Wetlands

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Abstract

Wetlands are globally diverse ecosystems that occur between terrestrial and aquatic environments. The degree of flooding is the main control on wetland vegetation, which varies from shallow water wetlands with submerged and floating-leaved plants, to emergent marsh and treed swamp. Wetlands support unique flora and fauna, from duckweed to mangrove trees and from frogs to hippopotamus. Humans exploit them for water, rice and fish, but wetlands also provide key services, such as flood attenuation, coastline protection, water purification and carbon regulation. Despite these benefits, humans have drained or converted over half of global wetlands. Extensive wetlands remain, but many are threatened by altered flooding regimes, invasive species, nutrient enrichment, contamination and climate change. Conservation efforts must focus on protecting wetlands and especially on maintaining key ecological processes on which wetlands rely.

What are Wetlands?

Wetlands, as their name suggests, occupy transitional zones between terrestrial environments and permanently-flooded or aquatic environments. They are dominated by wetland vascular plants, or macrophytes, and they occur where periodic or permanent flooding produces soils with low oxygen conditions, which forces the biota, particularly rooted plants, to adapt to flooding (Keddy, 2010). Wetlands have existed since vascular plants first evolved and colonized land, 430 million years ago in the early Silurian period (Greb et al., 2006).

We know wetlands by many names: bog, fen, peatland, moor, mire, muskeg, marsh, slough, prairie pothole, wet savannah, dambo, rice paddy, wet meadow, salt marsh, swamp, carr, pocosin, mangrove swamp, mangal, bottomland, and riparian zones, to give just a few names for wetlands in the English language. This list bears witness to the rich and regional language we use for wetlands. But this list also attests to the underlying diversity of wetland ecosystems.

Several regional systems categorize wetlands into different types, based on their landforms, flooding regimes, nutrient regimes, peat formation or their vegetation, but no global system exists to describe wetlands (Keddy, 2010; Mitsch and Gosselink, 2015). Two complementary approaches are commonly used to describe wetlands. The first considers their large-scale landscape setting, and the second considers their vegetation.

Wetlands occur in different broad landscape settings: slope wetlands, depression wetlands, extensive mineral flats, extensive organic flats or peatlands, riverine or floodplain wetlands, lacustrine fringe wetlands and tidal fringe or coastal wetlands; (Fig. 1; Brinson, 1993). Each wetland type occupies a distinct geomorphology setting, and each also has distinct water sources and patterns of water movement through the wetlands.

When wetland vegetation is considered, five broad wetland types are generally recognized: shallow water wetlands, marshes, swamps, bogs and fens.

1. Shallow water wetlands are the most aquatic wetland type. They occupy shallow riparian zones of rivers and littoral zones of lakes and ponds and are dominated by floating-leaved and submersed aquatic plants (Fig. 2A).
2. Marshes are mostly flooded but are occasionally exposed. They are dominated by rooted herbaceous plants with stems and leaves that emerge above the water level. They generally accumulate little peat (Fig. 2B). Freshwater marsh has distinct vegetation from salt marsh, a type of coastal wetland.
3. Swamps are at least periodically flooded but with less flooding than other wetland types. They are dominated by woody plants, either trees or shrubs. They also accumulate little peat (Fig. 2C). Mangrove swamps are a particular type of coastal wetland along protected subtropical or tropical coasts (Fig. 2D).

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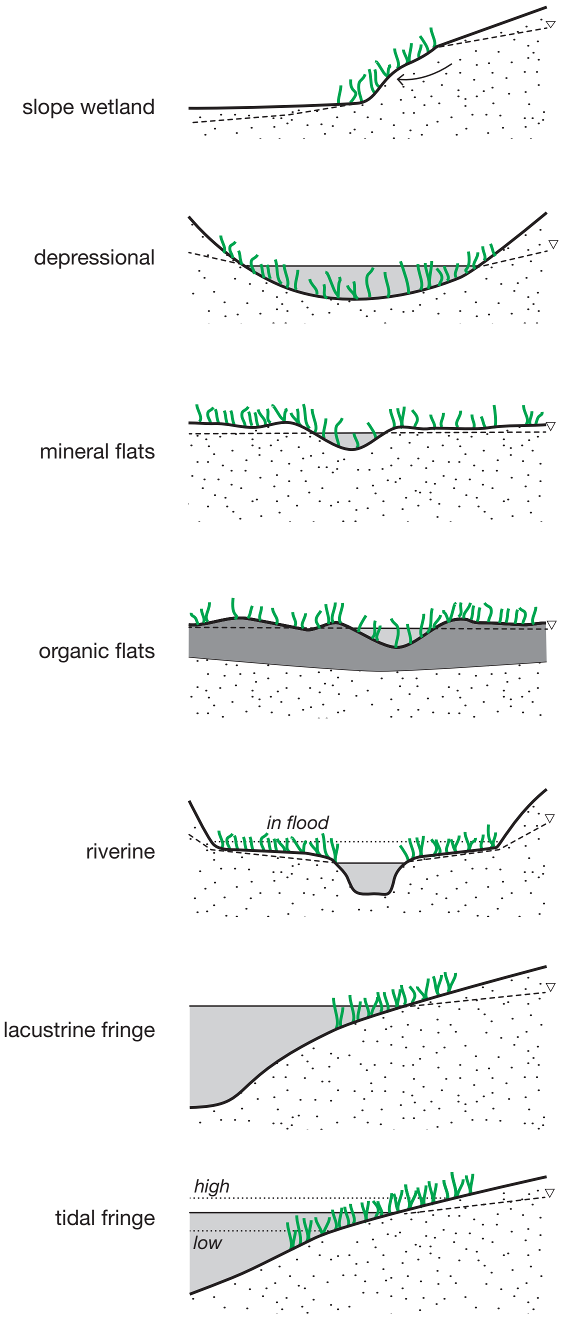

Fig. 1 General wetland landforms, following the hydrogeomorphic classification of wetlands (Brinson, 1993). The inverted triangle and dashed line indicates the water table in adjacent uplands.

4. Bogs are peat-accumulating wetlands, or peatlands, which are primarily rain-fed and are consequently nutrient-poor and acidic (pH 3–5.5). Bogs have a range of flooding environments and are dominated by peat mosses (*Sphagnum*), sedges, dwarf shrubs and scattered evergreen trees. Because they are rain-fed, bogs are also referred to as ombrotrophic peatlands (Fig. 2E).
5. Fens are another type of peatland that also receives groundwater inputs, and as such are less nutrient-poor and less acidic (pH $>$ 5.5) than bogs. Again, a range of flooding conditions occur. They are dominated by other mosses, sedges, grasses, and scattered shrubs and trees. They are also referred to as minerotrophic peatlands (Fig. 2F).

Other wetland types could be added, such as wet meadows between marsh and swamps. Many wetlands also do not easily fit into these classes, as for instance tropical peat swamps, which are treed swamps that accumulate thick peat deposits.

Fig. 2 Examples of wetland habitats: (A) shallow water wetland with giant water lily in the Amazon basin, Colombia; (B) emergent marsh at the mouth of the Atchafalaya River delta, Louisiana, United States; (C) hardwood swamp with tupelo in Louisiana, United States; (D) mangrove swamp at low tide, Australia; (E) bog in the Hudson Bay Lowland, Canada; and (F) string fen with alternate pools and raised ribs in the Hudson Bay Lowland. Photo credits: Daniel Campbell, except 2d by H. Bieser.

Wetlands and Flooding

Flooding is the key factor that controls wetland ecosystems. It dictates the type of vegetation and key ecological processes such as decomposition and nutrient cycling. The extent of flooding is a function of the hydrology of the wetland, and more specifically the water balance. The water balance is a simplified way to view how water enters and exits wetlands (Fig. 3). For inland wetlands, inputs include precipitation, surface inflow and groundwater discharge, and outputs are from evapotranspiration, surface outflow

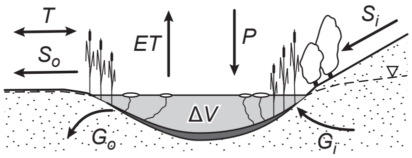

Fig. 3 Elements of a water balance in wetlands. Changes in water storage (ΔV) is a function of inputs of precipitation (P), surface runoff into the wetland (S_i) and groundwater discharge into the wetland (G_i), and outputs of evapotranspiration (ET), surface runoff out of the wetland (S_o) and groundwater recharge from the wetland (G_o). Where there is tidal influence, there are also tidal exchanges (T).

and groundwater recharge (Mitsch and Gosselink, 2015). Coastal wetlands also have tidal exchanges. When water inputs exceed outputs, flooding increases.

Oxygen diffuses 10,000 times slower in still water than in the air, and once a soil is flooded, oxygen diffuses even slower through the voids between the particles of wetland soils (Reddy and DeLaune, 2008). In consequence, once a wetland is flooded, the floodwaters and the surfaces of wetland soils are well-aerated, but oxygen below the soil surface is rapidly consumed by microbes and other biota (Fig. 4). Once flooded, wetland soils soon begin to suffer from low oxygen levels, a condition called hypoxia. With longer flooding duration, the oxygen becomes depleted, a state known as anoxia. Soil compounds of nitrogen, iron, manganese and sulfur also become chemically modified as flooding duration increases and oxygen is depleted (Ponnamperuma, 1972; Reddy and DeLaune, 2008). Methane gas is even produced from organic matter under anoxic conditions. Several of these modified compounds are toxic to plants (Kozlowski, 1984). As a result, plant roots and other wetland biota must not only survive through the low oxygen conditions found in flooded wetland soils, they must also contend with some toxic compounds produced by flooding.

Different wetlands have different duration of flooding, frequency of flooding and depth of the water table or the water level relative to the ground surface. The seasonal pattern of inundation above and below the soil surface is known as the hydroperiod (Reddy and DeLaune, 2008; Mitsch and Gosselink, 2015). However, sometimes the hydroperiod is defined more strictly as simply the duration of standing water in a wetland (Wellborn et al., 1996; Semlitsch, 2000; Batzer, 2013). The hydroperiod, along with the quality of soil organic matter and the availability of nutrients, determines the amount of oxygen that is available in wetland soils (Reddy and DeLaune, 2008). Plant roots, as discussed below, also strongly influence the amount of oxygen in wetland soils.

It is useful to contrast the seasonal hydroperiods of a few different wetland classes and consider the extent and timing of soil aeration with which wetland vegetation must contend.

Extensive organic wetlands, or large peatlands, such as bog and fen, have narrow water level fluctuations (Ingram, 1983; Fig. 5A). This produces extended anoxic conditions, which limit decomposition and the internal cycling of nutrients, and favor the accumulation of peat. Different flooding microhabitats occur in peatlands, from flooded pools >1 m deep to rarely flooded hummocks elevated 20–50 cm above the mean water table (Rydin and Jeglum, 2013), but all have relatively narrow water level fluctuations.

Lacustrine fringe wetlands, such as those along the Great Lakes of North America, are subject to wide seasonal water level fluctuations, with superimposed wind-driven short-term fluctuations, called seiches (Fig. 5B). Wetland vegetation types toward the upper end of this flooding gradient, such as swamp, wet meadow and, to a lesser extent, marsh, only have periodic flooding and consequently have respite from extended anoxic soil conditions. The water level fluctuations also allow more exchanges of nutrients and biota with the adjacent lake (Morrice et al., 2004).

Tidal fringe wetlands, or coastal wetlands, such as salt marshes or mangrove swamps, are subject to tides, with alternating flooded and exposed conditions once or twice each day (Fig. 5C; Friess et al., 2012; Van Loon et al., 2016). This flooding regime is superimposed upon longer-term water level fluctuations associated with lunar cycles, between neap tides and spring tides, and with those associated with occasional storm surges. Soils of tidal wetlands consequently alternate between hypoxic and more aerated

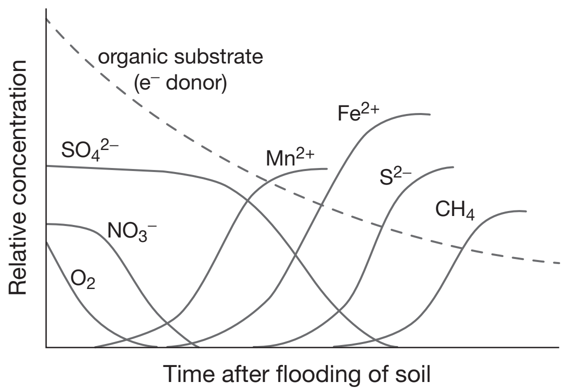

Fig. 4 Changes in relative concentration of soil compounds following flooding After: Reddy, K. R. and DeLaune, R. D. (2008). Biogeochemistry of wetlands: Science and applications, Boca Raton: CRC Press.

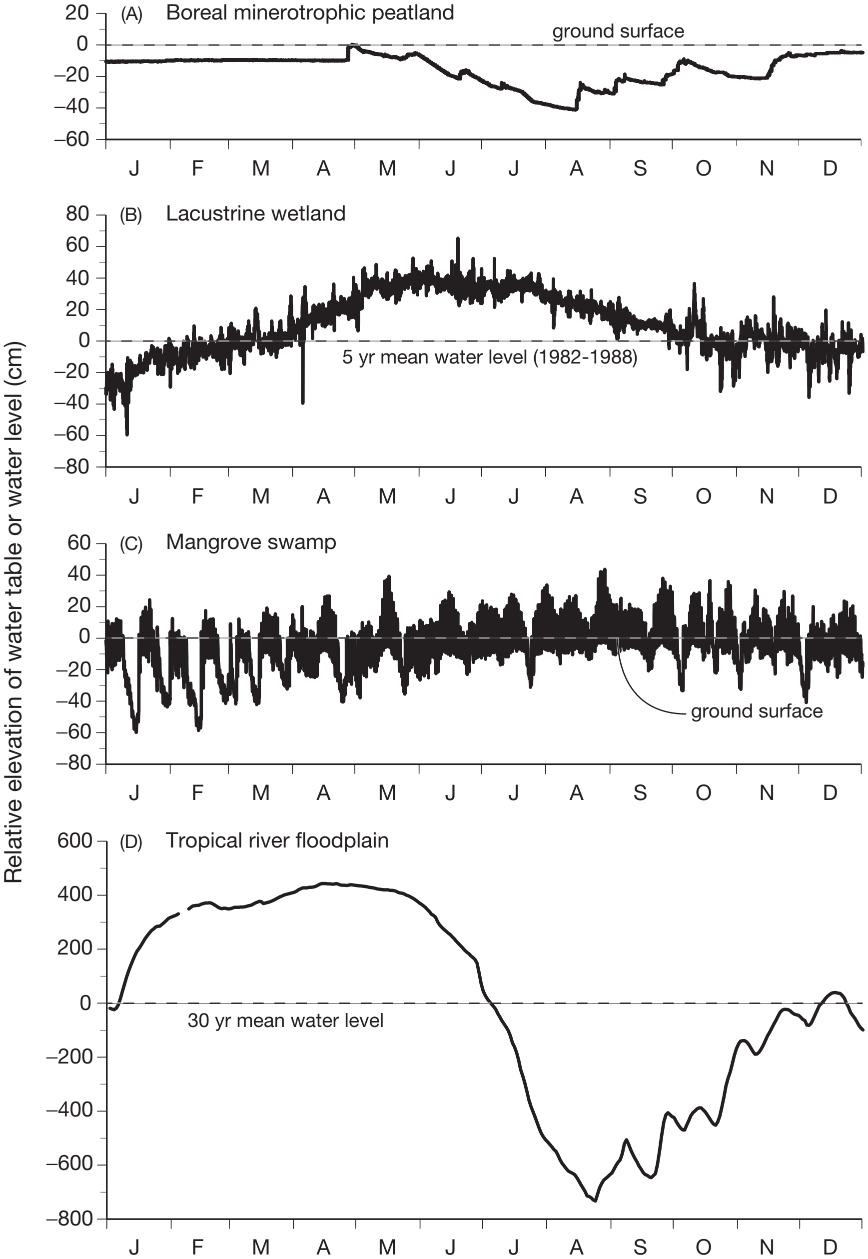

Fig. 5 Examples of annual hydroperiod curves in (A) a boreal minerotrophic peatland in Sweden in 2006 (Peichl et al., 2014); (B) a lacustrine wetlands along Lake Erie, USA/Canada, in 2017 (NOAA, 2018); (C) a microtidal mangrove swamp, in southern Florida, United States, in 2011 (Castañeda and Rivera-Monroy, 2018); and (D) a tropical floodplain along the Amazon River at Tabatinga, Brazil in 2017 (SO HYBAM, 2018). Elevations are relative to the ground surface or a local reference point, as indicated. Measurements were taken at hourly intervals (A–C) or daily intervals (D).

conditions on a frequent basis. The tides also allow for frequent exchanges of nutrients, organic matter and biota between the wetlands and the adjacent estuarine or marine environments.

Riverine wetlands are only inundated when the rivers flood. Extreme examples occur in the floodplain forests of the Amazon basin of South America, where water levels fluctuate over >12 m each year (Fig. 5D; Junk et al., 2011). These floodplain forests consequently shift from flooded anoxic environments to drained aerated environments, for several months at a time. The floods act as pulses that permit extensive exchanges of sediment, organic matter, nutrients and biota between the river channel and its floodplain (Junk et al., 1989).

Flooding and Wetland Vegetation

Flooding has profound but different impacts on different wetland plants (Sculthorpe, 1967; Hutchinson, 1975; Blom, 1999; Banach et al., 2009; Keddy, 2010). Consider an idealized transect along a water depth gradient bordering a river or lake, beginning from the most flooded to the least flooded wetlands sites (Fig. 6). Vegetation appears in zones depending on the extent of flooding.

Submerged aquatic macrophytes, such as milfoil (*Myriophyllum*) and bladderwort (*Utricularia*), and rooted floating-leaved macrophytes, such as water lilies (Nymphaceae), occur in shallow water wetlands, the most aquatic wetland habitats, which are predominantly to permanently flooded. Further upslope, in periodically exposed environments, is a zone of emergent macrophytes, such as cattail (*Typha*) and arrowhead (*Sagittaria*), rooted in wetland soils, but with their leaves extending above the water surface. This is marsh. Finally, shrubs, such as willows (*Salix*) or alders (*Alnus*), and trees, such as larch (*Larix*) or tupelo (*Nyssa*), occur toward the top of the flooding gradient in only periodically flooded environments, in swamp. Free-floating macrophytes, such as duckweeds (Lemnaceae) and water cabbage (*Pistia*), may occur across this flooding gradient. Algae also grow on plants and other surfaces across this gradient and can make up a substantial portion of primary productivity in some wetlands (McCormick et al., 1998; Adame et al., 2017). Bryophytes, such as peat mosses (*Sphagnum*) and brown mosses (Amblystegiaceae), are generally only abundant where water levels fluctuations are low, as in peatlands.

These different types of wetland plants have different adaptations to flooding. Submersed aquatic macrophytes are well adapted to completely aquatic environments. Their leaves lack a waxy cuticle, are thin and often have a large surface to volume ratio to facilitate the diffusion of oxygen and other substances between their tissues and the water column (Sculthorpe, 1967; Hutchinson, 1975). They can even use dissolved inorganic carbon during photosynthesis, instead of carbon dioxide, which makes them even more suitable to aquatic environments (Sculthorpe, 1967; Hutchinson, 1975; Pedersen et al., 2013).

Rooted floating-leaved macrophytes and emergent macrophytes extend their rhizomes and root systems into the flooded wetland soils. They can withstand some hypoxia in their roots and rhizomes, at least temporarily, through metabolic adaptations (Kozlowski, 1984; Blom, 1999). However, their principal strategy is to avoid hypoxia, through morphological adaptations. They have air channels within their stems and roots, called aerenchyma, which allow for air to circulate from leaves and stems above the water level to the rhizomes and roots in flooded wetland soils (Fig. 7; (Sculthorpe, 1967; Hutchinson, 1975; Jung et al., 2008; Sorrell and Hawes, 2010). The aerenchyma not only provides oxygen to the roots and rhizomes, it also can aerate the flooded soils immediately around the plant roots (Reddy and DeLaune, 2008; Lai et al., 2012). This effect can facilitate the survival of less flood-tolerant species in the wetland soils nearby (Callaway and King, 1996). However, many emergent plants still prefer less flood duration (Campbell et al., 2016), and many will die back when they are continuously flooded for three or more years (Harris and Marshall, 1963; van der Valk, 1994). Seeds of many emergent plants also prefer to germinate under unflooded conditions (van der Valk, 1981), and as a result, periodic exposed conditions are needed to regenerate many species of emergent marsh vegetation.

Most woody plants lack any morphological adaptations to oxygenate their roots (Kozlowski, 2002; Parolin, 2009). They must rely on physiological adaptations to withstand flooding. They die after a year of continuous flooding, although a few woody wetland species can withstand flooding for 2–3 years (Valle Ferreira and Stohlgren, 1999; Kozlowski, 2002). This is why trees and shrubs are limited to swamps, the wetland type with the least flooding duration. Mangroves are exceptions. They are shrubs and small trees, but they can survive longer flooding because they have aerial roots known as pneumatophores, which transport oxygen to buried roots via aerenchyma (Srikanth et al., 2016).

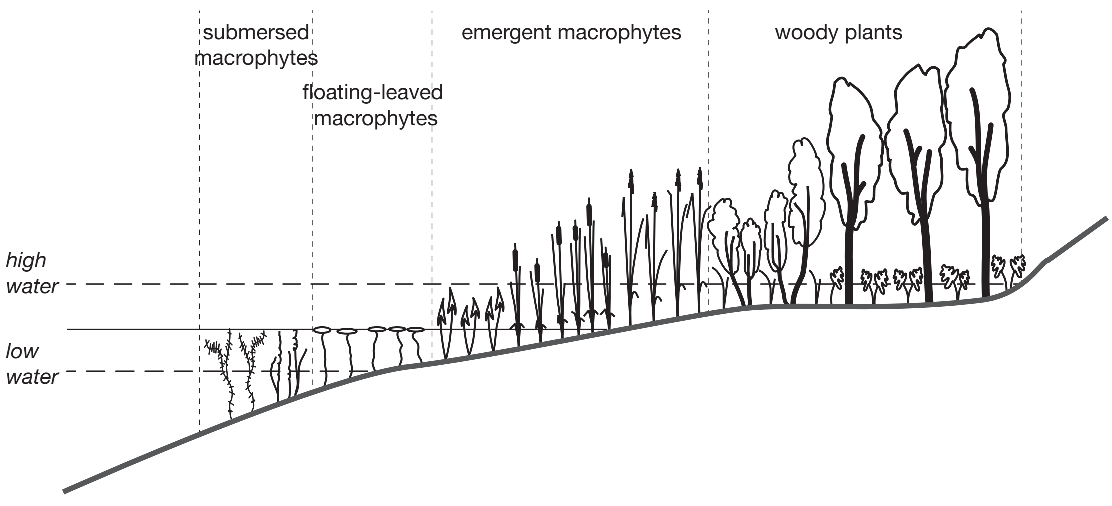

Fig. 6 An idealized transect across a wetland from shallow water wetlands through emergent marsh to swamp. The lower elevations are almost continuously flooded, while the upper elevations of the wetland are only periodically flooded during high water periods.

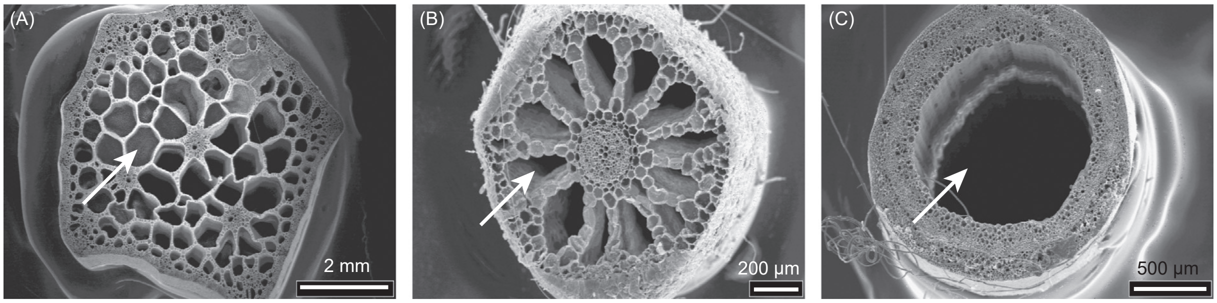

Fig. 7 Cross-sectional views of aerenchyma in shoots of wetland plants: (A) arrowhead, *Sagittaria sagitifolia* susbp. *Leucopelata* var. *edulis*, (B) water milfoil, *Myriophyllum spicatum* and (C) crowfoot, *Ranunculus cantoniensis*. The arrows indicate aerenchyma. After: Jung, J., Lee, S. C. and Choi, H. K. (2008). Anatomical patterns of aerenchyma in aquatic and wetland plants. *Journal of Plant Biology* **51,** 428–439.

Other Controls on Wetland Vegetation

Fertility is the second principal factor controlling wetland vegetation (Keddy, 2010). Many wetlands, such as salt marshes, freshwater marshes and swamps, are quite productive, with net primary productivity ranging between 1.5 and >2 kg m^{-2} $year^{-1}$ (Bradbury and Grace, 1983). Their productivity even exceeds that of intensively farmed agricultural land. However, not all wetlands are productive. Peatlands, for instance, have low net primary productivity, between 0.3 and 1 kg m^{-2} $year^{-1}$. The supply of macronutrients, mainly nitrogen and phosphorus, is responsible for these differences in productivity among wetlands.

For instance, diverse infertile herbaceous wetlands exist in temperate regions, each with their own assemblage of wetland species (Fig. 8). Because of the low nutrient supply, these wetlands have low productivity and are dominated by short-statured species. In contrast, fertile herbaceous wetlands with high nutrient supply become dominated by only a few tall productive species, such as cattail (*Typha*) or common reed (*Phragmites*; Moore et al., 1989). When infertile wetlands receive increasing nutrient supply, the few taller competitive dominants replace the diverse short-statured species, in a process mediated by the competition for light. Many species of conservation concern are also short-statured, and are consequently restricted to infertile, unproductive wetlands (Moore et al., 1989).

Differences in vegetation between wetlands can also be a result of differing micronutrient supply. For instance, both macronutrients such as nitrogen and phosphorus are scarce across peatlands, but fens have a larger supply of calcium than bogs (Fig. 9). This is because bogs are only rain-fed, while fens also receive groundwater inputs. Fens, in consequence, have different species assemblages from bogs, have more rapid nutrient cycling and are more productive (Sjörs, 1950; Bridgham et al., 1996; Wheeler and Proctor, 2000; Keller et al., 2006).

Disturbances, defined as processes that substantially reduce the biomass of vegetation, also have profound influences on the vegetation of wetlands (Keddy, 2010). For instance, flooding by beaver damming is a disturbance because it drowns trees and shrubs. Other examples of disturbance include high river flows which erode river floodplains, ice which gouges shorelines in boreal regions, tropical cyclones which produce erosive waves and high salinity pulses in coastal wetlands, and fire in subtropical and tropical wetlands (Salo et al., 1986; Guntenspergen et al., 1995; Kotze, 2013; Lind et al., 2014). Many wetlands, such as emergent marshes, are adapted to these disturbances. They accumulate large banks of seed in the soil. These seeds consequently allow the vegetation to rapidly recover following severe disturbances (van der Valk, 1981; Keddy and Reznicek, 1986).

Grazing by herbivores is a more targeted type of disturbance that affects some wetlands (Bakker et al., 2016; Wood et al., 2017). Extreme examples include the overgrazing of subarctic coastal marshes by snow geese, or subtropical marshes by nutria, or constructed marshes by muskrat (Kerbes et al., 1990; Shaffer et al., 1992; Kadlec et al., 2007). These herbivores can efficiently transform productive emergent marsh to unvegetated mud flats. Wetland vegetation, at least submersed, floating-leaved and emergent macrophytes are more nutrient-rich, with a lower ratio of carbon to nitrogen than terrestrial vegetation, which explains why fauna prefer wetland plants as food (Bakker et al., 2016).

Other factors that control wetland vegetation include competition among plants, the burial of vegetation by sediment in floodplain and deltaic wetlands and salinity in coastal wetlands (Keddy, 2010).

Wetland Fauna

Many animals are dependent upon wetland environments at some point during their life cycle. An eclectic list could include species of mosquitoes, dragonflies, caddisflies, aquatic beetles, crayfish, crabs, snails, fish, frogs, salamanders, turtles, crocodilians, waterfowl, wading birds, rodents and a few large mammals.

One way to consider the animals in wetlands is to examine the wetland food webs (Montague and Wiegert, 1990). Herbivore-based food chains, where animals directly eat vascular plants, are important in some wetlands, as pointed out above for waterfowl and large rodents (Bakker et al., 2016; Wood et al., 2017). But in many wetlands, the food webs are based upon plant detritus and the bacteria and fungi that feed off it, or upon the microalgae attached to wetland surfaces (Fig. 10). Invertebrate animals feed from

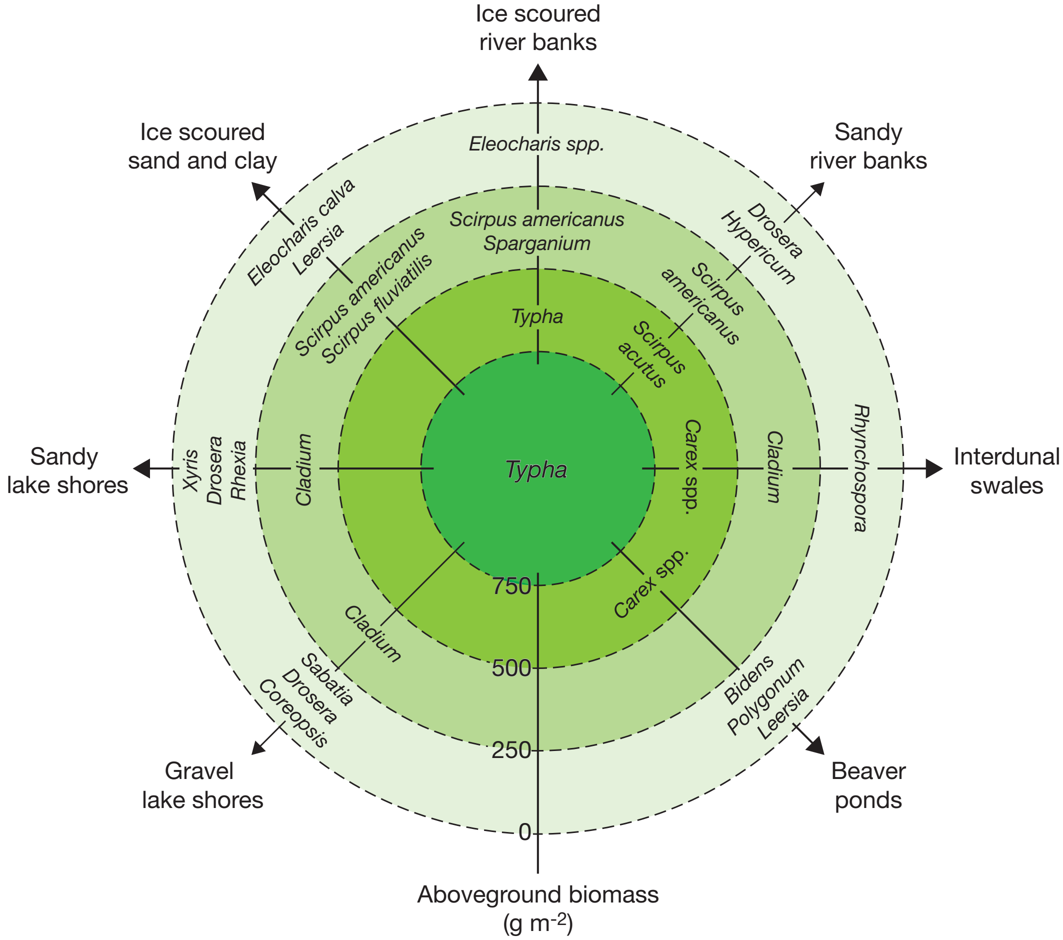

Fig. 8 Organization of herbaceous wetlands along gradients of above ground productivity. The peripheral habitats are infertile and have low productivity. The core habitats are fertile, with low disturbance, and have consequent high productivity. They are dominated by large canopy-forming herbaceous emergent species, such as *Typha*. After: Moore, D. R. J., Keddy, P. A., Gaudet, C. L. and Wisheu, I. C. (1989). Conservation of wetlands: Do infertile wetlands deserve a higher priority? *Biological Conservation* **47,** 203–217.

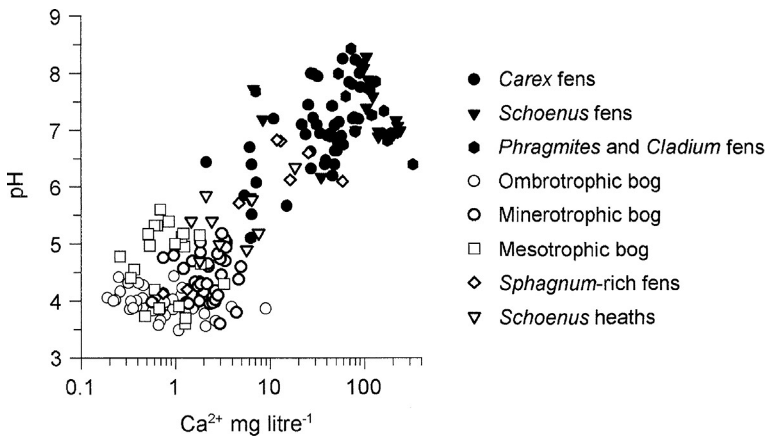

Fig. 9 Peatland vegetation types in Britain and Ireland along gradients of water pH and calcium ion concentration. After: Wheeler, B. D. and Proctor, M. C. F. (2000). Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology* **88,** 187–203.

the detritus, the microbes and the microalgae, and they, in turn, are food for fish and birds (Batzer and Wissinger, 1996; Minello et al., 2003). In coastal wetlands, invertebrates include diverse crustaceans, annelid worms and mollusks, but in freshwater wetlands, they are primarily insects. Wetlands with detritus and microalgae-based food webs include temperate marshes,

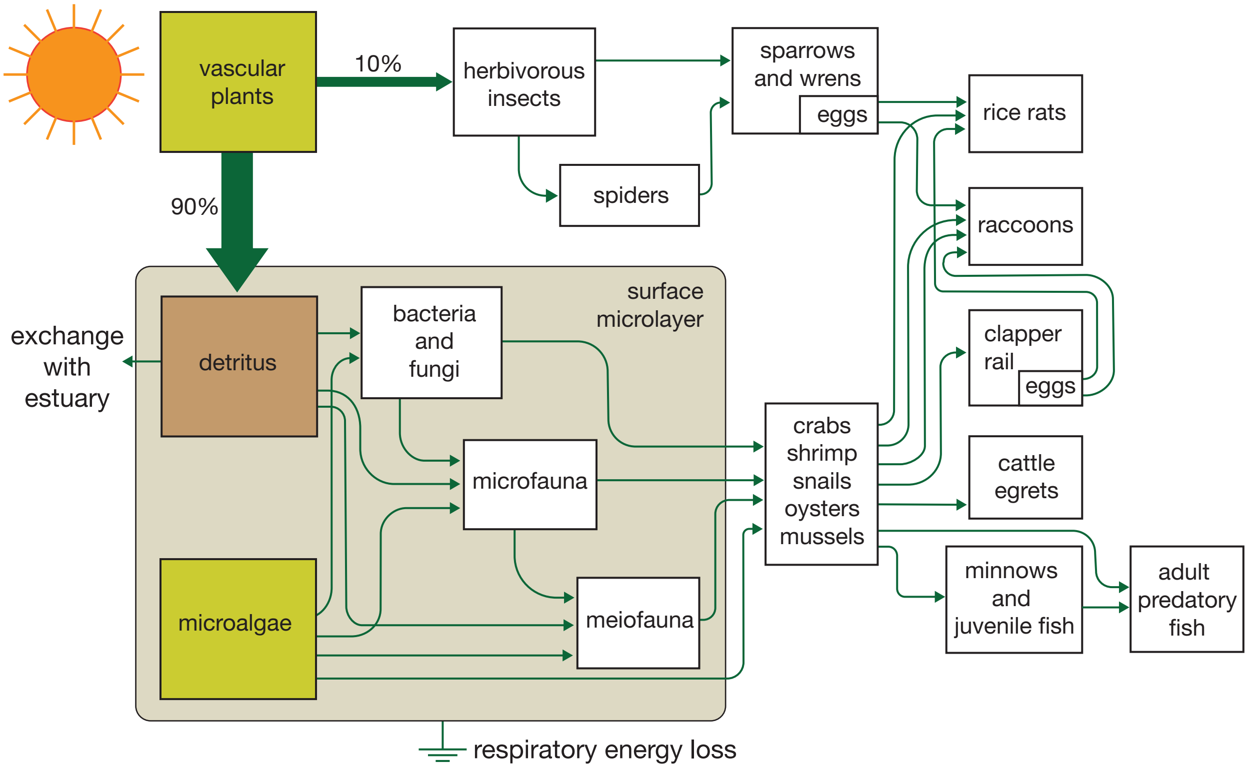

Fig. 10 Food web in a coastal salt marsh, with a grazing food chain along the top and a detrital and microalgal food chain on the bottom. After: Montague, C. L. and Wiegert, R. G. (1990). Salt marshes. In: Myers, R. L. and Ewel, J. J. (eds.) *Ecosystems in Florida.* pp 481–516. Orlando: University of Central Florida Press.

subtropical wet prairies, salt marshes, mangrove swamps and even peatlands (Murkin, 1989; Belicka et al., 2012; Jassey et al., 2013; Abrantes et al., 2015).

Fish utilize the more aquatic habitats found in wetlands. Different species use them as spawning grounds, nursery habitat for juveniles, or as feeding grounds for adult fish. Fish play important roles in the food webs of riverine wetlands, lacustrine wetlands, salt marsh and mangrove swamps (Minello et al., 2003; Petry et al., 2003; Junk et al., 2007; Nagelkerken et al., 2008; Lee et al., 2014; Trebitz and Hoffman, 2015). Fish also move from wetlands to more aquatic habitats. They consequently contribute to wider aquatic food webs in adjacent rivers, lakes, estuaries and nearshore marine ecosystems.

Amphibians are quintessentially associated with freshwater wetlands. They include frogs, toads, salamanders, newts, sirens, and amphiomas. Some amphibians use wetland habitats as larva and then inhabit more aquatic or terrestrial habitats as adults. Others, such as larger frogs, inhabit wetlands throughout their life cycle. Amphibian use of wetlands depends primarily on the duration of flooding and the presence of fish predators (Wellborn et al., 1996; Semlitsch, 2000; Baldwin et al., 2006). Small ephemeral depressional wetlands with only seasonal flooding can have high amphibian use and diversity, in part because they are fishless, whereas permanently flooded wetlands have different amphibian species, adapted to counter fish predation.

Several groups of birds depend on wetlands, including waterfowl, such as ducks, geese and swans, and wading birds, such as herons, cranes, flamingos, rails, jacanas, avocets, shorebirds and ibis (Batt et al., 1989; Sierszen et al., 2012; Holopainen et al., 2015). Many inland and coastal wetlands are globally recognized as Important Bird Areas for their role in providing nesting or migratory stopover habitat for wetland birds (http://www.birdlife.org/).

A few mammals are also emblematic of wetland habitats. For instance, beavers (*Castor* sp.) act as ecosystem engineers by damming small watercourses and creating wetlands in much of North America and parts of Eurasia (Naiman et al., 1988). Another noteworthy example, capybaras (*Hydrochoerus hydrochaeris*), the world's largest rodent, inhabit the vast floodplain wetlands in South America (Corriale and Herrera, 2014). Or consider hippopotamus (*Hippopotamus amphibius*) in sub-Saharan Africa, which, by means of their large bodies moving through wetlands, actually control the geomorphology of African wetlands (McCarthy et al., 1998). A less evident example would be the Bornean orangutan (*Pongo pygmaeus*), which has its last strongholds in the peat swamps of southeast Asia (Posa et al., 2011).

Where Are Wetlands Found?

Wetlands occur on all continents, except on Antarctica. They cover at least 12.1 million km^2 (Davidson et al., 2018), or roughly 9% of the global land area, excluding Antarctica (Fig. 11). Approximately 93% of wetland area occurs inland on the continents, while

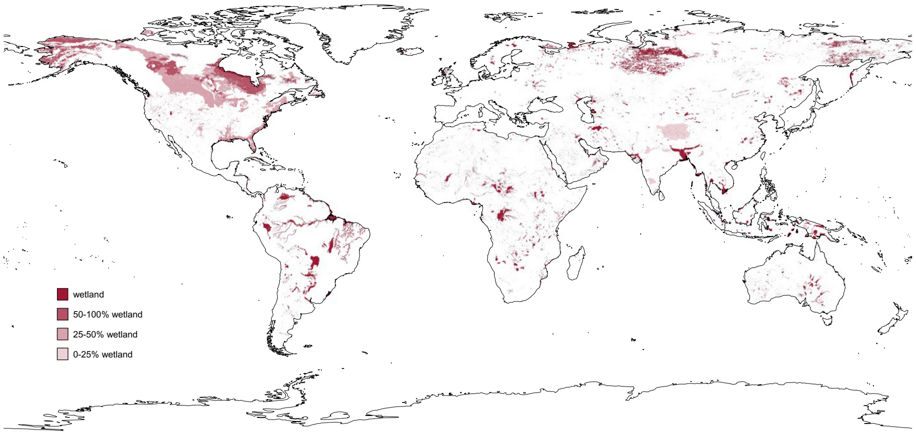

Fig. 11 World distribution of wetlands and wetland complexes. Data from the Global Lakes and Wetlands Database (Lehner and Döll, 2004).

the remaining 7% occurs along marine coasts or in estuaries (Davidson et al., 2018). A few wetlands are quite large, with the 11 largest wetlands or wetland complexes covering a total of 5.8 million km^2 (Fraser and Keddy, 2005; Keddy et al., 2009). The top four wetlands are representative and contrasting. They include two major boreal peatlands, the West Siberian Lowland in Russia and the Hudson Bay Lowland in Canada and two extensive tropical swamps in the Amazon River basin in South America and the Congo River basin in central Africa.

Wetland Ecosystem Goods and Services

Wetlands provide significant ecosystem goods and ecosystem services that support human well-being (Table 1; Millenium Ecosystem Assessment, 2005; Liquete et al., 2013; Reis et al., 2017; IPBES, 2018; Ramsar Convention on Wetlands, 2018). Ecosystem goods include foods such as fish and grains, water, fuels and other biotic products. For instance, riverine, lacustrine and coastal wetlands support critical fisheries of fish and crustaceans, which provide essential protein for nearby settlements (Welcomme et al., 2010; Lee et al., 2014; Abrantes et al., 2015; Trebitz and Hoffman, 2015). Rice (*Oryza sativa* [Asian rice] or *Oryza glaberrima* [African rice]) is also widely cultivated in subtropical and tropical wetlands that have been converted to agricultural use (Gopal, 2013). It is a staple food that feeds billions of people. Another key ecosystem good from wetlands is water. Humans extract water near wetlands for drinking water, irrigation and other uses, although water extraction affects the flooding regimes upon which wetlands depend (McCartney and Acreman, 2009). Some wetlands also provide non-food goods, such as timber, thatching material, fuel wood, honey and waxes (Uddin et al., 2013).

Wetlands not only provide goods for human use, but they also provide key ecosystem services, for which we do not pay, that help to regulate and support broader ecosystems and human societies. For instance, headwater and riverine wetlands store water

Table 1 Principal ecosystem goods and services provided by wetlands

Ecosystem services	*Examples in wetlands*
Ecosystem goods	
Food provision	Fisheries (fish, mollusks, crayfish, crab, shrimp), waterfowl, rice, wild rice, sago palm, wild vegetables
Water storage and provision	Replenishment of groundwater resources, water for human consumption
Biotic materials and biofuels	Non-food uses, including timber, fibers, resins, medicines, genetic resources, fuel peat
Regulating and supporting ecosystem services	
Water flow regulation	Reduction of flood risks in rivers and consequent reduction in erosion and flood damage
Coastal protection	Wave attenuation and protection against storm surges in coastal wetlands
Water purification	Filtering and degradation of nutrients, organic wastes and pollutants
Climate regulation	Carbon regulation through uptake, storage and sequestration of CO_2 as peat; release of methane
Cultural services	
Recreation and tourism	Birdwatching, ecotourism
Symbolic and aesthetic values	Spiritual and aesthetic enjoyment

Adapted from: Millenium Ecosystem Assessment (2005). *Ecosystems and human well-being: wetlands and water*, Washington, DC: World Resources Institute; Liquete, C., Piroddi, C., Drakou, E. G., Gurney, L., Katsanevakis, S., Charef, A. and Egoh, B. (2013). Current status and future prospects for the assessment of marine and coastal ecosystem services: A systematic review. *PLoS One* **8**, e67737.

and slowly release it, as a sponge does, which allows these wetlands to moderate flows and reduce flood peaks and flood damage in water courses downstream (Fritz et al., 2018; Lane et al., 2018). Headwater wetlands also recharge and replenish the groundwater table (Lane et al., 2018).

Coastal wetlands, both salt marshes and mangrove swamps, act as barriers for coastal defense. They attenuate wave energy and floodwaters and stabilize the shorelines in estuarine and marine ecosystems (Shepard et al., 2011; Leonardi et al., 2018; Reed et al., 2018). However, sufficient sediment supply is required to maintain the coastal defense function of coastal wetlands (Boesch et al., 1994).

Wetland ecosystems purify water by filtering out sediments, nutrients, wastes and some pollutants (Verhoeven et al., 2006; Reddy and DeLaune, 2008). Some wetlands are even designed and constructed to treat nutrient-enriched waters in urban, industrial or agricultural settings (Kadlec and Wallace, 2009).

Wetlands are also key ecosystems for the control of climate change (Moomaw et al., 2018). Over millennia, wetlands, especially coastal wetlands and boreal peatlands, have sequestered and stored large quantities of carbon as organic enriched sediments and peat, making them key carbon sinks with the potential for mitigating the impacts of climate change (Mitsch et al., 2013; Sjogersten et al., 2014). However, methane, an important greenhouse gas, is also released from some wetlands (Bridgham et al., 2013; Mitsch and Gosselink, 2015).

Many wetlands provide significant cultural services, such as opportunities for ecotourism, recreation and even spiritual and aesthetic enjoyment. Consider mangrove swamps. They were once avoided as zones of danger, darkness and disease, at least to western eyes (Friess, 2016). Today, mangrove swamps not only provide recreation opportunities for tourists, such as birdwatching and nature enjoyment (Uddin et al., 2013), they also give spiritual and cultural meaning to those who visit them (Thiagarajah et al., 2015).

Threats to Wetlands

Wetlands face many threats, including drainage and conversion, changes in their hydrology, excess nutrients, invasive species and climate change.

The conversion or drainage of wetlands is the most important threat facing wetlands (Junk et al., 2013; van Asselen et al., 2013). Between 54% and 57% of natural wetlands are estimated to have been lost since 1700 AD, with a more rapid loss of between 64% and 71% since 1900 AD (Davidson, 2014). The most significant causes for these losses of wetlands are the expansion of arable land and the expansion of urban land, although the construction of dams, dykes and other infrastructure is also an important cause in some regions (van Asselen et al., 2013). Large urban population centres are often present in deltas and floodplains, which explains why wetland losses to urbanization are high. Some of the natural wetlands that are converted to agriculture, such as rice paddies, still provide some ecosystem services such as flood control and faunal habitat (Verhoeven and Setter, 2010; Gopal, 2013). Institutional and regulatory frameworks, such as the use of subsidies to convert natural wetlands to cropland, are also still responsible for substantial wetland losses in some regions (van Asselen et al., 2013).

The remaining wetlands are often affected by changes in flooding regimes (Junk et al., 2013). For instance, water control structures along rivers reduce species diversity in remaining wetlands downstream (Nilsson et al., 2005). In coastal wetlands, ditching and canalizing does not necessarily drain the wetlands, but they can lead to saltwater intrusion and consequent vegetation shifts (Gedan et al., 2009).

Although wetlands are valued for their ability to filter nutrient-enriched waters, excess nutrients can shift vegetation and ecosystem processes, especially in historically infertile ecosystems (Moore et al., 1989; Verhoeven et al., 2006). For instance, in the subtropical Everglades wetlands in the United States, oligotrophic marshes that have received nutrient-enriched agricultural runoff shift their species composition from sawgrass to cattail (McCormick et al., 2011). Atmospheric pollution also impacts infertile wetland ecosystems. For instance, peatlands subject to nitrogen-enriched atmospheric pollution shift toward non-peat accumulating wetlands (Bubier et al., 2007). Depending on their landscape position, wetlands may also receive high loads of contaminants from nearby land uses. For instance, wetlands that receive pesticide-enriched runoff from intensive agricultural land have higher incidences of limb malformations in the amphibians that breed there (Mann et al., 2009).

Invasive species, both animals and plants, are also a serious threat to wetlands by changing dominance of wetland species, the structure of their habitat and the food webs (Shaffer et al., 1992; Zedler and Kercher, 2004). A quarter of the most invasive species of plants are found in wetlands (Zedler and Kercher, 2004). Examples in wetlands include common reed (*Phragmites australis*) in wetlands of temperate North American, salt-cedar (*Tamarix* spp.) in floodplain wetlands of arid southwestern North America, and water hyacinth (*Eichhornia crassipes*) in tropical to sub-tropical wetlands outside of its native South American range (Shafroth et al., 2005; Villamagna and Murphy, 2010; Hazelton et al., 2014).

Climate change is also threat to wetlands, since it has the potential to change the water balance and the consequent flooding regime of wetlands (Mitsch et al., 2013). More importantly, climate warming could lower the water tables in peatlands and transform these peatlands from carbon sinks to sources of greenhouse gases, causing further climate warming (Moomaw et al., 2018).

Coastal wetlands are also threatened by sea level rise associated with climate change (Kirwan and Megonigal, 2013). However, recent research indicates that coastal wetlands can keep up with sea-level rise, if sufficient space is available for these coastal wetlands to migrate upgradient and inland as sea levels rise, and if they receive sufficient sediment supply (Schuerch et al., 2018).

However, where shoreline hardening inland restricts their upward and inland migration, coastal wetlands may be caught in a "coastal squeeze," which limits their ability to migrate with sea level rise (Torio and Chmura, 2013).

Wetland Conservation and Restoration

Efforts to conserve and to restore wetlands have grown over the past half century. Arguments for their conservation are often based upon their high utilitarian value through the ecosystem goods and ecosystem services that they provide. But they are also intrinsically valuable as habitat for unique and often threatened biota. Both the utilitarian values and intrinsic values of wetlands should be considered in wetland conservation.

The Ramsar Convention on Wetlands was adopted in 1971 as an international treaty to promote the conservation and wise use of wetlands and their resources. Over 2300 wetlands, covering 2.5 million km^2 in 170 countries, are now designated as internationally important wetlands under this treaty (Ramsar Convention on Wetlands, 2018). Some countries, such as the United States and Canada, have few Ramsar sites, but they conserve wetlands through other protection systems. Nevertheless, only 10% of inland wetlands globally have protection status either as Ramsar sites or as other protected areas (Reis et al., 2017). Furthermore, few of these protected areas have safeguards to maintain their hydrology, their sediment dynamics and their water quality, upon which they depend (Reis et al., 2017). Wetland conservation must consider these key processes in order to retain the extent, quality and function of conserved wetlands.

A total of 73 countries have implemented national policies for wetland conservation (Ramsar Convention on Wetlands, 2018). The strength of these policies vary greatly, from countries with paper-only policies to countries with stringent policies where wetland loss is offset by the creation or restoration of wetlands elsewhere, as is attempted in the United States. Wetlands International (www.wetlands.org) is the primary non-governmental organization involved in the conservation of wetlands internationally, but national organizations operate in many countries toward the conservation of wetlands.

Wetland restoration or creation has increased substantially over the past half century as a strategy to mitigate the loss of wetlands, their ecosystem goods and services and their biodiversity (Darrah et al., 2019). However, data on the area of restored wetland are lacking in most regions. Restoration methods exist for several wetland types, including temperate swamps and marshes, bogs, vernal pools, floodplain wetlands, salt marshes and mangrove swamps (Broome et al., 1988; Quinty and Rochefort, 2003; Bosire et al., 2008; King et al., 2009; Calhoun et al., 2014; Biebighauser, 2015; Chimner et al., 2017). Further efforts are required to compile comprehensive restoration protocols across wetlands. Note that the biological structure and biochemical functioning of restored wetlands are lower than in natural wetlands nearby (Moreno-Mateos et al., 2012). This result, along with the high costs of wetland creation or restoration, suggest that the conservation and sound management of existing wetlands should take precedence over wetland creation and restoration, wherever possible. However, given the historical and current losses of wetlands, the restoration or creation of wetlands remains a useful strategy for wetland conservation.

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