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Impacts of salinization caused by sea level rise on the biological processes of coastal soils - A review

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Soil salinization caused by sea level rise threatens coastal agricultural soils and geochemically important wetlands worldwide. The aim of this review is to outline expected changes in soil biological activity by discussing the combined effects of salt stress and flooding on plants productivity and soil microbial communities, which determine consequences on fluxes of C, N and P. Finally, it outlines the expected repercussions on greenhouse gases emissions. The prediction of outcomes is made difficult by the concomitant and sometimes contrasting actions of flooding and seawater intrusion on partly acclimated and non-acclimated environments. Non-salt acclimated plants suffer from osmotic stress, but also from reduced O_2 solubility. Microbial biomass declines with increasing salinity and microbial communities shift in composition. Large concentrations of Cl^- inhibit nitrification, but salinity stimulates N_2O fluxes. Impacts on C mineralisation rates is variable but enhanced by the larger availability of terminal electron acceptors. The reduction of Fe combined with that of SO_4^{2-} could enhance P mobility. Salinization affects methanogenesis which is constrained in favour of SO_4^{2-} reduction. Consequences are largely site specific and difficult to predict because of the complex network of processes occurring simultaneously in different compartments (i.e., soil, microbiome, vegetation). The distinction between short and long term effects is also important. A reliable prediction of outcomes at a planetary scale will only result from more precise inventories and monitoring of areas displaying specific similarities and from the implementation from these well-defined data sets of specifically devised models whose results can be finally combined on a weighted basis.

KEYWORDS

salinization, see level rise, wetlands, GHG, coastal soils

Introduction

Salinization has occurred throughout the Earth's history *via* the natural accumulation of salts, released by the weathering of rocks. This process, nowadays intensified by rising temperature, is known as primary salinization. Associated changes in salinity occur over a time scale of approximately 100,000 years, though further variations arise over shorter orbital cycles of 23,000–41,000 years (Neukom et al., 2014). In contrast, much faster increases in salt concentrations caused by anthropogenic actions are known as secondary salinization. Since the onset of civilization, anthropogenic manipulations of the hydrologic cycle have artificially altered the balance between salt accumulation and water inputs, leading to increased salinity in some wetlands, inland aquatic systems and upland soils. Secondary salinization can take place over time scales as short as decades, or even more rapidly (Herbert et al., 2015).

Another threat, associated with climatic changes and the salinization of coastal agricultural soils and wetlands, is due to the worldwide sea level rise (SLR), which also endangers biodiversity, with coastal freshwater wetlands being among the most biodiverse environments on Earth. Wicke et al. (2011) estimated that, globally, 1.1×10^9 ha of land was salt-affected and 14% (1.5×10^8 ha) of this area is classified as forest, wetlands, or other legally protected areas. Blankespoor et al. (2012) projected that, following a 1 m rise in sea level, 64% of freshwater coastal wetlands would be lost and converted to saline systems, with the higher regional loss rates in the Middle East and North Africa (100%), Latin America and the Caribbean (74%), Sub-Saharan Africa (72.5%), East Asia and the Pacific (62.2%). Henman and Poulter (2008) estimated that, worldwide, there are approximately 15×10^6 ha of coastal wetlands below 5 m elevation above the mean sea level (MSL), and thus vulnerable to projected SLR. The Australian and New Zealand Environmental and Conservation Council predicts significantly high salt concentrations in 40,000 km of their waterways and associated wetlands by 2050 (Nielsen et al., 2003).

This review starts with a brief outline of the driving factors that determine the diversity of situations that arise from the combined action of the unprecedentedly rapid rise of sea level and the augmented probability of coast inundation events associated with the increased frequency of storms stemming from climatic changes. It then examines threats to coastal agricultural land and natural wetlands before focusing on the consequences of salinization on soil biological properties that regulate the contribution of coastal soils main to the biogeochemical cycles. The aim is to outline and clarify the complexity of affecting factors and feedbacks that arise from the often-contrasting actions of submergence, availability of electron acceptors and osmotic stress on acclimated (salt marshes) or non-acclimated (coastal freshwater wetlands and agricultural land) ecosystems. A specific discussion is devoted to the consequences on greenhouse gases (GHG) emissions.

Sea level rise and forecasted increases in sea water salinity

The fact that SLR is amongst the most important consequences of global climate change and a major threat to many countries on Earth is widely acknowledged. Habitat and infrastructures of the people living in coastal areas, which host about 10% of the total population of our planet, are likely to face increasingly frequent inundation events and eventually become permanently flooded (Carrasco et al., 2016). The global MSL was calculated to have increased, from 1993 to 2018, at a rate of 3.34 mm per year (based on near real-time satellite altimetry data, Aviso, 2003). As a consequence of global climate change, MSL is projected to increase by 0.26–0.82 m by 2100 (IPCC, 2013; IPCC, 2014), with some models projecting an upsurge of more than 1 m by 2100 (Richardson et al., 2009; Vermeer and Rahmstorf, 2009; Rignot et al., 2011). In addition to the melting of polar caps, the warming of the oceans will also contribute to the global SLR, because of the decrease in density of water with temperature. Vermeer and Rahmstorf (2009) used a semi-empirical method linking temperature changes to SLR, and the resulting projected global SLR by 2100 of 0.75–1.90 m is significantly higher than the IPCC projections (0.26–0.81 m, IPCC, 2013; IPCC, 2014).

Variations caused by gravitational effects resulting from land ice mass changes, thermal expansion and ocean dynamics will be observed at the regional scale. In fact, SLR does not manifest itself as a smooth, linear increase, rather its rates vary over time and between regions, complicating predictions for seawater intrusion. Mediterranean coasts and lands facing the Red Sea, the north-eastern part of the Indian Ocean, are potentially more at risk because of the high salinity of marine waters (Figure 1). Valjarević et al. (2020) updated the world maps of sea-surface salinity and calculated the expected increase in salinity (levels and distribution) caused by a 2°C increase in global mean temperature (by the CMIP5 climatological model). According to their projections, salinity levels above 39‰ will be experienced in the area of the Red Sea, the African countries in the Mediterranean, the countries in the Persian Gulf and the Bengal Gulf and Indochina, as well as the Victoria state and the Northern Territory in Australia (Figure 1). In fact, salinization prompted by the SLR varies geographically, because of the spatial variability of regional trends caused by smaller-scale alterations in water temperature, surface winds and geologic activity (IPCC, 2013). Heterogeneity is driven, among other factors, by the salinity of nearby sea surface layers. Climatic factors concur to exacerbate the phenomenon in some regions, e.g. a negative balance between precipitation and soil
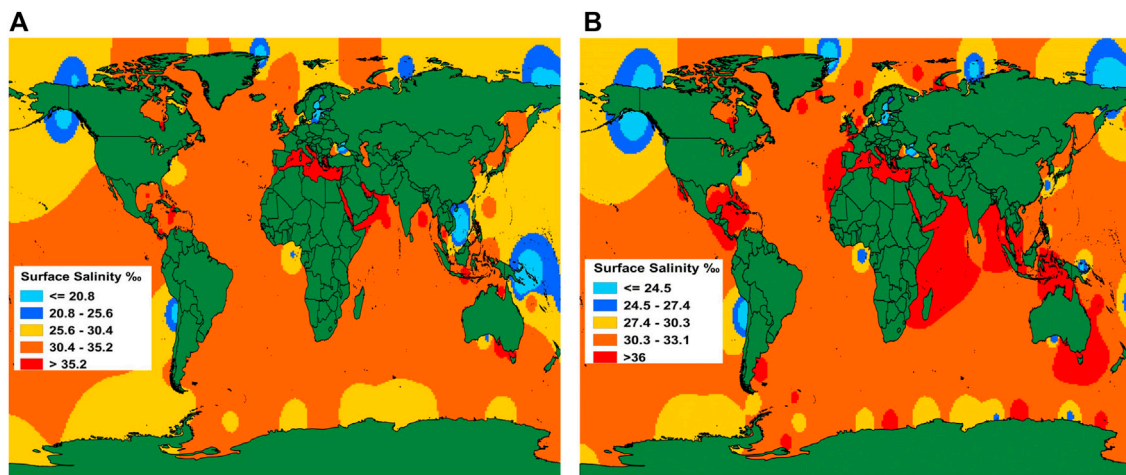
FIGURE 1
World map of sea surface salinity **(A)** shows current salinity distribution according to measured data from the world seas. A global mean temperature increase of 2°C will affect salinity levels and distribution in the world **(B)**. Modified from Valjarević et al. (2020).

evapotranspiration causes salts accumulation in the presence of saline groundwater (Rose et al., 2005).

It is estimated that global soil salinization will continue spreading at a rate of up to 2 Mha yr^{-1} (Abbas et al., 2013). Case studies showing the influence of SLR on lagoons and/or estuaries include Lagoa dos Patos, Brazil (Toldo et al., 2000), Lake Illawarra and St. Georges Basin, New South Wales, Australia (Sloss et al., 2006), Venice Lagoon, Italy (Ferla et al., 2007), Pamlico–Albemarle Sound, North Carolina, United States (Pilkey et al., 2009), Wadden Sea, Netherlands/Germany (Dissanayake et al., 2012), Ria Formosa, Portugal (Andrade et al., 2004), Vistula Lagoon, Baltic Sea (Navrotskaya and Chubarenko, 2013), and Manzala Lagoon, Egypt (Frihy and El-Sayed, 2013). Several aquifers along the densely populated Mediterranean Sea coasts are already suffering seawater intrusion. Speed up of this phenomenon could be particularly intense in this part of the world, because the Mediterranean region, and especially its semi-arid areas, are likely to be seriously affected by a decline in freshwater resources (Kundzewicz and Döll, 2009).

Spatio-temporal drivers of salinization

As sea levels rise, seawater intrusion into freshwater ecosystems increases in frequency, duration and spatial extent (Weissman and Tully, 2020). The risk of salinization of coastal soils is related to the frequency of inundation, which increases with proximity to the seashore and decreases with ground height above the MSL. Tides of unusual elevation are becoming more frequent due to a combination of SLR and extreme weather conditions fostered by climate change (IPCC, 2014), and

exacerbate the situation of submerging coastal soils and their salinization.

Strong winds may push the waves of high tides further inland and long drought periods will cause salts to accumulate in surface soil horizons. Once the soils have become submerged, salinity is expected to approach a steady-state equilibrium with brackish waters (Abbas et al., 2013), but even before this happens, evaporation from periodically inundated soils will cause soil salinity to increase at levels much higher than those of the recurrently invading waters. Geographical characteristics contribute to differentiate the effects: within a given tidal range, the frequency of inundation at a particular soil elevation in salt marshes is generally influenced by landscape characteristics, such as length and tortuosity of tidal creeks or distance from the shore. These factors may combine with local climate features, such as the direction of prevailing winds, and lead to locally different inundation patterns (Yang et al., 2015).

The main spatial drivers of variability in salinization intensity are local geomorphology, soil hydrology, textural composition and vegetation cover, which alter pathways and speed of the submarine water discharge, as well as the effects of tidal range and pore water exchange that determine the rates of pentration and drainage of sea water (Guimond and Tamborski, 2021).

Soil texture determines the thickness of the capillary fringe and the potential maximum flux of solutes to the soil surface (Fiola et al., 2020). The capillary rise is, in fact, lower in sandy layers and can retard the building up of salt accumulation. In the soils of estuarine and former floodplain areas, the succession and textural composition of soil horizons impact the height at which groundwater can rise. Textural discontinuities affect the hydrologic connectivity of the soil and reduce the flow of water and solutes to the surface (Gardner, 2005). Stratigraphic
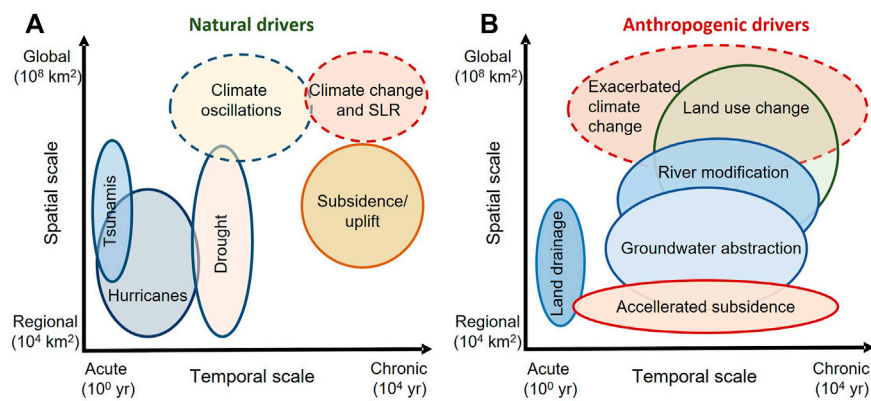
FIGURE 2
Time scales and affected surface areas of natural **(A)** and anthropogenic **(B)** drivers of salinization in coastal soils. Modified from White and Kaplan (2017).

constraints, such as mud layers, hamper the discharge flow leading to smaller and denser salt fingers where the effect is exacerbated by the eventual presence of buried sand lenses (Wu et al., 2022). These factors are however important only in low-lying soils where the depth of the water table is sufficiently shallow, so the steepness of the banks may zonally reduce the impact of infiltration of salty ground water.

Soil morphology influences the type of vegetation cover that, in turn, affects the flow of water and solutes towards the surface as the suction exerted by plant water uptake and transpiration can greatly accelerate the process (Carmona et al., 2021). Plants affect the distribution of salinity both quantitatively and qualitatively. In fact, Cl^- tends to be excluded from plant nutrient uptake and to accumulate in soil and groundwater as a function of evapotraspiration, with a decreasing gradient of Cl^- concentration with depth (Grimaldi et al., 2009). Presence of roots of neighbour trees exploring the soil, increase the complexity of the spatial variability of Cl^-, enhancing the risk of strong salinization during periods of drought concomitant to the growing season (Humphries et al., 2011). Salt reduces plant evaportraspiration of riparian species but, rising seawaters can lead to the die back of the riparian vegetation in favour of the establishment of halophytes and salt-tolerant woody species (e.g., *Tamarix* spp.). Salt-tolerant plants can take up water at very low soil water potential, thanks to the production of soluble osmolytes stored in the cell vacuoles to regulate the osmotic stress (Flowers et al., 2015). The consequent increase of evapotraspiration further enhances salt accumulation (with the exception of the very dry season where leaf stomata close and traspiration is reduced), exacerbating the process of soil salinization and increasing especially Na^+ levels in the soil. Moreover, vegetation cover is reduced in halophytic compared to riparian communities, entailing an increase in soil temperature that further boosts salt accumulation due to evaporation (Liu

et al., 2019) and causes changes in bacterial community structure (Zhao et al., 2022). Finally, plants can not avoid the passive accumulation of salt in their tissues: this salt is returned to the soil at the end of the growing season, during leaf/root renewal or plant death, supplying salt-enriched litter to the soil and altering OM decomposition.

The natural drivers of coastal soils salinization act through widely differentiated time and spatial spans (Figure 2). They may exacerbate soil salinity for less than a year affecting relatively limited areas or act across much longer periods and at a nearly planetary scale, such as the present climate change and past climate oscillations (White and Kaplan, 2017).

Transient drivers, such as tsunamis or hurricanes, cause direct salinization of groundwater and soils in coastal areas, but previous salt levels may be restored within a year in many geographical regions, as salts can be leached away by intense seasonal rains (Kume et al., 2009). However, in combination with dry climates or low soil permeability, the effects of marine inundation caused by transient exceptional events are expected to last longer. All these natural actions are amplified by anthropogenic drivers such as land drainage (Valipour, 2014), accelerated subsidence (Daliakopoulos et al., 2016), groundwater abstraction (White and Kaplan, 2017), land use changes (Gopalakrishnan et al., 2019), and by all those activities that fuel climatic changes (Figure 2). Anthropogenic drivers may act faster and cause, at the same time, effects that may persist over very long time spans. For instance, the low-lying coastal area near Ravenna (north-eastern Italy) is affected by groundwater salinization from seawater infiltrations fostered by an increase in pumping that will cause threats to freshwater availability (Giambastiani et al., 2020). Gonneea et al. (2013) showed that seasonally enhanced SLR leads to increases in the amount and salt concentrations of submarine ground discharge (in summer). Wood and Harrington (2015) further illustrated, by a two-

dimensional variable density model, that sea level fluctuations push saline water into inland groundwater-fed wetlands through the movement of the subterranean freshwater-saltwater interface.

It is therefore evident that the variety of drivers acting on coastal soils is matched by the large diversity of their spatio-temporal effects. Local factors and their combinations may greatly accelerate the process in specific areas or dampen consequences in others. A holistic approach is therefore necessary to understand the often contrasting outcomes of salinization from SLR on soil biological properties.

Salinization of coastal agricultural lands

Secondary salinization of agricultural soils is one of the most pressing environmental challenges that humankind will face in the current century (UNESCO, 2016). The Food and Agriculture Organization of the United Nations (FAO) estimates that, globally, over 830 M ha of arable land are affected by salinization (Martínez-Antonioand Collado-Vides, 2003). Salinization affects the 17 western states of the United States, up to 3 Mha in Europe, more than 5% of the arable land in Africa, about a fifth in West Asia and 30% in Australia (Chhabra, 1996; Rengasamy, 2006; IPCC, 2007; Ladeiro, 2012).

Albeit the salinity of the seas varies, the elemental composition of marine salts is worldwide the same so that constant relative proportions are always maintained among the elements (Millero et al., 2008). On the contrary the composition of the salts accumulated by inland saline soils depends on the type of rocks from which they formed or that had been in contact with the waters entering the soil, as well as climatic and pedogenetic factors. This large variability of affecting factors is reflected by the variability of the composition of groundwaters, that in general contain a larger proportion of less mobile cations, whereas anions are dominated by the bicarbonate ion and not by chloride (Shvartsev, 2008). As a consequence, salinization of coastal soils, being imposed by sea water, modifies the composition of the soil exchange complex and of the soil solution in relatively similar ways throughout the globe, whereas the salinity affecting inland soils primarily reflects local situations.

Coastal agricultural practices are less resilient than upland agriculture because they need to cope with more frequent changes in ground water salinity, occasional sea inundations, water stresses and waterlogging (Awal, 2014). The sustainability of coastal agriculture is influenced by both climatic and non-climatic factors, of which SLR is the most influential. Apart from SLR, climate change has the potential to affect coastal areas in several ways, such as through increases in temperature and changes in the frequency and intensity of rainfall and storms (Gopalakrishnan et al., 2019).

The deterioration of soil fertility due to soil salt accumulation is a growing concern in coastal areas. Salinity reduces soil quality (by reducing nutrient content and enzymatic activities, Xian et al., 2019), limits the growth of crops, constrains agricultural productivity, and in severe cases, leads to the abandonment of agricultural lands (Diome and Tine, 2015; Sambou et al., 2016). High salt levels in agricultural soil or irrigation waters make water and nutrient uptake difficult for salt-sensitive plants, such as rice, thereby reducing plant growth and crop yields (Kaniewski et al., 2016). Moreover, saltwater inundation mobilizes nutrients that add to the loading in adjacent water bodies, reducing water quality (Herbert et al., 2015). Coastal farming systems result severely affected. In Bangladesh, for example, coastal soil salinity in agricultural lands has been found to dramatically affect crop revenue and the internal migration of farmers (Chen and Mueller, 2018). In Vietnam, more than 30% of the sugarcane plantations have been either destroyed or significantly damaged by the inundation and intrusion of saltwater into the Mekong Delta, resulting in a significant financial loss (Gopalakrishnan et al., 2019).

The productivity of coastal agriculture is increasingly hampered by the biophysical and biochemical constraints imposed by salinity on crop growth (Duarte et al., 2014). Novel perspectives will be, however, offered by studies on biostimulants and plant growth-promoting microorganisms isolated from the rhizosphere of salt tolerant plants (Pereira et al., 2019; Otlewska et al., 2020; Pereira et al., 2021). Literature shows that isolation and inoculation of specific bacterial strains, by soil amendment or foliar spread, can improve nutrient uptake in the plant and decrease plant sensitivity to Na^+ (see, e.g., Etesami and Beattie, 2018).

Adoption of traditional amelioration practices on salt-affected coastal lands not only reducesthe direct impact of osmotic stress on crops, but also exerts a positive action on soil biological fertility by reverting the reduction in the biodiversity of the soil microbiome (Sun et al., 2022).

Impacts on freshwater coastal wetlands

The alteration of water chemistry caused by the ions brought in by marine water alters the chemical speciation of elements, their concentration in the soil solution and modifies habitat conditions and substrate availability for soil microorganisms (Shao et al., 2022), shifting the dominant biogeochemical processes within soil (Haywood et al., 2020) and ultimately altering the ability of wetlands to provide key ecosystem services (Wang et al., 2020).

Coastal wetlands are valuable transition environments, sensitive to changes in marine processes and freshwater flows from upstream catchments. Herbert et al. (2015) identified five mechanisms of salinization in coastal wetlands, including: 1)

surface or subsurface seawater intrusion linked to SLR, 2) reduction of riverine freshwater flow, 3) alteration of subsurface freshwater, 4) anthropogenic alteration of coastal geomorphology, and 5) storm surges. The main driver of salinization of coastal freshwater wetlands is undoubtedly surface or subsurface seawater intrusion. Mechanisms 2, 3 and 5 could be probably better considered as climate change-related processes that locally can exasperate salinization.

The third mechanism responsible for the salinization of coastal freshwater wetlands relates to changes in groundwater recharge and discharge (Galliari et al., 2021; Wu et al., 2022). Aquifers are often exploited so intensively that their natural hydrological regime is strongly disturbed and may be thrown out of balance (Custodio, 2010; Dymond et al., 2019). In particular, changes in seawater intrusion are highly non-linear and exhibit important thresholds, or tipping points, beyond which full seawater intrusion into a coastal aquifer may occur in response to even small sea level and/or groundwater management changes (Elliott et al., 2016). Several aquifers along the densely populated Mediterranean coasts are already suffering seawater intrusion (Mazi et al., 2014).

Anthropogenic manipulations of coastal geomorphology, the fourth mechanism, principally affect coastal floodplain wetlands (Dymond et al., 2019; Mancuso et al., 2020). In the Netherlands, for example, the combination of lowland reclamation in the past centuries and ongoing SLR is expected to lead to strong salinization (Oude Essink, 2001). Similar impacts are expected due to the dredging of deep water channels in the Yangtze and Pearl River Deltas in China (Zhang et al., 2014).

The fifth mechanism, storm surges, can introduce saline water into coastal freshwater wetlands along the estuarine continuum, and in near-shore lagoons and depressional wetlands that have no permanent hydrologic connection to the sea (Guimond and Michael, 2021). The increased frequency of extreme weather events associated with climate change will proportionally increase its contribution to coastal salinization in the near future.
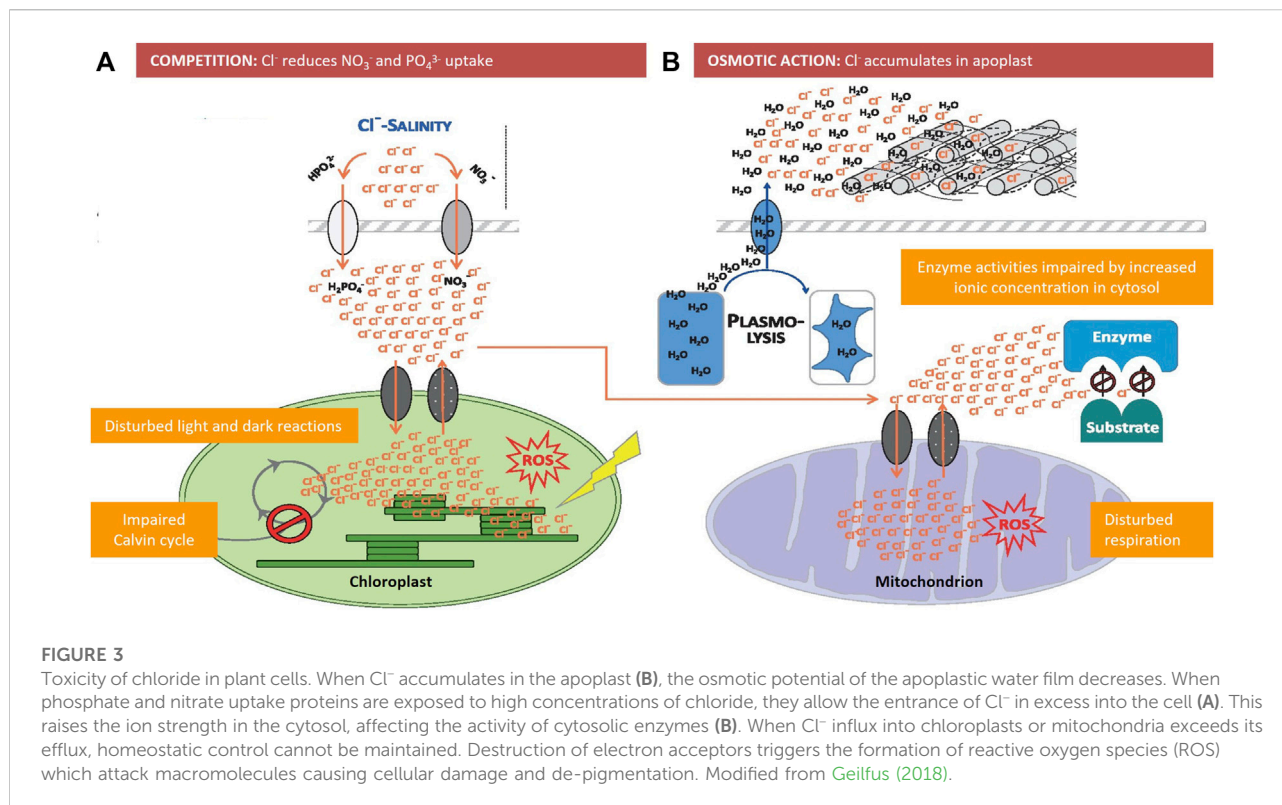
Effects of SLR on the biological activity of wetland soils are linked to O_2 availability, which is not only related to flooding. Elevated ionic concentrations caused by salinity reduce the solubility of gases (Stumm and Morgan, 1996). This affects the diffusion of O_2 in waterlogged soils, resulting in shallower penetration into the soil profile and more negative redox potential. Reduced gas solubility can accelerate GHG emissions by allowing a faster formation of bubbles, and reducing soil microorganisms accessibility to CO_2 and N_2O (McGinnis et al., 2006). In this way, CH_4 oxidation and N_2O reduction might become less efficient when soils are saturated with saline waters than similar soils saturated with fresh waters.

Saline water is denser than fresh water, and seawater intrusion via surface or groundwater movement can result in the establishment of strong stratification (and the formation of a halocline) in tidal rivers and depressional wetlands (Brock et al., 2005; Revsbech et al., 2005). Stratification is a barrier to the movement of O_2 between the lighter superficial freshwater and the underlying saline strata. Salt loads of merely 2 g L^{-1} are enough to alter the density of water and produce a degree of stratification similar to the temperature-derived density stratification observed in holomictic freshwater lakes (Findlay and Kelly, 2011).

Ionic displacement has been suggested as a mechanism for desorption of plant nutrients and other chemical species from salinizing wetland soils, particularly inorganic nitrogen (e.g., ammonium) and phosphate (PO_4^{3-}), with potential consequences for the fertility of these soils, but also eutrophication of down-stream waters. Therefore, the effects of salinization on wetland biogeochemistry typically include decreased inorganic N availability, decreased C inputs and increased generation of toxic sulfides. All this has negative effects on the biodiversity of wetlands, which include the direct loss of plant species diversity, reduced potential for plant population recruitment, reduction in primary production and subsequent loss of fauna diversity through the loss of habitat and food (Davis and Froend, 1999). Indeed, larger salt and sulfide concentrations induce physiological stress in wetland biota and ultimately can result in large shifts in wetland communities and their associated ecosystem functions (Herbert et al., 2015). Increased salinity is a stress that has been shown to reduce diversity in both terrestrial (Briggs and Taws, 2003; Hobbs et al., 2003) and freshwater aquatic systems (James et al., 2003; Brock et al., 2005). Ecological impacts are influenced by a range of factors including the sensitivity of a species to salt (for both sub-lethal and lethal effects), rates of salinity increase, length of exposure and the life stage at which a species is exposed to salt stress (Cocks, 2003). At soil conductivity above 1.5 dS m^{-1}, reduced growth rates and reduced development of roots and leaves are observed in aquatic plants (James et al., 2003; Nielsen et al., 2003). Smith et al. (2009) found that a considerable loss of freshwater macrophytes may occur after a relatively small increase in salinity and with a severe loss of species already at conductivities of about 1 dS m^{-1}.

Osmotic stress in salt-affected soils challenges the maintenance of turgor pressure in plants (Flowers et al., 2015). Acclimated species are able to accommodate high Na$^+$ and Cl$^-$ concentrations by intracellular ion compartmentation and the production of osmolytes, i.e., organic solutes that contribute to the osmotic adjustment such as non-structural carbohydrates or amino acids (Gil et al., 2013). Mitochondrial enzymes are sensitive to Na$^+$ and especially the cytochrome c, a crucial component of the electron transport chain (Figure 3). In fact, cell respiration was found to be inhibited in mitochondria isolated from salt-stressed plants compared to plants

FIGURE 3
Toxicity of chloride in plant cells. When Cl⁻ accumulates in the apoplast **(B)**, the osmotic potential of the apoplastic water film decreases. When phosphate and nitrate uptake proteins are exposed to high concentrations of chloride, they allow the entrance of Cl⁻ in excess into the cell **(A)**. This raises the ion strength in the cytosol, affecting the activity of cytosolic enzymes **(B)**. When Cl⁻ influx into chloroplasts or mitochondria exceeds its efflux, homeostatic control cannot be maintained. Destruction of electron acceptors triggers the formation of reactive oxygen species (ROS) which attack macromolecules causing cellular damage and de-pigmentation. Modified from Geilfus (2018).

inhabiting non-saline soils, although the response of overall respiration is very variable (Jacoby et al., 2011).

Chloride is an essential micronutrient in plants and regulates enzyme activities in the cytoplasm: it is a co-factor in photosynthesis, acts as a counter anion to stabilize membrane potential and is involved in turgor and pH regulation (White and Broadley, 2001). However, it can be toxic to plants (Geilfus, 2018) and triggers the production of reactive oxygen species (ROS, Figure 3). Critical concentrations for toxicity are estimated to be 4–7 mg g⁻¹ for Cl⁻-sensitive species and 15–50 mg g⁻¹ for Cl⁻-tolerant species (White and Broadley, 2001). Reduced rhizodeposition of labile organic compounds and an overall decrease in C inputs (due to the alteration of the Calvincycle) can be expected to have detrimental effects on soil microbial biomass abundance and activity.

Glycophytes, i.e., non-tolerant species to salt, could hardly acclimate to increasing salinity. Therefore, salt stress directly impacts species diversity and composition of plant communities, leading to vegetation shifts in favour of the acclimated halophytic vegetation. Salt-tolerant species are capable to handle the reduced O₂ solubility and mineral N availability (Flowers et al., 2015), osmotic stress and specific ion toxicity, determining the short and long term implications on the net primary productivity and, therefore, on the whole C and N inputs to soil.

Response of microbiota to salt toxicity

Soil contact with sea water is toxic for most soil organisms within 2 h and effects last for at least 48 h (Rath et al., 2016). Exposure to high concentrations of salts affects microorganisms in two ways: by osmotic stress and through specific ion toxicity (Serrano, 1996).

Similarly to plant cells, elevated concentrations of marine salts in the soil water phase cause abnormal Na⁺ and Cl⁻ accumulation in microbial cells and disrupt the uptake of water and essential ions (Figure 3), which may ultimately lead to mortality (Serrano, 1996; Zhang et al., 2019). Toxicity levels inhibiting bacterial growth by about 50% range between 30 and 100 mM Na or between electrical conductivities of 3.0 and 10.7 dS m⁻¹ (Rath et al., 2016).

Increasing salt concentrations in the surrounding medium elevate the osmolarity outside microbial cells and, as external salt concentrations rise, cells lose water. To maintain cell turgor and prevent dehydration, microorganisms produce and accumulate osmolytes in their cytoplasm (Empadinhas and Da Costa, 2008). They have evolved two different osmoadaptation strategies to achieve homeostasis with the surrounding environment, but both are energetically expensive (Gunde-Cimerman et al., 2018).

The first and more widespread strategy, adopted by microorganisms exposed to saline media, is the accumulation

of low molecular weight organic compounds (osmolytes) such as amino acids and carbohydrates within the cell (Oren, 2008). The synthesis of organic osmolytes requires energy in the form of ATP. Oren (1999) calculated that heterotrophic microorganisms need to use between 23 and 79 ATP molecules to produce one molecule of an osmotic solute. Extrusion of Na^+ and uptake of K^+ also consume ATP equivalents.

The second survival strategy, demonstrated in many halophilic prokaryotes, minimizes osmotic potential differences by taking up ions (predominantly potassium) from the medium. This, however, requires the adaptation of intracellular enzymes to elevated ionic concentrations in the cytoplasm, since they should keep their original conformation to preserve enzymatic activity (Oren, 2008). This is not easily achieved because excessive salt concentrations may eventually denature proteins (Frankenberger and Bingham, 1982) and affect enzymes. Even when their solubility is not diminished, the spatial arrangement of amino acids at the active site, which is crucial for maintaining the catalytic efficiency, may be altered at high ionic strengths (Leprince and Quiquampoix, 1996) which favour hydrophobic interactions and de-stabilize electrostatic attraction forces.

Some studies indicate that changes both in microbial community composition and function occur with changes in salinity (Jackson and Vallaire, 2009). The resilience ability of soil fauna seems, however, a function of ecosystem complexity and site specific factors. Salt stress can differently impact the community based on its composition and some organisms might be impacted only marginally (Pereira et al., 2019). Bacteria appear to be more resilient to salinization than fungi, and fungal contribution to microbially derived C is negatively affected by salinity (Shao et al., 2022). Rath et al. (2019) investigated microbial salt tolerance in several saline soils and found that high salt concentrations could inhibit fungal growth by more than 90%. Sardinha et al. (2003) found a strong decrease in the ratio of the fungal biomarker ergosterol to microbial biomass C and that in the least saline site fungi made up 90% of the microbial biomass, but only 17% at the most saline site. The inoculation of salt-tolerant beneficial microorganisms (bacteria in particular) can reduce the salt stress by which the autochthonous microbial community is affected, with consequent positive repercussions to plant or crop growth (Pereira et al., 2016). The variety of microbial responses to salt stress and the existence of beneficial strains could possibly support future strategies to actively face soil salinization, representing a promising perspective in agriculture.

Lower microbial diversity was found in saline soils of the Yellow River delta (Zhao et al., 2020). However, the phyla Proteobacteria, Bacteroidetes, Chloroflexi, Acidobacteria and Planctomycetes, represented more than 70% of the bacterial community 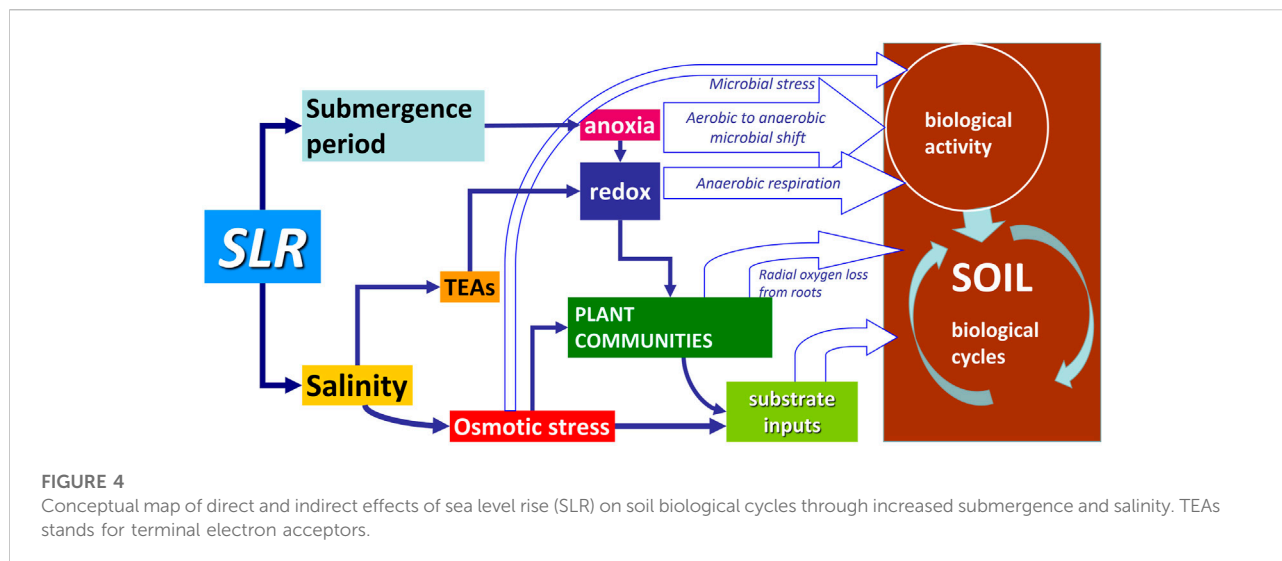in the three different wetlands, indicating the wide adaption of these phyla to salinity changes. Specifically, Proteobacteria, which were recognized as the most dominant phylum (35–39%), appeared not to be affected by salinity. However, the bacterial composition was different among the wetlands, as revealed by β-diversity, and specific bacterial taxa were suggested to serve as bioindicators of soil salinization (Rath et al., 2019).

The species-specific response of soil microorganisms to increased Cl^- concentration results in modifications of the soil microbial community. However, chlorine is naturally diffused in the environment because saltwater from the oceans is, with an average concentration of 19 g Cl L^{-1}, one of the main sources of atmospheric Cl^- (Stumm and Morgan, 1996). Inorganic chloride is a normal component of the soil solution which is more abundant in coastal regions, where it is carried by marine aerosols (Meira et al., 2006). Setia et al. (2010) suggested that, when chloride is the predominant anion of the soil solution, the nature of the accompanying cations is of little importance and that the osmotic effect plays an important role in reducing rates of organic matter decomposition. However, empirical data from a larger variety of habitats, range of scales and microbial functional groups are still needed to understand how the structure and function of microbial communities will be altered by salinization.

A substantial increase in Cl^- concentration inhibits both nitrification and denitrification, but the associated microbial communities appear to be able to adapt to high Cl^- concentrations over time (Hale and Groffman, 2006). Moreover, Soil anoxia tends to reduce the rate of chlorination of the soil organic matter (SOM) (Bastviken et al., 2007; Bastviken et al., 2009). By affecting the composition of soil microbial cenosis, the increase in chloride availability may even affect the chlorine flux from its inorganic form to organic compounds and *vice versa* (Gryndler et al., 2008) with consequences affecting the process of chlorination of SOM (Öberg et al., 2005).

The most consistently observed alteration in bacterial communities caused by inundation or infiltration of sea water is a change in the number of methanogenic archaea and a coincident decrease in CH_4 production (Baldwin et al., 2006). Observations suggest that Na^+ and Cl^- alone can inhibit methanogenesis in inland soils but, in coastal systems because of the concomitant increase in SO_4^{2-}, the inhibition is fostered by a less efficient competition with facultative anaerobes (Pattnaik et al., 2000; Mishra et al., 2003; Baldwin et al., 2006; Chambers et al., 2011).

Extracellular enzyme activities are generally larger in non-saline soils compared to naturally saline soils (Rietz and Haynes, 2003; Ghollarata and Raiesi, 2007), even if halophytic microorganisms had the time to adapt and colonize the latter. Enzymatic activity is therefore often measured to assess biological activity in soils affected by

FIGURE 4
Conceptual map of direct and indirect effects of sea level rise (SLR) on soil biological cycles through increased submergence and salinity. TEAs stands for terminal electron acceptors.

salinization. This provides a convenient way to monitor the consequences of increased salt concentrations on the biological activity of soils (Lemanowicz et al., 2019), however this approach is not without drawbacks. Assays that measure enzyme activities in soil usually test the potential activity at substrate saturation, which is a condition very far from that normally encountered in the substrate starved soil environment (Hobbie and Hobbie, 2013). Moreover, conditions such as temperature or pH can either be optimized or kept close to natural conditions (German et al., 2011; German et al., 2012), which leads to a considerable difference in results (Burns et al., 2013). Current methods which estimate enzyme activities at saturated substrate levels and optimized conditions do not estimate actual *in situ* activities, but rather maximum activities related to the abundance of enzymes, which is largely determined by the size of the soil microbial community (Rath and Rousk, 2015). The observed decrease, therefore, reflects lower microbial biomass contents and only secondarily, a change in functionality of the microbial community.

On the other side, microbial communities faced with unfavourable osmotic potentials can allocate lower energy resources to protein production and therefore release fewer extracellular enzymes. To highlight this, the determination of specific activities (mg substrate transformed per mg of microbial biomass C) would be much a better index of induced functional changes, than activities *per se*. Unfortunately, this approach has scarcely been adopted, although it would also allow direct comparison among different situations and a better generalization of consequences (Moorhead et al., 2013).

Another problem with using enzyme activities as an indicator of overall microbial status is that results can vary considerably between different soils and different enzymes

(Frankenberger and Bingham, 1982; Saviozzi et al., 2011). Therefore, it remains elusive to identify common general patterns from the assessments of extracellular enzyme activities in saline soils. This suggests that other metrics may be preferable to assess microbial functioning in saline soils, e.g., DNA/RNA-based molecular methods (Rath and Rousk, 2015).

Salinity effects on soil biogeochemical cycles

Increasing levels of chloride, sodium, potassium, magnesium and sulphates from sea water intrusion have major effects on biogeochemical processes (Weston et al., 2006; Setia et al., 2010) and the relationships between plants, soil and microbial communities (Nielsen et al., 2003; Munns and Tester, 2008) (Figure 4). SLR has important effects on soil biogeochemical cycles through the combined action of submergence and salinity on plant communities, in terms of productivity and type of vegetation (Hines et al., 2006). In fact, in addition to the anaerobic shift, imposed by the lack of O_2 that accompanies soil submergence, microbial respiration is supported by the larger availability of terminal electron acceptors (TEAs) in sea water with respect to fresh water. TEAs support anaerobic respiration, which partly compensates for the low efficiency of anaerobic transformations. At the same time, changes in plant communities contribute to altering microbial activity due to the different quantity and quality of litter available as a substrate for microorganisms (Barry et al., 2022).

In this paragraph, we will examine the complex interacting factors that drive the modifications in biological activities and govern the outcomes of SLR on the soil biogeochemical cycles of C, N and briefly on those of Fe, S and P.

Carbon cycle

Wetland soils have been estimated to contain from 45 to 70% of the terrestrial C pool (Mitra et al., 2005) and are assumed to play an important role in reducing atmospheric GHG concentrations, and mitigating climate change (McLeod et al., 2011). Coastal wetlands (i.e. salt marshes and mangrove swamps) sequester one order of magnitude more C than an equivalent area of terrestrial forests or peatlands (Chmura et al., 2003; McLeod et al., 2011). Considering that coastal wetland coverage will be reduced by 46–59% by the end of this century, based on current SLR predictions (Spencer et al., 2016), the reduction in C sequestration will have strong impacts on the terrestrial C cycle (Pfeffer et al., 2008; Vermeer and Rahmstorf., 2009), yet the overall effect is controversial and difficult to predict.

SLR will modify C cycling in coastal wetlands in two ways: 1) by increasing the length of submergence periods and, 2) by increasing salinity (Figure 4). The apparently contradictory results found in the literature may respond to the contrasting actions of these two concomitant factors that combine into a complex pattern. If sea rise *per se* will increase the incidence of soil anoxia, which is expected to favour C sequestration, salinity will increase the availability of TEAs and foster SOM mineralization (Stagg et al., 2017). Inundation by brackish waters may result, at least transiently in a negative C balance in freshwater wetlands, but is likely to have opposite effects in salt marsh sites with high elevation above the MSL. Effects of salinity on soil C depend on vegetation shifts (i.e., from non-halophytic to halophytic plant communities) that affect the quantity and quality of organic matter input to soil.

Salinity acts in contrasting ways on salt tolerant rather than salt sensitive plants. In a non-halophytic system inundated by saline waters, C inputs may dramatically diminish within a short period, because of the immediate anoxia and toxicity imposed by flooding and salt water, respectively (Figure 4). On the contrary, the same phenomenon may have a much lower impact on the productivity of the acclimated plant community (Glenn et al., 1992).
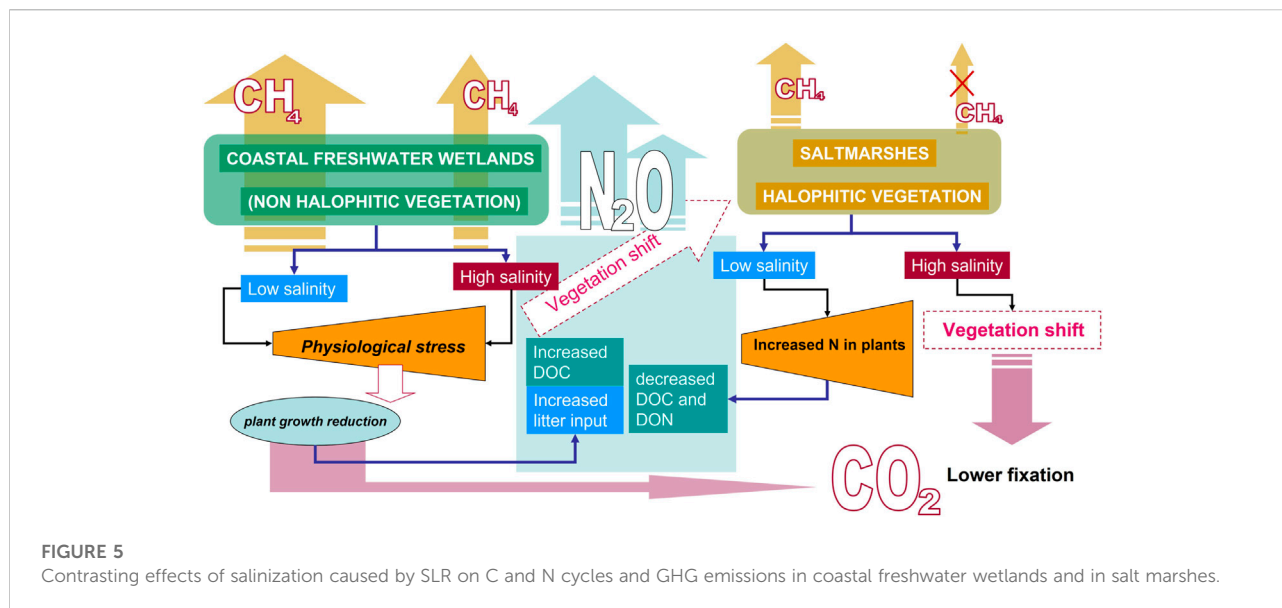
At the same time, in submerged soils, C mineralization efficiency depends on the availability of TEAs. Adverse effects on organic matter decomposition were found after the addition of salts to non-saline soils (Wichern et al., 2006; Wong et al., 2008), but sea salts composition and submergence interact in a complex pattern. Decomposition rates depend on the type of salt: for instance, Na_2SO_4 increased CO_2 emission from submerged soils during laboratory incubation, while NaCl decreased it (Li et al., 2006). The addition of sulphate ions sustains anaerobic respiration and therefore a more efficient decomposition of SOM, compared to strictly anaerobic systems, where microorganisms are forced to derive their energy from fermentation. It also inhibits the reduction of CO_2 to CH_4. So, the increased availability of TEAs which are normal components of seawater is crucial. In tidal freshwater forests, salinity

increased the amount of C mineralized (based on laboratory incubations) suggesting that even relatively low increases in salinity can alter the short-term C dynamics of coastal wetlands (Marton et al., 2012).

The primary consequence of increasing soil salinity on C dynamics of coastal freshwater wetlands is undoubtedly the decrease in plant productivity caused by osmotic stress, and hence, in the long term, the potentially diminished C inputs to the soil (Figures 3, 4). However, in the very short term or following transient pulses in salinity, caused by storms or tsunamis, a transient increase in C inputs to soil, e.g., caused by the more intense shredding of litter from salinity stressed plants, may also be observed. Over longer periods, when salt accumulates, stressed plants become less competitive, fostering changes in abundance and diversity of plant communities that can enforce feedbacks that affect soil formation processes (Ferronato et al., 2018; Pellegrini and Fernández, 2018). Neubauer et al. (2013) showed that the release of CO_2 from soil increased in response to a short-term salinity pulse, but declined over time in response to long-term (3.5 years) exposure. This was attributed to slow indirect feedbacks on soil that affect the composition of SOM (e.g., higher C:N ratios) and are potentially driven by changes in plant productivity and species composition and abundance. In one of the few long-term studies reported in the literature, soils containing larger SOM stocks appear to lose more C in response to salinization, with respect to soils of low C content (Marton et al., 2012). Forecasting the consequences of SLR on organic matter decomposition in wetlands, therefore, requires the integration of biogeochemical dynamics along with vegetation patterns (Figure 5).

Besides governing the release of CO_2 from soils, organic matter mineralization regulates the regeneration and availability of nutrients for plants, also in wetland systems (Reddy and DeLaune, 2020). In this respect, the ensuing decrease in soil microbial biomass and soil enzyme activities may reduce plant productivity in wetland soils, in which extracellular enzymes are crucial for the recycling of nutrients required to sustain plant growth (Pathak and Rao, 1998; Ghollarata and Raiesi, 2007).

Perduring submergence combined with salinity cause a decrease in soil microbial diversity: this reduction, besides being driven by a shift to anaerobic or facultative anaerobic microorganisms, is connected with the toxicity of sulfide and it eventually fosters slower SOM decomposition rates (Setia et al., 2013; Qu et al., 2019). Before this happens, any increase in salinity will be transiently accompanied by an increase in concentration in the soil solution of TEAs (such as iron, manganese and sulphate ions), that support anaerobic respiration and therefore stimulate CO_2 production via increased efficiency in the mineralization of organic matter (Chambers et al., 2011; Meiggs and Taillefert, 2011; Weston et al., 2011; Marton et al., 2012; Neubauer et al., 2013). The larger availability of TEAs supports the shift of the dominant pathway of anaerobic metabolism from methanogenesis towards higher

FIGURE 5
Contrasting effects of salinization caused by SLR on C and N cycles and GHG emissions in coastal freshwater wetlands and in salt marshes.

energy yielding pathways (e.g., SO_4^{2-} reduction). This, combined with lower plant productivity, could eventually lead to a reduced carbon sequestration potential (Herbert et al., 2015).

The best studied effect of increased salinity on microbial C cycling in freshwater wetlands is the suppression of methanogenesis caused by the availability of SO_4^{2-} (Weston et al., 2006; Chambers et al., 2011; Poffenbarger et al., 2011; Neubauer et al., 2013). This not only makes CO_2 reduction to CH_4 less advantageous, but even promotes CH_4 oxidation. Recently, tidal freshwater sediments have been shown to support high rates of anaerobic CH_4 oxidation coupled to SO_4^{2-} (Segarra et al., 2015) and Fe (III), Mn (IV), and NO_3^- reduction (Segarra et al., 2013). The interactions between increased SO_4^{2-} and methanogenesis and CH_4 oxidation (aerobic and anaerobic) are likely to vary with site specific factors such as soil and water chemistry, O_2 availability, vegetation type and water level fluctuations.

The balance between C inputs and mineralization rates does not only affect CO_2 emissions and C sequestration potential, but is also crucial in determining the capability of coastal marshes to keep up with SLR. In fact, their resilience depends on the enhanced organic matter accretion and accelerated sediment deposition (Kirwan and Guntenspergen., 2010). The latter may be seriously hampered by anthropic actions that are the main causes of sediment erosion and loss of wetland surfaces (Fontolan et al., 2012).

Nitrogen cycle

Nitrogen often acts as a limiting nutrient for coastal salt marshes and N availability has considerable impacts on the

structure and productivity of plant communities (Mitsch and Gosselink, 2015). Ammonification is the key process that converts organic N into inorganic N, but all the steps of the N cycle are impacted by inundation with marine waters. In tidal zones, increased sea level combined with tides may result in frequent alterations of the hydrologic status of soils, which stimulate decomposition of SOM and loss of N (Djaman et al., 2018). Bai et al. (2005), Bai et al. (2007) showed that flooding duration and frequencies could influence soil N distribution because submergence greatly influences soil properties.

A comprehensive meta-analysis of coastal soil salinization on N pools by Zhou et al. (2017) showed that soil salinization increased plant N content (+18%), soil NH_4^+ (+12%) and soil total N (+210%), although it decreased soil NO_3^- (−2%) and soil microbial biomass N (−74%). Therefore, we can expect the net primary production (NPP) of halophytic plant communities to benefit from this increased N availability, whereas effects on non-acclimated vegetation may be limited or even reversed by the action of osmotic stress.

Nitrate is the most efficient electron acceptor in submerged soils and helps to maintain the soil redox potential at more positive values. Nitrification, which may still go on in aerobic surface water and soil layers, provides a relatively low but continuous supply of this type of TEAs to the denitrifiers, facultative anaerobic bacteria, which produce the energy necessary for their metabolism by reducing NO_3^- to N_2 using electrons derived from the oxidation of substrates. Denitrification has often been observed to decline along salinity gradients (Rysgaard et al., 1999; Craft et al., 2009; Giblin et al., 2010). However, this detrimental effect is limited to ammonium oxidizing bacteria and nitrite oxidizing bacteria:

heterotrophic aerobic denitrifiers can thrive on the nitrate produced by heterotrophic nitrification and may successfully remove most of the N under different salinity conditions (Fu et al., 2019).

Isotopic analysis of N in ocean sediment layers covering the past 300 million years has shown that substantial variations in denitrification rates were associated with planetary climatic changes such as Quaternary glacial and interglacial periods. Enrichments in ^{15}N, indicative of intensified denitrification, regularly occurred during the stages of rapid sea level rise and were followed by a decrease as sea level subsided again (Algeo et al., 2008). We can therefore expect a similar trend to occur during the early stages of inundation of coastal areas by sea water.

Large increases in salinity (16.5 dS m^{-1}) ultimately inhibit soil nitrification (Ardón et al., 2018). In oxic zones, microbial nitrification converts NH_4^+ to nitrite (NO_2^-) and, finally, to nitrate (NO_3^-), but sulfide inhibits nitrifying bacteria (Joye and Hollibaugh, 1995). Therefore, with increased exposure to saltwater, nitrification rates may decrease and affect denitrification, because of the lower availability of substrate (Rysgaard et al., 1999; Noe et al., 2013). Sulfide ions inhibit denitrification directly by inhibiting the reductase enzymes that catalyze the final steps of denitrification, resulting in incomplete denitrification to NO_2^-, NO, or N_2O (Brunet and Garcia-Gil, 1996), or indirectly by reducing NO_3^- availability via the inhibition of nitrification. Increased ionic strength can also interfere with the enzymes associated with denitrification (Glass and Silverstein, 1999). Dissolved salts alter the configuration of the active site of enzymes (non-competitive inhibition), modifying kinetic parameters such as rate and saturation constants (Dinçer and Kargi, 2001).

Increasing soil salinity stimulated soil N_2O fluxes as well as hydrological NH_4^+ and NO_2^- fluxes more than threefold, although it decreased the hydrological dissolved organic nitrogen (DON) flux (−59%). Soil salinization also increased net N mineralization by 70%, although salinization effects were not observed on the net nitrification, denitrification and dissimilatory nitrate reduction to ammonium (Zhou et al., 2017).

Sulphur, iron and phosphorus cycling

In wetlands, S cycling is tightly coupled to Fe cycling, both of which are driven by biotic and abiotic redox reactions (Smolders et al., 2007; Burgin et al., 2011). In oxic or sub-oxic soils, S and Fe are in their oxidized forms, i.e., SO_4^{2-} and Fe^{3+}, and are reduced to sulfide (S^{2-}) and ferrous (Fe^{2+}) ions during anaerobic microbial respiration. Sulphate reduction results in the formation of sulfide species (H_2S, HS^-, S^{2-}), which are toxic to many organisms (Lamers et al., 2013). In many soils, this toxicity is controlled by the co-precipitation of insoluble forms. Released sulfide and Fe^{2+} ions combine abiotically to form, at first, highly insoluble iron monosulfide (FeS) (Schoepfer et al., 2014), regulating the

concentration of sulfide in the soil solution. Salinization generally favours the formation of FeS_x minerals in wetland soils such as mackinawite and pyrite (FeS_2, Rickard and Morse, 2005; Tobias and Neubauer, 2019). Nevertheless, the formation of FeS_x minerals retains S in sediments and can have potentially deleterious consequences. Reclamation of anaerobic soils with high concentrations of FeS_x may generate acid sulphate soils. If drained, FeS_x minerals react with O_2 releasing a large amount of H^+ (White et al., 1997), leading to soil acidification and the mobilization of aluminium (Al) and toxic metals (Johnston et al., 2003; Baldwin and Fraser, 2009; Lamers et al., 2013). These processes limit the reclamation of soils that have been submerged by sea water for a long time.

The interaction between S and Fe cycling indirectly also controls P cycling in periodically submerged soils. In fact, the reduction of Fe (III) to the more soluble ferrous Fe (II) form and its reaction in solution with sulfide results in the dissolution of Fe-PO$_4$ minerals, releasing phosphate ions (Reddy and DeLaune, 2020). The increased availability of P freed from iron-sulphur complexes goes on for weeks to months following saltwater intrusion, and may contribute to the eutrophication of overlying and downstream waters (Lamers et al., 2001; Lamers et al., 2002; Weston et al., 2006). The concomitant increased potential for H_2S build-up and toxicity, and for PO_4^{3-} release, have important implications for overall ecosystem health and downstream eutrophication, though these effects may not be apparent with short-term salinization.

It is obvious that Fe, S, and P dynamics are highly complex and, albeit driven by biological reduction, they are controlled largely by abiotic factors such as water chemistry, SOM, soil type, hydrology and other site-specific factors.

Emission of greenhouse gases

Prediction of trends in the release of greenhouse gases (GHG) from soils is a complex issue where ecosystem type, soil hydrological status and quantity and composition of salts with respect to divalent cations combine in different ways (Figure 4).

Vegetated coastal ecosystems are net C sinks that fix and sequester large amounts of both locally produced and allochthonous organic C. In fact, from 428 to 681 g C m^{-2} y^{-1} are fixed by vascular plants and microalgae in North American salt marshes and rates of salt marsh C accumulation, due to sediment burial, reached on average 218 g C m^{-2} y^{-1} over the last 50–100 years (McLeod et al., 2011). In tidal salt marshes, CO_2 emissions from soils (i.e., soil CO_2 efflux) are highly variable ranging from 240 to 720 g C m^{-2} y^{-1} and this heterogeneity arises from a variety of processes, including autotrophic and heterotrophic respiration and fermentation (Tobias and Neubauer, 2019). Even if the global net C sequestration potential of vegetated coastal ecosystems is difficult to predict, mangrove swamps and salt marshes greatly contribute to the

biological C pool (Chmura et al., 2003) and it would be important to predict changes brought by SLR.

An increase in sea level will obviously increase the length of submergence periods in tidal environments, eventually leading to permanent flooding of the lowest parts of coastland. As a consequence, the time allowed for oxygen diffusion will be restricted and anaerobic decomposition of SOMfostered by anoxia. In general, C mineralization is slower in submerged soils, because of thermodynamic impairments on decomposition, but submergence by sea water implies an increase in salinity, which drives a complex network of consequences.

Weston et al. (2006) observed a shift from methanogenesis to SO_4^{2-} reduction in ocean water-amended sediments, though this biogeochemical shift was not accompanied by changes in microbial community dominance (Edmonds et al., 2009). Poffenbarger et al. (2011) performed a meta-analysis on CH_4 fluxes along natural salinity gradients and showed that emissions decreased with increasing salinity. However, the decrease was significant only for salinity regimes above 18 g L^{-1} (polyhaline marshes), whereas for mesohaline marshes, about 52% of the positive GHG balance of the yearly sequestered C was offset by methane emissions that did not significantly differ from those of non-saline systems. This is indirectly confirmed by responses of GHG emissions to storm-surge reductions in salinity: Capooci et al. (2019) used a mixed effects models approach and found that a decrease in salinity can produce increased pulses up to 24% in GHG emissions.

Short-term laboratory incubations simulating saltwater intrusion in tidal forests (Marton et al., 2012) confirmed that CH_4 production was inhibited by salinity, decreasing up to 90% in 5‰ salinity treatment, but variable responses were observed for N_2O production. Tidal forest soils are capable of producing from 0.032 to 1.9 µg N_2O g^{-1} soil h^{-1}, but most of it is reduced to N_2, unless the acidity of the freshwater inputs inhibits the N_2O reductase activity. At high levels of seawater intrusion, however, the same enzyme may suffer from inhibition by sulfide ions caused by increased sulphate availability (Sorensen et al., 1980).

The production of GHG is regulated by the availability of TEAs that are preferentially used by microorganisms because of the greater thermodynamic yield compared to methanogenesis (Figure 4). Besides sulphate, the availability of other TEAs can also be influenced by SLR. For instance, humic substances are a widespread component of dissolved organic matter in rivers and can act as TEAs but, because of their poly-electrolytic nature, their solubility is suppressed in sea water. The normal trend can therefore be locally reversed with a lack of TEAs leading to increased methane production.

Conclusions and outlook on future investigation needs

Coastal soils feature some of the most densely inhabited and productive areas of the world and are natural hot spots of

biodiversity. They also harbour biological processes that govern interchange between terrestrial and marine environments and between soils and the atmosphere. Because of the large number of effecting factors acting often in contrasting directions, the consequences of salinization of coastal soils are still difficult to predict on the global scale. In particular, the effects of SLR on C and N cycles and consequently on GHG emissions from coastal soils are highly variable, depending on the contrasting and concomitant effects of flooding and salinity. At present, it is unlikely that this variability can be handled by models aiming to predict consequences at a planetary scale. A reliable evaluation at a planetary scale should result from more precise inventories and monitoring of areas displaying specific similarities and from the implementation from these well-defined data sets, of specifically devised models whose results can be finally combined on a weighted basis.

Besides the collection of data, a deeper knowledge of the mechanisms and effecting factors that act, in both the short and long term on the biological activity of soils affected by SLR is certainly needed. In this way most of the apparently contradictory results that are nowadays reported in literature could be embedded into a holistic insight, allowing scientists and decision makers to devise *ad hoc* strategies and mitigate unavoidable impacts of SLR and salinization at local and regional scales.

Author contributions

MD conceptualized the project and, with SM, developed the structure for the review. MD compiled data and prepared the initial text. EP contributed to the writing of the text. SM, CB, and MC contributed to the editing and finalization of the manuscript. All authors approved the text for publication.

Conflict of interest

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

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