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11 Services and functions

In the first chapter we encountered the concept of wetlands providing services such as food production and climate regulation. How much are they worth? One estimate is \$14 785/ha per year for interior wetlands and \$22 832/ha per year for coastal estuaries (Costanza *et al.* 1997). That is, a hectare of wetland produces services that are roughly the value of a small car or a year of university tuition, each year. Another estimate gives the global value of \$1.8 billion per year (Schuyt and Brander 2004). Where do such numbers come from? In this chapter we shall look at some examples of services provided by wetlands, focusing on three areas: production of food, regulation of the atmosphere, and culture/recreation. Efforts to quantify these services are not without their critics. There are those who resist putting dollar values on nature, since not everything that humans value has a price. None the less, the use of human currency to evaluate natural services is a growing field in economics (e.g. Costanza *et al.* 1997). Even if you have reservations about the approach, you need to understand how it is done.

11.1 Wetlands have high production

The capture of solar energy by plants is the foundation of virtually all life on Earth. The enormous production of human food in wetlands including rice, fish, amphibians, crustaceans, and mammals testifies to the rate of production in wetlands. The rate of organic production in wetlands is one of the highest in the world, matched nearly by tropical forest. In this section we will discuss the factors that make wetlands such important sites of production.

11.1.1 Wetlands are sites of high primary production

Figure 11.1 shows that swamps and marshes are some of the most productive ecosystems on Earth; they rival both rainforest and cultivated land. But, unlike agricultural fields, primary production in wild wetlands occurs with no fossil fuel inputs in the form of gasoline and fertilizer, no tending by humans, no artificial irrigation, and no heavy machinery. Wetlands can therefore be regarded as factories in the landscape that mass produce both organic matter and oxygen to support surrounding ecosystems. Draining such wetlands may therefore be compared to systematically smashing the factories that support life on Earth.

11.1.2 Wetlands have high secondary production

High rates of primary production provide raw materials for the construction of other life forms. The production of animal biomass in wetlands is some 9.0 g/m^2 per year, 3.5 times the value for terrestrial ecosystems (Turner 1982). This production has both direct economic values (e.g. fisheries, trapping, hunting) and values that are more difficult to measure (e.g. carbon flow, recreation, support of endangered species).

Let us begin with the obvious – some wetland-dwelling animals eat plants. Look at the stomach contents of turtles (Table 6.3) and waterfowl (Table 6.4). One could construct similar tables for

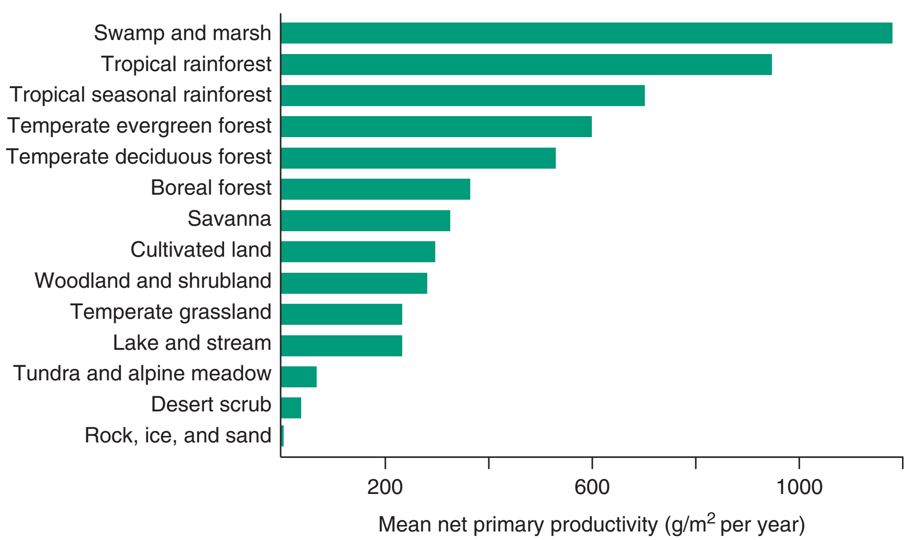

FIGURE 11.1 Mean net primary productivity of wetlands (top) compared with other ecosystems. (From data in Whittaker and Likens 1973.)

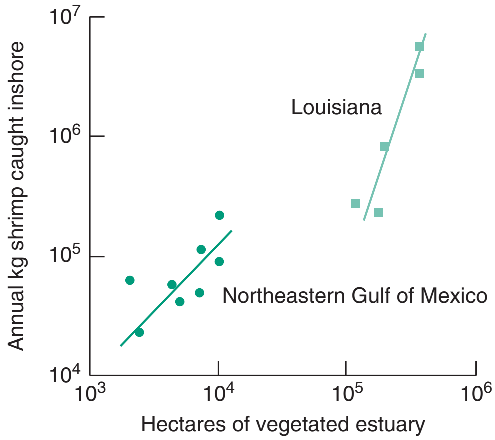

FIGURE 11.2 The relationship between the mean annual yield of shrimp caught inshore and the area of vegetated estuary. (From Turner 1977.)

nearly every animal in a wetland. Many wetland animals do not feed only on plants but on other secondary producers: the turtles in Table 6.3 feed also upon fish and mollusks. And turtles are in turn consumed by predators such as otters and alligators.

In some cases, the area of secondary production is distant from the area of primary production. Shrimp harvests in estuaries of the Gulf of Mexico are strikingly correlated with the area of salt marsh (Figure 11.2). Similarly, Welcomme (1976, 1979, 1986) has found that the area of floodplain in African rivers predicts the fish catch from these rivers. A production of 40–60 kg/ha for the maximum flooded area is typical for tropical floodplains throughout the world. Further, on a worldwide basis, there is a quantitative relationship:

$$\text{catch(kg)} = 5.46 \times \text{floodplain area(ha)}.$$

11.1.3 Much of the energy passes through a decomposer-based food web

In spite of such examples above, little of the primary production of world ecosystems is directly consumed by wildlife. This statement may seem remarkable. There is a great deal of production in wetlands, and many animals in wetlands, and we spent all of Chapter 6 looking at herbivores. The point, which you may recall from Chapter 6, is that most of the primary production passes directly to decomposers (Kurihara and Kikkawa 1986). That is, in most cases, wetland animals feed on other secondary producers that have fed on decomposers (Figure 11.3).

To put this in context, in a mixed deciduous forest, herbivores consume only 1% of primary production while in grassland, herbivores consume about 8%. Similar low figures are found in wetlands. Herbivores consumed only some 10% of primary production in both peatlands (Miller and Watson 1983) and salt marshes (Wiegert *et al.* 1981), although Lodge (1991) reports higher values for grazing on aquatic macrophytes. In salt marshes, decomposers are the base of a food chain that supports estuarine and oceanic fisheries (Turner 1977; Montague and Wiegert 1990), and a similar process appears to occur in rivers bordered by large floodplains (Welcomme 1976, 1986). In peatlands, the constant high water table and the acidic substrate reduce the activities of decomposers, so a substantial proportion of the plant debris accumulates as peat (Gorham 1957; Miller and Watson 1983).

At the risk of being repetitive, although the exact number varies among types of wetlands, overall, the preponderance of energy flow bypasses grazers (Figure 11.3). The processing of this ca. 90% of the energy requires the activity of decomposers. Kurihara and Kikkawa (1986) conclude: “For most ecosystems, the concept of secondary production must incorporate the . . . role of decomposers in making the energy of primary production available to animals.” The efficiency of decomposers in consuming primary production is illustrated by measurements showing that over 90% of the carbon fixed annually in peatlands is re-released as carbon dioxide (Silvola *et al.* 1996). Further explorations of decomposer activity can be found in Polunin (1984), Heal *et al.* (1978), Good *et al.* (1978), Dickinson (1983), and Brinson *et al.* (1981). If you look carefully at the cover of this book, you will see that some

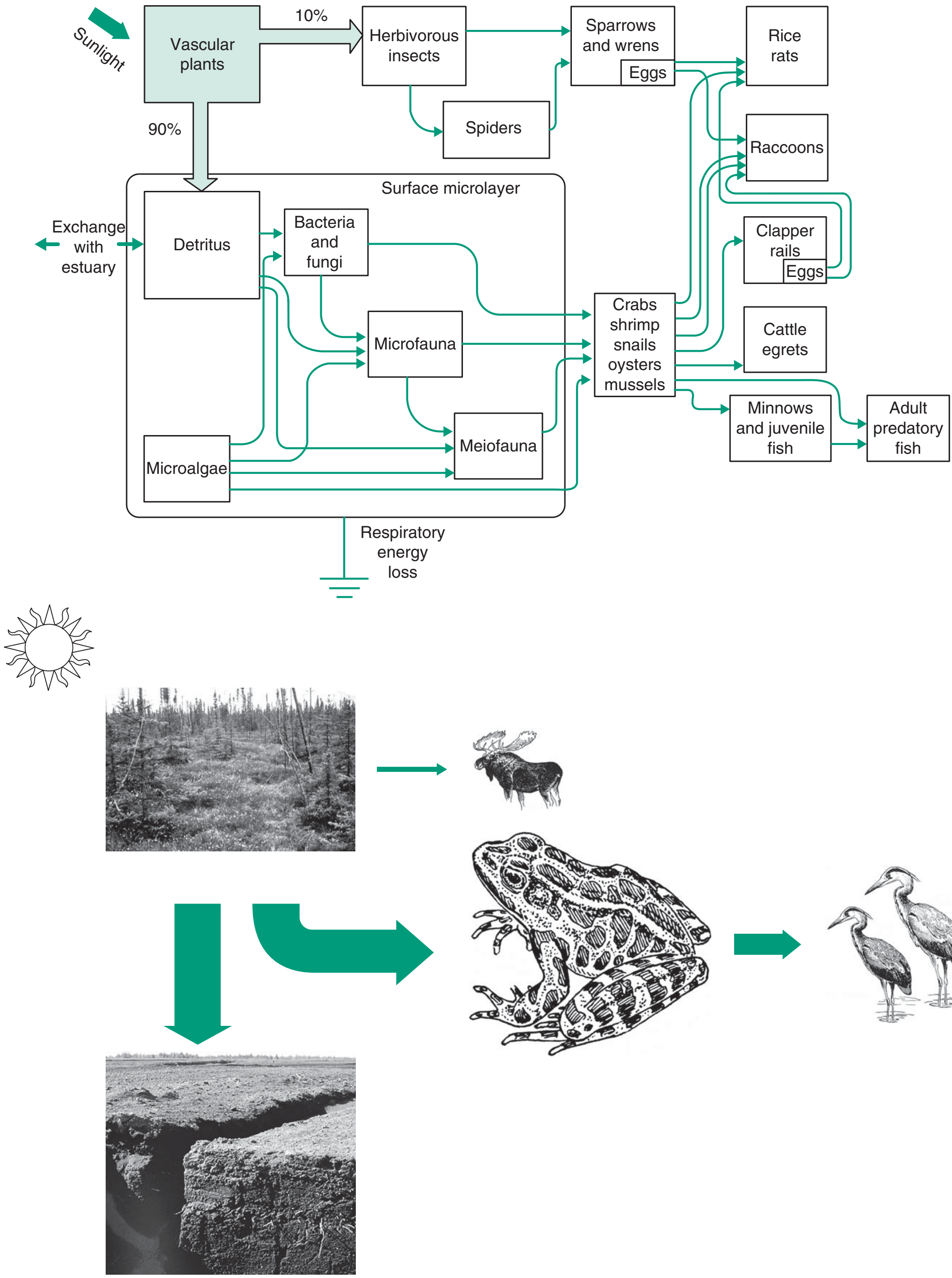

FIGURE 11.3 Wetlands are a major source of primary production. Some of this is consumed directly by wildlife, but a majority of the biomass is first processed by decomposers including insects and bacteria. The top figure shows a detailed analysis of energy flow in a coastal marsh, where no peat is accumulating (after Montague and Wiegert 1990). The bottom diagram shows a simplified version for a wetland where peat is accumulating (bog, peat, courtesy C. Rubec; moose, frog, heron courtesy B. Hines, U.S. Fish and Wildlife Service)

attempt has been made to include the often unseen invertebrates that process primary production, although, of course, many of them are microscopic bacteria.

In the end, the primary production that is not consumed directly by herbivores, nor processed by decomposers, accumulates as peat (Figure 11.3, bottom).

11.1.4 Wetlands may be used only seasonally

Many animals use wetlands for only part of the year. Consider, for example, the immense herds of grazing animals found on the East African plains that we covered in Section 6.3.2. Here let us add from two complementary sources for the story – Denny (1993a) for the botanist's perspective, and Sinclair and Fryxell (1985) for the zoologist's. To appreciate the processes, we must understand that water availability in this region changes at two timescales: annual cycles driven by rainy seasons, and longer fluctuations driven by variation in mean annual rainfall (Sinclair and Fryxell 1985). In semi-arid areas, the dry season forces grazing animals to converge on, and remain within, a 20-km radius of permanent water supplies such as rivers and swamps. In southern Sudan, for example, there are large areas of seasonally flooded and permanently flooded grasslands at the headwaters of the Nile (Denny 1993a). The deeper water areas may have the emergent *Cyperus papyrus* but the shallower areas have "lush, nutritious grasses much favoured by herbivorous browsers." Some 800 000 white-eared kob, a species of antelope, occur here. Each year when the rains stop, animals migrate from shorter grass areas into ephemeral wetlands. Even elephants use these wetlands (Mosepele *et al.* 2009). Overall, it appears that wetlands allow animal herds to move between wet lands and dry lands over the year, thereby allowing a landscape to support much larger mammal populations than would otherwise be possible.

11.1.5 There are exceptions

Having emphasized the high productivity of wetlands, we should note that aquatic plants do not appear to fit the above generalization, having relatively low production when compared to terrestrial plants (Figure 11.1). Three explanations have been offered for this observation: terrestrial plants have complex canopies with many leaf layers to intercept sunlight, their leaves can acclimate to high or low irradiance, and there is both rapid diffusion of gases and a large reservoir of carbon dioxide in the air (Sand-Jensen and Krause-Jensen 1997). These explanations, however, apply only to differences between aquatic communities and terrestrial communities. What about differences among types of wetlands? Low rates of production in aquatic wetlands are likely a consequence of limited supplies of carbon dioxide and light for submersed leaves.

Peatlands also have relatively low production, probably as a consequence of low nutrient levels and short growing seasons. The vast accumulations of peat found in northern wetlands like the West Siberian Lowland and the Hudson Bay Lowland have taken thousands of years to accumulate.

11.1.6 Some historical context

These basic patterns of primary production have only recently been determined. Leith (1975) recounts how photosynthesis itself was only discovered in the period from 1772 to 1779, and how in 1804 de Saussure gave the correct equation for photosynthesis. In 1919, Schroeder provided an estimate of dry matter production on land, 28×10^9 t. Future work required better mapping of world vegetation types, and better data on oceanic production. By 1960, Müller was able to estimate 10.3×10^9 t of carbon produced on land and 25×10^9 t in the sea.

The creation of the International Biological Program (IBP) in the early 1960s co-ordinated attempts to estimate primary production better in different ecosystems, and to incorporate these data into ecosystem and global models (Leith and Whittaker 1975). Detailed analyses of primary production and its use by different consumers were documented for coastal wetlands as well as other ecosystem types (Odum 1971; Leith and Whittaker 1975). I will not describe the different methods for measuring energy flow in wetlands; you can read about it books like Leith and Whittaker. What we are interested in is the results – the data from studies of energy flow provided the foundation for compiling Figure 11.1. Later work tried to put such measurements into large energy-flow models for ecosystems (Leith and Whittaker 1975). While the value of these systems models is doubted by some scientists (McIntosh 1985), they are still prominent in many publications on wetlands (e.g. Good *et al.* 1978; Patten 1990).

11.2 Wetlands regulate climate

Wetlands play an important role in regulating the climate through carbon storage, the production of methane, and their historical role in producing coal.

11.2.1 Carbon storage

The amount of carbon dioxide in the atmosphere is one factor that controls the Earth's temperature. Carbon dioxide is transparent to sunlight, but reflects heat back to Earth. This is the basic mechanism of a greenhouse, and hence the origin of the term greenhouse effect. Since the Industrial Revolution, the concentration of carbon dioxide in the atmosphere has been rising (Figure 11.4). This is thought to be an important cause of projected changes in climate.

Since swamps and marshes are ecosystems in which plants rapidly extract carbon dioxide from the atmosphere (roughly 1 kilogram for every square meter), it is reasonable to conclude that these wetlands are particularly important in removing carbon dioxide from the atmosphere and cooling the Earth. Of course, this also depends upon how much of the organic matter is consumed by other organisms, in which case the carbon dioxide may be rapidly cycled back into the atmosphere (Figure 11.3). Peatlands are one notable exception. Here the rate of decomposition is far lower than the rate of production, with the consequence that carbon remains stored in partially decayed plant material. Some 500 million hectares (nearly 4% of the Earth's ice-free land area) now consists of peatlands (Gorham 1990). These peatlands store carbon that would otherwise be released to the atmosphere as carbon dioxide. One estimate suggests that 500 billion metric tons of carbon would be released into the atmosphere if all the peatlands on Earth were destroyed (Dugan 1993). This means that the world's large peatlands may have an enormous importance in protecting the Earth from higher temperatures. The world's largest peatlands are in central Russia (the West Siberian Lowland), northern Canada (Hudson Bay Lowland, Mackenzie Valley Lowland), and southern South America (Magellanic moorlands). Many other smaller peatlands in Europe and Asia also store carbon.

The rate of carbon storage can be disrupted by human activities. Drainage of these wetlands can increase rates of decomposition, releasing carbon dioxide into the atmosphere (Silvola *et al.* 1996). Drainage can also increase fire frequencies, increasing carbon dioxide production (Gorham 1991; Hogg *et al.* 1992). Burning peat for electricity will have the same effects. Some countries with peatlands have few trees, in which case humans have learned to cut and dry peat for heating their homes (recall Figure 4.14).

There is concern that rising temperatures themselves may be sufficient to increase rates of decomposition, in which case we can expect significant climatic consequences (Gorham 1991; Woodwell *et al.* 1995), chiefly a further increase

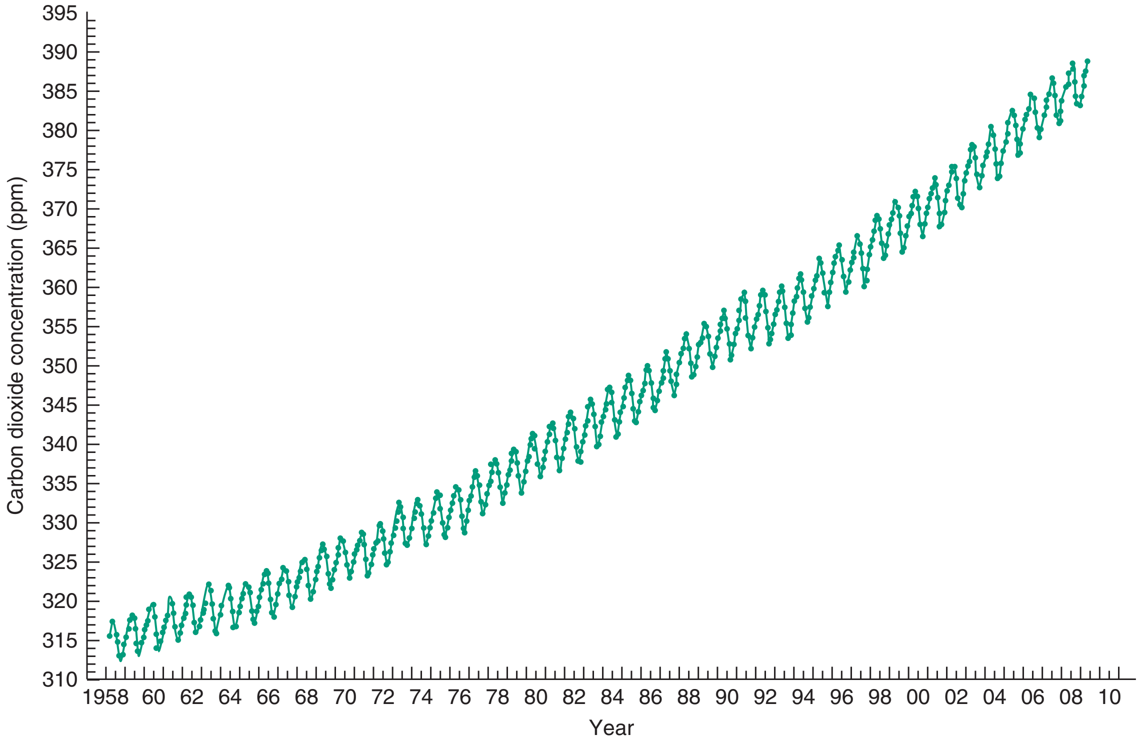

FIGURE 11.4 The concentration of carbon dioxide in the atmosphere (measured at the Mauna Loa observatory) is increasing with time. Note too that there is a cycle – each summer growing plants in the northern hemisphere reduce carbon dioxide levels by about 5 ppm. Decay returns this carbon dioxide to the atmosphere in the winter. Wetlands store carbon dioxide as peat and reduce the rate of increase. (From Keeling and Whorf 2005 and Tans 2009.)

in mean global temperature. This is not just speculation: Silvola *et al.* (1996) have shown that carbon dioxide production increases with higher temperature or with a lower water table. Warmer and drier summers may therefore speed up the rate of release of carbon dioxide from storage in peatlands, enhancing the greenhouse effect.

11.2.2 Methane production

Methane (CH_4) is a very simple molecule. It is also the most abundant organic chemical in the Earth's atmosphere, although its concentration is measured only in parts per billion (ppb). Because it absorbs infrared light, it is also an important greenhouse gas (Cicerone and Ormland 1988; Forster *et al.* 2007). Indeed, one molecule of methane generates as much greenhouse effect as 23 molecules of carbon dioxide, although methane degrades more rapidly, with a half-life of about 7 years (House and Brovkin 2005).

Over the past 650 000 years, methane has cycled between 400 ppb during glacial periods to about 700 ppb during interglacial periods. Air samples extracted from dated ice cores suggest that methane concentrations have slowly increased from ca. 700 to 1000 ppb over the last two millennia, with more rapid increases recently in the 1970s and 1980s (Figure 11.5). The level found in 2005 – 1774 ppb – is therefore more than twice the level recorded from other interglacial periods. Although methane levels continue to increase, the rate of increase appears to have slowed over the past few decades; the reasons are unclear (Forster *et al.* 2007).

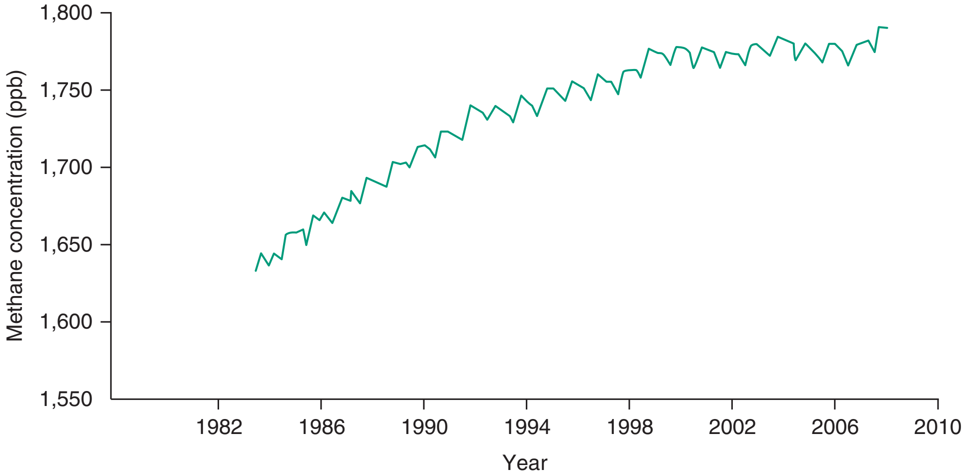

FIGURE 11.5 The concentration of methane in the atmosphere is increasing with time. Wetlands play an important, but poorly understood, role in regulating atmospheric methane levels. (Data from U.S. National Oceanographic and Atmospheric Administration.)

Natural wetlands contribute from one-third to one-half of the methane released to the atmosphere each year (Cicerone and Ormland 1988; Whiting and Chanton 1993; House and Brovkin 2005). This amounts to more than 100 Tg of methane (a Teragram $= 10^{12}$ g); 25% of this comes from tropical and subtropical swamps and marshes, whereas 60% is released from high-latitude peatlands (Matthews and Fung 1987). There is still considerable uncertainty on the figure of 100 Tg – the Millenium Ecosystem Assessment (House and Brovkin 2005) puts it between 92 and 237 Tg per year, while Whalen (2005) narrows it down to 145 Tg per year.

Human agriculture is certainly the other major source, also about one-third of the global total, and it comes largely from ruminant animals and rice paddies. Rice paddies contribute in the order of 100 Tg of methane (Aselman and Crutzen 1989). Rice paddies have higher emission rates on a m^2 basis, 300–1000 mg CH_4/m^2 per day, than natural wetlands (Table 11.1).

Part of the difficulty with making this kind of generalization is the inherent variation. Methane production varies among wetland types, among locations in wetlands, and with both temperature and flooding, making it difficult to generalize (Whalen 2005). So let us turn from global averages to look more at the processes involved in this service. We are particularly interested in the organisms that make methane and that consume methane, and how methane moves from the wetland to the atmosphere.

Methane is produced by a group of decomposers known as methanogenic archaebacteria, an ancient group of microorganisms that are strict anaerobes and live in highly reduced conditions. They do not break down organic matter themselves, but rather use the carbon dioxide generated by other decomposers as a substrate, and combine it with hydrogen: $4H_2 + CO^2 = CH_4 + 2H_2O$. One ATP is produced for each methane molecule produced. It also appears that other organic molecules such as acetate (CH_3COOH) can be used in this process (Valentine 2002).

Methane is consumed by other microorganisms. In anoxic conditions, methane oxidation apparently requires no fewer than three organisms, two different groups of archaebacteria existing in "consortia" with sulfate-reducing bacteria (Valentine 2002).

The emissions of methane from a wetland therefore depend ultimately upon how the local environment affects the relative abundance and activity of the above groups of microorganisms. Methane production will vary enormously with local

Table 11.1 **Global wetland methane emissions extrapolated from measured emission rates in field experiments**

Wetland type	Emission rate ($mg\ CH_4/m^2$ per day)	Area ($10^{12}\ m^2$)	Mean prod. period (days)	Emission (Tg/yr)
Lakes	43	0.12	365	2
Bogs	15	1.87	178	5
Floodplains	100	0.82	122	10
Marshes	253	0.27	249	17
Fens	80	1.48	169	20
Swamps	84	1.13	274	26
Rice fields[a]	310+	1.31	130	145
Total		7.00		100–300

[a] Rice fields have a second temperature-dependent term that leads to ranges from 300 to 1000 CH_4/m^2 per day.
Source: After Aselman and Crutzen (1989).

conditions. Roots of higher plants can reduce methane production by releasing oxygen and suppressing methane production, whereas root decay and root exudates can accelerate methane production (Segers 1998). It is likely that the oxidized upper levels of the wetland remove significant amounts of the methane produced in deeper layers (Segers 1998; Whalen 2005).

In some cases, the aerenchyma in plants provides a route for the diffusion of methane into the atmosphere. In one peatland, Shannon *et al.* (1996) found that a majority (64–90%) of the methane produced in an ombrotrophic peatland was emitted by one herbaceous plant, *Scheuchzeria palustris*. The aerenchyma of the plant transported the methane produced by methanogenic bacteria from below the soil surface into the atmosphere. Other plants such as *Carex* spp., *Peltandra virginiana*, and *Typha* are also known to emit methane.

Now back to the atmosphere (Figure 11.5). Once methane reaches the atmosphere, it is removed by reaction with the hydroxyl free radical (OH) which is produced photochemically in the atmosphere (Forster *et al.* 2007). A dramatic drop in growth of atmospheric concentrations occurred in 1992. It is thought that the Mt. Pinatubo volcanic eruption in July 1991 injected enough material into the low stratosphere of the tropics to shift photochemistry and accelerate removal of CH_4 by atmospheric OH.

11.2.3 And then there is coal

On a larger timescale, consider the degree to which our civilization is based upon another wetland product: coal. The ability to mine coal was a trigger of the Industrial Revolution, and by the 1980s we consumed in the order of 3 billion tons per year (Manfred 1982). Even highly industrialized countries such as the United States still depend upon coal for roughly one-fourth of their energy consumption (Manfred 1982). Emerging economies in India and China will increase the rate at which coal is mined and burned. Coal comes from swamps that existed long in the past (Figure 11.6). By burning the coal, humans are releasing carbon dioxide that was once extracted from the atmosphere by wetland plants – this is why coal is called a fossil fuel. The burning of coal is the most obvious (but not the only) cause of the rising trend in carbon dioxide levels in the atmosphere. To the degree that they remove carbon dioxide from the air and store it, wetlands provide a counterbalance. Coal mines also emit methane.

FIGURE 11.6 Coal was produced in vast wetlands such as this Carboniferous coal swamp. (© The Field Museum, #GE085637c.) When coal is burned, the stored carbon returns to the atmosphere as carbon dioxide. Stored nutrients such as nitrogen are also released. (See also color plate.)

11.3 Wetlands regulate the global nitrogen cycle

In Chapter 3 we learned about the effects of nitrogen availability on the distribution and abundance of plants and animals. Here we will learn about the significant role wetlands play in the nitrogen cycle.

11.3.1 Nitrogen is abundant in the air but scarce in organisms

We take it for granted that the atmosphere is 78% nitrogen and 21% oxygen with only trace amounts of carbon dioxide and methane. But why is the atmosphere the way it is? In his 1789 *Treatise on Chemistry,* published only a few years before he went to the guillotine, Lavoisier addressed in one of his first sections the composition of the atmosphere:

> We have already seen that the atmospheric air is composed of two gases . . . one of which is capable, by respiration of contributing to animal life . . . the other, on the contrary, is endowed with directly opposite qualities; it cannot be breathed by animals, neither will it admit of the combustion of inflammable bodies, nor of the calcination of metals.

The former we call oxygen, the latter nitrogen (although Lavoisier preferred the term azote). We now know some important further features of this azotic gas. First, the Earth's atmosphere differs from those of both neighboring planets (Venus and Mars) in having this gas predominant in its atmosphere. Second, nitrogen is essential for the construction of amino acids, the building blocks of proteins and life –

each has a nitrogen molecule in its structure. Third, only a few organisms can remove nitrogen from the atmosphere, so that both plant growth and animal growth is limited by the availability of nitrogen (e.g. Raven *et al.* 1992; White 1993). Finally, the enzyme that catalyzes the conversion of atmospheric nitrogen to biologically usable forms, nitrogenase, functions only under anoxic conditions, presumably because it originated early in the Earth's history when the atmosphere was still anoxic. Therefore, when cyanophytes reduce atmospheric nitrogen to a biologically usable form, they do so in special thick-walled cells called heterocysts in which the enzyme is protected from oxygen.

Overall, we can say that the shortage of nitrogen for making proteins is one of the central and unifying themes of plant and animal ecology. This is all the more strange given the abundance of nitrogen in the atmosphere.

11.3.2 Wetlands allow chemical transformation of nitrogen

Wetlands are an important part of the cycling of nitrogen because the hypoxic or anaerobic conditions allow chemical transformations of nitrogen. Moreover, since the water level changes "wetlands maintain the widest range of oxidation–reduction reactions of any ecosystem on the landscape. This allows them to function as effective transformers of nutrients and metals . . ." (Faulkner and Richardson 1989, p. 63). That is, wetlands are sites where elements are transformed among an array of chemical states (Rosswall 1983; Armentano and Verhoeven 1990; Patten 1990). The complex biogeochemical cycle of nitrogen involves multiple biotic and abiotic transformations involving seven valency states (+5 to −3). In wetlands, most nitrogen is stored in organic sediments. There are two scales at which nitrogen movement and transformation can be studied. At the within-wetland scale, the principal flows occur among three components: organic matter, the oxidized surface layer, and deeper anoxic layers. At a landscape scale, there are flows among three other components: the surrounding terrestrial landscape, the wetland, and the atmosphere. Since we have already seen how nitrogen moves in soils (Figure 1.14), let us consider the larger scale here.

At larger scales, inputs of nitrogen to wetlands include fixation, runoff, and precipitation. Outputs include runoff and gaseous nitrogen produced by denitrification.

Wetlands provide two services. They can increase or decrease nitrogen levels in the water.

Whether a wetland is a source or sink for nitrogen depends upon the relative rates of fixation and denitrification in turn (Table 11.2). Recall that these processes are largely dependent upon the proximity of the surface oxidized layer to the anoxic regions deeper in the wetland (Faulkner and Richardson 1989).

11.3.3 Increasing nitrogen levels through fixation

In areas where nitrogen is scarce, cyanobacteria can fix nitrogen and increase local productivity. This is an important process in rice paddies, and also in natural nutrient-limited systems like the Everglades.

During nitrogen fixation, bacteria reduce atmospheric nitrogen (N_2) to ammonium (NH_4^+), providing a continual flow of nitrogen from the atmosphere to the soil. Rates of fixation in wetlands are, however, usually rather low (from 1.0 to 3.5 g/m^2 per year) (Table 11.2). Exceptions may include rice fields, floodplains, and wetlands such as the Everglades where cyanobacteria fix nitrogen. Some published estimates are considerably higher than those in Table 11.2; Whitney *et al.* (1981) estimated nearly 15 g/m^2 per year for salt marshes in eastern North America.

The principal organisms involved in nitrogen fixation in wetlands are cyanobacteria such as *Nostoc*. Better known are the bacteria such as *Azotobacter* and *Clostridium* which form nodules on

Table 11.2 **Nitrogen fixation and denitrification in wetlands**

Wetland type	N fixation Mean rate (g/m^2 per year)	N fixation Total (Tg/yr)	Denitrification Mean rate (g/m^2 per year)	Denitrification Total (Tg/yr)
Temperate				
Peat mires	1.0	3.0	0.4	1.2
Floodplains	2.0	6.0	1.0	3.0
Tropical				
Peat mires	1.0	0.5	0.4	0.2
Swamp forest	3.5	7.8	1.0	2.2
Floodplains	3.5	5.2	1.0	1.5
Rice fields	3.5	5.0	7.5	10.8
Total		27.5		18.9
Total terrestrial		139		43–390

Source: From Armentano and Verhoeven (1990).

the roots of legumes, but legumes are relatively uncommon in most wetlands. A group of filamentous bacteria known as actinomycetes forms nodules on the roots of some trees aud shrubs associated with wetlands, notably the alders (*Alnus*) and wax myrtles (*Myrica*). *Rhizobium* is also associated with a family found in wetlands, the Ulmaceae. Finally, the cyanobacterium *Anabaena* often occurs in association with the floating water fern *Azolla*, and plays an important role in fixing nitrogen for rice paddies.

11.3.4 Lowering nitrogen levels through denitrification

Wetlands can reduce the nitrogen in water by capturing it in plant tissue, storing it in organic sediments, or converting it back to atmosphereic nitrogen. This service is of particular value in those cases where nitrogen is locally abundant and produces unwanted plant growth such as algal blooms. The importance of wetlands for denitrification has likely increased since industrial fixation of nitrogen (using the Haber process) has caused nitrogen enrichment (eutrophication) of both rivers and precipitation.

Denitrification is carried out by microorganisms living in anaerobic conditions, as we saw in Chapters 1 and 3. In this process, NO^{-3}, the biologically useful state, is converted back to N_2 or N_2O. These diffuse upward through the soil back into the atmosphere. Appreciable amounts are actually transported upward by aerenchyma in rooted plants (Faulkner and Richardson 1989). In general, denitrification rates are slightly lower than fixation rates. As a first, very rough approximation, nitrogen fixation is from 1–3 g/m^2 per year, while denitrification is about 1 g/m^2 per year (Table 11.2). Rice fields are an exception. The attempt to measure these processes accurately at the global scale (e.g. Lavelle *et al.* 2005) is a challenge, in part because the relative rates of nitrogen fixation and denitrificaton vary in so many ways. Not only do the rates vary among types of wetlands, but they vary spatially in wetlands – and then there is temporal variation on top of that, depending upon season and amount of flooding. Consider a few more examples. Bowden (1987) reported denitrification rates nearly an order of magnitude higher (30 g/m^2 per year), which would mean the wetlands are efficiently transforming organic nitrogen to atmospheric nitrogen. You can read more about biogeochemical cycling of nitrogen in sources such as Faulkner and

Richardson (1989), Armentano and Verhoeven (1990), and Lavelle *et al.* (2005).

In general, it appears that the rates of denitrification exceed rates of fixation, so that wetlands can be thought of as sites where organic nitrogen arrives in runoff and detritus, and is then returned to the atmosphere.

11.3.5 Treatment wetlands

Since nitrogen and phosphorus are significant causes of eutrophication, there is considerable interest in the use of wetlands to process wastewater and runoff. Here we have to recall the principal difference between nitrogen and phosphorus cycles, as introduced in Chapters 1 and 3. Nitrogen has a gaseous phase in its cycle, and it is possible to use artificial wetlands for denitrification, which returns nitrogen to the atmosphere as N_2 gas. Both nitrogen and phosphorus are necessary for construction of plant tissue. Hence plants can remove both of these nutrients from water. Of course, if the plants fall back into the water and decay, there was only temporary storage and the nutrients are returned to the water. If, however, the plants are harvested, or if they are eaten by herbivores that leave the site, then it is possible for nutrients to be removed from the location. Otherwise, nutrients accumulate in the wetland, which, as we say in Chapter 3, can have deleterious effects upon some of the species therein. Nutrient removal is worth re-emphasizing: if you burn a wetland, some nitrogen is lost to the atmosphere through volatilization, but the rest falls in place as ash. Hence, burning will be of limited use in controlling eutrophication – and note that you now know enough to predict it may be helpful with eutrophication by nitrogen, but will likely have minimal impact on eutrophication by phosphorus. Mowing and harvesting, as practiced in traditional cultures, actually removes the nutrients from the wetland and transports them elsewhere. Finally, both nitrogen and phosphorus can be stored in sediment. The only problem with storage in sediment is that this means that sediment (or possibly peat) is accumulating, in which case the wetland is slowly filling in.

Overall, then, wetlands can offer an important service by improving water quality. The service is greatly affected by how the wetland is managed, and may, if care is not taken, eventually lead to the loss of the wetland.

Many communities are finding that artificially constructed treatment wetlands are a useful way to treat wastewater (Figure 11.7), particularly surface runoff, and there is now an entire industry building around treatment wetlands (Hammer 1989; Knight

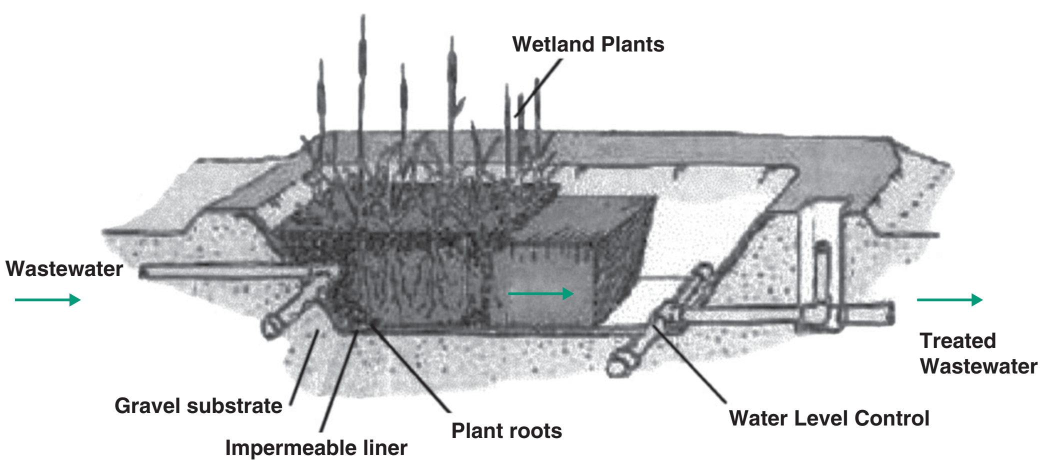

FIGURE 11.7 Treatment wetlands are constructed to reduce concentrations of nitrogen and phosphorus in wastewater. (From U.S. Environmental Protection Agency 2004.)

and Kadlec 2004). In coastal areas, constructed wetlands may provide both nutrients and fresh water. Several huge treatment wetlands are being built to try to reduce nutrient inputs to the Everglades (Sklar *et al.* 2005). Whether treatment wetlands will work at this scale is unknown, particularly as these treatment wetlands will have to deliver water with extremely low nutrient levels if they are to prevent cattail expansion in the Everglades.

11.4 Wetlands support biological diversity

The ability of wetlands to support large numbers of species enables them to perform an important service – wetlands act as storehouses of natural diversity. In this section we will discuss biodiversity as a service and the number of species that wetlands support.

11.4.1 Biodiversity storage is a service

We have already explored some of the factors that control biological diversity in wetlands in Chapter 9. When we talk about biodiversity as a service, we are describing just how many species the wetland supports. That is, we treat a wetland as a sort of warehouse of biological materials or of genetic diversity. Many species also provide other services that we explicitly measure in separate categories. For example, the presence of a particular species of cyanophyte would be one unit of the biodiversity of a wetland. The services of that cyanophyte might appear in several other categories: primary production, nitrogen fixation, food for an endangered species, carbon storage . . . it is entirely possible for one species to provide multiple services.

When we describe biodiversity as a service, particular value is given to species that are regionally or globally rare. This is because rare species represent a section of biodiversity that could be lost, and, generally, the fewer the individuals present, the greater the probability that they will disappear. I have tried to incorporate some examples of such species in this book, including the gopher frog (Figure 2.5*b*), furbish lousewort (Figure 2.5*e*) and Plymouth gentian (Figure 2.5*f*), Venus fly-trap and prairie white-fringed orchid (Figure 3.4), and bog turtle (Figure 5.13), as well as rhinoceros (Section 6.3.4), Bengal tigers (Section 8.5), and snail kites (Section 13.2.2). There are many, many more. Increasingly, every region, state, province, and nation has lists of significant species and their status. The usual three status levels are “species of concern” through “threatened species” to “endangered species.” Species of concern are normally on a watch list of species that appear to be declining, while endangered species are normally at imminent risk of disappearance. Great care is taken before assigning these status levels, and they are frequently adjusted as new information becomes available. Different regions of the world often use different terms for describing status, although there is a steady convergence of terminology. The ultimate world authority is the IUCN *Red List*, created in 1963. The *Red List* classifies species using status levels ranging from “least concern” to “critically endangered” (http://www.iucnredlist.org/). The list also includes the many species thought to be already extinct.

11.4.2 Services can be measured for whole wetlands or individual species

In principle, we can think about services in two ways. There is the service provided by a wetland as a whole, and the services provided by each individual or species. In this chapter, the focus has been on the services of whole wetlands. This is partly because it is usually this information that government agencies need to know for conservation planning.

In a general way, the service performed by a wetland is the total of the services provided by all the species. If we knew all the services performed by each individual in each species, and summed them all, we would have one estimate of the service

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performed by the wetland. Of course, the problem is that we do not know the services provided by many species, nor do we know how many individuals there are. Sometimes, their services may even cancel each other out – for example denitrifying bacteria may cancel out the effects of nitrogen-fixing bacteria. As a further complication, services like water storage and carbon storage in peat are clearly the consequence of many species together, some of which may have been dead for centuries. Hence, for studying services it is probably better to take a top–down approach, that is, to ask about the service of the whole wetland without first worrying about which species is providing which service. We may be able to measure oxygen production, methane production, water storage, fish production, or bird production, even if we do not yet understand all the different species in the wetland that contribute to that service.

All the same, some services may be provided by a small number of species. Sphagnum mosses store organic carbon. Cyanophytes fix atmospheric nitrogen. Fish provide human food. To illustrate, Table 11.3 shows some services provided by selected species. In most cases, we do not know what services, if any, a species performs. A wetland that stores biodiversity therefore stores an unknown number of services, often provided by an unknown number of species. It is likely that some species will provide enormous services, while others may provide minor services. The point is that we often do not yet know. As but one example, most people dislike mosquitoes; few know that if we somehow eliminated all the mosquitoes from a set of wetlands, we would not only take away a food supply for many other insects, fish, and birds (including species consumed by humans), but we would even prevent pollination of local forest orchids (Table 11.3). At the other extreme, rice is a staple food. Of course, when a wetland is turned into a rice paddy, many of the species that occur there naturally disappear, so the biodiversity service is reduced.

As science progresses, we will gain a better understanding of wetland services provided by individual species. In the interim, the mere presence of these species is itself a value. Indeed, as we shall see below, sometimes the cultural and recreational value of a selected species far outweighs any other known service.

11.4.3 Wetlands provide habitat for some 100 000 species of animals

Wetlands not only support large numbers of individual species, but they support many different kinds of species. Some 100 000 animal species alone require freshwater habitats (Lévêque *et al.* 2005). Of these, some 50 000 are insects; there are 21 000 vertebrate species, 10 000 crustacean species, and 5000 mollusk species. Among the vertebrates, amphibians occur solely in fresh water, with ca. 5500 species. To this list one would need to add species using coastal wetlands for a global total.

In Chapter 9 we saw what kinds of environmental factors determine the number and kind of species found in wetlands. Under the topic of services, let us add that wetlands support diversity in several ways. First, there are species that are obligately dependent upon wetlands. Amphibians are a typical example. Many other species, however, use wetlands only occasionally as a source of water, food, and shelter. The herds of African mammals are a typical example. Finally, since wetlands (like mountain ranges) are often among the last wild places in landscapes, those large carnivores that need large areas of habitat may find wetlands to be the last wild places for refuge – examples include the Bengal tiger in the Sundarbans, the Florida panther in the Everglades, and the Iberian lynx (the world's most endangered feline) in the Doñana wetlands of southern Spain.

11.4.4 Management for biodiversity

One of the great emerging challenges for biologists is the management of wetlands to maintain, or even enhance, biological diversity. At one time, biologists were expected to maximize production of a few species, like muskrats or ducks. In the history of Louisiana, for example, enormous areas of coastal

Table 11.3 Selected examples of ecological services provided by wetland species

Service	Example
Food	(a) Rice is a staple food for a large proportion of the human population. According to the FAO (2009), 600 million tons were grown in 2007, of which 220 million tons were consumed in India and China alone (IRRI 2009). (b) Fish provide food for many human populations, and are particularly important as a source of protein in poorer nations. (c) Vegetables that come from wetlands include Chinese water chestnut (the tuber on *Eleocharis dulcis*), wetland taro (*Colocasia esculenta*), and lotus root (*Nelumbo nucifera*). (d) Fruits from temperate wetlands include cranberries (*Vaccinium*) and elderberries (*Sambucus*). Fruits from tropical wetlands include Acai berries (*Euterpe oleracea*) and ungurahua fruits (*Oenocarpus bataua*), both of which are species of palm trees. (e) Wild rice (genus *Zizania*) requires little cultivation, and is of some importance to aboriginal North Americans, who increasingly collect the rice for sale as a natural food product.
Artistic inspiration and appreciation	(a) Claude Monet, the French impressionist, produced four water lily paintings. One, called *Le Bassin aux Nymphéas*, painted in 1919, sold for \$78.8 million in London in 2008. (b) Dragonflies, frogs, and turtles have all inspired artists to create work of beauty. Their representations can be found in many cultures, both ancient and modern.
Medicinal plants/Artistic inspiration	*Acorus calamus* has long been considered an aphrodisiac. It is also hallucinogenic. Walt Whitman's folio of poems *Leaves of Grass* has, in the third edition, a section called the "Calamus" poems.
Medicine	Aronia berries (*Aronia melanocarpa*) have high concentrations of antioxidants and are used in many herbal treatments.
Lumber	Cypress trees provide attractive and decay-resistant wood.
Pollination	*Aedes* mosquitoes carry pollinia for some *Platanthera* orchids.
Fertilization	Cyanophytes such as *Nostoc* and *Anabaena* enhance the fertility of rice paddies by fixing atmospheric nitrogen.
Clothing	Fur has provided humans with warm clothing for millennia. Fur can also be processed to make felt. (The author has a hat made in Argentina from nutria felt.)
Paper	The word paper actually comes from the plant papyrus (*Cyperus papyrus*), which is harvested from Egyptian wetlands and has been used to make paper for millennia. Other local uses include baskets, hats, fish traps, trays, floor mats, roofs, and rope. Reeds are collected as raw material for paper in China.
Construction material	Reeds are harvested for thatching on houses in Europe and for constructing boats and houses in Iraq.

marsh were burned, ditched, and impounded simply to increase the abundance of muskrats to produce more pelts (O'Neil 1949), and often with little consideration for impacts on other species or the long-term survival of the marshes themselves. Increasingly, biologists are being charged with managing wetlands for the benefit of all the species they contain. This is far more of a challenge than single-species management. It is however the way of the future. All of Chapter 9 was therefore devoted to biodiversity. If you skipped that chapter, it might be a good time to go back and read it.

11.5 Wetlands provide recreation and cultural services

There is no easy, and certainly no single, way to measure the value of recreation and culture. Civilized societies have always had museums and art galleries and theaters, but how do you assess their value? Do the Louvre or the Smithsonian Institution or the Great Wall of China have a cash value? Let's look at some methods of measuring economic value and their application to wetlands.

11.5.1 Three approaches to measuring economic value

Some philosophers would argue that trying to put an economic value on culture and recreation debases them. None the less, there are others who do believe it is possible to assign cash values even to culture and recreation. And even if these cash values are imperfect, they are better than nothing, so the argument goes. In order to fit culture and recreation into economic decision-making, we simply have to use the standard currency for measuring value: dollars, pounds, euros, yen, or roubles. There are many methods for attempting to put economic values on systems (Costanza *et al.* 1997; Daily 1997; Heal 2000; Krieger 2001), and there is a good deal of disagreement. For simplicity, consider three main options: hedonic price indices, replacement cost, and travel costs.

Hedonic price indices To put a value on views, you find the difference in sale prices of similar homes, one set with good views and one set without. This could be applied in some case to wetlands, such as comparing the value of homes with and without access to wetlands or coastline.

Replacement cost The value of good soil might be calculated by replacement cost. We might ask how much it would take to grow the equivalent amount of food using hydroponics. Or how much would it cost to buy fish that a wetland is currently producing. In a real example, New York was faced with securing its future water supply. A new water treatment plant would have cost them \$9 billion, including operating costs. Protecting 80 000 acres of land in the Catskills that provides clean water cost, instead, \$1.5 billion. Thus, there was a clear advantage to making use of a natural service. But as Heal (2000) observes, what then is the value of the water: \$1.5 billion, \$9 billion (replacement cost), or the difference between the two? And what if the land is also providing, as it certainly does, other ecological services such as oxygen production or recreation?

Travel costs When people have choices on how to spend their money, the amount that they allocate to travel to natural areas, or museums, or theaters, says something about the value they put on that activity. Since actual entry to many wetlands and parks is usually available at low cost (unlike say, opera tickets) the travel costs are a major component of a user's willingness to pay for an experience.

11.5.2 Two large examples

While none of these methods is perfect, we shall start with the travel costs, and see how that story develops. I will illustrate the process using two recent studies that have tried to put an economic value on nature and natural areas – a Canadian study on the value of nature based on a national poll of 87 000 people (Environment Canada 2000) and an American study into the economic value of wildlife refuges (Carver and Caudill 2007). These have the advantage of being large in scope; the disadvantage is that wetlands are not separated from other wild places.

Number of visitors

Those guest books you see in museums have a purpose – they allow the staff to count how many people enter, and thereby justify their budgets.

So always sign guest books. If there are gates where entry fees are paid, direct counts of visits to specific locations can been made. Here are some numbers from the United States in 2006:

National Parks	272.6 million visits
Bureau of Land Management	55 million visitors
National Wildlife Refuges	34.7 million visitors

While such figures show that people value wild areas, they say nothing about the economic return of such activity.

Expenditures

One obvious method is to measure the travel costs that a visitor pays in order to reach a site. This can include vehicle mileage, boat rental, or airline tickets (Carvalho 2007).

Travel costs, are however, insufficient for measuring expenditures. The Canadian study (Environment Canada 2000) found that travel was only about one-fourth of the expenditure associated with enjoyment of nature:

Equipment	28.4%
Transportation	23.5%
Food	18.4%
Accommodation	12.7%
Other items (e.g. entry fees)	5.8%

Equipment was the biggest expense: cameras and binoculars for the birdwatchers, guns and ammunition for hunters, rods and boats for fishermen, tents and canoes for the explorers. If you have priced a good set of binoculars or a good canoe, you can see how much people will spend to see a bird, shoot a deer, hook a shad, or travel a wild river. The total expenditure for 1 year, 1996, was $11 billion.

Multiplier effects

Expenditures alone do not include the multiplier effects or ripple effects of these expenditures in the economy as a whole. When you buy gas on the way to a wild area, or hire a guide, or stay in a lodge, the money you spend cycles through the economy. Again, there is no single way to measure these effects. The Canadian study produced five measures intended to reflect these multiplier effects. For every dollar spent on nature-related activities, almost $1.50 of gross business production was generated. Although the idea of multiplying the expenses by 1.5 gives some sense of multiplier effects, increasingly complex economic models are employed. These economic measures were determined:

Gross business production	$16.3 billion
Gross domestic product	$11.4 billion
Government revenue from taxes	$5.1 billion
Personal income	$5.5 billion
Number of jobs sustained	201 400

The American study used economic modeling to include effects on the economy including car repairs, shoes, and alcohol. They concluded that visitors to Wildlife Refuges contributed $1.7 billion to the economy and contributed 26 800 jobs.

Willingness to pay

Another method is to measure the willingness to pay. In the case of the Upper Paraná River floodplain, the interviewed tourists were asked how much they would be willing to contribute to a foundation dedicated to protecting the natural values of the area (Carvalho 2007). This is questionable since the user does not actually have to pay the funds, nor are they faced with alternative scenarios for use of the money.

Associated with willingness to pay you will often see "surplus value" being calculated. Surplus value reflects how much more people are willing to pay for a service above what it actually costs them. In the Canadian study, respondents reported that they would have been willing to pay an extra $2 billion before limiting their outdoor activity. Again, however, there is real difficulty with measuring surplus value, since it depends upon people's best guess of how much they would pay before ceasing their activity. They might, however, switch from a long visit to a shorter visit, from a distant site to a nearer one, or simply economize with cheaper binoculars. Anyone who knows a devoted fly fisherman or deer hunter or birdwatcher knows too that these activities have such a high value that they would not easily be given up. Asking such people how much more they would pay seems like an exercise in futility. None the less, it is done.

11.5.3 Estimates of economic value of wetlands for recreation

Since the above examples addressed the recreational value of nature rather than wetlands, you might wonder about values for wetlands alone. Here are a few examples that are specific to wetlands.

Floodplain in Brazil One undammed fragment of the Upper Paraná River floodplain in Brazil, 230 km in length, is a popular destination for tourists. By applying a combination of the methods above to tourists, Carvalho (2007) calculated an estimated value of $533.00 per hectare. The total value was $356.5 million per year.

Marshes in the Great Lakes Two wetland areas on the north shore of Lake Erie have been studied (Kreutzwiser 1981, pers. comm.) In 1978, 17 000 people used the Long Point marshes for recreation, and derived an estimated $213 000 of recreational value. Assuming 1460 ha of marshes, this yields $146/ha annually (in 1978 Canadian dollars). Similar studies in Point Pelee National Park produced higher values of $1425/ha annually. The higher figures for Point Pelee partly reflect the higher travel costs, since visitors tend to travel longer distances to reach Pelee. This likely reflects its international reputation, including special events such as spring bird migration.

Wetlands at the global scale Costanza *et al.* (1997) estimated the following values in $/ha per year for wetlands, using in most cases willingness to pay (WTP) approaches. I have also included coastal estuaries given their close association with tidal marshes and mangroves.

Recreational (e.g. ecotourism, sport fishing):

Tidal marsh/mangroves	658
Swamps/floodplains	491
Estuaries	381

Cultural (esthetic, educational, spiritual):

Tidal marsh/mangroves	(no information)
Swamps/floodplains	1761
Estuaries	29

11.6 Wetlands reduce flood peaks

Water levels in rivers change with time (Chapter 2). In temperate zones, high-water periods are caused by the melting of snow; in tropical areas, high-water periods are often associated with rainy seasons. Most wetland organisms can tolerate flooding, and many benefit from or depend upon it. From their perspective, flooding is necessary, and their life cycles are timed to exploit the flood peak. In this section we will look at how wetlands help to reduce flood peaks.

11.6.1 Flooding is natural and inevitable

When humans build on floodplains, flooding becomes a problem. What people call a river's “banks” are, after all, usually the river's edge during a seasonal low. Water levels that rise above those banks are inevitable. Yet too many people who live in floodplains seem surprised when the river rises. Many hectares of farms, factories, and cities are flooded every time the river enters a higher phase

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(recall Figure 2.1). Of course, as *The Epic of Gilgamesh* (Sanders 1972) reminds us, so long as people have built on floodplains, they have complained about floods.

11.6.2 Levees and flood walls often make the situation worse

The natural response to seeing a river in flood is to build a wall along the river bank to stop the "flood." These flood walls, artificial levees, dikes, impoundments, and so on, now line and confine rivers throughout the world (recall Figures 2.25, 7.8). All have many unfortunate consequences.

- Artificial levees end the natural link between the river and the floodplain, with negative effects on the organisms in both the floodplain and the river. The wetlands begin to desiccate, and growth slows from lack of nutrients; riverine fish are denied access to wetlands for feeding and rearing their young.
- Artificial levees encourage more people to move onto the floodplain, so the number of people at risk increases with time.
- Artificial levees prevent the floodplain from absorbing and storing water, which makes the floods even higher – particularly for people downstream.
- Artificial levees cause the land inside the levee to subside, so the land becomes even lower than the river, and even more prone to flooding.

As a consequence, human development of watersheds often leads to steadily increasing losses from floods. Whether you talk about the Mississippi River, the Rhine River, or the Yangtze, the story is more or less the same. This is not a new problem (Kelly 1975). When settlers moved into the deciduous forests of eastern North America, they first cleared forests in the soils most immediately useful for planting. Small wet patches could then be drained with ditches, and, as technology for drainage improved with the use of buried tiles, increasingly large areas of swamps could be undertaken. In southern Ontario, large areas of swamps were under-drained with tiles in the 1860s, thereby creating farmland described as "first class lands ... fit to produce any kind of crop." But almost immediately these projects generated flooding in adjacent lower lands, and by 1873 a county council had petitioned the provincial legislature to set up a system of arbitration to settle disputes about flood damage (Kelly 1975)!

We now know that wetlands provide the service of floodwater retention: water may be stored within the substrate (as in peatlands) or above the soil surface in the entire basin. Floodplain wetlands therefore reduce flooding downstream by allowing flows to spread out over larger areas of landscape, thereby reducing both the velocity and the depth of discharge.

11.6.3 You can estimate the value of flood protection

Thibodeau and Ostro (1981) attempted to put an economic value upon development of 8500 acres of marsh and wooded swamp in the Charles River basin in Massachusetts (Table 11.4). The benefits from these wetlands were divided into categories including flood control, water supply, increases in nearby land value, pollution reduction, and recreation and esthetics. Flood control values were estimated by forecasting flood damage that would have occurred without wetlands. In one case, during a 1995 storm, the U.S. Army Corps of Engineers estimated that the wetlands of the Charles River reduced peak river flows by 65% and delayed flooding over a period of 3 days after the actual storm. What property damage would have occurred if these wetlands had not been present? Thibodeau and Ostro estimate projected annual flood damage of nearly $18 million, which translates into a value of about $2000 per acre of wetland (Table 11.4). An asset that yields $2000 in perpetuity has a present economic value of more than $33 000 per acre.

Of course, a single private owner cannot capture most of these benefits. They are largely external benefits.

Table 11.4 **Summary of the benefits of 1 acre of Charles River wetland in New England**

Service	Estimate of value: Low	High
Increases in land value		
Flood prevention	$33 370	$33 370
Local amenity	$150	$480
Pollution reduction		
Nutrients and BOD	$16 960	$16 960
Toxic substances	+	+
Water supply	$100 730	$100 730
Recreation and esthetics		
Recreation	$2145	$38 469
Subtotal	$153 000	$190 009
Preservation and research	+	+
Vicarious consumption and option demand	+	+
Undiscovered benefits	+	+
Total including visual–cultural benefits	$153 535+	$190 009+

Source: From Thibodeau and Ostro (1981).

Table 11.5 **The economic value of 1 hectare of wetland, as estimated from the median value of 89 sites**

Service	Value (US$ per hectare per year in 2000)
Flood control	464
Recreational fishing	374
Amenity/recreation	492
Water filtering	288
Biodiversity	214
Habitat nursery	201
Recreational hunting	123
Water supply	45
Materials	45
Fuelwood	14

Source: From Schuyt and Brander (2004).

It may well be to his economic advantage to fill the land, reaping its development value. When this happens, it is the town, the watershed, and the region which suffer the loss.

Thibodeau and Ostro (1981) are describing the “tragedy of the commons” (Hardin and Baden 1977), which, as Hardin (1968) first presented it for grazing communities, leads each citizen to make apparently rational decisions in their best short-term interest. Yet, when each individual in the community goes through the same decision-making process, and acts in this apparently rational manner, the result is destruction for the entire community. The property owner filling in the acre of wetland, the multinational logging executive felling the next tract of tropical forest, and the herdsman deciding to graze an additional animal upon the communal pasture, all are making a decision that produces short-term economic benefits to the individual or corporation, but which ultimately damages the larger community.

11.6.4 Adapting to life on floodplains

In short, losses from flooding are inevitable once floodplains are settled. When wetlands are drained, and levees built, it gets worse. As I write this, a flood peak is rolling down the Mississippi River in Missouri. Cedar Rapids and Des Moines have water flowing through their streets. No doubt, as you are reading this, a flood peak is rolling down some other river in the world. One can read about flood storage, and see lines in tables (e.g. Tables 11.4 and 11.5) that put a value on wetlands, but often we still miss the simple message. As a personal example, which does offer some psychological insight into human attitudes, my father bought a home overlooking a floodplain. I grew up there. Every spring he complains to me about how high the water is. I used to try to explain that that is what happens to

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a floodplain, and encourage him to enjoy the wood ducks and the great blue herons. Now I just save my breath. At some instinctive level it seems to offend his sense of order that the river should flow at a level other than its typical July level. Period. However deeply ingrained such views are in our fellow human beings, our professional challenge is to build systems which take advantage of wetlands yet remove people from risk.

The quite remarkable story about the service of flood storage is how the construction of artificial levees has caused flooding, even though the levees are supposed to protect from floods. When a levee breaks, and the flood waters re-enter what was an old piece of floodplain, the flood peak immediately falls. If several levees upstream break, the polders (the areas that were once floodplain and wetland) often are able to absorb most of the floodwaters and end the flooding. Hence, people downstream find themselves hoping that the levees upstream will break before the flood peak arrives at their own doorsteps! What this shows very clearly is that if the floodplains upstream had been left undeveloped, they would be performing their flood control service by absorbing the floodwaters, and there would have been no dangerous flood downstream in the first place. In his book *The Control of Nature* John McPhee (1989) describes how The Great Flood of 1927 in the Mississippi River "tore the valley apart" (p. 42). Yet it was nowhere near a record flood, it was not even a 100-year flood. It was a consequence of levees that left the water confined into a narrow channel. It was not an act of God, he says, it was an act of engineers.

The commonsense approach is to ensure that valuable infrastructure is built at higher elevations, and that structures at lower elevations either be elevated on pilings, or be expendable (Nicholls and Mimura 1998; Keller and Day 2007; Vasseur and Catto 2008). Many regions now have floodplain maps that restrict development within frequently flooded areas. This is a basic principle of land use planning, and can be found in older, although classic, books such as *Design with Nature* (McHarg 1969).

Of course, private landowners often complain that they cannot build on their property because it is zoned floodplain and demand compensation. They obstruct zoning and planning. Of course, had they been allowed to build on the floodplain, the same people would be demanding government compensation when their house or factory was damaged by a flood. Given that some people have to complain about something, it is generally easier and cheaper to allow them to complain about not being able to build than to complain about having their house destroyed. Over time, the message sinks in that land on floodplains should be left as land.

Of course, there are always going to be a few people who avoid rational discussion. Barbara Tuchman has written about such people in *The March of Folly* (1984). I doubt, however, that any of those people are reading this book.

11.6.5 There is money to be made from engineered disasters

Continuing on that theme, Mark Twain once noted, roughly, "there is no point trying to convince someone to believe something when he will profit from not believing it." Hence, we should not expect everyone to accept the need to make commonsense planning decisions. When I was in Louisiana, private landowners were demanding the right to do whatever they wanted with their land, even turning land below sea level into subdivisions, while at the same time they were insisting that the federal government step in and protect their land with levees and restore their wetlands, too, free, all while keeping taxes low. There is, apparently, no federal statute that says landowners have to be logically consistent.

It is unfortunate that bad decisions by one community force other communities to make the same bad decision. *A community that builds taller levees and impounds bigger areas exports its flooding to neighbors*. Levee building pits one community against another, each building its levees higher, in the hope that it will be a neighboring community that floods instead of them. There is no end to the cycle.

Thus one begins an expensive and never-ending vicious cycle of levee construction up and down the river valley. It is likely to be far more economical to buy wetlands and leave them for flood storage in the first place, instead of building enormous levees downstream to handle the flood.

There is an enormous industry that benefits from money spent on flood control. Indeed, some have said that in Louisiana, levee construction has less to do with flood control than with obtaining federal money (Houck 2006). Buying and restoring wetlands upstream to provide long-term flood storage is an obvious solution to recurring flooding, as is restricting building in the most flood-prone areas. The more levees we build along rivers, the higher the floods will become. Hence, it is time to plan adaptively for life on floodplains.

- Protect existing wetlands for flood storage
- Reduce the area of land protected by levees to enhance flood storage
- Move critical infrastructure to higher land
- Elevate critical infrastructure that cannot be moved.

Given the enormous value of the services of flood control, and recreation, wetlands should increasingly become part of land use planning in watersheds. It is happening, and levees are being removed in parts of North America, Europe, and Asia. You will see some examples in the next chapter.

11.7 Wetlands record history

Plant and animal debris often accumulates in wetlands owing to the low oxygen levels, and the resulting layers of peat and sediment can record the sequence of plant species that occupied a site over millennia. Since we know what environmental conditions these plants required, one can reconstruct how the environment has changed. Peatlands are particularly important and well studied. One frequently finds that the accumulations of organic matter provide a nearly complete record of the plant associations that occurred on the site over thousands, or tens of thousands, of years. This record most commonly takes the form of pollen and plant fragments, but can be supplemented by insect parts, charcoal fragments, archeological artefacts, and even rooted trees that have been buried over the years (e.g. Watts and Winter 1966; Walker 1970; Moore 1973; Godwin 1981; Delcourt and Delcourt 1988, 1991). They can also record contaminants such as lead and show us how deposition rates changed with time. (Exceptions include alluvial flood plains, where the sediments are constantly reworked by meandering rivers, so that the sedimentary record is lost [e.g. Nanson and Beach 1977; Salo *et al.* 1986]).

Let us take Ireland as an example. Figure 11.8 shows the types of pollen recovered from a peat bog near Tipperary. More than 8 meters of peat now cover the original soil surface. Some 10 000 years ago the site was open tundra, as indicated by the abundant birch and sedge pollen. Pine woods developed some 8000 years ago, to be replaced by elm–oak woodland some 6000 years ago. This suggests a steady amelioration of climate. About 3000 years ago, *Ulmus* (elm) pollen declines and herb pollen increases; this appears to reflect woodland clearance by Neolithic farmers. About 1800 years ago the clearances become more extensive, apparently due to the arrival of Bronze Age farmers. At many sites, wooden trackways constructed from branches or split logs were apparently constructed to cross bogs and link farming communities (Godwin 1981). At about AD 300, there was a reduction in intensity of farming, but since then there has been a steady increase in amounts of grass and herb pollen, indicating greater human impacts upon the Irish landscape.

Such records provide important opportunities to study long-term changes in vegetation and climate, the impacts of human cultures upon

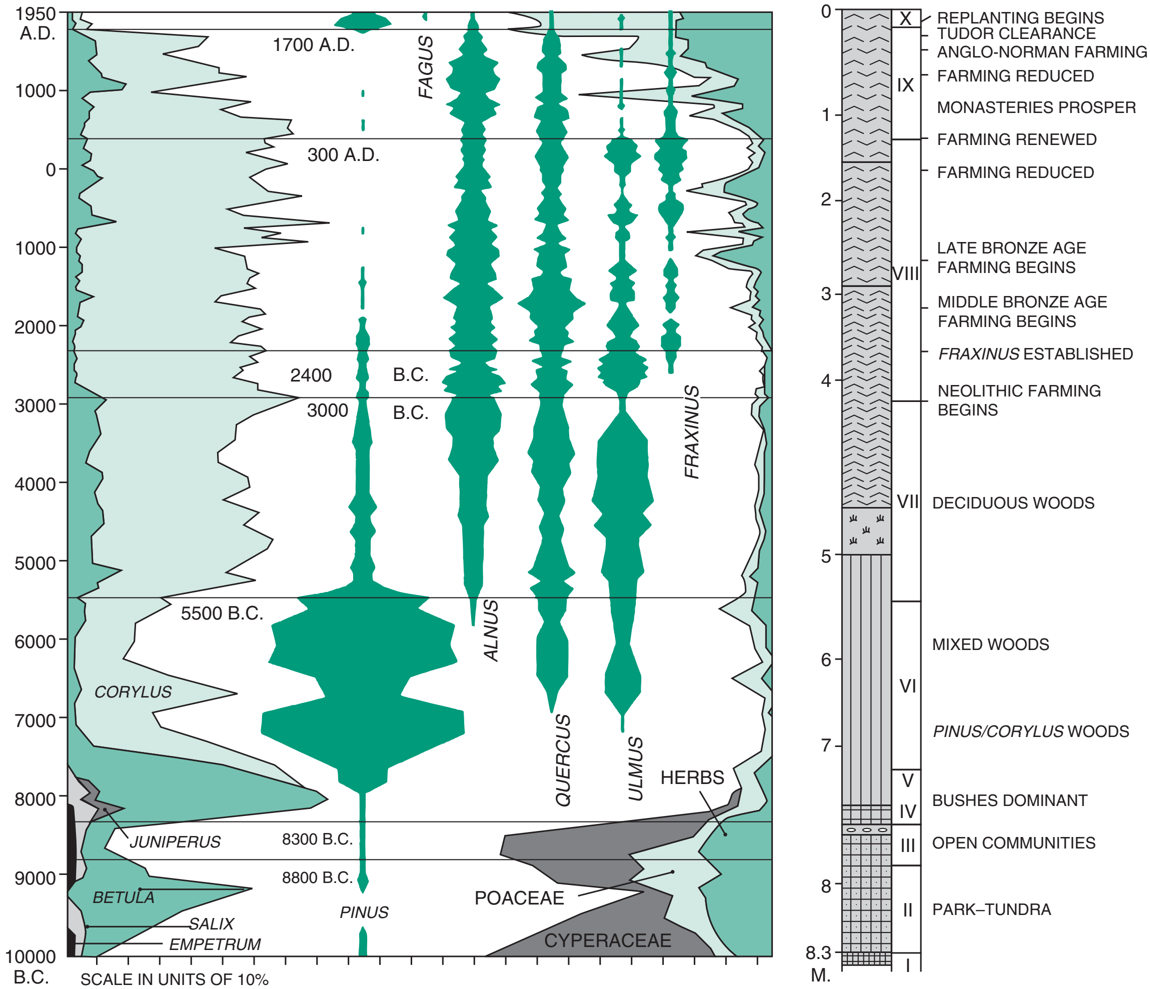

FIGURE 11.8 A 10 000-year profile through the Littleton Bog, Ireland, shows how tundra gradually turned into deciduous forest, and then how humans stripped the land of its forests. (After Mitchell 1965, from Taylor 1983.)

vegetation, and natural processes such as succession in wetlands. In many cases peatlands can be considered to be archives for adjoining regions of the Earth's surface (Godwin 1981). Changes in vegetation and land use are not the only records stored in bogs. A Danish almanac of 1837 records: "There is a strange power in bog water which prevents decay. Bodies have been found which must have lain in bogs for more than a thousand years, but which, though admittedly somewhat shrunken and brown, are in other respects unchanged." More than 690 human bodies have been recovered from peat bogs. The most famous are perhaps Lindow Man and Tollund Man. The bodies are distributed across Germany, Denmark, Holland, England, Scotland, Ireland, Norway, and Sweden (Stead *et al.* 1986; Coles and Coles 1989). Most are from the period between 100 BC and AD 500. Men, women, and children have been found, the outstanding feature being that they are so well preserved that they are sometimes first assumed to be the result of a recent murder. Some, such as the Tollund

Man, were apparently strangled, with the plaited skin noose still attached to the neck; others appear to have been pegged down while still alive (Glob 1969). The bodies give the appearance of having been tanned, a process now attributed to a polysaccharide (sphagnan) produced by *Sphagnum* (Painter 1991).

Many studies of wetland services do not explicitly include the role of wetlands in preserving archeological and climatological data. Growing concerns about human impacts on climate, and about rates of deposition of atmosphere comtaminants like lead and mercury, are likely to further increase the value of such records.

11.8 Adding up the services: WWF and MEA evaluate wetland services

The World Wildlife Fund undertook a review and meta-analysis of 89 wetland evaluation studies (Schuyt and Brander 2004). Their objective was to better quantify the global value of wetlands, particularly in light of the criticisms of the Constanza *et al.* (1997) studies, and the lack of detail on the types of wetlands. The task, is of course, complicated by the many services that wetlands perform, combined with the many different types of wetlands and the many geographical regions in which they occur.

To combine the 89 existing studies, they divided wetlands into five types and found the economic value (in US dollars in the year 2000) for each. Their first example, the Pantanal, was shown in Table 1.8. The median values were:

Unvegetated sediment	$374/ha
Freshwater wood	$206/ha
Salt/brackish marsh	$165/ha
Freshwater marsh	$145/ha
Mangrove	$120/ha

The high value of unvegetated sediments is unexpected, and is partly explained by the value in storm protection and as nursery grounds for commercial fisheries in areas like the Wadden Sea in the Netherlands and the Rufiji delta in Tanzania. Migratory waterbirds also feed in mud flats, and invertebrate populations may be higher that in the nearby vegetated areas (Peterson *et al.* 1989). The low value of mangroves, in contrast, may reflect the predominance of their use for fuelwood in areas of low income.

Using these data, WWF next extrapolated to the rest of the world using a database on 3800 wetlands representing about 63 million hectares, yielding a value of $1.8 billion per year. Wetlands in Asia had particularly high values, likely a reflection of the high population density of this part of the world.

These values are conservative. First, as the list of services in Table 11.5 shows, some services were not included, such as water supply (extractive use by industry), erosion control, climatic stabilization, carbon sequestration, maintenance of ecosystem stability, medicinal resources, and genetic resources. Second, the figure of 63 million hectares is on the low side. Other estimates are 10 or even 20 times higher. If you use the Ramsar estimate (12.8 million km^2), the total economic value of the world's wetlands, based on the services examined in the WWF report (and therefore not all services) could be around $70 billion per year. This larger figure would be consistent with the study valuing the services of the Pantanal alone at $15 billion per year (Table 1.8).

The Millenium Ecosystem Assessment (2005) provided a comprehensive overview of human impacts on the biosphere. This assessment tabulated a list of 17 services provided by ecosystems in general. These services were assigned to one of four categories: provisioning, regulating, cultural and supporting. The MEA then assigned relative values for each of these services for inland wetlands (Figure 11.9) and coastal wetlands (Figure 11.10). Compare these figures to Table 1.7.

It appears that we have been significantly undervaluing wetlands. As knowledge of services increases, the value of wetlands is likely to increase further.

Services	Comments and Examples	Permanent and Temporary Rivers and Streams	Permanent Lakes, Reservoirs	Seasonal Lakes, Marshes, and Swamps, including Floodplains	Forested Wetlands, Marshes, and Swamps, Including Floodplains	Alpine and Tundra Wetlands	Springs and Oases	Geothermal Wetlands	Undeground Wetlands, Including Caves and Groundwater systems
Inland Wetlands									
Provisioning									
Food	production of fish, wild game, fruits, grains, and so on	●	●	●	●	·	·		
Fresh water	storage and retention of water; provision of water for irrgation and for drinking	●	●	•	·	·	·		●
Fiber and fuel	production of timber, fuelwood, peat, fodder, aggregates	•	•	·	●	•	·	·	
Biochemical products	extraction of materials from biota	·	·	?	?	?	?	?	?
Genetic materials	medicine, genes for resistance to plant pathogens, ornamental species, and so on	·	·	?	·	?	?	?	?
Regulating									
Climate regulation	regulation of greenhouse gases, temperature, precipitation, and other climatic processes; chemical composition of the atmosphere	·	●	·	●	·	·	·	·
Hydrological regimes	groundwater recharge and discharge; storage of water for agriculture or industry	●	●	•	•	·	·		·
Pollution control and detoxification	retention, recovery, and removal of excess nutrients and pollutants	●	•	·	•	·	·		•
Erosion protection	retention of soils and prevention of structural change (such as coastal erosion, bank slumping, and so on)	•	·	·	•	?	·		·
Natural hazards	flood control; storm protection	•	●	●	•	•	·		·
Cultural									
Spiritual and inspirational	personal feelings and well-being; religious significance	●	●	•	•	·	•	·	·
Recreational	opportunities for tourism and recreational activities	●	●	•	·	·	·	·	·
Aesthetic	appreciation of natural features	•	•	·	•	·	·	·	·
Educational	opportunities for formal and informal education and training	●	●	•	•	·	·	·	·
Supporting									
Biodiversity	habitats for resident or transient species	●	●	•	•	·	·	·	·
Soil formation	sediment retention and accumulation of organic matter	●	·	•	●	·	?	?	
Nutrient cycling	storage, recycling, processing, and acquisition of nutrients	●	●	●	●	·	·	?	·
Pollination	support for pollinators	·	·	·	•	·	·		

FIGURE 11.9 The relative magnitude (per unit area) of ecosystem services provided by inland wetlands: low (small dot), medium (intermediate dot), high (large dot), ? = unknown; blank cells indicate that the service is not considered applicable to inland wetlands. The figure shows the global average pattern according to expert opinion. (From Millennium Ecosystem Assessment 2005.)

Services	Comments and Examples	Estuaries and Marshes	Mangroves	Lagons, Including Salt Ponds	Intertidal Flats, Beaches, and Dunes	Kelp	Rock and Shell Reefs	Seagrass Beds	Coral Reefs
Coastal Wetlands									
Provisioning									
Food	production of fish, algae, and invertebrates	●	●	·	•	·	•	·	•
Fresh water	storage and retention of water; provision of water for irrigation and for drinking	·		·					
Fiber, timber, fuel	production of timber, fuelwood, peat, fodder, aggregates	●	●	•					
Biochemical products	extraction of materials from biota	·	·			·			·
Genetic materials	medicine; genes for resistance to plant pathogens, ornamental species, and so on	·	·	·		•			·
Regulating									
Climate regulation	regulation of greenhouse gases, temperature, precipitation, and other climatic processesses; chemical composition of the atmosphere	•	•	•	·		·	·	•
Biological regulation	resistance of species invasions; regulating interactions between different trophic levels; preserving functional diversity and interactions	•	●	•	·				·
Hydrological regimes	groundwater recharge/discharge; storage of water for agriculture or industry	·		·					
Pollution control and detoxification	retention, recovery, and removal of excess nutrients and pollutants	●	●	•		?	·	·	·
Erosion protection	retention of soils	•	●	·				·	·
Natural hazards	flood control; storm protection	●	●	·	·	·	•	•	●
Cultural									
Spiritual and inspirational	personal feelings and well-being	●	·	•	●	·	·	·	●
Recreational	opportunities for tourism and recreational activities	●	·	·	●	·			●
Aesthetic	appreciation of natural features	•	·	•	•				●
Educational	opportunities for formal and informal education and training	·	·	·	·		·		·
Supporting									
Biodiversity	habitats for resident or transient species	•	•	·	●	·	●	·	●
Soil formation	sediment retention and accumulation of organic matter	•	•	·	·				
Nutrient cycling	storage, recycling, processing and acquisition of nutrients	•	•	•	·	·	·		•

FIGURE 11.10 The relative magnitude (per unit area) of ecosystem services provided by coastal wetlands: low (small dot), medium (intermediate dot), high (large dot), ? = unknown; blank cells indicate that the service is not considered applicable to coastal wetlands. The figure shows the global average pattern according to expert opinion. (From Millennium Ecosystem Assessment 2005.)

CONCLUSION

We began with the challenge of measuring ecological services. We have now examined some of the principal services provided by wetlands. Some, like the value of fish, are easy to measure. Others, like regulation of climate are equally important, but much harder to measure. And others still, like the value of wetlands to culture, seem immeasurable. Of course, when a painting like Claude Monet's *Le Bassin aux Nymphéas* sells for $78.8 million, this neatly translates art into dollars.

Here are two more examples.

When the young Polish novelist Józef Konrad Korzeniowski took the aging *Roi des Belges* up the Congo River in 1899, who would have guessed that it would give us Joseph Conrad (a new name) and the darkly famous novella *Heart of Darkness* (Figure 11.11, top)? And who could have guessed then that an entirely

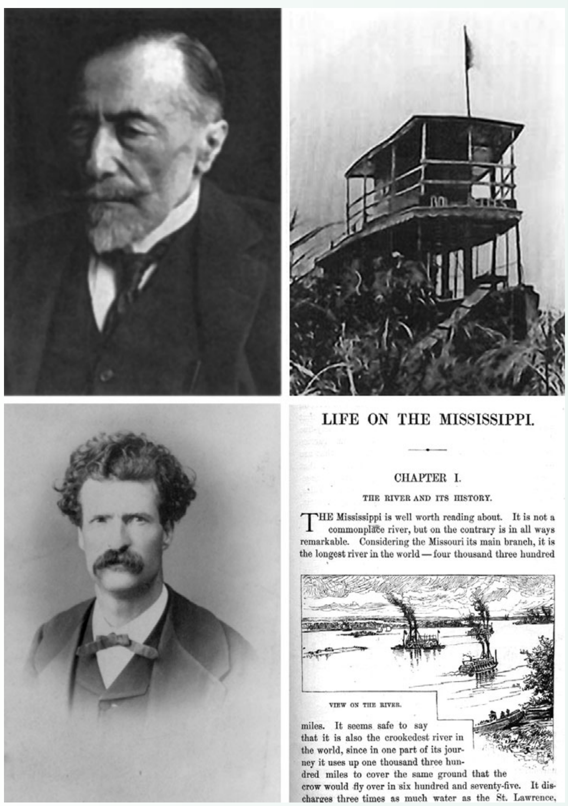

FIGURE 11.11 Wetlands have played a prominent role in the world's literature. Top: Joseph Conrad (1857–1924) sailed up the Congo River in 1899 in the *Roi des Belges* (built 1887, only this ancient photo survives; from en.wikipedia.org), inspiring his book *Heart of Darkness* (1902). Bottom: Mark Twain (1835–1910) (courtesy Library of Congress, P&P) worked as a riverboat pilot and wrote several books based upon his experience, including *Life on the Mississippi* (1883).

new medium, color film, would be used to tell stories, and that *Heart of Darkness* would metamorphose into *Apocalypse Now*?

And then there was the young typesetter Samuel Clemens who decided, in 1856, to give up a journalistic assignment from the Keokuk *Saturday Post* for a series of comic letters about travel in South America, and instead become a riverboat pilot on the Mississippi River. Who would have guessed that this event would eventually give us Mark Twain (another new name) and legacies like *Life on the Mississippi* (1883) (Figure 11.9, bottom) and, only a year later, *The Adventures of Huckleberry Finn*?

There are just two of many famous artists whose lives were inextricably bound up with wetlands. In this chapter I have tried to lay out the fundamentals of putting economic values on wetlands. It is an issue that is likely to grow in importance and sophistication. And, at the same time, Claude Monet, Joseph Conrad, and Mark Twain are just three people who illustrate the power of wetlands to influence human creativity in ways that are hard to predict and even harder to measure.