P Keddy. 2008. Freshwater Marshes. In S.E. Jørgensen and B.D. Fath (Editor-in-Chief), Ecosystems. Vol. 2 of Encyclopedia of Ecology, 5 vols. pp. 1690-1697. Oxford: Elsevier.

Freshwater Marshes

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Six Types of Wetlands
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Wetlands are produced by flooding, and as a consequence, have distinctive soils, microorganisms, plants, and animals. The soils are usually anoxic or hypoxic, as water contains less oxygen than air, and any oxygen that is dissolved in the water is rapidly consumed by soil microorganisms. Vast numbers of microorganisms, particularly bacteria, thrive under the wet and hypoxic conditions found in marsh soils. These microbes transform elements including nitrogen, phosphorus, and sulfur among different chemical states. Therefore, wetlands are closely connected to major biogeochemical cycles. The plants in wetlands often have hollow stems to permit movement of atmospheric oxygen downward into their rhizomes and roots. Many species of animals are adapted to living in shallow water, and in habitats that frequently flood. Some of these are small invertebrates (e.g., plankton, shrimp, and clams), while others are larger and more conspicuous (fish, salamanders, frogs, turtles, snakes, alligators, birds, and mammals).

Figure 1 Marshes occur in flooded areas, such as this depression flooded by beavers in Ontario, Canada. As the photo illustrates, marshes form at the interface of land and water. Courtesy of Paul Keddy.

Six Types of Wetlands

There are six major types of wetlands: swamp, marsh, fen, bog, wet meadow, and shallow water (aquatic). These six types are produced by different combinations of flooding, soil nutrients, and climate. A seventh group, saline wetlands, which includes salt marshes and mangroves, is often treated as a distinct wetland type. Saline wetlands occur mostly along coastlines (see Mangrove Wetlands), but also occasionally in noncoastal areas where evaporation exceeds rainfall, such as in arid western North America, northern Africa, or central Eurasia.

Swamps and marshes have mineral soils with sand, silt, or clay. Swamps are dominated by trees or shrubs (see Swamps), whereas marshes are dominated by herbaceous plants such as cattails and reeds (Figure 1). Such wetlands tend to occur along the margins of rivers (Figure 2) or lakes, and often receive fresh layers of sediment during annual spring flooding. Marshes are among the world's most biologically productive ecosystems. As a consequence, they are very important for producing wildlife, and for producing human food in the form of shrimp, fish, and waterfowl.

Figure 2 Extensive bulrush (*Schoenoplectus* spp.) marshes along the Ottawa River in central Canada. The stalks of purple flowers indicate the invasion of this marsh by purple loosestrife (*Lythrum salicaria*), a native of Eurasia. Courtesy of Paul Keddy.

Fens and bogs have organic soils (peat), formed from the accumulation of partially decayed plants. Most peatlands occur at high latitudes in landscapes that were glaciated during the last ice ages. In fens, the layer of peat is relatively thin, allowing the longer roots of the plants to reach the mineral soil beneath. In bogs, plants are entirely rooted in the peat. As peat becomes deeper (the natural trend as fens become bogs), plants become increasingly dependent upon nutrients dissolved in rainwater, eventually producing an 'ombrotrophic' bog. The large amounts of organic carbon stored in peatlands help reduce global warming.

Wet meadows occur where land is flooded in some seasons and moist in others, such as along the shores of rivers or lakes. Wet meadows often have high plant diversity, including carnivorous plants and orchids. Examples of wet meadows include wet prairies, slacks between sand dunes, and wet pine savannas. Pine savannas may have up to 40 species of plants in a single square meter, and hundreds of species in a hundred hectares.

Aquatic wetlands are covered in water, usually with plants rooted in the sediment but possessing leaves that extend into the atmosphere. Grasses, sedges, and reeds emerge from shallow water, whereas water lilies and pondweeds with floating leaves occur in deeper water. Aquatic wetlands provide important habitat for breeding fish and migratory waterfowl. Animals can create aquatic wetlands: beavers build dams to flood stream valleys, and alligators dig small ponds in marshes or wet meadows.

The Distribution of Marshes

Wetlands can occur wherever water affects the soil. Not only are there therefore many kinds of wetlands, but their size and shape is very variable. Wetlands can include small pools in deserts and seepage areas on mountainsides, or they can be long but narrow strips on shorelines of large lakes (**Figure 3**), or they may cover vast river floodplains (**Figure 4**) and expanses of northern plains. The two largest wetlands in the world (both >750 000 km^2) are the West Siberian lowland and the Amazon River basin. The West Siberian Lowland consists largely of fens and bogs, but marshes occur along rivers, particularly in the more southern regions (**Figure 5**). The Amazon is a tropical lowland with freshwater swamps and marshes containing more kinds of trees and fish than any other region of the world.

Water as the Critical Factor

Water is a critical factor in all marshes. The duration of flooding is the most important factor determining the kind of wetland that occurs. Water can arrive as short pulses of flooding by rivers, as rainfall, or as slow and steady seepage. Each mode of arrival produces different kinds of wetlands. In order to better understand marshes, let us consider four examples of wetlands with very different flooding regimes.

Floodplains. Wetlands along rivers are often flooded by annual pulses of water (see Riparian Wetlands). These pulses may deposit thick layers of sediment or dissolved nutrients that stimulate plant growth. In floodplains (see Floodplains), animal life cycles are often precisely determined by the timing of the flood. Fish may depend upon feeding and breeding in the shallow warm pools left by retreating floodwaters. Birds may time their nesting to be able to feed their young on the fish and amphibians left

Figure 3 Sedges, grasses, and forbs compose this marsh on the leeward side of a narrow peninsula projecting into one of the Great Lakes (Lake Michigan), Michigan, USA. Courtesy of Cathy Keddy.

Figure 4 Extensive marshes of bulltongue (*Sagittaria lancifolia*) and American bulrush (*Schoenoplectus americanus*) now occur in coastal Louisiana, USA, where logging destroyed baldcypress forest. Courtesy of Paul Keddy.

Figure 5 The largest wetland in the world occurs in the Western Siberian Lowland. Although much of this is peatland, marshes occur along the watercourses, particularly in the southern areas. Courtesy of M. Teliatnikov.

Figure 6 Southern marshes on the coastal plain of North America may be dominated by a single grass, maidencane (*Panicum hemitomon*). This marsh occupies an opening within a baldcypress swamp, Louisiana, USA. Courtesy of Cathy Keddy.

behind by receding water. Marshes are often intermixed with swamps, depending upon the duration of flooding (Figure 6). Early human civilizations developed in this type of habitat, along the Nile, Indus, Euphrates and Hwang Ho, where the annual flooding provided fertilized soil and free irrigation.

Peat bogs. Some peat bogs receive water only as rainfall. As a consequence, the water moves slowly, if at all, and contains very few nutrients. Hence, these types of wetlands often are dominated by slow growing mosses and evergreen plants (see Peatlands). Most such wetlands occur in the far north in glaciated landscapes. Humans have developed a number of uses for the peat – in Ireland, the peat is cut into blocks and used for fuel. In Canada, the peat is harvested and bagged for sale to gardeners. In Russia, peat is used to fuel electrical plants. Marshes may form on the edges of bogs where nutrients accumulate from runoff, or along river courses where nutrients are more available.

Seepage wetlands. In gently sloping landscapes water can seep slowly through the soil. In northern glaciated landscapes, such seepage can produce fens, which have distinctive species of mosses and plants, and may develop in distinctive parallel ridges. In more southern landscapes, seepage can produce pitcher plant savannas or wet prairies. Often these seepage areas are rather small (only a few hectares in extent) but are locally important because of the rare plants and animals they support. Seepage areas can be larger, and when the water flow is sufficiently abundant, shallow water can move across a landscape in a phenomenon known as sheet flow. The vast Everglades, with its distinctive animals, is a product of sheet flow of water from Lake Okeechobee in south central Florida southward to the ocean.

Temporary wetlands. In many parts of the world, small temporary (or ephemeral) pools form after heavy rain or when snow melts. These pools can go by a variety of local names including vernal pools, woodland ponds, playas or potholes (see Temporary Waters). The aquatic life in these pools is forced to adopt a life cycle that is closely tied to the water levels. Many species of frogs and salamanders breed in such pools, and the young must metamorphose before the pond dries up. Wetland plants may produce large numbers of seeds that remain dormant until rain refills the pond.

Since water has such a critical effect on wetlands, where water levels change, plant and animal communities will change as well. A typical shoreline marsh will often show distinct bands of vegetation ('zonation'), with each kind of plant occupying a narrow range of water depths (Figure 7). Most kinds of animals, including frogs and birds, also have their own set of preferred water depths. Wading birds (egrets, ibis, herons) may feed in different depths of water depending upon the length of their legs. Ducks, geese, and swans can feed at different water depths depending upon the length of their necks. Some water birds (Northern Shoveler, flamingos) strain microorganism from shallow water, while others (cormorants, loons) dive to feed further below the surface. Some ducks prefer wetlands that are densely vegetated, while others prefer more open water. Hence, even small changes in the duration of flooding or depth of water can produce very different plant and animal communities.

Many marsh plants adapt to flooding by producing hollow shoots, which allow oxygen to be transmitted to the rooting zone. The tissue that allows the flow of oxygen is known as aerenchyma. Not only can oxygen move by diffusion, but there are a number of methods in which oxygen moves more rapidly through large clones of plants, entering at one shoot and leaving at another. Consequently, plants can play an important role in oxidizing the soil

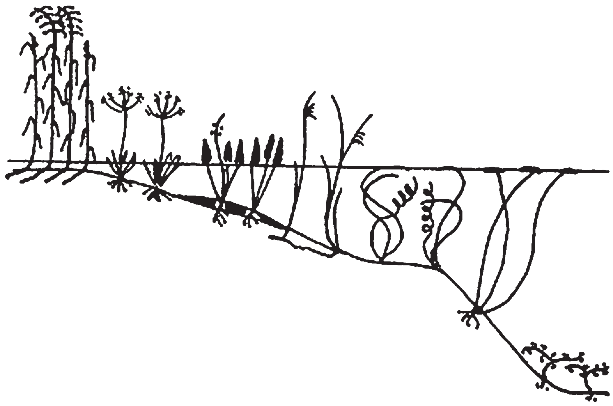

Figure 7 Different marsh plants tolerate different water levels. Hence, as the water level changes from shallow water (left; seasonally flooded) to deeper water (right; permanently flooded), the plants appear to occur in different zones. Courtesy of Rochelle Lawson.

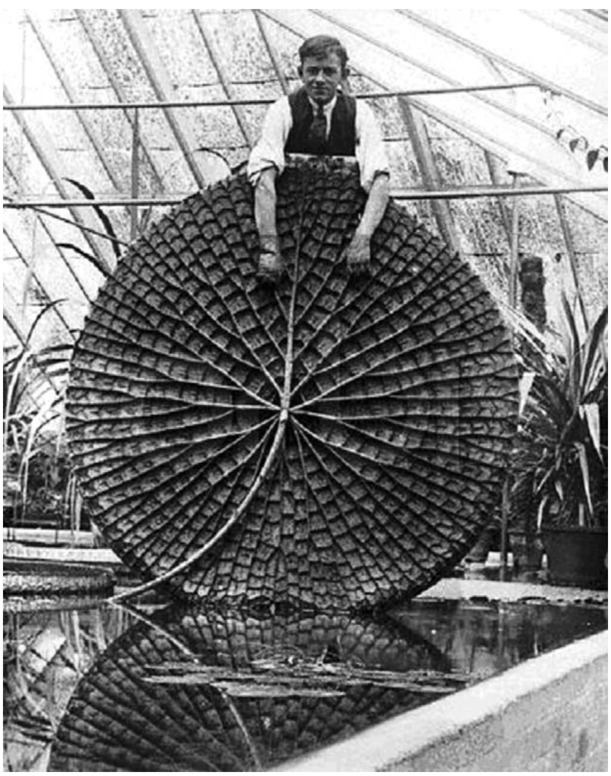

Figure 8 The Amazon water lily has the largest floating leaves of any wetland plant. Note the prominent ribs on the underside of the leaf. Courtesy of Corbis.

around their rhizomes, allowing distinctive microbial communities to form. Some marsh plants also have floating leaves (e.g., water lilies) or even float entirely on the surface (e.g., duckweeds). The largest floating leaves in the world (Figure 8) are those of the Amazon water lily (*Victoria amazonica*). The gargantuan leaves can be 2 m in diameter with an elevated lip around the circumference. There are two gaps in the lip to allow water to drain, and large spines to protect the underwater sections of the foliage.

Other Environmental Factors Affecting Marshes

Nutrients

The main nutrients that affect the growth of marsh plants, and plants in general, are nitrogen and phosphorus. As described above, flood pulses that carry sediment down river courses can produce particularly fertile and productive marshes. Floodplains can therefore be thought of as one natural extreme along a gradient of nutrient supply. At the other end of the gradient lie peat bogs, which depend partly or entirely upon rainfall, and which therefore receive few nutrients. Sphagnum moss is well adapted to peatlands, and often comprises a large portion of the peat. In between the natural extremes of river floodplains (high nutrients) and peat bogs (low nutrients), one can arrange most other types of wetlands. The type of plants, and their rate of growth, will depend where along this gradient they occur, but most marshes generally occur in more fertile conditions.

While nutrients enhance productivity, paradoxically they can often reduce the diversity of plants and animals. Often, the high productivity is channeled into a few dominant species. One finds large numbers of common species, while the rarer species disappear. Humans often increase nutrient levels in watersheds and wetlands, thereby changing the species present and reducing their diversity. Carnivorous plants are known for tolerating low nutrient levels, because they can obtain added nutrients from their prey. Common examples include pitcher plants (*Sarracenia* spp.), bladderworts (*Utricularia* spp.), and butterworts (*Pinguicula* spp.). Cattails (*Typha* spp.) and certain grasses (*Phalaris arundinacea*) are particularly well known for rapid growth and an ability to dominate marshes at higher nutrient levels.

Disturbance

A disturbance can be narrowly defined as any factor that removes biomass from a plant. In marshes, sources of disturbance may include waves in lakes, fire, grazing, or (in the north) scouring by winter ice. One of the principal effects of disturbances is the creation of gaps in the vegetation, allowing new kinds of plants to establish from buried seeds. Most marshes have large densities of buried seeds, often more than 1000 seeds m^{-2}. After disturbance, marsh plants can also re-emerge from buried rhizomes. Hence, cycles of disturbance play an important role in creating marshes.

Although the presence of fire in wetlands may seem paradoxical, fire can often occur during periods of drought. Northern peatlands, cattail marshes on lakeshores, wet prairies, and seepage areas in savannas can burn under the appropriate conditions. In northern peatlands, a fire can remove thousands of years of peat accumulation in a few days, even uncovering boulders and rock ridges that were buried beneath the peat. In marshes, fire can selectively remove shrubs and small trees, preventing the marsh from turning into a swamp. In the Everglades, burning can create depressions that then cause marshes to revert to aquatic conditions.

Animals that feed upon plants often cause only small and local effects. Think of a moose grazing on water lilies, a muskrat feeding on grasses, or a hippopotamus feeding on water hyacinth. Often the small patch of removed foliage is quickly replaced by new growth. But when herbivores become overly abundant, they can destroy the marsh vegetation entirely. In northern North America along Hudson Bay, Canada geese (*Branta canadensis*) are now so abundant that they remove all vegetation from expanses of coastal marsh. In southern North America, along the Gulf of Mexico, an introduced mammal, nutria (*Myocastor coypus*), similarly can strip marsh vegetation to coastal mudflats. To some extent, disturbance by herbivores is a natural phenomenon, one that has occurred cyclically throughout history. However, in the above two examples, one suspects humans may be the ultimate cause of the large-scale overgrazing (see the next section).

Periodic droughts may at times function like a natural disturbance by killing adult plants, and allowing new species to re-establish from buried seeds. Vernal pools and prairie potholes both have plant and animal species that are adapted to this kind of cyclical disturbance.

Plant and Animal Diversity in Wetlands

Wetlands are important for protecting biological diversity. Their high productivity provides abundant food, and the water provides an important added resource. Hence, wetlands often have large populations of animals and wading birds. The Camargue in Southern Europe, for example, is considered to be the European equivalent of the Everglades. Both have species of wading birds such as storks and flamingos (Figure 9). Large numbers of other kinds of species including fish, frogs, salamanders, turtles, alligators (Figure 10), crocodiles, and mammals require flooded conditions for all or at least part of the year. If the wetlands are drained, all of the species dependent upon them will disappear.

All wetlands, however, do not support the same species. Often, as already noted in the section entitled 'Disturbance', small differences in water level or nutrient supplies will produce distinctive types of wetlands. Hence, wetlands that are variable in water levels and fertility will frequently support more kinds of species than wetlands that are uniform. Along the Amazon River floodplain, for example, different kinds of swamp, marsh, grassland, and aquatic communities form in response to different flooding regimes, and each has its own complement of animal species. In the Great Lakes,

Figure 9 Marshes provide essential habitat for many kinds of wading birds including flamingos, Jurong Bird Park, Singapore. Courtesy of Corbis.

Figure 10 Alligators are one of the many species that benefit from protected marshes such as the Everglades, Loxahatchee National Wildlife Refuge, Florida, USA. Courtesy of Paul Keddy.

different flood durations similarly produce different types of wetlands, from aquatic situations in deeper water, to marshes and wet meadows in shallower water. Some types of frogs, such as bullfrogs, require deeper water, while others, such as gray tree frogs, require shrubs.

Human Impacts

Humans have had, and continue to have, serious impacts upon wetlands in general, and marshes in particular. Some human impacts include draining, damming, eutrophication, and alteration of food webs. Let us consider these in turn.

One of the most obvious ways in which humans affect wetlands is by draining them. When the wetlands are drained, the soil becomes oxidized, and terrestrial plants and animals replace the wetland plants and animals. Often, drainage is followed by conversion to agriculture or human settlement, entirely removing the marshes that once existed. Vast areas of farmland in Europe, Asia, and North America were once marshes and have now been converted to crops for human consumption. Many countries now have laws to protect wetlands from further development, although the degree of protection provided, and the degree of enforcement, varies from one region of the world to another. Wetlands are also often included in protected areas such as national parks and ecological reserves.

Construction of dams can also have severe negative effects upon wetlands. The dams may be built for flood control, irrigation, or generating electricity. The wetland behind the dam may be destroyed by the prolonged flooding, whereas the wetlands downstream are disrupted by the lack of normal flood pulses. A single dam can therefore affect a vast area of wetlands. The degree of damage depends upon the pattern of water level fluctuations in the reservoir behind the dam, but in general large areas of marsh are lost both upstream and downstream from the dam. Sediment that would have expanded and fertilized wetlands during periodic floods becomes trapped behind the dam. Most of the world's large rivers have now been significantly affected by dams. To protect wetlands, it is necessary to identify rivers that are still relatively natural and to prevent further dams from being constructed. In other cases, it is possible to remove dams and allow natural processes to resume. An artificial levee can be considered a special type of dam that is built parallel to a river to prevent it from flooding into adjoining lands. Levees harm marshes by preventing the annual flooding, and by allowing cropland and cities to move into floodplains.

Humans can also affect wetlands by changing the nutrients in the water. Sewage from cities provides a specific 'point source' of nutrients, particularly nitrogen and phosphorus, that enter water courses then spread into wetlands. Activities such as agriculture and forestry provide 'diffuse sources' of nutrients, where runoff from large areas carries dissolved nutrients, and nutrients attached to clay particles, into the water and into adjoining marshes. The added nutrients can stimulate plant growth, which may seem to be beneficial – but it often leads to significant changes in the biota. Rarer plants and animals that are adapted to low fertility are replaced by more common plants and animals that exploit fertile conditions. Rapid growth of algae, followed by decay, can eliminate oxygen from lakes, causing fish kills. Protecting the quality of marshes therefore requires two sets of actions. First, it is necessary to control the obvious point sources of pollution by building sewage treatment plants. Second, it is necessary to use entire landscapes with care, with the broad objective of reducing nutrients in runoff. This can involve carefully timing the fertilization of crops, maintaining areas of natural vegetation along watercourses, fencing cattle away from stream valleys, minimizing construction of new logging roads, and avoiding construction on steep hill sides.

Herbivores are common in wetlands, and a natural part of energy flow from plants to carnivores. Common examples of large herbivores include moose, geese, muskrats, and hippopotamuses. Humans can disrupt wetlands by disrupting the natural balance between herbivores and plants. Herbivores can increase to destructive levels in several ways. When humans introduce new species of herbivores, rates of damage to plants may increase greatly – for example, nutria introduced from South America are causing significant damage to coastal wetlands in Louisiana. When humans reduce predation on herbivores, they may also increase to higher than natural levels. Killing alligators may damage wetlands by allowing herbivores such as nutria to reach high population densities; similarly, the loss of natural predators may be one of the reasons that Canada geese have multiplied to levels where they can destroy wetlands around Hudson Bay. There is also evidence that when humans harvest blue crabs, snails that the crabs normally eat begin to multiply and damage coastal marshes. These types of effects are difficult to study, since the effects may be indirect and take place over the long term.

Road networks are a final cause of damage to wetlands. The obvious effects of roads include the filling of wetlands, and the blocking of lateral flow of water into or out of wetlands. But there are many other effects. When amphibians migrate across roads to breeding sites, vast numbers can be killed by cars. In northern climates, the road salt put on roads as a de-icer can flow into adjoining wetlands. Snakes may be attracted to the warm asphalt and killed by passing cars. Invasive plant species can arrive along newly constructed ditches. Overall, roads change a landscape by accelerating logging, agriculture, hunting, and urban development. As a consequence, the quality of the marshes in a landscape is linked to two

Table 1 The world's largest wetlands (areas rounded to the nearest 1000 km^2)

Rank	*Continent*	*Wetland*	*Description*	*Area (km^2)*	*Source*
1	Eurasia	West Siberian Lowland	Bogs, mires, fens	2 745 000	Solomeshch, chapter 2
2	South America	Amazon River basin	Savanna and forested floodplain	1 738 000	Junk and Piedade, chapter 3
3	North America	Hudson Bay Lowland	Bogs, fens, swamps, marshes	374 000	Abraham and Keddy, chapter 4
4	Africa	Congo River basin	Swamps, riverine forest, wet prairie	189 000	Campbell, chapter 5
5	North America	Mackenzie River basin	Bogs, fens, swamps, marshes	166 000	Vitt *et al.*, chapter 6
6	South America	Pantanal	Savannas, grasslands, riverine forest	138 000	Alho, chapter 7
7	North America	Mississippi River basin	Bottomland hardwood forest, swamps, marshes	108 000	Shaffer *et al.*, chapter 8
8	Africa	Lake Chad basin	Grass and shrub savanna, shrub steppe, marshes	106 000	Lemoalle, chapter 9
9	Africa	River Nile basin	Swamps, marshes	92 000	Springuel and Ali, chapter 10
10	North America	Prairie potholes	Marshes, meadows	63 000	van der Valk, chapter 11
11	South America	Magellanic moorland	Peatlands	44 000	Arroyo *et al.*, chapter 12

Modified from Fraser LH and Keddy PA (eds.) (2005) *The World's Largest Wetlands: Ecology and Conservation*. Cambridge: Cambridge University Press.

factors: the abundance of roads (a negative effect) and the abundance of forest (a positive effect). Although it may not be obvious, halting road construction (or removing unwanted roads) and protecting forests (or replanting new areas of forest) may have important consequences for all the marshes in a landscape.

Wetland Restoration

Humans have caused much damage to wetlands over the past thousand years, and the effects have increased as human populations and technological power have grown. We have seen some examples of damage in the preceding section. In response to such past abuses, humans have also begun consciously re-creating wetlands. There are a growing number of efforts to create new wetlands and enhance existing wetlands. Along both the Rhine River and the Mississippi River, some levees have been breached, allowing floodwater to return and marshes to recover. Depressions left by mining, or deliberately constructed for wetlands, can be flooded to recreate small marshes in highly developed landscapes. Construction of dams and roads has been more carefully regulated.

The future of marshes will likely depend upon two human activities: our success at protecting existing marshes from damage and our success at restoring marshes that have already been damaged. The list of the world's largest wetlands in Table 1 provides an important set of targets for global conservation.

Summary

Marshes are produced by flooding, and, as a consequence, have distinctive soils, microorganisms, plants, and animals. The soils are usually anoxic or hypoxic, allowing vast numbers of microorganisms, particularly bacteria, to transform elements including nitrogen, phosphorus, and sulfur among different chemical states. Marsh plants often have hollow stems to permit movement of atmospheric oxygen downward into their rhizomes and roots. Marshes are some of the most biologically productive habitats in the world, and therefore support large numbers of animals, from shrimps and fish through to birds and mammals. Marshes are one of six types of wetlands, the others being swamp, fen, bog, wet meadow, and shallow water. Humans can affect marshes by changing water levels with drainage ditches, canals, dams, or levees. Other human impacts can arise from pollution by added nutrients, overharvesting of selected species, or building road networks in landscapes.

See also: Floodplains; Mangrove Wetlands; Peatlands; Riparian Wetlands; Swamps; Temporary Waters.

Further Reading

Fraser LH and Keddy PA (eds.) (2005) *The World's Largest Wetlands: Ecology and Conservation*. Cambridge: Cambridge University Press.

Keddy PA (2000) *Wetland Ecology*. Cambridge: Cambridge University Press.

Middleton BA (ed.) (2002) *Flood Pulsing in Wetlands: Restoring the Natural Hydrological Balance*. New York: Wiley.

Mitsch WJ and Gosselink JG (2000) *Wetlands*, 3rd edn. New York: Wiley.

Patten BC (ed.) (1990) *Wetlands and Shallow Continental Water Bodies, Vol. 1: Natural and Human Relationships*. The Hague: SPB Academic Publishing.

Whigham DF, Dykyjova D, and Hejnyt S (eds.) (1992) *Wetlands of the World 1*. Dordrecht: Kluwer Academic Publishers.

Fundamental Laws in Ecology

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The Need for Fundamental Laws
Systems Ecology in the Jet Stream of Scientific Development
Systems Ecology: Ten Tentative Fundamental Laws – An Attempt to Formulate an Ecosystem Theory
Other Ecosystem Theories
Summary
Further Reading

The Need for Fundamental Laws

Humans have always strived toward finding a structure or a pattern in their observations – to develop a theory. Science does not make sense without theory. Without theory, our observations become only a beautiful collection of impressions without explanation or application to solve problems of human interest. The alternative to scientific theory is to observe everything which is not possible. A well-developed theory can be used to make predictions.

Our scientific knowledge has to be coherent in order to apply the underlying theory and explain our observations. Ecology has only partially been able to condense the systematic collection of observations and knowledge about ecosystems into testable laws and principles. During the last few decades systems ecologists have developed hypotheses that together with basic laws from biochemistry and thermodynamics are proposed as a first attempt to formulate fundamental laws in ecology. The inherent complexity of ecosystems means that it is necessary to break from the long reductionistic scientific tradition to a new holistic ecological approach. Reductionistic science has had a continuous chain of successes since Descartes and Newton. Lately, however, there is an increasing understanding for the need of knowledge syntheses to a more holistic image. Today this search for a holistic understanding of complex systems is considered one of the greatest scientific challenges of the twenty-first century by many scientists.

Several important contributions to systems ecology have attempted to capture the features and characteristics of ecosystems, their processes, and their dynamics. The different theories and approaches look inconsistent at first glance, but when examined more closely, their complementarity becomes evident . This commonality and consensus regarding ecosystem dynamics was asserted by Jørgensen in the first edition of *Integration of Ecosystem Theories: A Pattern* (1992), and later editions (2nd edn. 1997 and 3rd edn. 2002) have only enhanced the perception that the theories form a pattern and that they are highly consistent. It is clear from recent meetings and discussions that today we have a general ecosystem theory which is rooted in a consensus of the pattern of ecosystem dynamics. The ecosystem theory presented here combines the work of several scientists, and provides a foundation for further progress in systems ecology, ecosystem theory, and ecology. Furthermore, it may be feasible to use a few fundamental laws to derive other laws to explain most observations. We do not know yet to what extent this is possible in ecology, but at least we propose a promising direction for a useful, comprehensive ecosystem theory. Only by the application of the theory can we assess how and where the theory needs improvements.

Systems Ecology in the Jet Stream of Scientific Development

Seven general scientific theories have changed our perception of nature radically during the last 100 years: general and special relativity, quantum theory, quantum complementarity, Gödel's theorem, chaos theory, and