discussed in this chapter. Examples include the responses of extracellular enzymes to water table manipulation and the influence of plant traits related to $O_2$ transport on rates of organic matter decomposition, $CH_4$ production, and $CH_4$ oxidation. Advances in wetland carbon biogeochemistry can be incorporated into management plans to enhance carbon preservation, prevent the destabilization of accumulated soil carbon, and reduce greenhouse gas emissions, thus maintaining the role of wetlands as regulators of global climate. Given the present limits on our ability to optimize wetland creation and restoration for specific carbon and greenhouse gas emission goals, it is wise to prioritize conservation of existing wetland carbon stocks over restoration and management (Moomaw et al., 2018; Neubauer & Verhoeven, 2019). In addition to the biogeochemical considerations we have discussed in this chapter, the cost effectiveness of various restoration and management actions (e.g., Taillardat et al., 2020) has real-world implications for how wetlands are managed. Managing wetlands for climate regulation should be one facet of a comprehensive plan that also considers valuable co-benefits of wetlands including water quality improvement, wildlife support, water storage, and cultural services.

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## TABLES

**Table 1:** Radiative balance and radiative forcing for two hypothetical wetlands at two time periods.

| Wetland | Time | Long-term carbon preservation rate | $CH_4$ emission rate | | Radiative balance | Radiative forcing |
|---|---|---|---|---|---|---|
| | | (g $CO_2$ $m^{-2}$ $yr^{-1}$) | (g $CH_4$ $m^{-2}$ $yr^{-1}$) | (g $CO_2$-eq $m^{-2}$ $yr^{-1}$) | (g $CO_2$-eq $m^{-2}$ $yr^{-1}$) | (g $CO_2$-eq $m^{-2}$ $yr^{-1}$) |
| Wetland 1 | Time 1 | 75 | 10 | 450 | 375 | 0 |
| | Time 2 | 75 | 10 | 450 | 375 | |
| Wetland 2 | Time 1 | 150 | 40 | 1800 | 1650 | -1080 |
| | Time 2 | 150 | 16 | 720 | 570 | |

For Wetland 1, we assume there is no change in rates of carbon preservation or $CH_4$ emission over time. For Wetland 2, we assume that a management action lowered $CH_4$ emissions but did not affect long-term carbon preservation. Note that the carbon preservation and $CH_4$ emission rates are mass fluxes (e.g., kg $CH_4$ per area per time, not kg C or mol C per area per time). The $CH_4$ mass flux is converted to a $CO_2$-equivalent ($CO_2$-eq) flux by multiplying the mass flux by the 100-year SGWP value of 45 (Neubauer & Megonigal, 2015). The radiative balance of a site is the difference between the warming due to $CH_4$ emissions and the cooling due to carbon preservation, with a positive radiative balance indicating that the wetland has a net warming effect over a 100-year period. Radiative forcing is the difference in the radiative balance between the two time periods, with negative radiative forcing indicating that a wetland is having a smaller warming effect (or a greater cooling effect) in Time 2 vs. Time 1.

**Table 2:** Ratios of aerobic to anaerobic metabolism in different wetland types.

| | Aerobic : anaerobic ratio | |
|---|---|---|
| Wetland type | $CO_2$ production | $CO_2$ + $CH_4$ production |
| bog | 3.8 ± 3.7 | 4.3 ± 1.8 |
| fen | 7.0 ± 8.2 | 6.5 ± 7.6 |
| moor | 2.9 ± 1.3 | *n.a.* |
| swamp | 3.8 ± 1.1 | 5.0 ± 0.7 |
| tropical wetland | 16.0 ± 10.3 | 13.4 ± 9.4 |
| pocosin | 2.2 ± 0.7 | *n.a.* |
| Overall mean | 7.1 ± 1.2 | 8.2 ± 11.6 |

Values are means ± standard errors. n = 2 to 15 per wetland type. *n.a.* indicates data were not available for that wetland type. Data from Chapman et al. (2019)

**Table 3:** Nominal oxidation state of carbon for major classes of organic matter.

| Compound | NOSC |
|---|---|
| $CO_2$ | + 4 |
| tannins | + 0.64 |
| carbohydrates | + 0.03 |
| lignin | - 0.27 |
| protein | - 0.82 |
| lipids | - 1.34 |
| $CH_4$ | - 4 |

Average NOSC values for organic matter in sulfidic floodplain sediments are from Figure S4 in Boye et al. (2017). The NOSC values for other systems and sites will vary depending on the identity of the specific molecules that make up each broad class of organic matter. Values for $CO_2$ and $CH_4$ were calculated following LaRowe and Van Cappellen (2011)

## FIGURE LEGENDS

**Figure 1:** Wetland carbon inflows, outflows, and preservation. Only a small fraction of the carbon inputs to a wetland is typically preserved over decades to centuries, with an even smaller fraction preserved for millennia. The sizes of the arrows are illustrative of the relative magnitude of different carbon flows in some wetlands, but the figure does not represent any specific wetland type.

**Figure 2:** Subsidence due to peatland drainage in California, Florida, Malaysia, Sumatra, and the United Kingdom. Data for the United Kingdom are from Hutchinson (1980); all other data were extracted from Hooijer et al. (2012). Curves with dashed lines indicate that individual data points were not available for plotting.

**Figure 3:** Effects of $O_2$ availability on enzyme activity and organic matter decomposition. A cascade starts when increased $O_2$ supply stimulates microbial aerobic respiration (A), triggering increased phenol oxidase synthesis (B) and a decline in inhibitory phenolics (C). Lower inhibition causes higher hydrolase activity (D) and organic matter decomposition (E) releasing $CO_2$ and nutrients (E), which can feed back on microbial activity through pH effects related to $CO_2$ production and nutrition effects due to release of nitrogen, phosphorus, and other nutrients. After Fenner & Freeman (2011).

**Figure 4:** $CO_2$ production from peat as a function of the concentration of O-alkyl carbon. Data points represent peat soils at a single site and from different soil depths. OC = organic carbon. Reproduced from Leifeld et al. (2012).

**Figure 5:** Contributions of $CO_2$, $CH_4$, and $N_2O$ to radiative forcing due to land use / land cover change. Colored bar segments show the radiative forcing from each individual gas. Black circles show the overall radiative forcing from all three gases combined. Data from Tan et al. (2020).

## FIGURES

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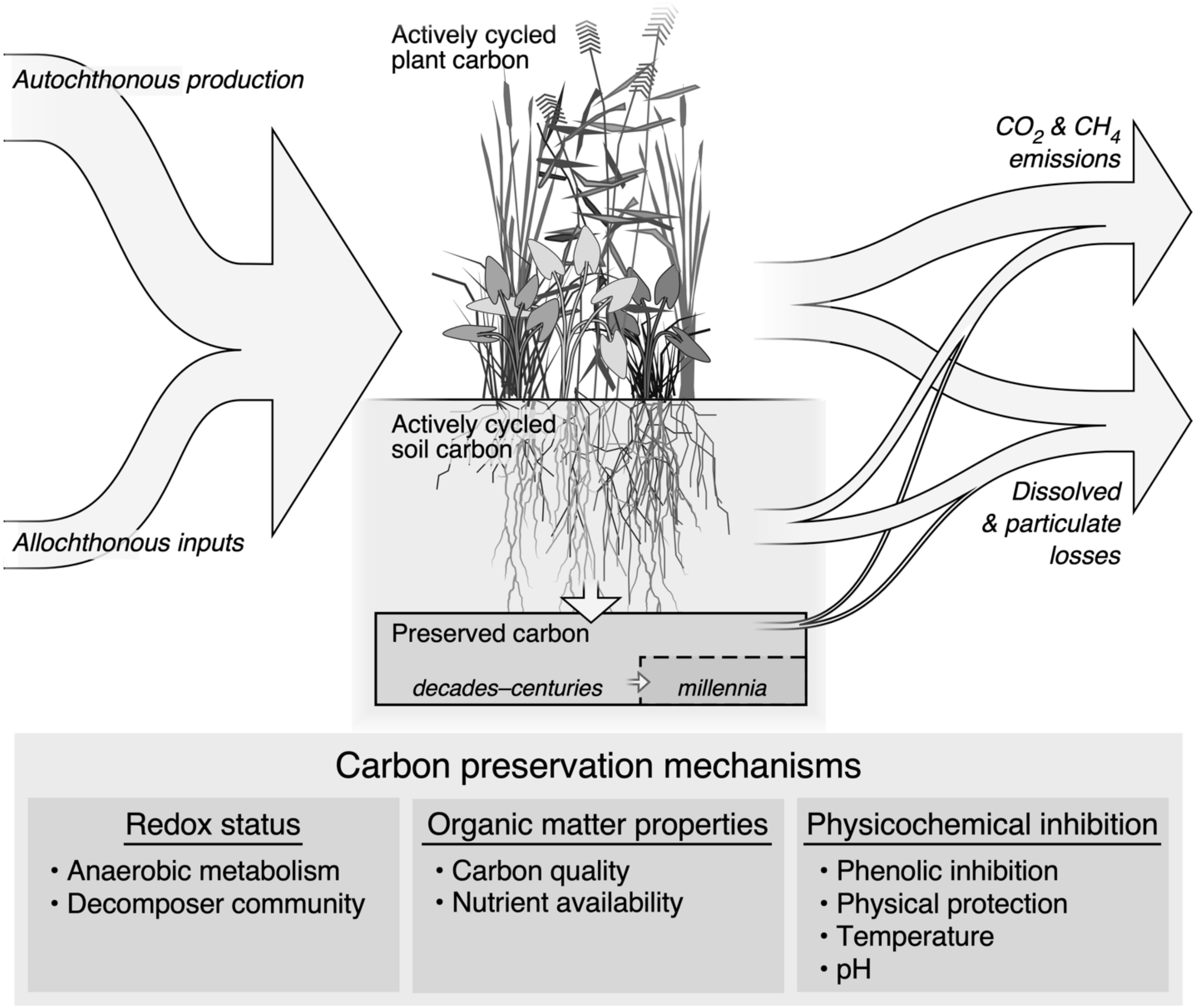

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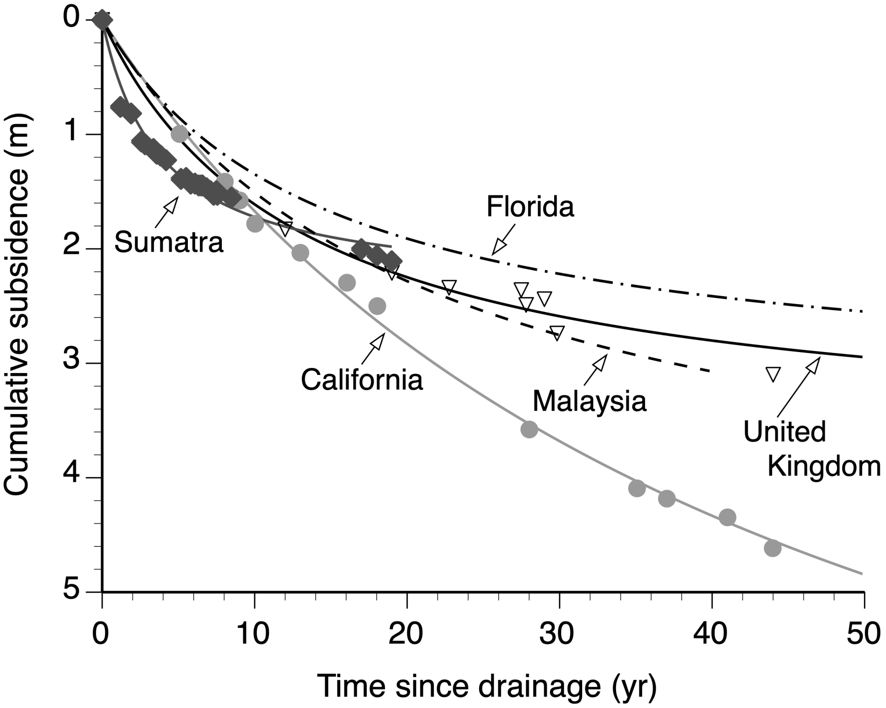

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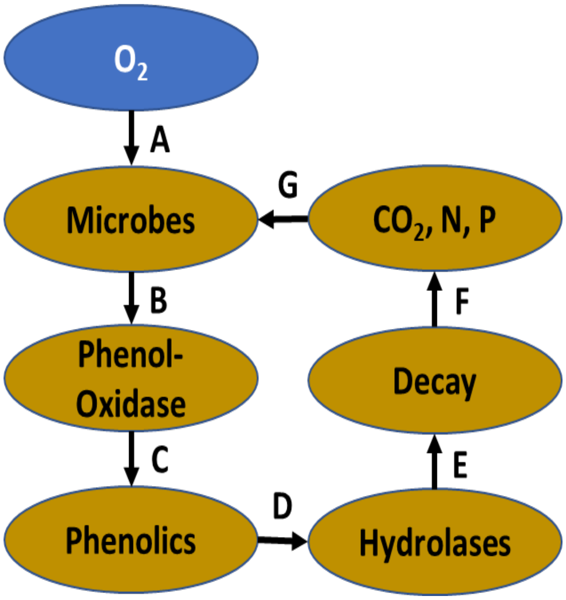

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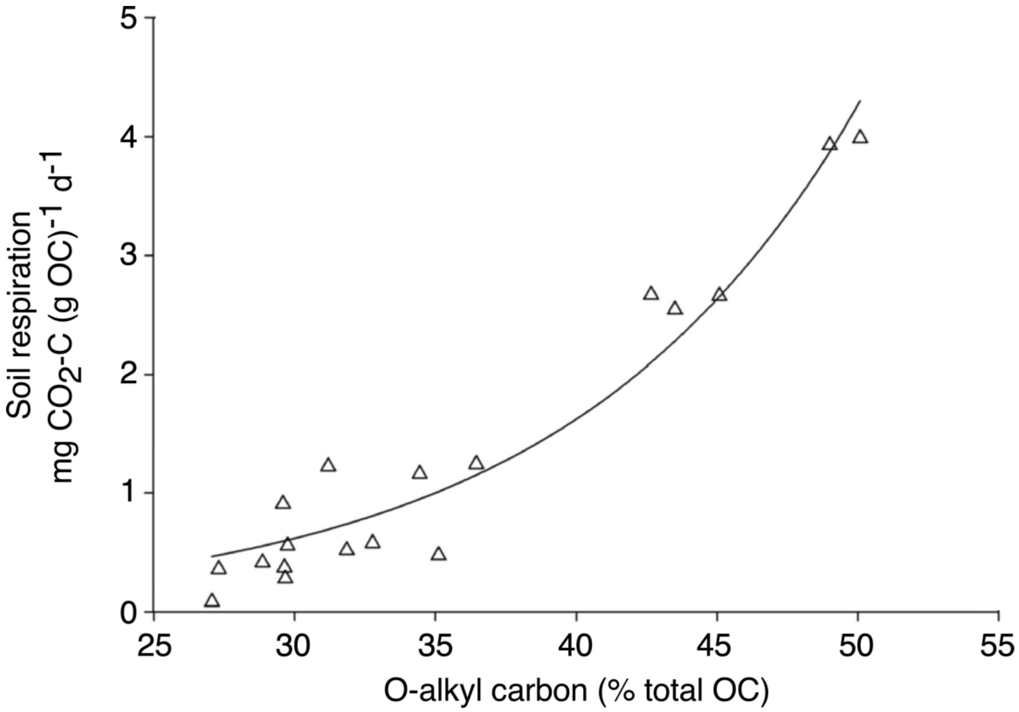

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