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WETLAND RESOURCES: Status, Trends, Ecosystem Services, and Restorability

Joy B. Zedler and Suzanne Kercher
Botany Department, University of Wisconsin, Madison, Wisconsin 53706; email: jbzedler@wisc.edu, skercher@wisc.edu

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■ **Abstract** Estimates of global wetland area range from 5.3 to 12.8 million km^2. About half the global wetland area has been lost, but an international treaty (the 1971 Ramsar Convention) has helped 144 nations protect the most significant remaining wetlands. Because most nations lack wetland inventories, changes in the quantity and quality of the world's wetlands cannot be tracked adequately. Despite the likelihood that remaining wetlands occupy less than 9% of the earth's land area, they contribute more to annually renewable ecosystem services than their small area implies. Biodiversity support, water quality improvement, flood abatement, and carbon sequestration are key functions that are impaired when wetlands are lost or degraded. Restoration techniques are improving, although the recovery of lost biodiversity is challenged by invasive species, which thrive under disturbance and displace natives. Not all damages to wetlands are reversible, but it is not always clear how much can be retained through restoration. Hence, we recommend adaptive approaches in which alternative techniques are tested at large scales in actual restoration sites.

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INTRODUCTION

Wetlands are areas "where water is the primary factor controlling the environment and the associated plant and animal life" (1). They are considered a resource because they supply useful products, such as peat, and perform valued functions, such as water purification and carbon storage. A status report on the resource involves evaluation of both the area and condition of wetlands. Knowledge of wetland resources and the research capacities of various nations are uneven among continents. Aware of the inequities, we consider the status and trends of wetlands globally and regionally, the ecosystem services provided by wetlands, and restoration potential. A global comparison, however, requires a common definition of wetlands. Although all definitions of wetlands are based on hydrologic conditions, the degree of wetness is a major variable. Wetlands are wetter than uplands but not as wet as aquatic habitats. How wet is wet enough, and how wet is too wet?

The Ramsar Convention is a 1971 international treaty, signed in Ramsar, Iran, which lays out a framework for national action and international cooperation for the conservation and wise use of wetlands and their resources (2). The definition of wetlands under this treaty is broad, including both natural and human-made wetlands and extending to 6 m below low tide along ocean shorelines (3). Nearly 124 million ha (hectares) of wetlands in 1421 sites around the world have been designated as Wetlands of International Importance (4); of these, only 19 sites are in the United States (1,192,730 ha—less than 1% of the total U.S. land).

The U.S. Fish and Wildlife Service (FWS) definition (5) is much narrower, but still includes shallow aquatic systems: "Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. For purposes of this classification wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes (plants that grow in water); (2) the substrate is predominantly undrained hydric soil (wet and periodically anaerobic); and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of the year."

Still narrower is the definition used in the U.S. regulatory process. The Army Corps of Engineers and the Environmental Protection Agency both have jurisdiction over specific areas that are regulated by the Clean Water Act. "Jurisdictional wetlands" must have evidence of all three indicators (wetland hydrology, wetland soil, and wetland plants), whereas FWS wetlands have "one or more" of the indicators. Disagreements over jurisdictional wetlands sparked national debate and a review of wetland boundary determination procedures by the National Research Council (6). Regulators now use a detailed federal guidebook and additional state and local guidelines to draw specific boundaries around jurisdictional wetlands (6).

This review covers literature on wetlands of many types defined by many criteria. Although it would be preferable to select studies that use the same definition of wetland for comparison of status and trends, inventories are not yet standardized. We do, however, focus most of our specific examples on wetlands dominated by herbaceous vegetation, with which we have personal experience.

STATUS AND TRENDS OF WETLAND AREA

Five key points about the status of wetlands are consistent with our experience and the literature: Wetland area and conditions continually change; pest plants readily invade many wetlands; half of global wetland area has been lost; wetlands cover less than 9% of global land area; and much of the remaining wetland area is degraded. These points, elaborated below, lead to the subsequent discussion of ecosystem services that are lost as wetland area and quality decline.

Wetland Area and Conditions Continually Change

Because hydrologic conditions define wetlands, any alteration of water volume (increases, decreases, or timing of high and low waters) threatens the area and integrity of wetlands. And because the quality of the water further defines the type of wetland, increases in nutrient loadings (eutrophication) often threaten wetland integrity. The examples below illustrate the complexity of causes of wetland loss and degradation. For further information about causes and impacts of one class of wetlands (temperate freshwater) continent by continent, see Brinson & Malvarez (7).

Like many major rivers, the Mississippi is extensively leveed to protect cities and other developments from flooding. Former floodplains are no longer considered wetland when they fail to flood. Loss of flooding leads to other alterations. Downstream, the coastal wetlands are deprived of sediment supplies. With insufficient sedimentation, coastal wetlands can be overwhelmed by rising sea level. Such is the case for large areas of Louisiana coastal marsh. In addition, canals have been dredged, and spoils have been piled alongside, repeating the problems of levees. The spoil banks isolate wetlands from their sediment-rich water sources and negatively affect marsh plant growth. The loss of vegetation further impairs the capacity of coastal wetlands to combat rising sea level (8–10). More subtly, as the coastline subsides, saline water creeps inland, stressing freshwater wetlands and shifting composition toward brackish species. Shifts in the relative area of tidal water and marsh vegetation can change the amount of marsh-edge habitat that is available for shellfish and finfish (11). With less marsh vegetation and less marsh:plant edge, fisheries are threatened. Considerable efforts are underway to track changes in both the area and condition of Gulf of Mexico wetlands (12).

Global warming is of specific concern to coastal wetlands because sea levels are rising (eliminating wetlands along the ocean edge) and because human populations are expanding (filling wetlands on the upland side). Globally, 21% of the human population lives within 30 km of the coast, and coastal populations are increasing at twice the average rate (13). Development is already eliminating coastal wetlands at a rate of 1% per year. Nicholls et al. (13) predict that a global sea-level rise of 20 cm by the 2080s would result in substantial damage, while a 1-m rise would eliminate 46% of the world's coastal wetlands. In addition, coastal wetlands would experience increased flooding. Their model indicates geographically different impacts, with wetland loss most extensive along the Mediterranean, Baltic, and Atlantic coasts, plus the Caribbean islands (Figure 1) and coastal flooding greatest for wetlands in the southern Mediterranean, Africa, and South and Southeast Asia. Their prediction that small islands of the Caribbean, Indian Ocean, and the Pacific Ocean would receive the largest impacts of flooding was illustrated tragically by the 2004 tsunami that devastated small islands and coastal areas in Indonesia and Sri Lanka (Figure 2).

Drainage is the main cause of wetland loss in agricultural regions. The example of Hula Valley, Israel, shows how drainage leads to a chain reaction of impacts. There, some 45–85 km^2 of shallow lake and papyrus swamps were drained, and 119 species of plants and animals were lost (14). As the soils dried, peat decomposed, and some became like powder, forming dust storms with local winds. Decomposition and wind erosion caused the ground surface to subside about 10 cm per year. Chemical changes were also documented. Sulfur and nitrates were released during decomposition; these were leached into the Jordan River and transported to Lake Kinneret. Gypsum (calcium sulfate) formed in the Jordan River, and sulfate was later released to Lake Kinneret, where drinking water supplies were contaminated (14).

Eutrophication is a common problem for wetlands downstream from agricultural and urban lands, in part because nutrients allow aggressive plants to gain a competitive advantage and displace native species. For example, in New York State, inflows of nutrient-rich surface and groundwater led a few species to form monotypic stands in what was otherwise a species-rich fen (15). Although the species that form monotypes can be natives, more often they are nonnatives, hybrids, or introduced strains of native plants (16). In the Netherlands, wetland researchers have identified an internal eutrophication process that occurs when water levels are lowered, and aerobic conditions lead to the release of nutrients that would otherwise be unavailable to plants (17). Additional impacts of eutrophication occur when nutrients reach the water column. In the Chesapeake Bay, nitrogen and phosphorus loadings (increases of up to 7- and 18-fold, respectively) have caused algal blooms that shade out sea grasses, reduce oxygen in the water column (hypoxia), and harm fish and shellfish (18). Detailed modeling of sources and transport of nutrients has led to specific targets for reducing inputs, but the ability to reduce nonpoint sources remains challenging for a large watershed with agricultural and urban land uses (18).

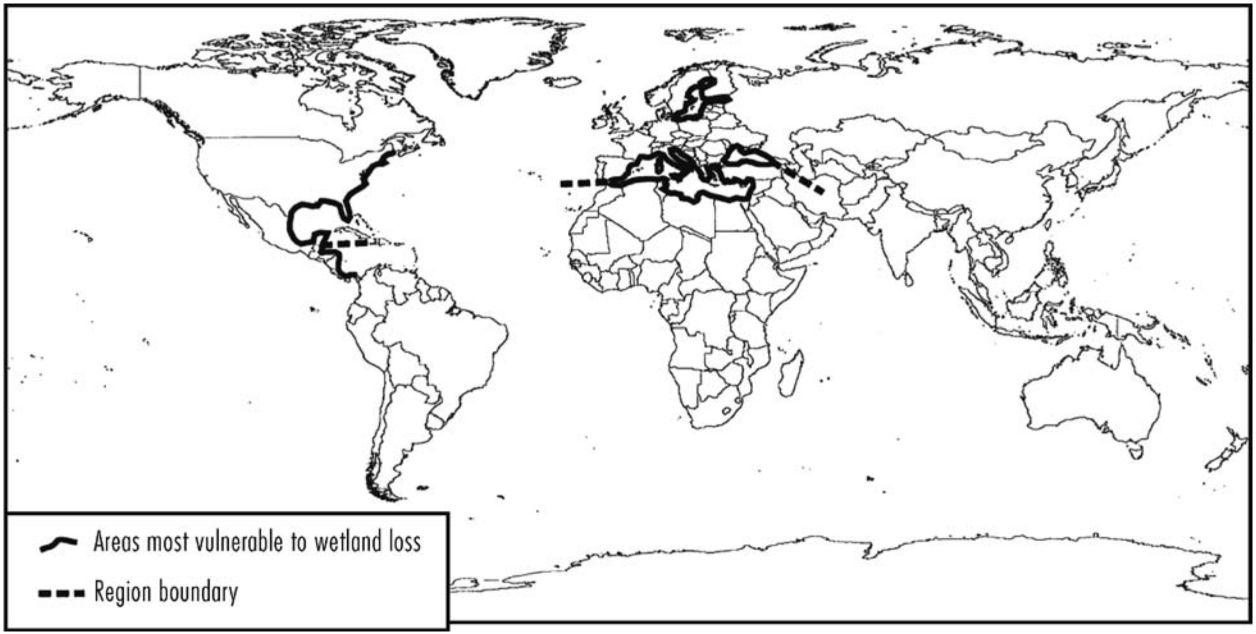

Figure 1 Global regions predicted to lose the largest area of wetland, given 1-m rise in sea level (from Reference 13, with permission from Elsevier).

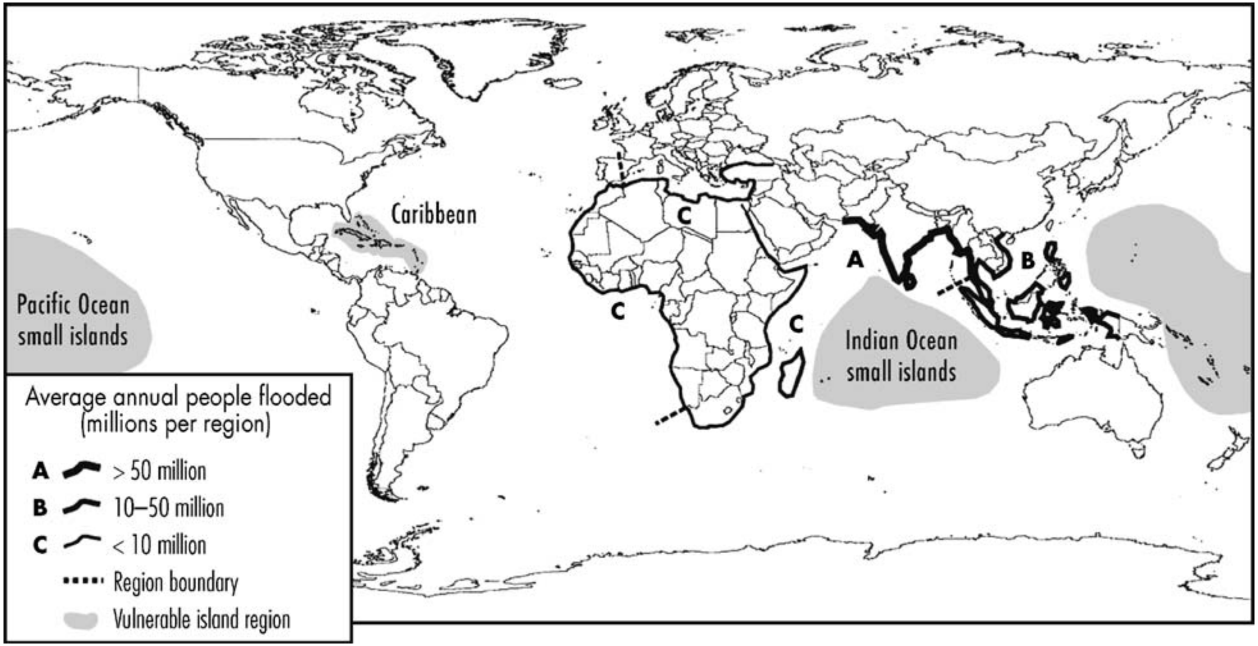

Figure 2 Global regions at greatest risk to flood impacts associated with global warming (from Reference 13, with permission from Elsevier).

Pest Plants Readily Invade Many Wetlands

Wetlands are landscape sinks where nutrients are augmented by runoff or enriched groundwater, allowing invasive species to establish, spread, and displace native species (16). Native sedge meadows, for example, support 60 or more species but 15 or fewer when invaded by *Phalaris arundinacea* (19). In a recent survey of ~80 Great Lakes coastal wetlands (C.B. Frieswyk, C. Johnston, and J.B. Zedler, article in review) found invasive cattails (the exotic *Typha angustifolia* and the hybrid *Typha x glauca*) to be the most common dominant, and native plant species richness was decidedly lower as a result. Here, "dominant" is the species judged to have the greatest influence on the community based on cover and associated species (C.B. Frieswyk, C. Johnston, and J.B. Zedler, article in review). In contrast, native plant dominants had many co-occurring species.

The mechanism whereby invasive plants suppress other species include dense rhizomes and roots that leave little space for neighbors (as in *T. x glauca)*, strong competition for nutrients (20), and tall dense canopies that usurp light (as in *P. arundinacea*) (20a). Canopies that usurp light for longer periods of time certainly have an advantage over native species with more ephemeral canopies. For example, *P. arundinacea* initiates growth well in advance of native vegetation in Wisconsin and continues growth well into November, after natives have gone dormant. Allelopathins might be involved in suppressing native species, but evidence is limited (21).

Attitudes about exotic species differ greatly among cultures, however. A recent article from China (22) extols the virtues of *Spartina alterniflora*, which was deliberately transported from the U.S. Atlantic Coast to the eastern China coast (~30° N). At present, 410 of 954 km of coastline in Jiangsu Province are protected by *S. alterniflora,* and 137 km^2 of former mudflats have developed into salt marsh after just 20 years. Continuing expansion of this plant suggests a bright future for the Chinese. Meanwhile, the same species transported to the Pacific Coast of Washington, Oregon, and northern California is considered ecologically damaging to shorebirds, oyster fisheries, and native ecosystems.

Half of Global Wetland Area Has Been Lost

The world's wetlands and rivers have felt the brunt of human impacts; in Asia alone, about 5000 km^2 of wetland are lost annually to agriculture, dam construction, and other uses (23). In Punjab, Ladhar (24) reported that the main causes of wetland loss have been drainage, reduced inflows, siltation, and encroachment, although Dudgeon (25) found the effects of habitat loss to be very poorly documented for all of Asia.

Estimates of historical wetland area are crude, at best, because few countries have accurate maps for a century or two ago. One estimate is that about 50% of the global wetland area has been lost as a result of human activities (26). Much of this loss occurred in the northern countries during the first half of the twentieth century, but increasing conversions of wetlands to alternative land uses have accelerated wetland loss in tropical and subtropical areas since the 1950s (27). Drainage for agriculture has been the primary cause of wetland loss to date, and as of 1985, it was estimated that 26% of the global wetland area had been drained for intensive agriculture. Of the available wetland area, 56% to 65% was drained in Europe and North America, 27% in Asia, 6% in South America, and 2% in Africa (27). Water diversions in support of irrigated agriculture are also responsible for large areas of wetland loss, as has occurred around the Aral Sea in Uzbekistan and Kazakhstan.

Wetland loss among the 48 conterminous states of the United States was estimated at 53% for the 1780s to 1980s (28). A recent update (29) concluded that the conterminous states had 42,700,000 ha of wetland in 1997 [coefficient of variation (C.V.), 2.8%]. Between 1986 and 1997, 260,700 ha (C.V. 36%) were lost. Of these, freshwater wetlands absorbed 98% of the losses. Causes were attributed to urbanization (30%), agriculture (26%), silviculture (23%), and rural development (21%). Coastal wetland losses are lower than inland losses, but states along the northern Gulf of Mexico continue to lose 0.86% of their wetland area per year (9).

The annual rate of wetland loss in the United States (for 1986 to 1997) is about 80% lower than for the preceding 200 years. Since the 1950s, freshwater emergent wetlands have suffered the greatest percentage loss (24%), and freshwater forested wetlands have experienced the greatest area loss (29). Given data on more recent declines in area (Table 1) and changes in type, it is clear that the nation is not meeting its policy goal of no net loss. The goal of no net loss in acreage and function was developed by a National Wetlands Policy Forum convened by the Conservation Foundation (30) and subsequently established as national policy by Presidents G.H.W. Bush, W. Clinton, and G.W. Bush.

TABLE 1 Percent change in wetland area for selected wetland and deepwater categories, 1986 to 1997 (from Reference 29)

Marine intertidal	−1.7
Estuarine intertidal nonvegetated	−0.1
Estuarine intertidal vegetated	−0.2
Freshwater nonvegetated	12.6
Freshwater vegetated	−1.4
Freshwater emergent	−4.6
Freshwater forested	−2.3
Freshwater shrub	6.6
All freshwater wetlands	−0.6
Lacustrine habitats	0.8
Riverine habitats	−0.6
Estuarine subtidal habitats	0.1

A few types of wetlands have increased in area. In the United States, landowners like to create freshwater ponds in order to attract wildlife; nationwide, ponds have increased in area by ~13% in the past decade (29). Freshwater shrub area has also expanded (29), perhaps owing to fewer fires or drainage, and floodplains have formed in new places because of dam building by beavers (7). Reservoirs and rice paddies have been created by humans, and some wetlands have formed accidentally. The Salton Sea became a 10,000-ha shallow-water body when the Colorado River flooded in 1905, aided by an irrigation canal that directed flows into the landscape sink (31). Overall, however, the conversion of drylands to wetlands is far outweighed by the conversion of wetlands to drylands (or to deep water, as behind dams).

Although wetland loss statistics are not precise, it is clear that a substantial portion of historical wetland area has been lost. The effect on landscapes is virtually unknown. It seems likely that a watershed with two 10-ha wetlands would function differently if it lost two areas ~5 ha versus one area ~10 ha. Wetland area, landscape position, and type are keys to wetland functioning (32, 33).

Wetlands Cover Less than 9% of Global Land Area

Topography and hydrologic conditions dictate the location and extent of wetlands. Most wetlands occur in low-topographic conditions or "landscape sinks," where ground and/or surface water collects. Others occur on hills or slopes where groundwater emerges as springs or seeps, or they depend solely on rainfall as a water source.

Globally and regionally, wetlands cover a tiny fraction of the earth's surface. The area is ~5.3 million km^2 according to Matthews & Fung (34), who obtained independent digital data on vegetation, soil properties, and inundation. The Ramsar Convention estimate is somewhat higher at 7.48–7.78 million km^2, not including salt marshes, coastal flats, sea-grass meadows, and other habitats that they do not consider wetlands. Finlayson et al. (35) acknowledge that estimates are not reliable and that the "tentative minimum" could be as high as 12.8 million km^2 (Table 2). Finlayson et al. (35) based their estimates of global wetland area on results from three international projects; two of these were international workshops organized in 1998 by Wetlands International and the third was the Ramsar "Global Review of Wetland Resources and Priorities for Wetland Inventory" (GRoWI). GRoWI analyzed 188 sources of national wetland inventory data and 45 international, continental, and global inventories, which included books, published papers, unpublished reports, conference proceedings, doctoral theses, papers, electronic databases, and information available on the World Wide Web. Of the 188 sources of national-level inventories, Finlayson et al. report that only 18% could be considered comprehensive, 74% were partial inventories that considered either wetlands of international importance only or specific types of wetlands only, and 7% of 206 countries had what Finlayson et al. consider adequate wetland

TABLE 2 Minimum estimates of global wetland area by region, as summarized in Reference 35

Region	Area (million square kilometers)
Africa	1.21–1.24
Asia	2.04
Eastern Europe	2.29
Western Europe	0.29
Neotropics	4.15
North America	2.42
Oceania	0.36
Total	12.76–12.79

inventories. Using the 12.8 million km^2 as a base, less than 10% of this area has been designated as wetlands of international significance (2).

Current data indicate that wetlands comprise <3% of the globe's 516.25 milllion km^2 surface area and less than 8.6% of the 148.9 million km^2 of land, using the 12.8 million km^2 estimate of Finlayson et al. (35). These percentages may well be underestimates because small wetlands are difficult to quantify; however, it is clear that wetlands occupy a small area of the Earth. Still, there are places where large wetlands dominate the landscape. The ten largest wetlands make up about 2.9 million km^2 (Table 3).

In the United States, 11.9% of the area of the 50 states is wetland, mostly contributed by Alaska (∼70,000,000 ha). For the 48 contiguous states, the figure is 5% (28). Florida has the largest area of wetlands and the largest proportion of its area in wetland (29.5%) (28); Nevada has the least (0.3%). Of the 42,700,000 ha of wetland in the conterminous United States, 95% are freshwater wetlands, and 5% are saline (estuarine or marine). For these 48 states, Niering (1) recognizes nine types of wetlands on the basis of their hydrologic conditions and vegetation: bogs, marshes, the Everglades, northern swamps and floodplain wetlands, shrub swamps, cypress swamps, southern bottomland hardwood swamps, lakes and ponds, and rivers and streams. Many more wetland types are recognized regionally, e.g., fens and sedge meadows are distinguished from bogs and marshes in the upper Midwest (37). Most ecoregions have multiple types of wetlands, and most wetland types occur in multiple ecoregions. An exception is the Everglades, which once covered one million ha. This huge system is unique in its large size, extremely low-nutrient status, and diverse animal life.

New remote-sensing technology promises to improve mapping, particularly for developing countries, where inventories are poorly developed and wetlands have suffered the greatest losses in area since the 1950s (26). Since the 1990s, satellite data have been increasingly used to map and document changes in wetland

TABLE 3 The largest global wetlands (in square kilometers), estimated as totaling ~2,900,000 square kilometers[a]

West Siberian lowlands, Russia	780,000–1,000,000
Amazon River, S. America	>890,000
Hudson Bay lowlands, Canada	200,000–320,000
Pantanal, S. America	120,000–200,000
Upper Nile River, Africa	50,000 → 90,000
Chari-Logone River, Africa	90,000
Mississippi River floodplain, N. America	86,000
Papua New Guinea, Eurasia	69,000
Congo River, Zaire, Africa	40,000–80,000
Upper Mackenzie River, N. America	60,000
Chilean fjordlands, S. America	55,000
Prairie potholes, N. America	40,000
Orinoco River delta, S. America	30,000

[a]From Reference 36.

area. Radar imaging is also useful because it can differentiate open water and flooded vegetation. One of the goals of the European Space Agency is to use Earth observation satellite data to aid in the implementation of global environmental treaties, including the Ramsar Convention (38). In the United States, the National Wetlands Inventory of the Fish and Wildlife Service maps wetlands and reports changes at 10-year intervals (39).

Much of the Remaining Wetland Area Is Degraded

If a wetland has survived filling, draining, or diversion, its integrity has not necessarily been preserved, nor is it safe from future degradation. The main causes of degradation are hydrological alterations, salinization, eutrophication, sedimentation, filling, and exotic species invasions. Studies of global pollution suggest that few areas on Earth are free of contaminants. Because wetlands primarily occur in landscape sinks, pollutants flow into and collect in wetlands. It seems likely that all wetlands are degraded; the variables are the magnitude and type of degradation.

Brinson & Malvarez (7) group alterations into four categories: (*a*) geomorphic and hydrologic (water diversions and dams, disconnection of floodplains from flood flows, filling, diking, and draining); (*b*) nutrients and contaminants (eutrophication, loading with toxic materials); (*c*) harvests, extinctions, and invasions (grazing, harvests of plants and animals, exotic species), and (*d*) climate change (global warming, increased storm intensity and frequency).

The detailed effects of degradation on biota are poorly known, but it is clear that biodiversity declines (7, 24, 40). The rate of decline likely increases when alterations are combined. In a recent experimental test, Kercher & Zedler (41) showed strong synergisms between increased flooding and eutrophication on experimental wetlands (grown in 1.1-m^2 $\times$ 0.9-m deep tubs known as mesocosms), such that the growth of an invasive grass doubled when both disturbances were present—as is common with storm water inflows. Increased dominance by the invasive correlated with decreased species richness (i.e., loss of natives). Synergistic interactions of this type need to be understood in field settings, however, not just mesocosms.

The degradation of wetland functions is even less well known because functioning is difficult to quantify. Also, functions differ with type, size, and position in the watershed, as well as the source and quality of water that flows into them.

LOSS OF ECOSYSTEM SERVICES

As wetland area is lost, key functions (ecosystem services) are also lost. Four of the functions performed by wetlands (42) stand out as having global significance and value as an "ecosystem service": biodiversity support, water quality improvement, flood abatement, and carbon management. Each of these functions results from many physical-biological interactions.

Biodiversity Support

Most efforts to protect wetlands are based on concern for biodiversity, especially waterfowl, shellfish, fish, and sometimes rare plants. About half of the United States' potentially extirpated species of animals and plants are dependent on wetlands (23). Wetlands support high productivity of plants but not always high plant diversity, e.g., the U.S. Atlantic coastal wetlands contain mostly monotypic *S. alterniflora* and the Everglades has widespread dominance of saw grass (*Cladium jamaicense*). Animals are more diverse. The presence of water, high plant productivity, and other habitat qualities attracts high numbers of animals and animal species, many of which depend entirely on wetlands. The Pantanal, which spans parts of Brazil, Bolivia, and Paraguay, supports 260 species of fish, 650 species of birds, and a high concentration of large animals (43). Wetland area determines biodiversity-support potential, but habitat heterogeneity is also a factor. The tidal flats, sandbanks, salt marshes, and islands of Europe's largest intertidal wetland (the Wadden Sea, 8000 km^2) supports diverse waterfowl, even though one third of the intertidal area has been lost since the 1930s (44). Aquatic animal diversity in streams and in rivers is partly a function of flow regimes, and conservationists are working to define "ecosystem flow requirements" (45).

In the United States, extensive research has quantified the coupling of primary and secondary productivity. Breeding waterfowl are censused annually and related to wetland condition (46). Nongame species (freshwater mollusks and amphibians) have become recognized as indicators of wetland loss and degradation because of their high sensitivity to changes in water quantity and quality. Threats to 135 imperiled freshwater species (fishes, crayfishes, dragonflies, damselflies, mussels, and amphibians) have been shown to differ for the eastern and western United States, with low water quality and impoundments at fault in the east and exotic species, lost habitat, and altered water flows in the west (47). Because amphibians move among small wetlands, forming metapopulations, specific criteria for buffers and distances between ponds have been developed for their conservation (48).

Vascular plant diversity is especially high in wetlands that do not receive much surface water runoff. Fens are fed by low-nutrient groundwater and support up to a hundred or more species (49). Many species can coexist where nutrients are in short supply, total productivity is low, canopies are short, light penetrates through the canopy, and no species has a strong competitive advantage (49, 50). Such wetlands are confined to landscape positions where the purest groundwater moves to the surface.

Water Quality Improvement

Runoff water from agricultural and urban areas typically contains large amounts of nitrate-nitrogen ($NO_3{}^-N$) and phosphorus, nutrients that stimulate algal growth in water bodies. With eutrophication, the decay of algae lowers oxygen concentrations, sometimes causing fish kills and disrupting the aquatic food chain. Such conditions are unappealing and occasionally toxic to humans. In the Gulf of Mexico, hypoxia occurs every summer, forming a "Dead Zone." Measured at 15,000 km^2 in the summer of 2004, the Dead Zone is linked to fertilizer-rich runoff from the Mississippi River basin, which covers 41% of the continental United States and contains 47% of the nation's rural population as well as 52% of U.S. farms (51).

In tandem with better nutrient management on farms and in cities, wetlands can serve a major role in ameliorating the global problem of nutrient overloading. Hey et al. (52) have even proposed "nitrogen farming," i.e., the restoration of wetlands for the specific purpose of removing nitrates from agricultural and urban runoff, on a massive scale in wetlands of the Mississippi River basin to abate hypoxia in the Gulf of Mexico. Wetlands are well known for their ability to remove sediments, nutrients, and other contaminants from water, functions that have led to the widespread harnessing of wetlands for wastewater treatment (53). In fact, a wealth of published studies consider wastewater treatment in constructed wetlands, but comparatively few studies concern water quality improvement in natural wetlands.

Wetlands with shallow water are effective in removing nitrates from through-flowing water, because denitrification is a coupled process wherein nitrates (present in aerated water) are reduced by anaerobic bacteria (found in anoxic soil) to nitrogen gas. Phosphorus (P) tends to attach to soil particles, so the best strategy for removing phosphorus is to trap sediment-rich water and hold it long enough for soil particles to settle out. A high concentration of aluminum or iron increases the phosphorus-binding capacity and hence phosphorus removal (54).

It is often assumed that nutrient removal is highest where species richness is low; that is, wetlands cannot be both species rich and excel at nutrient removal because high nutrient loadings allow a few aggressive plants to displace many of the natives. The assumption of a trade-off is largely untested. However, Herr-Turoff & Zedler (20a) demonstrated that *P. arundinacea* did not remove more nitrogen than a diverse wet prairie assemblage in mesocosms.

There is typically a threshold level of nutrient loading above which aggressive species can come to dominate a wetland. For example, The Everglades Forever Act of 1994 identifies P concentrations of ~10–50 ppb (parts per billion) in surface water as a threat to the Everglades. Continuous loading at low levels threatens to alter productivity and shift the native saw grass–dominated communities to dominance by the invasive *Typha domingensis* (55). Keenan & Lowe (56) propose a very general model for acceptable P loads to maintain diversity in wetlands, but acceptable nutrient loads will no doubt vary depending upon the wetland type.

Preserving and restoring wetlands to improve the quality of water that flows through a watershed require a landscape approach, e.g., finding sites that can intercept a significant fraction of a watershed's nutrient-rich runoff (57, reviewed in 33). Determining the wetland area needed to provide this function requires considerable investigation (45). On the scale of individual sites, research to date suggests that even narrow bands of vegetation (as little as 4 m) immediately adjacent to streams can remove up to 85% to 90% of NO_3^-N, P, and sediments carried in runoff (reviewed in 58). At the watershed level, estimates are that 1% to 5% of the total watershed would be needed to cleanse waters of the Des Plaines River in Illinois and up to 15% for the Great Lakes basin in Michigan, USA (reviewed in 59).

Flood Abatement

Economic costs associated with flood damage have risen considerably over the past 100 years, owing in large part to increased agricultural and urban encroachment into floodplains. The flooding of the Mississippi River in 1993 cost $12–$16 billion, and the 1998 floods in China displaced 20 million people and cost an estimated US$32 billion (2). Wetlands are becoming appreciated for their role in storing and slowing the flow of floodwaters. For example, along the Charles River in Massachusetts, USA, the conservation of 3800 ha of wetlands along the main stream reduces flood damage by an estimated $17 million each year (2). There is also an increased interest in restoring wetlands in flood-prone areas.

The wetlands that best abate flooding are those occurring upstream of places where flooding is a problem, namely urban areas and fields that have been planted with crops. Opinions differ on the advantages and disadvantages of preserving and restoring wetlands in the upper reaches of a watershed (reviewed in 59), but floodplains are known to be critical in mitigating flood damage, as they store large quantities of water, effectively reducing the height of flood peaks and the risk of flooding downstream. Hey et al. (52) found six sites in the upper Midwest that could reduce flood peaks of the Mississippi River by storing large volumes of water at strategic times.

The Mississippi River flood of 1993 would probably not have been so catastrophic and costly if more of the historical wetlands in the river basin had retained their flood-abatement service. A key question is how much wetland area is necessary for flood control? According to Hey & Philippi (60) the restoration of 5.3 million ha of wetlands within the Mississippi River valley would have abated the flooding and prevented most of the economic damage. That figure translates to restoring about 3% of total land area in the upper Mississippi and Missouri River basins, along with maintaining the current 4% of land area that is already wetlands. Overall, Mitsch & Gosselink (59) estimate that 3% to 7% of the area of a watershed in temperate zones should be maintained as wetlands to provide both adequate flood control and water quality improvement functions.

Carbon Management

Understanding of the role of wetlands as climate regulators is growing, and their role in sequestering carbon (C) in long-lived pools is becoming appreciated. To help implement the Kyoto Protocol, negotiated by 84 nations in 1997, researchers have increased their attention to quantifying global C stores, C sequestration rates in various ecosystems, and greenhouse gas sources and sinks. Upland forest and cropland ecosystems have been emphasized in much of the C management research to date [e.g., the U.S. Department of Energy's Carbon Sequestration in Terrestrial Ecosystems (61)]. Wetlands, however, are known to store vast quantities of C, especially in their soils (62) (Figure 3). Globally, wetlands are the largest component (up to 44% to 71%) of the terrestrial biological C pool, storing as much as 535 Gt (gigaton) C (reviewed in 62).

Although wetlands store vast quantities of C in vegetation and especially in their soils, they also contribute more than 10% of the annual global emissions of the greenhouse gas methane (CH_4) and can also be a significant source of CO_2 under some conditions (62). To what degree wetlands function as net sinks or sources of greenhouse gases appears to depend on interactions involving the physical conditions in the soil, microbial processes, and vegetation characteristics (63). In a review of several experimental studies focused on greenhouse gas exchange between the soil and atmosphere, Smith et al. (63) conclude that CO_2 release from the soil (primarily through heterotrophic respiration, especially decomposition of organic matter) increases exponentially with increasing temperature and decreases both with soil saturation and drought. Thus when natural wetlands are drained for cultivation or peat mining, large quantities of stored organic C decompose and are lost to the atmosphere as CO_2. Increasing temperatures expected to result from global warming are predicted to exacerbate the release of CO_2 from wetland soils, particularly in peatlands and where a temperature increase coincides with a drier climate.

CH_4, a potent greenhouse gas with a warming potential 23 times greater than CO_2, is formed in soils characterized by low-redox potential, an anaerobic

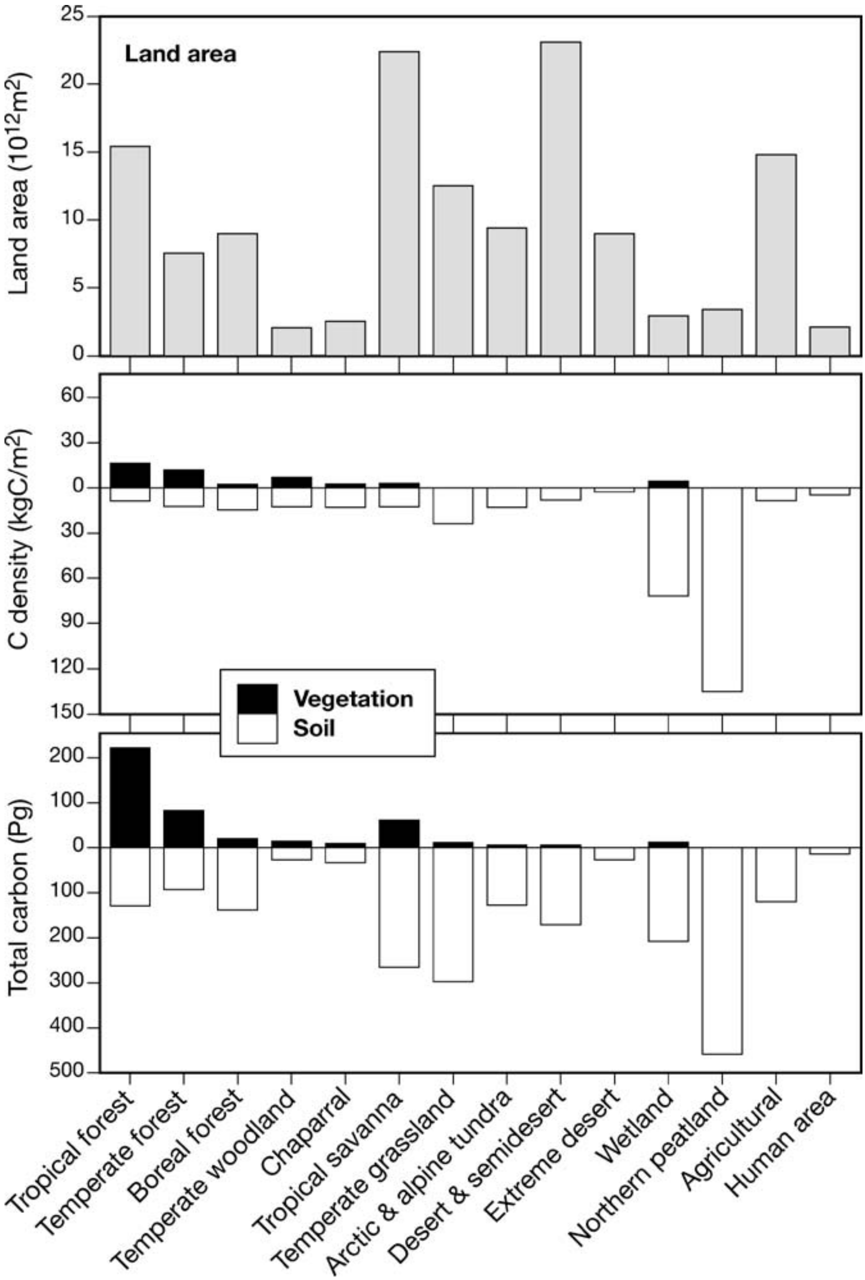

Figure 3 Wetland and peatland area, C density, and total C storage relative to other ecosystems and land uses (redrawn image from Reference 61, courtesy of Oak Ridge National Laboratory, managed by UT-Battell, LLC, for the U.S. Department of Energy, and data from Reference 71).

condition, which results from prolonged waterlogging and occurs in natural and managed wetlands, such as lake sediments and rice fields (63). CH_4 is released to the atmosphere from wetland soils by diffusion through water, ebullition (bubble formation), and diffusion through aerenchyma tissue in plants (64). Although the major factor controlling the production and release of CH_4 is soil redox, emissions are also believed to vary depending upon the type of vegetation present in a wetland, the texture of the soil, the quantity of plant litter present, and possibly soil acidity (63). In a study of Canadian peatlands, Roulet (65) indicates that, once the "global warming potential" of CH_4 is factored in, many peatlands are neither sinks nor sources of greenhouse gases, although Mitra et al. (62) claim that "pristine wetlands" should be considered a relatively small net source of greenhouse gases. Even so, Mitra et al. warn that the destruction of a pristine wetland would emit more C from decomposition of the soil and vegetation C pools than 175–500 years of CH_4 emissions from the same wetland. If future C sequestration potential of the wetland is factored into the calculation, destroying the wetland would cause more C emissions than several thousand years of net greenhouse gas emissions in the pristine wetland. Mitra et al. (62) thus conclude that the role of wetlands in global climate change will largely be determined by future development of wetland areas, rather than the arguably still ambiguous balance between C sequestration and CH_4 emission rates.

Existing wetlands must be preserved to the greatest extent possible to prevent further releases of terrestrial C to the atmosphere, but it is less clear what role created and restored wetlands will play in managing C, considering they are sources of CH_4 and considering C sequestration rates appear to vary across wetland types. For example, extant peatlands store vast amounts of C (Figure 3), but restored peatlands do not appear to accumulate C rapidly. Glatzel et al. (66) found that the high decomposability of new peat in a restored peatland resulted in very slow C sequestration and net emissions of both CO_2 and CH_4 in the short term. In contrast, coastal wetlands may offer excellent potential for C sequestration.

Empirical studies in California and Florida suggest that coastal wetlands offer excellent potential for C sequestration, as they appear to accumulate C over long time periods at higher rates than other ecosystems, probably because they continuously accrete and bury nutrient-rich sediments (67, 68). Chmura et al. (69) also report that, in contrast to peatlands, salt marshes and mangroves release negligible amounts of greenhouse gases and store more C per unit area (globally, $\sim 44.6 \times 10^9$ kg) C year^{-1}, albeit an underestimate due to lack of area data from China and South America). Because coastal wetlands are among the fastest disappearing ecosystems worldwide, only carefully controlled coastal development will prevent further losses.

Forested wetlands also sequester C effectively, and restoration of large areas of floodplain that have been converted to agriculture may be especially beneficial. In North America and Europe, 90% of floodplain areas are currently under cultivation (70); hence, the restoration of floodplain hydrology and the restoration of forested wetlands in floodplains would very likely contribute to C sequestration and indeed to biodiversity support, water quality improvement, and flood abatement functions.

The Loss of Wetland Functions Has a High Annual Cost

The ecosystem services provided by wetlands include the purification of air and water; regulation of rainwater runoff and drought; waste assimilation and detoxification; soil formation and maintenance; control of pests and disease; plant pollination; seed dispersal and nutrient cycling; maintaining biodiversity for agriculture, pharmaceutical research and development, and other industrial processes; protection from harmful UV radiation; climate stabilization (for example, through C sequestration); and moderating extremes of temperature, wind, and waves (72). These functions can be grouped as provisioning (e.g., food and water), regulating (flood and disease control), cultural (e.g., spiritual, recreational), and supporting services that maintain the conditions for life on Earth (e.g., nutrient cycling) (73).

The functions of wetlands are disproportionate to their area. Although wetlands cover <3% of the globe, they contribute up to 40% of global annual renewable ecosystem services (Table 4). Of these, providing water of high quality ranks highest.

TABLE 4 The 1994 U.S. dollar value of annually renewable ecosystem services provided by wetlands[a,b]

Wetland service	Dollars/ha/year	Billion dollars/year
Hydrologic services		
Water regulation	15–30	
Water supply	3,800–7,600	
Gas regulation	38–265	
Water quality services		
Nutrient cycling	3,677–21,100	
Waste treatment	58–6,696	
Biodiversity services		
Biological control	5–78	
Habitat/refugia	8–439	
Food production	47–521	
Raw materials	2–162	
Recreation	2–3,008	
Cultural	1–1,761	
Disturbance regulation	567–7,240	
Global totals		
Coastal wetlands		8,286
Inland wetlands		4,879
Total for global wetlands		13,165
Total services for all ecosystems for entire globe		33,268
Percentage provided by wetlands 39.6%		

[a]Includes tidal marshes, mangroves, swamps, floodplains, estuaries, sea-grass/algal beds, and coral reefs.

[b]Data from Reference 74 with ecosystems selected by Reference 33.

The above total for wetlands is estimated to be ~\$13 trillion per year (33). However, a meta-analysis of 89 wetland valuation studies (excluding climate regulation and tourism) by Schuyt & Brander (75) suggested that the global annual value of wetlands is \$70 billion, with an average annual value of \$3000/ha/year and a median annual value of \$150/ha/year. The 10 functions with the highest values (U.S. dollars per ha per year) include recreation (\$492), flood control and storm buffering (\$464), recreational fishing (\$374), water filtering (\$288), biodiversity support (\$214), habitat nursery (\$201), recreational hunting (\$123), water supply (\$45), materials (\$45), and fuel wood (\$14) (75). The United Nations' comprehensive Millennium Ecosystem Assessment will further map the health of wetlands and "assess consequences of ecosystem change for human well-being and options for responding to those changes" (73).

THE POTENTIAL TO RESTORE WETLANDS

In considering how much of the lost wetland area and lost ecosystem services might be recovered, we drew three conclusions: Restoration can reverse some degradation but many damages are not reversible; wetland restoration approaches and techniques are improving; and restoration policies can improve with time and experience. Still, every project has unique features, making it difficult to develop templates for restoration. Therefore, we argue that adaptive restoration offers great potential to learn how to restore specific sites.

Restoration Can Reverse Some Degradation but Many Damages Are not Reversible

Wetland loss and degradation have substantial and lasting effects, most notably the loss of ecosystem services. The process of restoration (assisting ecosystem recovery from degradation, damage, or destruction) (76) is gaining in popularity and improving in effectiveness. Restoration can solve many of the problems in Hula Valley (77). For example, peat dust storms could be abated by restoring wetness to Hula Valley wetlands, and emergent vegetation could be grown where peat surfaces have not subsided too much. In the northeastern United States, Able & Hagan (78) and Jivoff & Able (79) reported high use of diked wetlands by fish once tidal flushing was restored. Where aggressive plants crowd out competitors, as in the Netherlands, mowing can reduce growth and foster diverse vegetation (50). Questions that remain are which damages are not reversible, how much of the predamage structure and functioning can be restored, and what methods are most effective? Once species have been forced to extinction, the loss is permanent. Lesser, more localized degradations, however, can also resist restoration efforts. This is true of both abiotic and biotic changes.

ABIOTIC RESISTANCE The abiotic factors that cause ecosystem degradation are related to irreversible changes in landscapes and watersheds. Sometimes, the problem is the cessation of natural disturbances, such as hot wildfires and major flooding. More often, the problem is an introduced disturbance, such as increased surface-water runoff from city streets and fields or eutrophication from applications of fertilizer to fields and lawns. To reverse these changes, restoration has to begin at landscape scales—and this is rarely practical.

Many local damages to ecosystems are also irreversible, at least in the time frame of most restoration projects (often 3 to 5 years, sometimes 10 to 20 years, rarely 50 years). In a recent paper, Suding et al. (80) argue that internal feedbacks can begin to operate such that a site cannot return to native vegetation even if the external factors are reversed. For example, if a wetland becomes eutrophic and dominated by an invasive species that capitalizes on high-nutrient soils, the invader will likely exclude the native species and retain dominance as a monotype indefinitely. Removal of the external nutrient source will not necessarily reverse the invader's hold on the site.

Natural hydroperiods (timing, duration, and frequency of inundation) are variable at multiple temporal scales and hence difficult to restore. Wet soil is entirely different from dry soil, in large part because oxygen is rapidly depleted by microorganisms in the presence of water. Hydric soils develop under anoxic conditions, and various biogeochemical transformations follow, including nitrate reduction to nitrogen gas, sulfur reduction to hydrogen sulfide, C reduction to CH_4, and increased solubility (depending on soil pH and redox potential) (cf. 81). Although impacts of changing the temporal pattern of wetness and dryness are rarely known in detail, the complexity of the relationships suggests that natural hydroperiods are critical to wetland function; the question is how much they can be altered before services decline; and conversely, how much of the natural variation needs to be restored or can be restored to regain services? Temporary wetlands, intertidal marshes, vernal pools, and prairie potholes are difficult to restore because they depend on a variable hydroperiod with saturated conditions early in the growing season, followed by unsaturated conditions. A small error in elevation of the site or the water control structure can produce a wetland that is constantly inundated or one that is never or too-rarely inundated.

Groundwater-fed wetlands provide examples of the difficulties of restoring clean water in sufficient quantities. In Wisconsin, hydrologists determined that one site designed for restoration of sedge meadows (which are normally fed by groundwater) was strongly dependent on rainfall (82), which is not a good indication of long-term sustainability because slight deficits in water supply can lead to drought and plant mortality.

Flow rates are a major determinant of biota in streams, through their effect on substrate particle size, oxygenation, and related factors (25). When flows are altered, exotic and introduced species often benefit (83). Water supplies that are of low quality often constrain restoration efforts, with nutrient-rich water a near-universal problem and acidic water (caused by acid rain) a threat in some regions. Many studies demonstrate that diverse vegetation is not sustainable in eutrophic conditions (41, 49, 84–86). Sources of nutrients and acids are often well outside the restoration project area.

Soil conditions can also constrain wetland restoration efforts. Soils provide multiple services for the plants and animals being restored, i.e., soils conduct groundwater, transform nutrients, improve water quality, support seed germination and rooting, store seeds and rhizomes, and support mycorrhizae, symbiotic bacteria, and soil macrofauna (32). If the texture, nutrient status, seed banks, or microbiota are substantially altered, related functions are also altered. In some coastal wetland restoration projects (but less so in freshwater wetlands with lower sulfur content), the simple act of draining the soil allows chemical reactions that are damaging to microorganisms, plants, and soil animals. This is because drainage aerates the soil, changing conditions from reducing to oxidizing. Pyrite becomes oxidized, and the sulfur reacts with oxygen to form acid-sulfate soil. Soil pH can drop below 4.0. Decomposition increases, and the marsh surface subsides. While subsidence is hard to overcome, some of the chemical changes are readily reversed. Portnoy (87) tested soils within drained and diked wetlands of Delaware Bay to predict their behavior after restoring tidal flushing. As expected, pH levels returned to normal, and sulfur was precipitated by complexing with iron. At the same time, ammonium and P were mobilized (87). Soil texture can be limiting where soils have been removed or covered with material that is too fine or too coarse. Altered texture is not easily restorable. In one well-documented effort to restore habitat for an endangered salt marsh bird, a substrate that was too sandy (dredged material from San Diego Bay) proved to be too coarse to supply or retain nitrogen. The paucity of nitrogen proved to be the factor that limited growth of the target plant cover (cordgrass, *Spartina foliosa*), and the short stature of the vegetation not only failed to attract the endangered light-footed clapper rail (*Rallus longirostris levipes*) to nest, it also failed to attract a native beetle (*Coleomegilla fuscilabris*). Both the rail and the beetles require tall cordgrass, and without the predatory beetle, the scale insect (*Haliaspis spartina*) population grew exponentially and further diminished plant cover (88). No one imagined that starting with a soil that was predominantly sand instead of clay would have effects up the food chain. Additional abiotic constraints include inadequate soil development (89), hypersalinity, erosion, and sedimentation (90).

BIOTIC RESISTANCE Biota can and do limit restoration. Forested wetlands are slow to recover from deforestation because the key species take decades to mature (91). Peatlands are slow to recover from peat harvesting because the accumulation of organic matter depends on slow-growing mosses (92). Sedge meadows, dominated by tussock-forming species, might not regain their characteristic tussock topography for decades, possibly a century. Wetlands that are extremely rich in species are unlikely to recover their full diversity, even with planting, because restoration sites typically favor aggressive species, rather than the rarer plants that depend on host plants, facilitators, specific microsites, or specific pollinators (88, 88a).

Finally, and often most importantly, the presence of invasive species can make restoration of wetlands incomplete at best and impossible in the worst cases. Wetlands that occur in landscape sinks are subject to direct and indirect effects of disturbances occurring throughout their watersheds (16). Excess water, nutrients, sediments, and propagules all move downslope or downstream into wetlands, where a small disturbance can create a canopy gap that allows an invasive species's propagule to establish. Species capable of vegetative reproduction then take advantage of the nutrient-rich conditions, expanding to dominate the site and exclude native vegetation (19).

Wetland Restoration Approaches and Techniques Are Improving

Despite the difficulties posed by irreversible abiotic and/or biotic conditions, suitable targets for individual restoration sites can be achieved. The full potential of each site is rarely known, however. Below, we argue for experimental approaches to demonstrate restoration potential; here, we describe examples of past efforts.

Where hydrological conditions are altered or where developments could be flooded once natural water levels are restored, restorationists try to reproduce key features of what is a very complicated temporal pattern of wetness. For example, hydroperiods of wet meadows, emergent marshes, bogs, and fens differ only slightly, yet their vegetation is distinctive (37).

Removing dikes to restore tidal flushing is a common restoration approach in New England (93). Blocking drainage restores some of the qualities of prairie potholes (84). Adding water control structures to slow runoff is not ideal (32), but it may be necessary in drained agricultural lands (94) and other circumstances. Along Lake Erie, a dike was added and water levels controlled so the marsh seed bank could regenerate vegetation during low-water periods (95). Restoring wetlands that rely on groundwater is more difficult (96, 97).

Restoration of the long-duration flood pulse of the Kissimmee River flood plain is intended to undo the channelization of this formerly meandering river that feeds the Everglades. Prior to excavation of the 9-m-deep, 75-m-wide flood control channel, the floodplain was inundated 25% to 50% of the time (98). Dominant plants included willows (*Salix caroliniana*), buttonbush (*Cephalanthus occidentalis*), and emergent hydrophytes. In 2001, 24 km of river were reconnected in the first phase of this ambitious restoration program (99). However, seed banks were considered inadequate to restore the full diversity of plants (100).

In Louisiana, several techniques are used to slow wetland loss. Terracing is the construction of ridges from sediment (with plantings to stabilize the substrate); these are arranged to reduce fetch and hence erosion (101). Discarded Christmas trees are sometimes used to trap sediments and raise the elevation of the marsh plain; this is also employed in Great Lakes wetland restoration (95). More ambitious is the rediversion of sediment-rich flows from the Mississippi River to subsiding marshlands, a technique that requires multimillion-dollar water-control structures at key locations along the region's extensive levee system (cf. 102 for effects of the 1991 Caernarvon diversion on Breton Sound estuary).

An 8-ha lagoon in California (Famosa Slough) is separated from Mission Bay by a multilane freeway and a flood control channel. Prior to restoration, stormwater runoff facilitated invasions by *T. domingensis* and caused algal blooms (103). Citizens (J. Peugh & B. Peugh) led the rehabilitation effort, and the City of San Diego built impoundments to trap stormwater inflows and reduce nitrogen loading, and the city repaired tide gates to increase tidal flushing. Native salt marsh vegetation recovered, and the "muted" tidal regime sustained mudflat habitat, rewarding citizens with enhanced views of waterbirds.

TOPOGRAPHY Where topography is artificially flattened, natural slopes and heterogeneity can be restored by various means (89, 104, 104a). An elevation difference as small as 10 cm can eliminate some species and allow others to dominate (96). Rough surfaces can slow water flows by increasing friction and water in depressions. Shallow pockets of water can warm up rapidly and lose their dissolved oxygen, thereby promoting the growth of microorganisms involved in denitrification. Depressions also act to settle out sediments and adsorbed P. Both elevation and microtopographic variability are important. Although the full range of functions that rely on topographic heterogeneity is unknown, studies of mycorrhizae in New Jersey's monotypic white cedar (*Chamaecyparis thyoides*) swamps showed greater abundance on hummock tops than the wetter bases (105).

SOIL Where soils are altered, corrective measures need to be tailored to counter the damage. Soils with decreased organic matter or nutrients have been restored by adding soil amendments (106); soils with increased nutrients can be defertilized by removing soil or organic matter so that microorganisms can tie up the nitrogen (20). Restoration sites that have lost soil because of mining or gravel extraction have benefited from importation of fine-particle materials. Transplanted soils supported diverse vegetation in New York wetlands (107); however, benefits were short-lived for a Wisconsin sedge meadow that converted to cattails just five years after restoration (108, 109).

At Des Plaines Wetland Demonstration Site near Wadsworth, Illinois, the Chicago Wetlands Initiative, Inc., removed soil that had accreted at one site and moved it to another to convert a gravel pit into a wetland. Removal at the first site exposed historical wetland soil; addition at the gravel pit provided a substrate for native wetland plant introductions (D. Hey, personal communication).

The Wisconsin Waterfowl Association bulldozes nutrient-rich sod that is infested with the invasive *P. arundinacea*, rolls it up, and deposits it in drainage ditches, thereby removing sediment where it has accreted (exposing wetland soils) and disposing it where it can reduce drainage (restoring the potential for water to accumulate). If the resulting water levels are high enough, invasives do not reestablish (J. Nania, personal communication).

At Tijuana Estuary, California, the removal of 1–2 m of accreted sediment from an 8-ha restoration site exposed historical salt marsh soil that was compacted and lacking a seed bank. Test plots were (*a*) conditioned with rototilling and (*b*) amended by rototilling in kelp compost (organic hydrophilic material with 50% perlite), and unaltered plots were controls. Desired plant species (e.g., *S. foliosa*) were introduced as plugs at two densities and grew most vigorously in areas with compost and high-density plantings (E. O'Brien & J.B. Zedler, in review).

At Everglades National Park, the Hole-in-the-Donut Project is removing an invasive tree (Brazilian pepper, *Schinus terebinthifolius*) from many square kilometers of former agricultural land that was "rock plowed" to create soil from porous limestone. Because rock plowing made the substrate nutrient rich, restoration requires removal of the surface soil and exposure of underlying limestone, after which native plants reestablish and pepper trees are unable to reinvade (110). This effort, which is very heavy handed and costly, is being accomplished with mitigation funds. Trees are bulldozed, ground up, and mixed with the soil to form large mounds that are intended to support oak woodland among the grassy wetlands.

Drainage of saline wetlands sometimes leads to acid sulfate soils, as discussed above. Restoring tidal flushing can abate some damages (87), although organic matter and nitrogen stores are slow to recover (111).

VEGETATION Where the plant cover or diversity has been depleted, species might or might not recolonize on their own (112). When a dike that excluded seawater was accidentally breached, agricultural fields became mudflats that were rapidly colonized by halophytes and invertebrates (113). In contrast, rewetted prairie potholes that were drained and farmed for many decades recovered only a portion of their native species, attributed to poor dispersal (94, 114).

Target species can be encouraged to reoccupy a site or deliberately introduced. Microorganisms (e.g., mycorrhizae) are easily introduced with an inoculum of soil from a natural wetland, but this can be disruptive to the donor site. Mycorrhizae that are available from biological supply houses are not likely to be locally adapted genotypes. For wetlands, the roles of mycorrhizae are poorly known, so adding soil inocula is mainly a precautionary measure.

The need to plant wetland restoration sites has fostered debate among wetland restoration ecologists (115). Experimental evidence in salt marshes of southern California demonstrates the need to plant seven of the eight marsh-plain halophytes (116) but not the widespread dominant, *Salicornia virginica.* As predicted by the experiment, only *S. virginica* was able to colonize an 8-ha restoration site in Tijuana Estuary (90). In riparian wetlands, however, the vegetation is adapted to recolonize bare ground after flood scouring, and planting might not be necessary (91).

Species-rich plantings accelerate the development of a California salt marsh. Comparing plantings of zero-, one-, three-, and six-species assemblages, the plant canopy had more layers with six species, and productivity and N accumulation were also greater (117–119).

In stressful sites, tight clusters of plantings can be more effective than low-density plantings, e.g., in strip mine restoration (120) and salt marsh restoration

(E. O'Brien & J.B. Zedler, in review). Soil amendments can also reduce stress. For example, kelp compost is hydrophilic and aids plant growth in hypersaline tidal marsh soils (120).

In wetlands with plants that are ecosystem engineers (121), restoration should focus on that key species. For example, *Carex stricta* (tussock sedge) is the architect of tussock meadows, and the structures it builds support 10–11 plant species per 30-cm-tall tussock (122).

FAUNA Where animal populations are depleted, reintroductions and habitat reconstruction are considered. Structures might need to be added as nesting sites (e.g., tree snags for birds). The entire wetland landscape needs to be restored in order to attract some animal species. Amphibians are a good example because these animals move among ponds and cannot survive where pond-to-pond distances are too great (123, 124). Tidal wetland restoration is often aimed at attracting fish and shellfish (shrimp and crabs). Minello et al. (125) have demonstrated the importance of providing patchy vegetation, with a large proportion of edge between plants and water.

In southern California, tidal creek networks need to be incised into marsh plains that are restored by removing a meter or more of accreted sediments (117). Creeks are conduits for small fish to move into vegetated areas and feed on the marsh plain; given access to invertebrates on the marsh surface, killifish (*Fundulus parvipinnus*) find more food and grow much faster than if confined to deep channels (126, 127). Restored tidal creeks also benefit the endangered light-footed clapper rail (*Rallus longirostris levipes*) by providing feeding (crab) habitat and tall cordgrass (*S. foliosa*) for nesting. However, in San Diego Bay, restored cordgrass would not grow tall because there was little nitrogen in the sandy soil (88).

Prairie potholes that were recently restored were found to have fewer nesting birds than natural examples (128). However, bird use of some restored prairie wetlands (129) and in selected New York wetlands (130) did not differ from that in natural wetlands.

INVASIVE SPECIES Where unwanted plants and/or animals have invaded, undesirable species can be managed to reduce abundance. When invasive plants are a serious threat to restoration, cover crops are often used to usurp space and light, thereby reducing chances of early dominance by weeds. Invasive species that establish and persist are a great threat to wetland restoration projects because weeds thrive in disturbed sites.

Lesser snow geese are native to Hudson Bay, but they can be very damaging to vegetation. The salt marsh grass, *Puccinellia phyrganoides,* was more easily established where geese were fenced out of the research plots (131). Geese were detrimental in two ways, directly by feeding on plants and indirectly by trampling and compacting soil, which in turn increased soil salinity. Peat mulch was used to reduce compaction (131).

MICROORGANISMS Where microorganisms have been altered, ecosystem functions might be impaired. Wetzel (132) argues that because >90% of the metabolism in aquatic food webs is due to microorganisms, earlier paradigms with predation-based food webs need to be updated. As he states, "Massive amounts of organic matter that are produced within the drainage basin of the aquatic ecosystem. . .are never consumed by particulate-ingesting metazoans. . .up to 99% of the ecosystem organic carbon budget, particularly in rivers, can be detrital based and imported to lakes and rivers. . .."

Nitrogen fixation was lower in the surface soil of a restored salt marsh than its San Diego Bay reference site (133). In North Carolina, however, Currin et al. (134) found 5–10 times more nitrogen fixation by microbial mats in a restoration site with low plant cover and coarse sediments, and Piehler et al. (135) conclude that microbial nitrogen fixers are critical to salt marsh restoration because they supply a limiting nutrient to plants and provide food for marsh infauna.

Microorganisms can be reintroduced to restoration sites by adding small amounts of native soil to planting holes. In uplands, e.g., prairies, mycorrhizae are often added, but the need to do so in wetland restoration has not been demonstrated, despite the widespread abundance of these fungi in wetlands (136–139).

Restoration Policies Can Improve with Time and Experience

Following passage of the Clean Water Act (1977), the United States began to require the restoration of wetlands in exchange for permits to damage existing wetlands (32). As part of a national review of compensatory mitigation procedures, a National Resource Council (NRC) panel reviewed studies of on-site, in-kind projects intended to compensate for nearby damages. This policy allowed the following two major problems to develop:

- To fulfill the "in-kind" policy, undesirable wetlands were replaced by undesirable wetlands, such as those dominated by invasive *Typha* and stormwater runoff.
- To satisfy the "on-site" policy, wetlands were often created from uplands instead of restoring former wetlands.

Panel members found that restored wetlands were more likely to achieve ecological goals than were created wetlands (32).

The principal recommendation of NRC (32) was to develop strategies for restoring wetlands at watershed or landscape scales. Examples of how to proceed include restoring wetlands in optimal locations to remove nitrates from drained farmlands in Iowa (57), identifying priority landscape subunits within the prairie pothole region to attenuate flooding (140), prioritizing sites for sediment trapping in a southern Wisconsin landscape (141), and prioritizing wetland protection efforts for sustaining biodiversity (142). Although research on ecosystem services addresses individual functions, there are no examples of how to restore wetlands so that biodiversity support, water quality improvement, and flood abatement can all be accomplished within a single watershed (33), and there is no process to coordinate restoration planning for entire watersheds.

The U.S. Army Corps of Engineers (CoE) and the Environmental Protection Agency (EPA) have begun to meet annually to review, revise, and improve procedures (M. Sudol, CoE, & P. Hough, EPA, personal communication). On-site, in-kind compensation is still preferred, but the potential for mitigation banking and in-lieu fees to develop plans for strategic restoration at the watershed scale are becoming clearer. Mitigation banking requires "up-front" provision of new wetland habitat for which credits are later sold to developers who have permits to fill or dredge wetlands. Because criteria can be set in advance of permitting wetland damages, mitigation banks could be located strategically, and larger sites could be restored. The questions are whether high standards will be demanded, achieved, and sustained in the long term. A concern is that ecosystem services are moved from urbanizing areas (which might need the water-cleansing function) to rural bank sites.

Another alternative for mitigators is to pay in-lieu fees, which, like banks, can be used to fulfill a strategic, landscape- or watershed-scale wetland restoration plan. In general, wetland restoration needs to become more strategic at basin and watershed scales (33).

Every Project Has Unique Features

Surprise is a common element in restoration; even 40 years of experience in wetland restoration in the Netherlands have not eliminated the unexpected (143). The same has been said of efforts in the University of Wisconsin-Madison Arboretum, where prairie restoration began in 1934 (144). Curtis Prairie, a former pasture, is one of the oldest and most widely known ecological restorations; it was followed by burning and replanting of Greene Prairie in the 1950s. Today, these prairies support ~200 native plant species and unknown numbers of animal species; however, the wetter parts of both sites have resisted restoration attempts. The urbanizing watersheds allow stormwater to flow into the Arboretum and to foster the growth of invasive species, notably reed canary grass (*P. arundinacea*). Despite construction of stormwater detention basins, urban runoff continually flows into the lowlands, where it gives invasive species a competitive edge (41). We have been surprised by the difficulty of replacing this invasive species with a diversity of native plants. Where stormwater inflows cannot be curtailed, existing restoration tools cannot predictably restore native vegetation to wetlands. An adaptive restoration approach is called for, with multiple alternatives tested in phased experiments.

Adaptive Restoration Offers Great Potential to Learn How to Restore Specific Sites

Adaptive restoration can identify the most effective methods while reestablishing wetness and the biota. Thom (145) promoted the adaptive management approach to coastal wetland restoration. Later, Zedler & Callaway (146) described adaptive restoration as the process of conducting restoration as phased experiments, involving the establishment of replicated experimental treatments in subareas of the project site. The following steps are included:

1. Acknowledge what is not known that needs to be known to restore a specific site
2. Identify alternative restoration tools to test
3. Plan the restoration to occur in phased modules
4. Select basic tests for the first module and implement comparisons
5. Assess results and include researchers in the decision-making process
6. Use knowledge gained to plan subsequent phases
7. Adapt the restoration in response to experimental results.

This process is underway at Tijuana River National Estuarine Research Reserve.

KNOWLEDGE GAPS

At the global scale, inventories of wetland areas by type are needed at 5- to 10-year intervals, using classification systems and methods that are congruent across nations (35). Needs are most urgent for Asia, Africa, eastern Europe, the Pacific Islands, Australia, and South America (especially tropical wetlands) (7, 44). Tropical Asia is particularly in need of data on its aquatic biodiversity (25). Even Great Britain, with its long history of field research, lacks complete inventories of its coastal wetlands (147).

Once comparable inventory data are available, the trends in area loss can be determined and rates of degradation and restoration assessed (7). While the United Nations' Millennium Ecosystem Assessment will report the status of wetland ecosystems and project conditions for the future, more detailed, site-specific information will still be needed for regional and local decision makers. The approach of Norris et al. (40) for Australia's Murray-Darling basin (with a river length of 77,366 km) is a potential model for inventory and characterization of ecosystem integrity. They used environmental features, disturbance factors, hydrologic conditions, habitat, water quality, and biotic indicators to show that >95% of the river length is degraded, that 40% of the river length assessed had biota that were significantly impaired, and 10% of the length had lost at least 50% of the expected aquatic invertebrates (40).

Understanding how watersheds function in biodiversity support, water quality improvement, flood abatement, and C management with different amounts and types of wetland loss (or restoration) is a large knowledge gap for policy and decision makers. Additionally, we need a more complete understanding of how nutrient removal occurs in wetlands, what nutrient loads can be accommodated without threatening biodiversity, and where wetlands should be positioned in the landscape to improve water quality and flood abatement. We also recommend more attention be paid to contrasting functions across a range of wetland types. Such ambitious research goals will require a landscape approach in many cases. In Illinois, the Nature Conservancy (TNC) offers one example of how this can be accomplished: TNC is comparing paired watersheds (with and without concerted efforts to restore wetlands and improve agricultural practices), and water quality has improved where more wetlands have been restored (148). Such efforts should be expanded as replicated experiments with more watershed types and at multiple spatial scales.

Experimental, manipulative approaches are needed for restoring wetlands. The design of restoration sites to test alternative approaches can simultaneously restore a site while generating information on the practices that work best. When restoration is phased over time, as in adaptive restoration, techniques that work well in the earlier experimental modules can be adopted more broadly in later modules. At present, most projects are trials, without guarantees that targets will be met. The situation can only improve with science-based approaches that allow learning while doing.

Knowledge of wetland resources has improved substantially in the past two to three decades. Still, research is needed to produce accurate inventories of wetlands, using congruent classification schemes, assessments of condition, and information on rates of both loss/degradation and restoration/enhancement (7). Scientists do not yet know in detail where, how, and why wetlands are changing and how damages can be repaired in order to sustain global wetland resources. The information gaps are specific—exactly what happened, which specific changes can be reversed, and which restoration techniques are most effective in improving wetland functioning? Such questions are best tackled through adaptive restoration at the sites where attempts are being made to restore wetland resources.

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LITERATURE CITED

1. Niering W. 1985. *Wetlands*. New York: Knopf
2. Ramsar. 2002. *Fact Sheet on Wetland Values and Functions: Flood Control*. Ramsar, Gland, Switz. http://www.ramsar.org/values_floodcontrol_e.htm
3. Ramsar. 1982. *The Convention on Wetlands text*. http://www.ramsar.org/key_conv_e.htm
4. Ramsar. 2005. *Home page*. http://www.ramsar.org
5. Cowardin LM, Carter V, Golet FC, LaRoe ET. 1979. *Classification of Wetlands and Deepwater Habitats of the*

United States. Washington, DC: US Dep. Inter., Fish Wildl. Serv., Off. Biol. Serv. 129 pp.

6. Natl. Res. Counc. Comm. Wetland Mitig. 1995. *Wetlands: Characterization and Boundaries*. Washington, DC: Natl. Acad.
7. Brinson MM, Malvarez AI. 2002. Temperate freshwater wetlands: types, status, and threats. *Environ. Conserv.* 29:115–33
8. Turner RE, Boyer ME. 1997. Mississippi River diversions, coastal wetland restoration/creation and an economy of scale. *Ecol. Eng.* 8:117–28
9. Turner RE. 1997. Wetland loss in the northern Gulf of Mexico: multiple working hypotheses. *Estuaries* 20:1–13
10. Turner RE. 2001. Estimating the indirect effects of hydrologic change on wetland loss: If the earth is curved, then how would we know it? *Estuaries* 24:639–46
11. Delaney T, Webb JW, Minello TJ. 2000. Comparison of physical characteristics between created and natural estuarine marshes in Galveston Bay, Texas. *Wetlands Ecol. Manag.* 8:343–52
12. US Geol. Surv. 2004. *NWRC issues and capabilities*. http://www.nwrc.usgs.gov/issues.htm
13. Nicholls RJ, Hoozemans FMJ, Marchand M. 1999. Increasing flood risk and wetland losses due to global sea-level rise: regional and global analyses. *Glob. Environ. Change* 9:S69–87
14. Hambright KD, Zohary T. 1999. The Hula Valley (northern Israel wetlands rehabilitation project). In *An International Perspective on Wetland Rehabilitation*, ed. W Streever, pp. 173–80. Boston: Kluwer Acad.
15. Drexler JZ, Bedford B. 2002. Pathways of nutrient loading and impacts on plant diversity in a New York peatland. *Wetlands* 22:263–81
16. Zedler JB, Kercher S. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Crit. Rev. Plant Sci.* 23:431–52
17. Koerselman W, Vankerkhoven MB, Verhoeven JTA. 1993. Release of inorganic N, P and K in peat soils—effect of temperature, water chemistry, and water-level. *Biogeochemistry* 20:63–81
18. Boesch DF, Brinsfield RB, Magnien RE. 2001. Chesapeake Bay eutrophication: scientific understanding, ecosystem restoration, and challenges for agriculture. *J. Environ. Q.* 30:303–20
19. Kercher SM, Carpenter Q, Zedler JB. 2004. Interrelationships of hydrologic disturbances, reed canary grass (*Phalaris arundinacea* L.), and native plants in Wisconsin wet meadows. *Natural Areas J.* 24:316–25
20. Perry L, Galatowitsch SM, Rosen CJ. 2004. Competitive control of invasive vegetation: a native wetland sedge suppresses *Phalaris arundinacea* in carbon-enriched soil. *J. Appl. Ecol.* 41:151–62

20a. Herr-Turoff A. 2005. Does wet prairie vegetation retain more nitrogen with our without *Phalaris* invasion. *Plant Soil*. In press

21. Ervin GN, Wetzel RG. 2003. An ecological perspective of allelochemical interference in land–water interface communities. *Plant Soil* 256:3–28
22. Zhang RS, Shen YM, Lu LY, Yan SG, Wang YH, et al. 2004. Formation of *Spartina alterniflora* salt marshes on the coast of Jiangsu Province, China. *Ecol. Eng.* 23:85–94
23. McAllister DE, Craig JF, Davidson N, Delany S, Seddon M. 2001. *Biodiversity impacts of large dams.* Int. Union Conserv. Nat. Natural Resour./UN Environ. Programme Rep. http://www1.unep.org/depi/icarm/envdams/Report1BiodiversityImpacts.PDF
24. Ladhar SS. 2002. Status of ecological health of wetlands in Punjab, India. *Aquat. Ecosyst. Health Manag.* 5:457–65

25. Dudgeon D. 2003. The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. *Hydrobiologia* 500:295–14
26. Organ. Econ. Co-op. Dev./World Conserv. Union (IUCN). 1996. *Guidelines for Aid Agencies for Improved Conservation and Sustainable Use of Tropical and Sub-Tropical Wetlands*. Paris: Organ. Econ. Co-op. Dev.
27. Moser M, Prentice C, Frazier S. 1996. *A global overview of wetland loss and degradation*. http://www.ramsar.org/about_wetland_loss.htm
28. Dahl TE. 1990. *Wetlands Losses in the United States 1780's to 1980's*. Washington, DC: US Dep. Inter., Fish Wildl. Serv. 21 pp.
29. Dahl TE. 2000. *Report to Congress on the Status and Trends of Wetlands in the Conterminous United States 1986 to 1997*. US Dep. Inter., Fish Wildl. Serv., Washington, DC. 82 pp. http://wetlands.fws.gov/statusandtrends.htm
30. Conserv. Foundation. 1988. Protecting America's wetlands: an action agenda. *Rep. Natl. Wetlands Policy Forum.* Washington, DC
31. Salton Sea Auth. 2000. *About the Salton Sea*. http://www.saltonsea.ca.gov/thesea.htm
32. Natl. Res. Counc. Comm. Wetland Mitig. 2001. *Compensating for Wetland Loss Under the Clean Water Act*. Washington DC: Natl. Acad.
33. Zedler JB. 2003. Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Front. Ecol. Environ.* 1:65–72
34. Matthews E, Fung I. 1987. Methane emissions from natural wetlands: global distribution, area, and environmental characteristics of sources. *Glob. Biogeochem. Cycles* 1:61–86
35. Finlayson CM, Davidson NC, Spiers AG, Stevenson NJ. 1999. Global wetland inventory—current status and future priorities. *Mar. Freshw. Res.* 50:717–27
36. Keddy P. 2000. *Wetland Ecology*. Cambridge, UK: Cambridge Univ. Press
37. Amon JP, Thompson CA, Carpenter QJ, Miner J. 2002. Temperate zone fens of the glaciated midwestern USA. *Wetlands* 22:301–17
38. Atlantis Sci. Inc. 2002. Treaty enforcement services using Earth observation: wetlands monitoring. *Rep. to ESRIN Contract. Serv.*, Rome, Italy. 208 pp.
39. US Fish Wildl. Serv. 2004. *Homepage*. http://www.fws.gov
40. Norris RH, Liston P, Davies N, Coysh J, Dyer F, et al. 2001. Snapshot of the Murray-Darling basin river condition. *CSIRO Land Water Rep. to Murray Darling Basin Comm*. Canberra, Aust.
41. Kercher SM, Zedler JB. 2004. Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. *Oecologia* 138:455–64
42. Greeson PE, Clark JR, Clark JE, eds. 1979. *Wetland Functions and Values: The State of Our Understanding*. Minneapolis, MN: Am. Water Resour. Assoc.
43. Living Lakes. 2004. *Pantanal wetlands*. http://www.livinglakes.org/pantanal/
44. Spiers AG. 1999. Review of international/continental wetland resources. In *Global Review of Wetland Resources and Priorities for Inventory*, ed. CM Finlayson, AG Spiers, pp. 63–104. *Superv. Sci. Rep. 144*, Canberra, Aust.
45. Richter BD, Mathews R, Harrison DL, Wigington R. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. *Ecol. Appl.* 13:206–24
46. US Fish Wildl. Serv. 2004. *Waterfowl population status, 2004. Rep*. http://migratorybirds.fws.gov/reports/reports.html
47. Richter BD, Braun DP, Mendelson MA, Master LL. 1997. Threats to imperiled

freshwater fauna. *Conserv. Biol.* 11:1081–93

48. Semlitsch RD. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conserv. Biol.* 16:619–29
49. Bedford BL, Walbridge MR, Aldous A. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology* 80:2151–69
50. Grootjans AP, Fresco LFM, de Leeuw CC, Schipper PC. 1996. Degeneration of species-rich *Calthion palustris* hay meadows; some considerations on the community concept. *J. Veg. Sci.* 7:185–94
51. Turner RE, Rabalais NN. 2003. Linking landscape and water quality in the Mississippi River basin for 200 years. *BioScience* 53:563–72
52. Hey DL, McGuiness D, Beorkrem MN, Conrad DR, Hulsey BD. 2002. *Flood Damage Reduction in the Upper Mississippi River Basin: An Ecological Means*. Minneapolis, MN: McKnight Foundation
53. Kadlec R, Knight R. 1996. *Treatment Wetlands*. Boca Raton, FL: CRC Press
54. Smil V. 2000. Phosphorus in the environment: Natural flows and human interferences. *Annu. Rev. Energy Environ.* 25:53–88
55. Noe GB, Childers DL, Jones RD. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique? *Ecosystems* 4:603–24
56. Keenan LW, Lowe EF. 2001. Determining ecologically acceptable nutrient loads to natural wetlands for water quality improvement. *Water Sci. Technol.* 44:289–94
57. Crumpton WG. 2001. Using wetlands for water quality improvement in agricultural watersheds; the importance of a watershed scale approach. *Water Sci. Technol.* 44:559–64
58. Evans R, Gilliam JW, Lilly JP. 1996. *Wetlands and water quality*. North Carolina Coop. Ext. Serv. Pub. AG 473–7. http://www.bae.ncsu.edu/programs/extension/evans/ag.html 473–7
59. Mitsch WJ, Gosselink JG. 2000. The value of wetlands: importance of scale and landscape setting. *Ecol. Econ.* 35:25–33
60. Hey DL, Philippi NS. 1995. Flood reduction through wetland restoration: the upper Mississippi River basin as a case history. *Restor. Ecol.* 3:4–17
61. US Dep. Energy Consort. Res. Enhanc. 2004. *CSiTE, Carbon sequestration in terrestrial ecosystems*. http://csite.esd.ornl.gov/
62. Mitra S, Wassman R, Vlek PLG. 2005. An appraisal of global wetland area and its organic carbon stock. *Curr. Sci.* 88:25–35
63. Smith KA, Ball T, Conen F, Dobbie KE, Massheder J, Rey A. 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. *Eur. J. Soil Sci.* 54:779–91
64. Barbier EB, Acreman M, Knowler D. 1997. *Economic Valuation of Wetlands*. Gland, Switz.: Ramsar Conv. Bur. 138 pp.
65. Roulet NT. 2000. Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: prospects and significance for Canada. *Wetlands* 20:605–15
66. Glatzel S, Basiliko N, Moore T. 2004. Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, Eastern Québec, Canada. *Wetlands* 24:261–67
67. Brevik EC, Homburg JA. 2004. A 5000 year record of carbon sequestration from a coastal lagoon and wetland complex, southern California, USA. *Catena* 57:221–32
68. Choi YH, Wang Y. 2004. Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Glob. Biogeochem. Cycles* 18: Article GB4016

69. Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC. 2003. Global carbon sequestration in tidal, saline wetland soils. *Glob. Biogeochem. Cycles* 17: Article 11
70. Tockner K, Stanford JA. 2002. Riverine flood plains: present state and future trends. *Environ. Conserv.* 29:308–30
71. Amthor JS, Members Ecosyst. Work. Group. 1998. Terrestrial ecosystem responses to global change: a research strategy. *ORNL Tech. Memo. 1998/27, Publ. 4821. Oak Ridge Natl. Lab.*, Oak Ridge, TN. 46 pp.
72. Pagiola S, von Ritter K, Bishop J. 2004. *How much is an ecosystem worth? Assessing the economic value of conservation*. Washington, DC: World Conserv. Union/Nat. Conserv./World Bank
73. Millenn. Ecosyst. Assess. 2004. *Milennium ecosystem assessment updates*. http://www.millenniumassessment.org/en/index.aspx
74. Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, et al. 1999. The value of the world's ecosystem services and natural capital. *Nature* 387:253–59
75. Schuyt K, Brander L. 2004. *The Economic Value of the World's Wetlands*. World Wildl. Fund, Gland/Amsterdam, Neth. 32 pp.
76. Soc. Ecol. Restor. Int. 2004. *The SER international primer on ecological restoration*. http://www.ser.org/content/ecological_restoration_primer.asp
77. Dobson AP, Bradshaw AD, Baker AJM. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* 277:515–22
78. Able KW, Hagan SM. 2000. Effects of common reed (*Phragmites australis*) invasion on marsh surface macrofauna: response of fishes and decapod crustaceans. *Estuaries* 23:633–46
79. Jivoff PR, Able KW. 2003. Evaluating salt marsh restoration in Delaware Bay: the response of blue crabs, *Callinectes sapidus*, at former salt hay farms. *Estuaries* 26:709–19
80. Suding KN, Gross KL, Houseman G. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19:46–53
81. Richardson J, Vepraskas M. 2001. *Wetland Soils: Genesis, Hydrology, Landscapes, and Classification*. Boca Raton, FL: CRC Press/Lewis
82. Hunt R. 1996. Do created wetlands replace the wetlands that are destroyed? *USGS Fact Sheet FS-246-96*, US Geol. Surv., Middleton, WI
83. Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ. Manage*. 30:492–507
84. Galatowitsch SM, van der Valk AG. 1996. Characteristics of recently restored wetlands in the prairie pothole region. *Wetlands* 16:75–83
85. Galatowitsch SM, Whited DC, Lehtinen R, Husveth J, Schik K. 2000. The vegetation of wet meadows in relation to their land-use. *Environ. Monit. Assess*. 60:121–44
86. Green EK, Galatowitsch SM. 2001. Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha xglauca*). *Can. J. Bot./Revue Can. Bot.* 79:170–78
87. Portnoy JW. 1999. Salt marsh diking and restoration: biogeochemical implications of altered wetland hydrology. *Environ. Manage*. 24:111–20
88. Zedler JB. 1998. Replacing endangered species habitat: the acid test of wetland ecology. In *Conservation Biology for the Coming Age*, pp. 364–79, ed. PL Fiedler, PM Kareiva. New York: Chapman & Hall
88a. Fellows M, Zedler JB. 2005. Effects of the non-native grass, *Parapholis incurva* (Poaceae), on the rare and endangered hemiparasite, *Cordylanthus maritimus* subsp. *maritimus* (Scrophulariaceae). *Madroño* 52:91–98

89. Whisenant SG. 1999. *Repairing Damaged Wildlands*. Cambridge, UK: Cambridge Univ. Press
90. Zedler JB, Morzaria-Luna HN, Ward K. 2003. The challenge of restoring vegetation on tidal, hypersaline substrates. *Plant Soil* 253:259–73
91. Mitsch WJ, Wilson RF. 1996. Improving the success of wetland creation and restoration with know-how, time and self-design. *Ecol. Appl.* 6:77–83
92. Gorham E, Rochefort L. 2003. Peatland restoration: a brief assessment with special reference to *Sphagnum* bogs. *Wetlands Ecol. Manag.* 11:109–19
93. Warren RS, Fell PE, Rozsa R, Brawley AH, Orsted AC, et al. 2002. Salt marsh restoration in Connecticut: 20 years of science and management. *Restor. Ecol.* 10:497–513
94. Thompson AL, Luthin CS. 2004. *Wetland Restoration Handbook for Wisconsin Landowners*. Madison, WI: Bur. Integr. Sci. Serv., Wisconsin Dep. Natural Resour.
95. Wilcox DA, Whillans TH. 1999. Techniques for restoration of disturbed coastal wetlands of the Great Lakes. *Wetlands* 19:835–57
96. Bledsoe BP, Shear TH. 2000. Vegetation along hydrologic and edaphic gradients in a North Carolina coastal plain creek bottom and implications for restoration. *Weltlands* 20:126–47
97. Sidle WC, Arihood L, Bayless R. 2000. Isotope hydrology dynamics of riverine wetlands in the Kankakee watershed, Indiana. *J. Am. Water Resour. Assoc.* 36: 771–90
98. Toth LA, Koebel JW Jr, Warne AG, Chamberlain J. 2002. Implications of reestablishing prolonged flood pulse characteristics fo the Kissimmee River and floodplain ecosystem. In *Flood Pulsing in Wetlands: Restoring the Natural Hydrological Balance*, pp. 191–221, ed. B. Middleton. New York: Wiley
99. Whalen PJ, Toth LA, Koebel JW, Strayer PK. 2002. Kissimmee River restoration: a case study. *Water Sci. Technol.* 45:55–62
100. Wetzel PR, van der Valk AG, Toth LA. 2001. Restoration of wetland vegetation on the Kissimmee River floodplain: potential role of seed banks. *Wetlands* 21:189–98
101. Rozas LP, Minello TJ. 2001. Marsh terracing as a wetland restoration tool for creating fishery habitat. *Wetlands* 21:327–41
102. DeLaune RD, Jugsujinda A, Peterson GW, Patrick WH. 2003. Impact of Mississippi River freshwater reintroduction on enhancing marsh accretionary processes in a Louisiana estuary. *Estuarine Coast. Shelf Sci.* 58:653–62
103. Fong P, Zedler JB. 2000. Sources, sinks, and fluxes of nutrients (N+P) in a small highly modified urban estuary in southern California. *Urban Ecosyst.* 4:125–44
104. Boeken B, Shachak M. 1994. Desert plant-communities in human-made patches—implications for management. *Ecol. Appl.* 4:702–16
104a. Larkin DJ, Vivian-Smith G, Zedler JB. 2005. Topographic heterogeneity theory and applications to ecological restoration. In *Foundations of Restoration Ecology*, ed. D Falk, M Palmer, JB Zedler, pp. XX–XX. Washington, DC: Island. In press
105. Cantelmo AJ, Ehrenfeld JG. 1999. Effects of microtopography on mycorrhizal infection in Atlantic white cedar (*Chamaecyparis thyoides* (L.) Mills.). *Mycorrhizae* 8:175–80
106. Callaway JC. 2001. Hydrology and substrate. In *Handbook for Restoring Tidal Wetlands*, ed. JB Zedler, pp. 89–118. Boca Raton, FL: CRC Press
107. Brown SC, Bedford BL. 1997. Restoration of wetland vegetation with transplanted wetland soil: an experimental study. *Wetlands* 17:424–37
108. Ashworth SM. 1997. Comparison be-

tween restored and reference sedge meadow wetlands in south-central Wisconsin. *Wetlands* 17:518–27

109. Hey DL, Philippi NS. 1999. *A Case for Wetland Restoration*. New York: Wiley Intersci.
110. Dalrymple GH, Doren RF, O'Hare NK, Norland MR, Armentano TV. 2003. Plant colonization after complete and partial removal of disturbed soils for wetland restoration of former agricultural fields in Everglades National Park. *Wetlands* 23:1015–29
111. Craft C, Megonigal P, Broome S, Stevenson J, Freese R, et al. 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecol. Appl.* 13:1417–32
112. Parker TP. 1997. The scale of successional models and restoration objectives. *Restor. Ecol.* 5:301–6
113. Eertman RHM, Kornman BA, Stikvoort E, Verbeek H. 2002. Restoration of the Sieperda tidal marsh in the Scheldt estuary, the Netherlands. *Restor. Ecol.* 10:438–49
114. Seabloom EW, van der Valk AG. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. *Wetlands* 23:1–12
115. Streever W, Zedler JB. 2000. To plant or not to plant? *BioScience* 50:188–89
116. Lindig-Cisneros R, Zedler JB. 2002. Halophyte recruitment in a salt marsh restoration site. *Estuaries* 25:1174–83
117. Zedler JB, Callaway JC, Sullivan G. 2001. Declining biodiversity: why species matter and how their functions might be restored. *BioScience* 51:1005–17
118. Keer G, Zedler JB. 2002. Salt marsh canopy architecture differs with the number and composition of species. *Ecol. Appl.* 12:456–73
119. Callaway JC, Sullivan G, Zedler JB. 2003. Species-rich plantings increase biomass and nitrogen accumulation in a wetland restoration experiment. *Ecol. Appl.* 13:1626–39
120. MacMahon J. 1998. Empirical and theoretical ecology as a basis for restoration: an ecological success story. In *Successes, Limitations, and Frontiers in Ecosystem Science*, ed. ML Pace, PM Groffman, pp. 220–46. New York: Springer-Verlag
121. Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–86
122. Werner KJ, Zedler JB. 2002. How sedge meadow soils, microtopography, and vegetation respond to sedimentation. *Wetlands* 22:451–66
123. Knutson MG, Sauer JR, Olsen DA, Mossman MJ, Hemesath LM, Lannoo MJ. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. *Conserv. Biol.* 13:1437–46
124. Semlitsch RD, Bodie JR. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conserv. Biol.* 17:1219–28
125. Minello TJ, Zimmerman RJ, Medina R. 1994. The importance of edge for natant macrofauna in a created salt marsh. *Wetlands* 14:184–98
126. West JM, Zedler JB. 2000. Marsh-creek connectivity: fish use of a tidal salt marsh in southern California. *Estuaries* 23:699–710
127. Madon SP, Williams GD, West JM, Zedler JB. 2001. The importance of marsh access to growth of the California killifish, *Fundulus parvipinnis*, evaluated through bioenergetics modeling. *Ecol. Model.* 136:149–65
128. Delphey PJ, Dinsmore JJ. 1993. Breeding bird communities of recently restored and natural prairie potholes. *Wetlands* 13:200–6
129. Ratti JT, Rocklage M, Garton EO, Giu-

dice JH, Golner DP. 2001. Comparison of avian communities on restored and natural wetlands in North and South Dakota. *J. Wildl. Manag.* 65:676–84
130. Brown SC, Smith CR. 1998. Breeding season bird use of recently restored versus natural wetlands in New York. *J. Wildl. Manag.* 62:1480–91
131. Handa IT, Jefferies RL. 2000. Assisted revegetation trials in degraded salt-marshes. *J. Appl. Ecol.* 37:944–58
132. Wetzel RG. 2003. Freshwater and wetland ecology: challenges and future frontiers. In *Achieving Sustainable Freshwater Systems: A Web of Connections*, ed. MJ Holland, E Blood, L Shaffer, pp. 111–23. Washington, DC: Island
133. Langis R, Zalejko M, Zedler JB. 1991. Nitrogen assessments in a constructed and a natural salt marsh of San Diego Bay, California. *Ecol. Appl.* 1:40–51
134. Currin CA, Joye SB, Paerl HW. 1996. Diel rates of N-2-fixation and denitrification in a transplanted *Spartina alterniflora* marsh: implications for N-flux dynamics. *Estuarine Coast. Shelf Sci.* 42:597–616
135. Piehler MP, Currin CA, Cassanova R, Paerl HW. 1998. Development and N_2-fixing activity of the benthic microbial community in transplanted *Spartina alterniflora* marshes in North Carolina. *Restor. Ecol.* 6:290–96
136. Cooke JC, Lefor MW. 1998. The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. *Restor. Ecol.* 6:214–22
137. Turner SD, Friese CF. 1998. Plant-mycorrhizal community dynamics associated with a moisture gradient within a rehabilitated prairie fen. *Restor. Ecol.* 6:44–51
138. Turner SD, Amon JP, Schneble RM, Friese CF. 2000. Mycorrhizal fungi associated with plants in ground-water fed wetlands. *Wetlands* 20:200–4
139. Bauer CR, Kellogg CH, Bridgham SD, Lamberti GA. 2003. Mycorrhizal colonization across hydrologic gradients in restored and reference freshwater wetlands. *Wetlands* 23:961–68
140. McAllister LS, Peniston BE, Leibowitz SG, Abbruzzese B, Hyman JB. 2000. A synoptic assessment for prioritizing wetland restoration efforts to optimize flood attenuation. *Wetlands* 20:70–83
141. Richardson MS, Gatti RC. 1999. Prioritizing wetland restoration activity within a Wisconsin watershed using GIS modeling. *J. Soil Water Conserv.* 54:537–42
142. Schweiger EW, Leibowitz S, Hyman J, Foster W, Downing M. 2002. Synoptic assessment of wetland function: a planning tool for protection of wetland species biodiversity. *Biodivers. Conserv.* 11:379–406
143. Klotzli F, Grootjans AP. 2001. Restoration of natural and semi-natural wetland systems in Central Europe: progress and predictability of developments. *Restor. Ecol.* 9:209–19
144. Cottam G. 1987. Community dynamics on an artificial prairie. In *Restoration Ecology: A Synthetic Approach to Ecological Research*, ed. W Jordan III, ME Gilpin, JD Aber, pp. 257–70. Cambridge, UK: Cambridge Univ. Press
145. Thom RM. 2000. Adaptive management of coastal ecosystem restoration projects. *Ecol. Eng.* 15:365–72
146. Zedler JB, Callaway JC. 2003. Adaptive restoration: a strategic approach for integrating research into restoration projects. In *Managing for Healthy Ecosystems*, ed. DJ Rapport, WL Lasley, DE Rolston, NO Nielsen, CO Qualset, AB Damania, pp. 167–74. Boca Raton, FL: Lewis
147. Adam P. 2002. Saltmarshes in a time of change. *Environ. Conserv.* 29:39–61
148. The Nat. Conserv. 2004. *The Mackinaw River watershed*. http://nature.org/wherewework/northamerica/states/illinois/preserves/art7559.html

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