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MODULE 5: WETLAND COMMUNITY ASSEMBLY

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OVERVIEW

Wetland habitats are occupied by species that can tolerate flooded and—in the case of coastal wetlands—salty soils (Figure 1). Relatively few species can tolerate these conditions, but species with the right adaptations can be very abundant in wetland habitats. Wetlands vary in how stressful the conditions are, and plant and animal biomass varies correspondingly, from almost zero to extremely high. Within a wetland, plants and animals are often arranged in "zones" along a gradient of physical stress, with the best competitors occupying the least stressful habitats and excluding all others. In turn, the species that are best able to tolerate stress, but are poor competitors, occupy the most stressful habitats. In contrast to the negative effects of competition, the presence of stress-tolerant plants and animals may reduce the level of physical stress in the habitat and benefit other species, a process called "facilitation." In addition, wetland species are negatively affected by consumers. Animals that eat plants may strongly reduce plant biomass, the abundance of these "herbivores" may be reduced by predators, and organisms on all trophic levels may be affected by parasites. Most wetlands vary over time in how "wet" they are, and this variation creates constantly changing abiotic conditions that affect all these organisms and their interactions. Wetland organisms are also affected by a variety of disturbances such as floating mats of dead vegetation, sediment deposited by floating ice, and fire. These and other disturbances reduce competition and create opportunities for species that would otherwise be excluded from the habitat. Due to global change, individual wetlands will transform over time as climate and water inputs vary. At the same time, humans directly affect wetlands by increasing nutrient supplies, removing predators, and filling or draining wetlands. All these factors—abiotic stress, species interactions, disturbance, global change, and human impacts—vary geographically, meaning that an understanding of a particular wetland requires an understanding of its geographic context.

Figure 1. Diverse plant community in a Netherlands salt marsh. (Photo: Steve Pennings)

THE BASICS OF WETLAND COMMUNITY ASSEMBLY

We know a great deal about how wetland communities are assembled. Wetlands have been attractive study systems for research on community ecology, because they combine simplicity in plant biodiversity with strong abiotic gradients that produce striking community patterns. In addition, the soft sediments of wetlands make them suitable for some kinds of experiments, such as transplant experiments (moving plants and animals around and among different ecological conditions), because organisms are easy to excavate and relocate. At the same time, the importance of wetlands in regulating water chemistry, mediating the global carbon cycle, supporting fisheries and other wildlife, and protecting coastal communities from storms has generated a high level of interest in wetland processes and conservation. One lesson we have learned is that not all wetlands are the same: different types of wetlands in different parts of the world can function in different ways. What follows are broad generalizations that may not apply everywhere.

Plant species richness is low in most wetlands, compared with neighboring terrestrial communities, because most plant species cannot tolerate the abiotic stresses present in flooded soil (Module 3, Introduction to wetland plants; https://www.sws.org/education-modules-wetland-science/). For example, the anoxic soils caused by waterlogging prevent the majority of plant species that might occur in a terrestrial grassland from colonizing a freshwater wetland. The high porewater salinity encountered in brackish and saltwater wetlands further reduces the number of plant species that can persist in coastal and other saline wetland ecosystems. The flooded soils and high salinity can be conceptualized as two major "filters" that prevent species from colonizing wetlands (Figure 2). The low water potential and sulfidic conditions caused by flooding with seawater further prevent the majority of flood-tolerant plants from colonizing saline wetlands. Despite low species richness in wetlands, the plant species that do occur in wetlands are usually different from those found in terrestrial habitats, so wetlands contribute to plant diversity across the broader landscape.

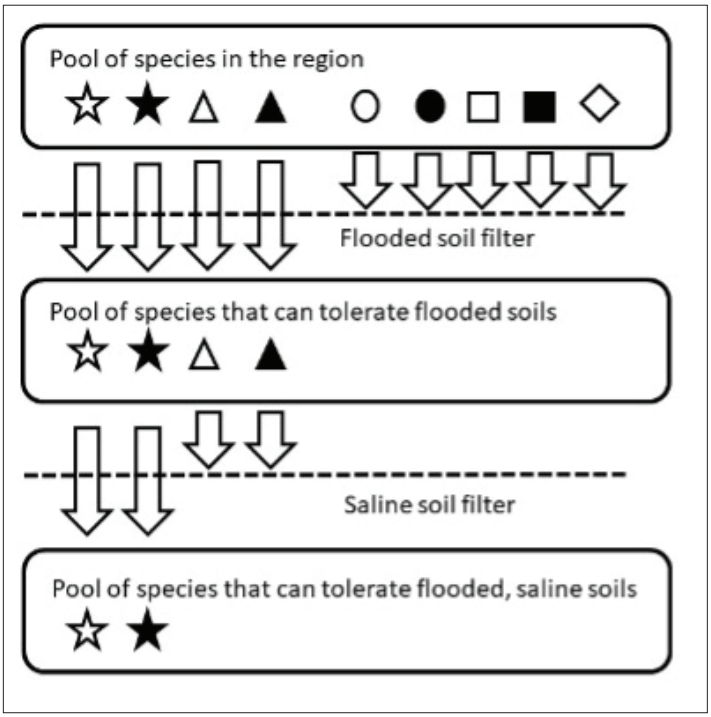

Figure 2. Species richness in wetlands is limited by two strong abiotic "filters." The lack of oxygen in flooded, waterlogged soils prevents many species that occur in a region from establishing in freshwater wetlands. The high salt and sulfide concentrations in saline soils prevent many species that could live in freshwater wetlands from establishing in saline wetlands.

Animal species richness is low in wetlands for similar reasons (Module 4, Basic biology of wetland animals; https://www.sws.org/education-modules-wetland-science/). Animals must not only be able to tolerate the abiotic conditions presented by flooded, and perhaps saline, soils, but often must also be able to tolerate alternating periods of flooding and exposure due to variable wetland hydroperiods (temporal variation in water depth due to tides, seasonal rainfall, etc.). Moreover, because many herbivores and pollinators only interact with a limited number of plant species, the low plant species richness of wetlands favors low species richness in the herbivore and pollinator fauna. Nevertheless, wetlands can be important in the conservation of declining species by providing safe habitat within otherwise developed regions (Fantinato and Bufa 2019). Moreover, as with plants, wetlands support groups of animal species such as aquatic insects and amphibians that are rare in terrestrial habitats, and so contribute to animal diversity across the broader landscape. In particular, wetlands provide essential habitat for many birds, some of which use wetlands occasionally and others of which are

wetland specialists. As parts of a landscape, wetlands also provide access to drinking water for a variety of terrestrial organisms.

Although species richness is usually low, some wetlands are highly productive. Species that have evolved the necessary physiological mechanisms may flourish in wetlands where they have access to abundant water and nutrients, and experience limited competition from other species. Standing above-ground plant biomass in freshwater wetlands dominated by cattails (*Typha*), *Phragmites*, or wild rice (*Zizaniopsis*) is on the order of 1,000-2,000 g m^{-2}, and in forested wetlands above-ground biomass can exceed 10,000 g m^{-2} (Mitsch and Gosselink 1993). Similarly, the marine invertebrates found in salt marshes, such as snails and burrowing crabs, can reach densities well over 50 m^{-2} (Silliman and Bortolus 2003). Productive wetlands often support high densities of birds adapted to wetlands. Not all wetlands are highly productive, however. Those with extreme levels of abiotic stress, such as highly saline salt marshes in regions with little rainfall, or low nutrients such as bogs, may not be able to support higher plants at all (Osland et al. 2014), and have correspondingly low animal biomass.

In many wetlands, plants and animals occur in distinct zonation patterns, in which one species replaces another over one or more spatial gradients of abiotic stress. These patterns are usually understood as resulting from a tradeoff between stress tolerance at one end of a gradient and competitive ability at the other end (Figure 3). According to this understanding, species that are competitively dominant occupy the least stressful habitats, but are excluded from the more stressful habitats by an inability to tolerate abiotic stress. The more stressful habitats are occupied by species that are more tolerant to the locally prevailing stress(es), but are poorer competitors—a consequence of tradeoffs in resource allocation to traits favoring stress tolerance versus competition. For example, in freshwater wetlands in North America, *Typha latifolia* occupies less-flooded habitats and limits *Typha angustifolia* to more stressful, more flooded habitats (Grace and Wetzel 1981). Similarly, in northeastern USA salt marshes, the competitively dominant species *Juncus gerardii* occurs in less-flooded high marsh habitats, and limits the more stress-tolerant but poorer competitor, *Spartina patens*, to lower, more-flooded elevations (Bertness 1991a). *S. patens* in turn limits *S. alterniflora* to the most-flooded marsh habitats (Bertness 1991b). Finally, along estuaries, it is common for tidal fresh marshes (the less stressful habitat) to be dominated by highly competitive plant species, and tidal salt marshes (the more stressful habitat) to be dominated by stress-tolerant but competitively inferior species (Crain et al. 2004; Engels and Jensen 2010).

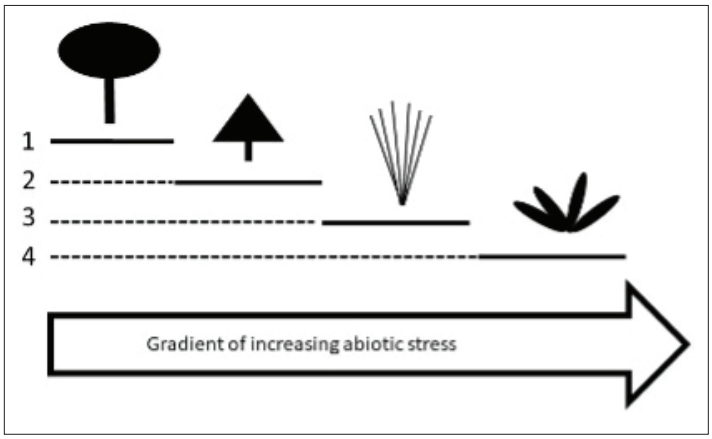

Figure 3. Competition-stress tolerance tradeoff. Four hypothetical species occur (solid lines) in zones across a gradient of abiotic stress, with species 1 in the least-stressful habitat and species 4 in the most-stressful habitat. Species 2 could survive where species 1 occurs, but is excluded from this habitat (dotted line) by competition. Similarly, species 3 and 4 could survive in less-stressful parts of the gradient (dotted lines) but are excluded from these areas by competition.

In cases where there are multiple types of stressful habitats, one can conceptualize this as a "centrifugal" model (Figure 4), in which a single, low-stress "core habitat" is occupied by the competitive dominant, and the various peripheral habitats, each with its own type of abiotic stress, are occupied by species tolerant of those particular stresses (Keddy 1990). Although the ecological processes creating these zonation patterns have been studied most extensively in plants, similar zonation patterns do occur in wetland animals. For example, in salt marshes in North and South America, crab species segregate both across elevation, from high to low marsh, and also along estuarine gradients from marine to freshwater (Teal 1958; Costa and Davy 1992). Herbivorous insects also segregate across elevation in response to variation in plant quality and abiotic factors (Denno et al. 1996; Denno et al. 2000).

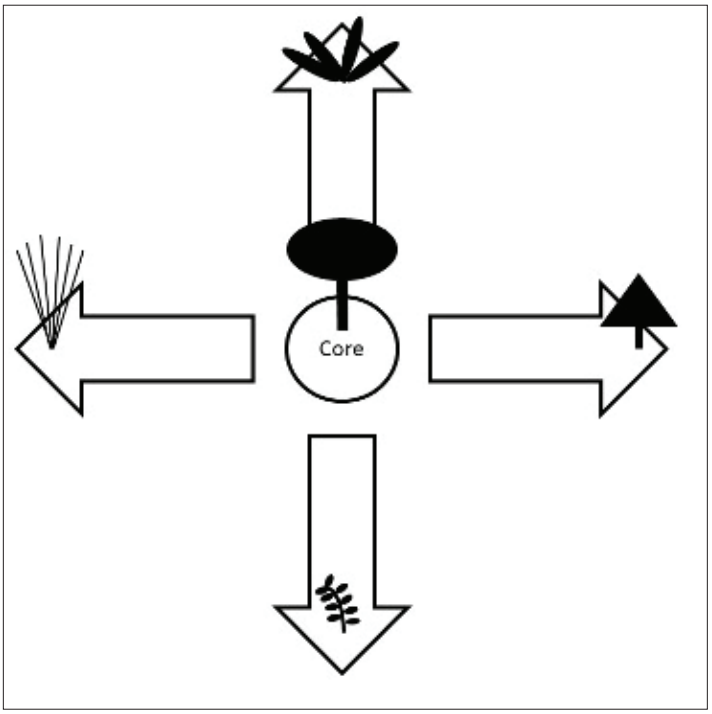

Figure 4. Centrifugal model. The competition-stress tolerance tradeoff can be generalized to scenarios in which there are multiple gradients of abiotic stress. The core habitat is the least-stressful habitat, and is occupied by the competitively dominant species. Different species, all of which are excluded by competition from the core habitat, occupy peripheral habitats representing different types of abiotic stress. These might include, for example, gradients in flooding, low nutrient availability, high wave action, and so on. Although for clarity the figure shows only one species at the extreme of each gradient, there might be intermediate species along each gradient as shown in Figure 3.

FACILITATION

The severe abiotic stresses present in wetlands create the opportunity for species to benefit each other by ameliorating harsh physical conditions in a process called facilitation (Figure 5). Plants that are capable of transporting oxygen from shoots to roots, for example, may oxidize the rhizosphere, improving conditions for other plant species (Callaway and King 1996). Plants that shade the substrate and block the wind may reduce heat stress on the soil surface while also limiting evaporation that concentrates salts in the rhizosphere of salt marshes, benefiting neighboring plant species (Bertness and Shumway 1993) and associated invertebrates (Bortolus et al. 2002; Sueiro et al. 2013). Burrowing crabs may improve soil conditions for plants by improving oxygenation of the soil and nitrogen availability (Montague 1982). Marsh bivalves may benefit both plants and other invertebrates by fertilizing the soil, enhancing water storage and reducing salinity stress (Angelini et al. 2016) and increasing the biotic complexity of the intertidal communities. Finally, the physical structure of wetland plants may benefit other organisms, for example by trapping mangrove propagules and enhancing establishment (Peterson and Bell 2012) or by altering the effectiveness of predators (Denno et al. 2002).

Figure 5. Burrowing crabs and bivalves are examples of wetland invertebrates that may benefit plants by decreasing abiotic stress or increasing soil nutrients.

TOP-DOWN CONTROL, ABIOTIC VARIABILITY AND DISTURBANCE

Although wetland organisms may benefit from positive interactions with other species, they may also be subject to top-down pressure from consumers such as herbivores, predators, and parasites. When conditions favor either high herbivore density or reduced plant resistance, herbivores can strongly suppress plant biomass (Silliman and Bortolus 2003). Herbivores in turn may be strongly suppressed by their predators. For example, in southeast USA salt marshes, predators largely exclude marsh snails from creekbank habitats that are easily accessed by fish and swimming crabs (Silliman and Bertness 2002). Human activity has largely removed the largest predators, such as tigers, alligators, seals and sea otters, from modern marshes, but where these species are protected they are increasing in abundance and resuming important ecological roles as apex predators (Gaskins et al. 2020). Finally, many wetland species support multiple parasite species that can strongly suppress the abundance and performance of their hosts (Lafferty and Morris 1996; Pennings and Callaway 1996).

While abiotic stress, competition, facilitation, and consumer pressure can combine to create strong patterns in community composition in wetlands, a variety of other factors may combine to create changing conditions that obscure these patterns. The

most obvious of these is changing water levels. Water levels in many freshwater wetlands vary seasonally and among years as a function of rainfall. As a result, abiotic conditions are constantly changing, and this increases local species diversity because changing conditions limit the ability of any single species to competitively exclude others (van der Valk 1981; Seabloom et al. 2001).

Another common ecological process that creates spatial and temporal variation in wetlands is disturbance. A wide variety of disturbances can remove plant biomass at particular locations in wetlands, creating opportunities for species that are not strong competitors and initiating secondary succession. In some wetlands, periodic drought can kill vegetation, which allows a new set of plants to establish from seeds. Another well-studied example is wrack (floating plant debris), which is deposited into the marsh at high tide, smothering underlying vegetation (Bertness and Ellison 1987). When wrack decomposes or is later rafted away by the tides, a series of competitively inferior plants can temporarily occupy the disturbed patches until such time as the competitively dominant plants recolonize. In high latitude marshes of North America, ice may raft chunks of sediment onto the marsh platform, with similar effects (Hardwick-Witman 1985). In other areas, fire may burn aboveground vegetation and leaf litter, again creating opportunities for suppressed plant species (Baldwin and Mendelssohn 1998). When common, herbivores may also suppress dominant plants and favor species that are weaker competitors but less palatable (Bazely and Jefferies 1986; He et al. 2015). Finally, a number of wetlands experience periodic large-scale dieback of vegetation for reasons that are not yet fully understood (McKee et al. 2004). These factors tend to obscure the simple zonation patterns that might otherwise have been present across abiotic gradients in a wetland (Brewer et al. 1998).

Over long time periods, wetland community structure may change due to changing abiotic conditions, such as those caused by climate change or long-term internal dynamics. Freshwater wetlands may disappear if groundwater supplies dry up or climate change reduces precipitation. Coastal marshes may experience more flooding if relative sea level rise outpaces sediment accretion, or less flooding if the land is rising out of the ocean. Depressional wetlands in terrestrial habitats may become more terrestrial as they gradually fill in with soil and organic matter. In a warming climate, marsh plants and animals may migrate to higher latitudes, such that community composition changes. Because global climate change is altering patterns of precipitation and sea level, it is likely that many wetlands will experience changes in species composition and structure in coming decades.

HUMAN ACTIVITIES

The species composition of today's wetlands is also strongly affected by human activities on the landscape. Humans have deliberately or accidentally introduced many species into geographic locations where they historically did not exist. For example, non-native genotypes of *Phragmites australis* have been introduced into North America where they have spread widely, invading brackish marshes where *Phragmites* previously did not occur (Kettenring and Mock 2012). Similarly, the salt marsh grass *Spartina alterniflora* has been introduced around the world, where it transforms estuaries from mudflats into salt marshes, often hybridizes with native species of *Spartina*, and dramatically changes the composition of the local biota (Strong and Ayres 2013). One of the most dramatic examples of the invasive potential of *Spartina alterniflora* comes from China, where it was deliberately introduced. In 40 years, *Spartina alterniflora* has spread to cover most of the Chinese coastline, replacing native intertidal ecosystems and obliterating the human industries, such as aquaculture, that depended on them (Nie et al. 2022). Another example comes from Central and South America, where the introduction of *S. alterniflora* was overlooked for centuries, leading to a radical misunderstanding of "native" coastal landscapes (Bortolus et al. 2015). Although ecologically and economically devastating, introductions like these offer ecologists novel opportunities to understand how communities assemble and are structured, and in this sense can provide valuable insights into wetland ecology.

Humans have had other important effects on wetlands. We have increased nitrogen availability in many wetlands, favoring large, competitively dominant

plants at the expense of weaker competitors (Levine et al. 1998). Humans have also removed many predator species, likely contributing to increased densities of herbivores (Coverdale et al. 2013). Finally, humans have filled or drained many wetlands, removing the habitat entirely.

All of the factors affecting the community structure of wetlands are likely to vary geographically as a function of climate and human population density, even within a particular wetland type (Osland et al. 2014). For example, the standing biomass of coastal salt marshes varies with latitude on the east coasts of both China and the United States due to variation in temperature and tidal range (Liu et al. 2020). Ice rafting is a known disturbance in high-latitude salt marshes, whereas hypersaline, low-productivity salt marshes are most common in warm, low-latitude climates (Osland et al. 2014).

This chapter has provided a brief introduction to the assembly of wetland communities, but has only touched on what is a vast literature. There are a wide variety of types of wetlands, and the generalities in this short chapter don't always apply to every specific situation. Readers wanting more information can turn to many review chapters and book length treatments of wetland ecology for more examples, greater detail, and treatment of specific wetland types. Although we know a great deal about community assembly of wetlands, a disproportionate share of this knowledge comes from temperate latitudes of North America and Europe. Studies from other parts of the world still have much to teach us about how processes that mediate the assembly of wetland communities vary geographically. Studying wetlands around the world will increase the generality of our concepts of wetland community assembly and improve local management of wetlands in all the places where they occur.

OTHER ELEMENTS

The figures from this module and supplemental photographs are provided in a PowerPoint file online at https://www.sws.org/education-modules-wetland-science/.

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