MODULE 1: AN INTRODUCTION TO WETLANDS

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OVERVIEW

Wetlands are a unique kind of habitat defined by shallow waters and/or periodic flooded soils, which dictates the environmental conditions (soils, water chemistry) and biota (microbes, plants, and animals) that occur. Like upland habitats, wetlands typically support lush plant growth (herbaceous plants, grasses, trees and shrubs), but these plants must be able to tolerate both flooding and drought. Like aquatic and marine habitats (oceans, lakes, rivers, streams), wetlands support aquatic invertebrates, amphibians, and fishes, but these organisms must cope with periodic drying and low oxygen conditions. Many birds, and a few mammals, are wetland specialists. Wetlands can be freshwater or saltwater, with this difference being another important control on the resident organisms.

The term "wetlands" is generic and includes a range of habitat types, including grassy and herbaceous marshes (freshwater or saltwater), swamps (with trees), bogs and fens (peatlands), and mangroves (tidal forests). Wetlands are common on the edges of lakes and rivers (floodplains) and seacoasts (saltmarshes and mangroves); peatlands and small depression wetlands are common in historically glaciated areas or on flat coastal plains. Some iconic wetlands include the Amazon floodplain and Pantanal of South America, the Everglades and Prairie Pothole region of North America, the tundra of Canada, Siberia and Scandinavia, bogs of northern Europe, Canada, and Russia, billabongs of Australia, the Okavango Delta of Africa, and the Sundarbans mangroves of India, among many others. Wetlands have many values to humans including flood control, water purification, coastal protection, and the support of a biodiversity that occurs nowhere else. Wetlands are threatened by human drainage and filling, and a changing climate.

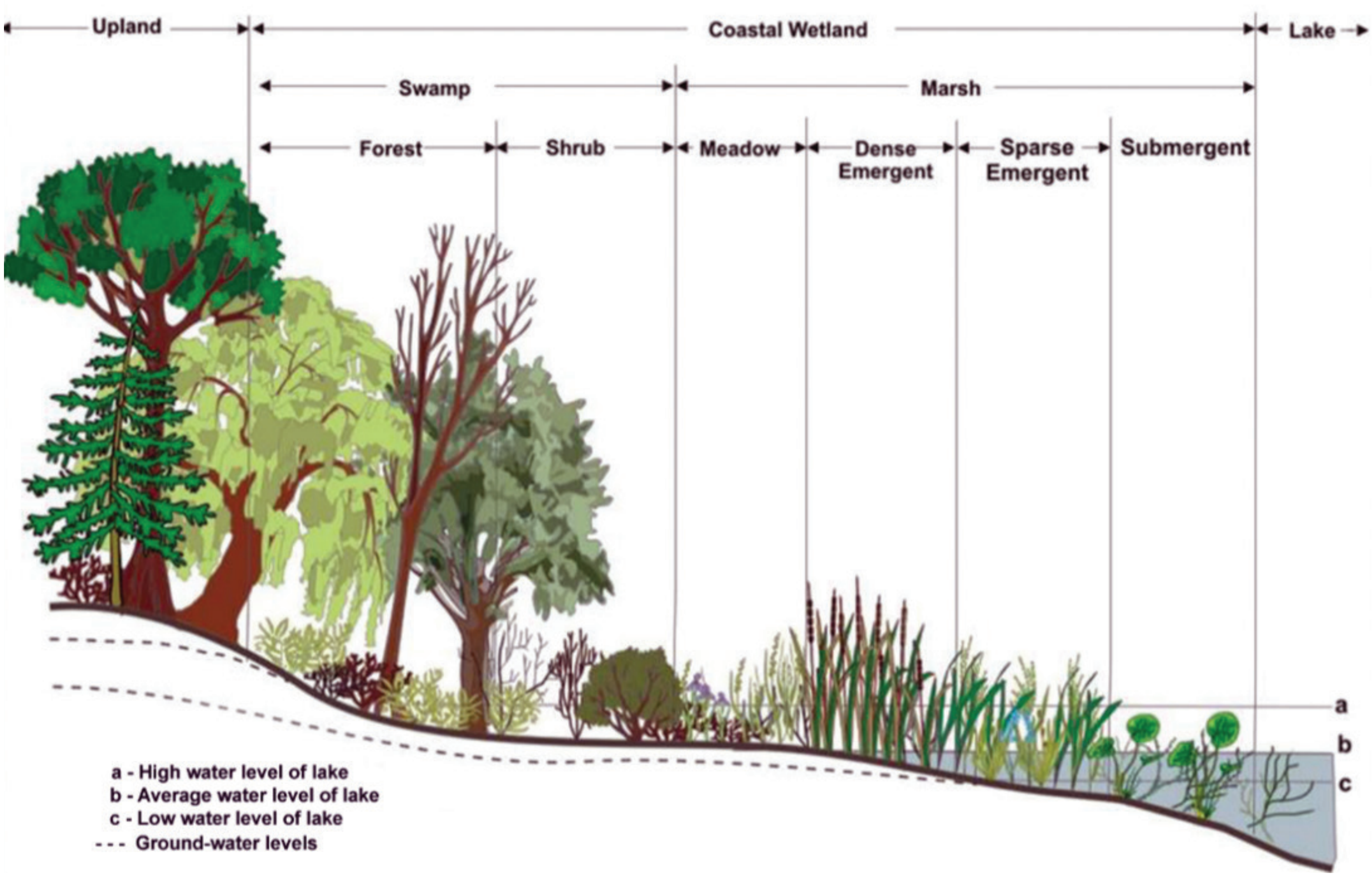

Figure 1. Diagram of different kinds of wetlands along a lake shore. (Courtesy of Doug Wilcox)

WHAT IS A WETLAND?

The term "wetland" is a catch-all term used to label a host of different kinds of habitat, such as marshes, swamps, fens, bogs, and many others (see below). The Oxford English Dictionary defines wetland as: *an area of land that is usually saturated with water.*

A more detailed international definition has been provided by the RAMSAR convention (an international conference held in 1979): *Wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres.*

A legal definition used in the United States (US) is: *"The term "wetlands" means those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas."* (Environmental Laboratory 1987).

All of these definitions emphasize that the presence of water is important to wetlands, although it does not necessarily have to be on the surface. The legal definition in the US also notes that water affects the soils by saturating them (becoming hydric soils) and the combination of water and hydric soils results in characteristic plants growing in wetlands. Thus, flooding, hydric soils, and/or wetland vegetation are key elements in most definitions of wetlands. More detail on a range of definitions for wetlands can be found in Sharitz et al. (2014).

Definitions of wetlands have scientific importance, as the biota and biological processes that occur in wetlands are unique from other kinds of habitats (terrestrial uplands, aquatic lakes, streams, rivers, oceans). A peculiarity of working in wetlands is that one may have to define one's study habitat for others, which is usually not the case for people working in forests, grasslands, streams, rivers, lakes, or oceans. A clear definition of wetland is also required in the legal arena because it may determine whether certain regulations apply (such as the Clean Water Act in the US). Legal definitions tend to draw lines between where a wetland starts or where it stops (called delineation; Environmental Laboratory 1987). As you become familiar with wetlands, however, you will find this concept arbitrary, as "lines" for wetlands are fuzzy and many wetland organisms do not adhere to these lines.

WETLAND FORMATION

Wetlands often occur in specific geographic landscapes (Jackson et al. 2014), where past and current geologic features tend to determine how prevalent wetlands are, as well as how they function.

Freshwater wetlands are common adjacent to rivers and lakes (floodplains, shallow littoral zones; see figures below and above). In flat coastal plains, floodplain wetlands of rivers can be expansive. In steep terrain, however, floodplains may be narrow. The extent to which water in the rivers or lakes fluctuates will affect floodplain development. Floodplains are especially important to people because they lessen impacts of floods by providing water storage, with the added benefit that water travelling through floodplains is purified (Costanza et al. 1997).

Figure 2. River floodplain wetlands. (Courtesy of USGS)

Historically glaciated areas tend to support numerous wetlands, which develop in low lying depressions formed via past glacial action such as scouring and moraine development during ice ages. The prairie pothole region of the northern central plain of North America (below; Galatowitsch 2012) is a prime example of a glacially molded landscape where literally millions of small wetlands occur. Larger "potholes" may be called lakes, and the formative process of both potholes and lakes can be similar. "Lake" districts around the world tend to also support many wetlands.

Figure 3. Prairie pothole wetlands, North Dakota. (Courtesy of USGS Northern Prairie Wildlife Research Center)

The greatest extent of wetlands in the world occur in the tundra regions of Siberia, Canada, Alaska, and Scandinavia (Bridgham et al. 2006). Permafrost in these areas prevents water from percolating down from the surface, and thus surface soils remain saturated, and wetland conditions develop (Gough 2012). Past glacial scouring in the tundra also created a landscape where many wetlands can develop (as was the case in areas south of the tundra). These wetlands are particularly important given a warming climate, as they may dry out in the future, and the organic soils (peat) may start to decompose, exacerbating warming by releasing more greenhouse gases (Bridgham et al. 2006; Gough 2012).

Figure 4. Tundra peatland, Alaska. (Courtesy of NOAA)

In landscapes with underlying limestone bedrock (called karstic), the dissolution of the limestone over time can cause depressions to develop in areas where the surface slumps or collapses. Many of the cypress dome and limesink wetlands of the Southeastern Coastal Plain of the US (Kirkman 2012), and turloughs of Ireland (Reynolds 2016) are examples of wetlands formed by this process. Freshwater springs are also common in karstic landscapes, and distinctive wetlands can develop at these groundwater discharge areas (see below).

Figure 5. Wetland associated with a freshwater spring, Utah. (Photo by Mary Jane Keleher with permission of University of California Press)

Oceanic tides create many wetlands along continental coastlines, including saltmarshes in cool high latitudes (see below; Pennings et al. 2012) and mangrove swamps in the warm tropics and subtropics (McKee 2012). Daily tides inundate the soils with saline water, creating conditions where unique wetland plants (such as cordgrasses and mangrove trees) flourish. At the mouths of larger rivers, where water and dissolved nutrients from the ocean and the rivers mix to create rich, moderately-saline (brackish) areas, expansive areas of estuarine wetlands can develop. These estuarine wetlands tend to be among the most productive wetlands on earth for plants and animals. Like freshwater floodplains, tidal wetlands are important buffers to flooding from storm surge.

Figure 6. Saltmarsh and egret, Georgia, USA. (Courtesy of Steve Pennings)

WETLAND HYDROLOGY

Because wetlands are created by the presence of water, the source of that water can have important consequences for how the habitats function (what processes and biota occur). Water for wetlands tends to come from three sources. One is from above in the form of direct rainfall or snowfall, i.e., precipitation. A second is from below - from groundwater that discharges to the surface into wetlands. The third is from lateral flow of water which can enter and move through wetlands via overland flow, stream flow, flooding from adjacent rivers or lakes, or flooding from tides. The specific source of lateral flow can be a key factor determining wetland functions.

How the water leaves a wetland is also important. It can leave vertically from evaporation or from transpiration from plants; collectively this water movement is called ET (for evapotranspiration). Water can also move downward from wetlands into the groundwater aquifers below. Wetlands are often touted for their abilities to recharge groundwater. While this is true, it should be recognized that most deep groundwater aquifers are filled by rainfall on uplands, where impervious clay layers (aquitards) may not occur and water moves down through the soil rapidly. Wetlands are more likely to recharge surficial aquifers. Finally, water in wetlands can move laterally back into rivers, lakes or the oceans, or out via streamflow.

Conceptually it is useful to view wetlands in terms of what are the most important sources of water to the wetland (inputs) and what are the important ways that water leaves the wetlands (outputs) (Jackson et al. 2014). This is called a water budget (but be aware that accurately measuring inputs and outputs can in many cases be a very, very difficult endeavor). The below water budget formula encapsulates the major inputs and outputs of water for most wetlands:

Inputs
(Precipitation + groundwater in + lateral flows in)
=
Outputs
(ET + groundwater out + lateral flows out) + Storage

When inputs are greater than outputs the storage is a positive number (i.e., the wetland is flooding). However, if the reverse is true, the habitat has a water deficit and is drying. As a result, many wetlands are dry during part of the year.

Most of us find a formula to be daunting to comprehend. But for some wetlands the water budgets can be very simple. Rockpools and some depression wetlands are filled almost exclusively by direct rainfall and lose water almost exclusively from evapotranspiration. The groundwater and lateral flow parts of their water budget equation are essentially zero. On the other hand, some wetlands have incredibly complex water budgets (beyond the formula above).

Water volume is not the only consideration of importance of water sources. For example, floodplains and tidal wetlands may receive their greatest volumes of water via lateral inputs from a river or the ocean, with a comparably small contribution from direct rainfall and groundwater discharge. Nevertheless, those precipitation inputs and groundwater discharge can be very important to resident plants and animals, by keeping soils wet between floods, even though they are a small part of the overall water budget.

The following "wetland hydrologic triangle" pictorial visualizes the relative importance of different water inputs (precipitation, groundwater, or surface-lateral sources) to wetland formation (from Sharitz et al. 2014). The lower right corner of the triangle is where lateral sources dominate (such as from tides or river floods) and floodplains, saltmarshes, and mangroves occur in that portion. In the lower left of the triangle, groundwater inputs dominate, and spring-associated wetlands occur. In the upper point of the triangle, precipitation dominates as is characteristic of bogs and some depressional (ephemeral) wetlands. In the middle of the triangle are wetlands where all water sources

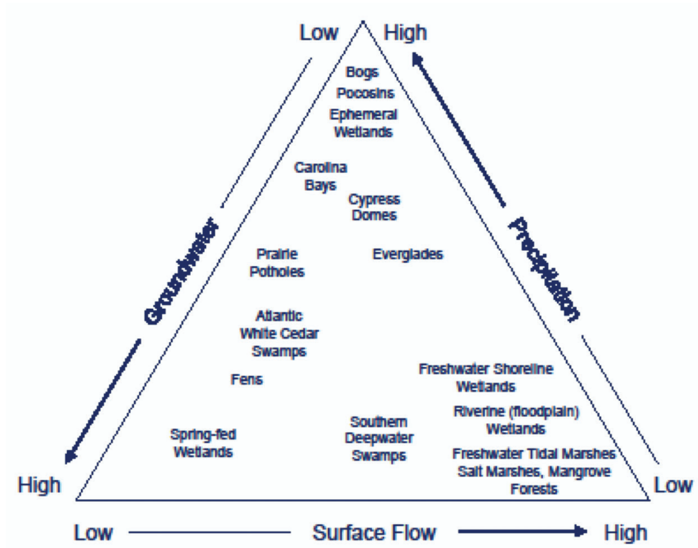

Figure 7. Hydrologic triangle showing relative inputs of water from groundwater, precipitation, and lateral flows into different wetland types. (Diagram by Rebecca Sharitz and Mark Brinson, with permission of University of California Press)

are important such as the Florida Everglades. If you are interested in how water in a particular wetland of interest to you affects its ecology, it might be a useful exercise to try to fit it into the triangle.

WETLAND SOILS AND MICROBES

Wetlands tend to retain water for long periods because, over time, deep layers of impervious clay or organic soils develop that impede water movements downward (termed an aquitard) (Jackson et al. 2014). One of the challenges of artificially creating a new wetland is that the unique soil conditions in wetlands require long periods to develop, and newly created wetlands often dry more quickly than natural habitats. One of the virtues of natural wetlands is that their impermeable soils help the habitats store and retain water on the landscape.

Wetlands soils also host unique bacterial communities because decay of organic matter saps the oxygen from the water, creating hypoxic (low oxygen) or anoxic (no oxygen) conditions. Most bacteria in upland soils are aerobic (use oxygen to respire) but in wetland soils the bacteria must use elements other than oxygen to "respire" and are called anaerobes. Common alternatives to oxygen for anaerobic bacteria include nitrate, sulfate, and iron oxide. When these alternative chemicals are exhausted, soil bacteria called methanogens may reduce CO_2 to methane. Because methane is such a potent greenhouse gas, some wetlands may be naturally contributing to climate warming. The situation may become concerning if the release of CO_2 through decay of organic matter accelerates to the point that more greenhouse gases are released than are absorbed.

Upland soils are often colored orange (from iron oxide, i.e., rust) or yellow (from manganese), but when these soils are flooded and become anoxic, the anaerobic bacteria convert these oxides to reduced forms, and the soils change to a grey or blackish color (see below). This color change in soils is one way that people trying to assess wetland conditions determine if the hydric soil criterion used to define wetlands is met. Thus, besides being a place where important ecosystem processes like decomposition take place, soil conditions also have importance to regulations.

Figure 8. Oxidized (rust colored) and reduced (grey colored) wetland soils. (Courtesy of Derek Faust)

PLANTS IN WETLANDS

Due to flooding and anaerobic conditions in wetlands, plant communities tend to be dominated by a flora adapted to tolerate these harsh conditions. The kinds of plant that inhabit particular wetlands are often used to define the habitats, and many common names for different wetlands reflect these plants.

Marshes are freshwater or saltwater wetlands dominated by emergent plants such as cattails, grasses, sedges, and reeds (freshwater marshes) or cordgrasses, rushes, and pickleweed (salt marshes; see photo above). Deep water areas of freshwater marshes may support floating or submersed plants such as water lilies or pond weeds. For germination, the seeds of marsh plants usually require exposure to the air, and thus following a drying and reflooding episode, a flush of emergent plant growth often occurs. In the absence of proper germination conditions, these seeds can remain on the bottom of flooded wetlands for long periods and accumulate in what is called the "seed bank."

Swamps are wetlands dominated by woody vegetation (trees and shrubs; see photo below). In Europe, there are wetlands called "reedswamps" but they would be referred to as a type of marsh, more broadly. As you can see, the use of local common names can cause confusion. The kinds of trees or shrubs that dominate swamps varies geographically and locally. Cypress (*Taxodium* spp.) swamps are an important wetland in the Southeast and Southcentral US, often on the floodplains of rivers (King et al. 2012) or in depressional wetlands (Carolina bays, Cypress domes) (Kirkman et al. 2012). Bottomland hardwood forests (often dominated by oaks) also occur on river floodplains (King et al. 2012). Much of the Amazon floodplain is swamp forest. Mangroves, a group of salt-tolerant tree species, occur as coastal tidal swamps in the warm tropics and subtropics across the globe. Other trees that can create swamp forests include Atlantic white cedar, red maple, red gum, black ash, and cottonwoods. Many peatlands support trees, but generally the term "swamp" is not applied to forested peatlands.

Peatlands are wetlands defined by dead plants and occur where plant growth rates exceed decay rates and organic materials slowly accumulate over years or centuries as peat. *Sphagnum* mosses tend to be the most important source of peat development in bogs and tundra wetlands. But emergent plants like sedges (in fens) and sawgrass (in the Everglades) or dead tree trunks (in the Okefenokee Swamp) can also form into peat.

Figure 9. Wetland swamp, Georgia USA. (Courtesy of Darold Batzer)

ANIMALS IN WETLANDS

Because wetlands have both aquatic and terrestrial characteristics, a diverse array of animals exploit the habitats, but they must deal with the unique environmental conditions that prevail. For the aquatic fauna (invertebrates, fishes), the organisms must tolerate low oxygen conditions as well as periodic drying. For the terrestrial fauna (invertebrates, birds, mammals), organisms must tolerate periodic flooding and be adapted to live and feed around water. Perhaps it is not surprising that amphibians (frogs, toads, salamanders), which live both aquatically and terrestrially, are particularly well represented in freshwater wetlands.

The fauna that occurs in wetlands that dry frequently is unique from the fauna that lives in wetlands that rarely dry (Wellborn et al. 1996). In tidal wetlands, salinity becomes an important regulator of animals, with compositional changes occurring along salinity gradients (saltwater to brackish-water to freshwater).

Compared to most uplands, aquatic habitats, and marine habitats, the animal fauna of most wetlands is comprised of relatively few species. Most of that diversity, in terms of numbers of species, can be found in the invertebrate fauna (insects, crustaceans, mollusks). However, because the animals that live in wetlands are unique from those that live elsewhere, wetland animals can contribute substantially to the overall biodiversity of a region. Wetlands support many animals that are endangered, with amphibians and birds being noteworthy examples of threatened species. Some of the best-known wetland animals include crocodiles and alligators, snakes, and beavers.

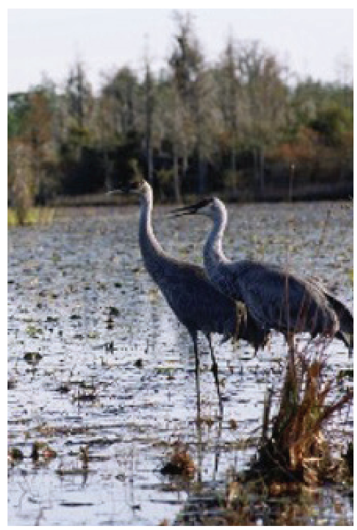

Figure 10. Sandhill cranes (Courtesy of Okefenokee National Wildlife Refuge)

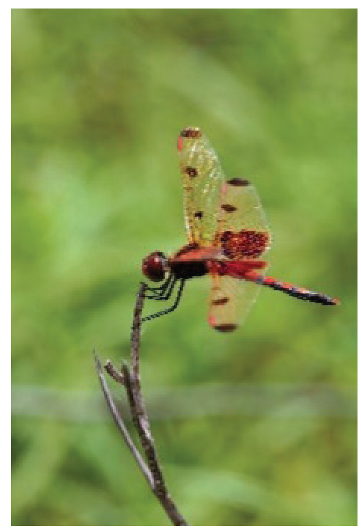

Figure 11. Dragonfly (Courtesy of Clesson Higashi)

Figure 12. Chorus frogs (Courtesy of Kevin Enge)

ACKNOWLEDGEMENTS

We thank Beth Middleton and Greg Noe for reviews of this module.

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