28 Wolf, J.B. *et al.* (1999) The role of maternal and paternal effects in the evolution of parental quality by sexual selection. *J. Evol. Biol.* 12, 1157–1167
29 Higashi, M. *et al.* (1999) Sympatric speciation by sexual selection. *Nature* 402, 523–526
30 Møller, A.P. and Alatalo, R.V. (1999) Good genes effects in sexual selection. *Proc. R. Soc. London Ser. B* 266, 85–91
31 Zann, R. (1994) Effects of band color on survivorship, body condition and reproductive effort of free-living Australian zebra finches. *Auk* 111, 131–142
32 Kose, M. *et al.* (1999) Sexual selection for white tail spots in the barn swallow in relation to habitat choice by feather lice. *Anim. Behav.* 58, 1201–1205
33 Forkman, B. and Corr, S. (1996) Influence of size and asymmetry of sexual characters in the rooster and hen on the number of eggs laid. *Appl. Anim. Behav. Sci.* 49, 285–291
34 Thornhill, R. (1983) Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am. Nat.* 122, 765–788
35 Simmons, L.W. (1987) Female choice contributes to offspring fitness in the field cricket *Gryllus bimaculatus* (De Geer). *Behav. Ecol. Sociobiol.* 21, 313–321
36 Oksanen, T.A. *et al.* (1999) Maternal effort and male quality in the bank vole. *Proc. R. Soc. London Ser. B* 266, 1495–1499
37 Drickamer, L.C. *et al.* (2000) Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Anim. Behav.* 59, 371–378
38 Welch, A.M. *et al.* (1998) Call duration as an indicator of genetic quality in male gray tree frogs. *Science* 280, 1928–1930
39 Sheldon, B.C. *et al.* (1997) Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. London Ser. B* 264, 297–302
40 Johnsen, A. *et al.* (2000) Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature* 406, 296–299
41 Petrie, M. (1994) Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* 371, 598–599
42 Birkhead, T.R. *et al.* (2000) Testosterone and maternal effects – integrating mechanisms and function. *Trends Ecol. Evol.* 15, 86–87

Progress in wetland restoration ecology

Joy B. Zedler

It takes more than water to restore a wetland. Now, scientists are documenting how landscape setting, habitat type, hydrological regime, soil properties, topography, nutrient supplies, disturbance regimes, invasive species, seed banks and declining biodiversity can constrain the restoration process. Although many outcomes can be explained *post hoc*, we have little ability to predict the path that sites will follow when restored in alternative ways, and no insurance that specific targets will be met. To become predictive, bolder approaches are now being developed, which rely more on field experimentation at multiple spatial and temporal scales, and in many restoration contexts.

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Upland and wetland restoration (Box 1) have much in common because efforts are made to reintroduce species and recover ecosystem functions, but the environmental and institutional contexts are substantially different. First, the hydrological regimes of wetlands (Box 1) are complex and are modified more often than those of uplands (Box 2). Second, the drainage of wetlands has eliminated highly valued functions[1] (e.g. fish and waterfowl production), leading to regulations that require compensation for damaging wetlands[2] (Box 3). The dollar value of wetland functions (Box 1) is particularly high. Data in Costanza *et al.*[1] indicate that 40% of global renewable ecosystem services (worth US$33 trillion per year) are provided by shallow waters, even though these ecosystems cover only 1.5% of the earth's surface.

Typically, wetland restoration aims to restore lost biodiversity or provide services, such as flood-peak reduction and water quality improvement (Fig. 1). The effectiveness of attempts to restore lost services is debated, because project proponents need to claim 'success' to justify the high costs of restoration and because standards for evaluating project outcomes are uneven[3]. Here, I consider recent progress in understanding how both biodiversity and functions develop, although these lines of scientific inquiry are often separate[4]. Biodiversity and function are not necessarily maximized at the same wetland. Species richness is often highest where nutrient supply is low (as in groundwater-fed wetlands). However, maximum nutrient removal requires abundant nutrient supplies (eutrophic conditions), where dominance is often by single plant species (e.g. cattail, *Typha* spp.). Although there is a need to restore wetlands to support both a diversity of species and ecosystem services, simple models for achieving these dual roles are not realistic[4].

Limitations of the scientific database

A central goal of restoration ecology is to predict the outcomes of specific restoration actions; however, the demand for restoration guidelines has outpaced the science[2]. Few sites are assessed beyond what is needed to satisfy specific permit conditions[3] and the results of such monitoring rarely appear in the peer-reviewed literature. Of 26 papers on coastal marshes (Box 1), most concerned small, recently restored sites, and most of the assessments were based only on short-term studies, a few sampling episodes and a few attributes[5]. Except for a 25-year study of soils in coastal North Carolina (USA) marshes[6], the long-term development of restored wetland ecosystems is poorly recorded.

Wetland restoration is more complex than implied by early concepts of ecosystem degradation and restoration. For example, degradation and restoration have been depicted as straight arrows proceeding in opposite directions along parallel paths[7]. In reality, degradation involves many paths of change in species abundances and ecosystem functions, and restoration is at least as complex. Furthermore, models developed for one wetland type appear not to transfer readily to other types[4]. There is considerable need for more habitat-specific advice, such as is available for prairie potholes[8], riverine wetlands[9] and tidal wetlands[10].

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Ecological theory has much to offer the practitioner (Table 1), but predictions remain vague (Box 4). Predictability should improve if generalities are sought where the restoration context and specific restoration actions are held constant[11]. To date, there are too few studies to draw generalizations within contexts, let alone between different site types and landscape settings.

Ecological principles

A review of the literature indicates that at least ten ecological principles are ignored or violated in many wetland restoration efforts. For each principle, I provide examples of the problems that are being identified and suggest where a more scientific approach is needed.

Landscape context and position are crucial to wetland restoration

Because wetland function is closely related to landscape position[12], Bedford[13] concludes that cumulative alteration of landscapes is the greatest constraint on wetland restoration. Several mitigation projects have been misplaced. In an urbanized area of Puget Sound (Washington, DC, USA), habitats excavated for salmon (Salmonidae) rapidly became filled with sediment[14]. In Pennsylvania (USA), groundwater-fed wetlands on a ridge were 'replaced' by wetlands on the floodplain, where surface-water inflows dominated[15]. Near Portland (Oregon, USA), 44 out of 51 mitigation wetlands were placed in novel positions[16]. Although poorly placed wetlands are unlikely to compensate for lost natural habitats, they do offer unique opportunities for researchers to quantify landscape–position effects. We have still to learn how watershed position interacts with degraded water quality and quantity to constrain restoration efforts.

Natural habitat types are the appropriate reference systems

Ponds are the easiest type of wetland to build; however, wetland ecologists warn that a shift towards 'generic' or 'novel' wetland types will not sustain regional biodiversity. Ponds are often restored to support waterfowl[13], but a generic pond design will not support all such species. For example, early migrants need shallow ponds that thaw in early spring[2]. In Oregon, ponds are often created to mitigate losses of natural marshes and wet meadows, thus shifting habitat type[17]. In a Pennsylvanian comparison, restored wetlands had more open water than reference systems, thus changing the distribution of habitat types[15]. Researchers need to explore how biodiversity and functions are affected by adding novel systems and changing the distribution of wetland types.

The specific hydrological regime is crucial to restoring biodiversity and function

Wetland hydrology has been altered through drainage, filling, dams, levees, water diversions and groundwater pumping, all of which alter the timing, amplitude, frequency and duration of high water. Restoration needs to begin by determining how the hydrology has changed[2,18]. Thus, plans to restore the Everglades[19] are based on extensive modeling of historical water flows. Likewise, Middleton[9] emphasizes the importance of flood pulses to community structure and ecosystem functioning. However, it is not clear how much of the natural hydrological regime has to be restored. We need to know if partial improvements to hydroperiods and water chemistry can restore the biota and biogeochemical functioning. Research on the many effects of timing, magnitude, frequency and duration of inundation is needed to complement assessments of the chemical content of water (pH, calcium, nutrients, salinity and contaminants, etc.). According to Hunt *et al.*[18], restoring depleted groundwater is especially challenging; near-surface local sources and deep regional sources interact to discharge water with a specific range of hydroperiods and unique chemical quality[18].

Ecosystem attributes develop at different paces

In constructed salt marshes of both the Atlantic and Pacific coasts, vegetation rapidly achieves 100% cover, although soil nitrogen (N) and organic matter (OM) are slow to accumulate[10]. Salt marshes constructed in North Carolina 25 years ago have lower soil organic carbon (C) and total N reservoirs than a 2000-year-old natural marsh[6]. Their C accumulation rates are similar to those of reference sites, but N accumulation rates are higher, thus C:N ratios have declined over time.

Box 1. Glossary

Marsh: wetlands dominated by emergent, herbaceous vascular plants, where the vegetation is primarily nonwoody.

Mitigation: is used here to mean compensation (through wetland restoration or construction) for wetlands being lost to development.

Mitigation policy: requires that developers avoid or minimize damage to wetlands before being given permission to compensate for unavoidable damage.

Wetland: shallow-water ecosystems, including marshes, bogs, vernal pools and seagrass beds.

Wetland functions: processes, such as productivity, biodiversity support, nutrient cycling and floodwater storage.

Wetland services: those processes with societal value.

Wetland restoration: is used here in a broad sense, including the return of predisturbance conditions and efforts to restore regional biodiversity or function by converting upland to wetland, as sometimes occurs in mitigation.

Box 2. Hydrological considerations are basic to wetland restoration

It is widely recognized that hydrological conditions provide the basic control of wetland structure and functioning[39]. Throughout history, streamflows have been modified so that water levels are neither too high nor too low. Today, most rivers have been altered to provide flood protection and supply water, using levees, channels, diversion structures and over 2.5 million dams[2] in the USA. In many places the 'natural hydrological regimes' are unknown, because structures precede streamflow gauging and because few wetlands have been sufficiently instrumented to characterize hydroperiods. In general, structures stabilize water levels. However, extreme floods can be crucial to wetlands. Because hydrological regimes can be readily modified, wetland restorationists begin by considering how water should influence the site. This requires greater understanding than currently exists of how water controls composition and function. How much of the natural hydrological regime must be restored to sustain the regional diversity and functions of wetlands is unknown. Although natural wetlands might experience floods every 50 to 500 years, providing 10- or 25-year events might suffice for some desired functions, such as scouring of marshes and re-establishment of sandy beaches on the Lower Colorado River.

Also unknown is the degree to which other aspects of the natural hydrological regimes must be mimicked to restore biodiversity and wetland functioning at the local scale. Hydrological regimes differ not only in the frequency and magnitude of high water, but also the duration, timing and temporal sequences of high and low water. Hence, there is much to learn about how hydroperiods affect plant and animal communities. Experiments typically vary one or two of the many aspects of flooding (e.g. water depth and duration), and few studies have documented the long-term aspects (legacies) of single flood events or particular sequences of events. Experimental research is needed to explain the impacts of past disruptions to hydrological regimes as well as to guide efforts to restore wetlands through manipulation of this basic wetland attribute. The fact that wetlands are products of their hydrology and that hydrological regimes are readily modified, offers wetland ecologists unique opportunities to uncover the details of cause–effect relationships and to use this knowledge in wetland restoration.

Box 3. Constraints imposed by the regulatory context of many wetland restoration projects

Under the US Clean Water Act, permits are needed to discharge materials into wetlands; the resulting damages must be compensated in some way, commonly through restoration or creation of wetlands[2]. Mitigation policy imposes unique demands on restoration, namely, the need for outcomes to match some reference site or a specific impact site, the need to emphasize one or a few attributes that can be measured to assess compliance with permit conditions, and the need to achieve specific standards in a short time frame, usually five years[3]. To determine if standards are met, permits generally require that some monitoring be done.

The stakes are high in the mitigation context, because project proponents are liable for outcomes, and regulators are increasingly tracking the progress of mitigation efforts. The specificity of requirements allows surveys (e.g. in Indiana[40]) of how often projects meet goals and how much wetland area is still being lost. The regulatory context ensures continuing controversy and re-evaluation and increasing opportunities for science; for example, through government funding of indicators of ecosystem health for use in rapid assessments and projections of long-term outcomes. Even though permits generally have few conditions (e.g. high cover of native plants), the intent of regulation is to sustain specific wetland services, such as water quality improvement. Hence, research needs to bridge the gap between structural attributes that can be easily measured and ecosystem functions.

Many wetland restoration efforts take place outside the regulatory context; in such cases, goals are likely to be broad and funds limited for quantitative evaluation (as with many upland restoration projects). What is unique for wetland restoration ecology is the impetus regulation provides for addressing specific aspects of ecosystem development.

In Oregon, 95 restored freshwater marshes had lower soil OM than natural marshes and no evidence of accumulation[20]. Even *Typha* stands of between 2 and 20 years of age can be slow to accumulate soil OM (Ref. 15). The restoration of harvested peatlands presents a particular challenge, owing to low productivity in northern latitudes[21]. For various attributes, we need predictability in the rates of change and understanding of the consequences of slow restoration rates.

Nutrient supply rates affect biodiversity recovery

Fens are typically rich in species, but the vegetation is difficult to restore when N and phosphorus (P) levels are elevated in either the soil or surface-water inflows. Nutrients increase the productivity of grasses, which tend to exclude other fen species[22]. High concentrations of P persist in farmed wet meadows[23] and plant species richness is correspondingly low. To predict outcomes of restoration efforts, we need to determine the thresholds of tolerance to eutrophication for representative plant communities.

At least one restoration site had insufficient nutrients. In San Diego Bay (California, USA), coarse soil (sandy dredge spoil) was 'leaky' and supplied too little N to support tall cordgrass (*Spartina foliosa).* Tall grass was needed by predatory beetles that limit populations of herbivorous scale insects[10]. Although N fertilizer initially increased the height of cordgrass, it later favored the growth of a succulent competitor. Without tall cordgrass, the endangered clapper rail *(Rallus longirostris levipes)* did not nest[10]. This illustrates that more long-term, whole-system research is needed to show how specific nutrient supply regimes affect entire food webs.

Specific disturbance regimes can increase species richness

In western Europe, the restoration of heavily grazed salt marshes[24] and monotypic reedbeds[25] (*Phragmites australis)* is aided by moderate grazing. However, intensively grazed marshes are more useful to certain bird species. Large, long-term experiments in Germany varied grazing by sheep and showed that two species of geese declined when grasses were allowed to mature[24]. The effects of hay cutting are not the same, because trampling by grazers can negatively affect ground-nesting species, whereas hay cutting retains a denser turf[24]. Hay cutting is recommended for aggressive stands of reed canary grass *(Phalaris arundinacea)* in the Czech Republic[26], where three cuts in one year nearly doubled the number of plant species per square metre. Research is needed on the types and intensity of disturbances that maximize species richness of both plants and animals.

Seed banks and dispersal can limit recovery of plant species richness

The restoration of biodiversity requires that propagules are present or can 'find' restoration sites. Not all vascular plant species return to drained and farmed prairie potholes after they are rewetted[27], because seed banks are depleted in potholes that have been farmed for many years. Sedge meadow and wet prairie species are affected more than readily dispersed mudflat annuals and emergent and floating aquatic plants[9,27]. By comparison, some native plants and many exotics are aggressive colonists. The longevity of seeds and constraints on seed dispersal deserve more study, especially to compare native versus exotic species.

Fig. 1. A 2.6 km segment of Nippersink Creek, Illinois, USA, was filled in to make farming more efficient. Here, the meandering creek is being restored by excavating the historical channel, contouring the banks, anchoring mats to control erosion, adding a mulching blanket and seeds to encourage native vegetation, and planting propagules of aquatic plants. The project has multiple goals: reduction of flooding downstream; improved water quality; habitat for fish, wading birds and waterfowl; and involvement of youngsters in the process (Ed Collins, project director and restoration ecologist with the McHenry County Conservation District, pers. commun.). Photo by J. Zedler.

Environmental conditions and life history traits must be considered when restoring biodiversity

A current debate[9] over 'self-design' and 'designer-wetland' approaches concerns the need to create conditions that foster natural recruitment and allow

Table 1. Relevant theories and concepts of community development and methods for overcoming constraints on community maturation[a–c]

Ecological theory	Potential actions
Island biogeography theory	
Dispersal limitation	Sow seeds, plant propagules and add perches to facilitate bird dispersal
Establishment limitation	Provide high habitat heterogeneity, import substrate, amend soil and eliminate undesired species or competitors
Persistence limitation	Restore large habitat blocks, minimize fragmentation and provide corridors between habitat blocks
Niche theory	
Safe sites	Increase micropographic heterogeneity to improve germination
Fundamental and realized niches	Plant species in suitable microsites, conduct pilot plantings to identify suitable habitats and plant more broadly in Phase 2[d]
Ecotypic variation	Plant appropriate genotypes and provide genetic variation for future selection
Self-design theory	Establish physical and chemical conditions that will favor desired species, anticipate changes, and assume that species (planted or volunteer) will 'find' suitable habitats
Assembly rules	Prepare site so that it will support late-succession species, plant them early and combine compatible species (e.g. members of different functional groups)
Hydrarch succession	Plant submergents, floating aquatics and emergents at appropriate water depths
Population theory	
Minimum viable populations	Introduce larger numbers of propagules
Metapopulation dynamics	Provide multiple habitat patches and dispersal corridors
Competition theory – competitive exclusion	Tend plantings to speed growth (fertilize, mulch, weed, control herbivory and treat disease)
Priority effects	Introduce desired species early and introduce larger and/or older individuals to shorten the time to dominance
Facilitation	Provide nurse plants or surrogate structures to trap seeds and/or reduce stress on seedlings; plant individuals in clusters; and inoculate soil with mycorrhizae
Invasion theory (exotic species)	Remove invaders by hand or machine; use herbicides or pesticides; smother with black plastic or mulch; introduce fast-growing cover crops
Trophic theory	
Herbivory theory (intermediate grazing hypothesis)	Employ moderate grazing and/or mowing to reduce dominance by a few species and to promote species richness
Trophic cascade	Introduce carnivores to regulate herbivores and promote plant growth
Keystone species	Introduce top carnivores that feed opportunistically and increase animal diversity (e.g. starfish on rocky shores); and introduce animals that increase habitat heterogeneity (e.g. alligators and beavers)
Disturbance theory	Provide flood pulses at appropriate intervals for streams and rivers; burn wetlands to control shrubs and trees; and fence out animals that disturb sites in undesirable ways or introduce animals that enhance diversity by opening patches in dense canopies

[a]See Box 4 for relevant theories and concepts of development.
[b]Data compiled from ecology textbooks and Refs 9,15.
[c]Many theories and concepts could be considered components of succession theory and are relevant to the wetland restoration. The list is not exhaustive, but the selections illustrate how complex restoration can be and how difficult it is to predict how a specific wetland ecosystem will develop.
[d]Phase 2: species are planted in suitable microsites, pilot plantings are conducted to identify suitable habitats and then the results are used to plant more broadly in subsequent phases.

the ecosystem to design itself over time[28] versus the planting of desired species required to achieve specific outcomes. Early similarities of two riverine wetlands, one planted with 12 species and one not planted, led Mitsch *et al.*[28] to assert that extensive planting is not necessary in the long term. This approach was rejected by van der Valk[29] for prairie potholes, where constraints on dispersal kept many species from reappearing. However, observations of marshes in both riverine and pothole settings concur that when hydrological regimes are restored, wetlands are readily colonized by some species, whereas rarer, more conservative or dispersal-limited species are unlikely to appear.

We need to know which environmental conditions favor the desired assemblage, which species need to be planted and what difference it will make if some species are missing. A restoration site in Tijuana Estuary (California, USA) was designed to support such research. In an experiment with eight marsh-plain halophytes, only three recruited readily; the other five would need to be planted to achieve biodiversity goals[10]. More species-rich plots achieved greater canopy complexity; thus, diversity enhanced the potential for wildlife support.

Predicting wetland restoration begins with succession theory

Although many restoration scientists[29] equate restoration with accelerating succession, restoration sites offer many challenges that have not been explored in naturally recovering ecosystems, thus requiring that we apply a broader knowledge of population and community dynamics (Box 4). There is high potential for exotic species to dominate and persist, thus halting succession. Cole[15] found two exotic species, reed canary grass and purple loosestrife (*Lythrum salicaria*), to dominate restored wetlands in Pennsylvania even though native species were planted. Also, hydrological conditions are likely to change rapidly in managed areas. Peterson and Teal[30] describe the breaching of dikes in Delaware Bay (Delaware, USA) to restore tidal

Box 4. Ecological theory: its (in)adequacy for predicting wetland restoration outcomes

Succession theory is central to ecological restoration[9,15]. In nature, a disturbed habitat immediately begins to change and it continues to develop over centuries. Ecologists recognize broad patterns where sites of different ages occur within a region or when large-scale disturbances are followed over time[41]. However, following the eruption of Mount Saint Helens, 'reality defied predictions'[42]. Community development occurred more rapidly than expected and small refuges played a larger role than predicted[42]. Although ecosystem recovery can be perceived as an orderly progression when viewed over long periods at a regional scale (e.g. 200 years for spruce forests that follow glacial melting in Alaska), shorter term, smaller scale patterns are hard to predict.

Restorationists seek to achieve a mature community in a short time by overcoming many constraints (Box 3). Further complicating predictability, restorationists employ site-specific actions to accelerate the developmental process (Table 1), and each action has the potential to change the trajectory of ecosystem development in ways that are largely uncharted. One can argue that following larger restoration sites for longer periods would show that succession theory can predict outcomes. One can also argue that the outcomes of many restoration sites cannot be predicted, because succession theory does not accommodate smaller scale, shorter term, site-specific patterns. The fact remains that wetland restorationists are often charged with achieving specific outcomes on small sites in short periods (Box 3), although the ability to predict specific outcomes is lacking for such settings, even for well studied communities.

marshes as 'sudden destruction (of the extant vegetation) rather than progressive succession'. The appearance of vegetation is sudden and unnaturally synchronized when seedlings or plants of uniform size are introduced to large areas. By contrast, during succession, vegetation develops in patches and involves vegetative expansion from the wetland edge. Such unnatural plantings can attract herbivores en masse; for example, herbivore damage at the San Diego Bay and Tijuana Estuary restoration sites was greater than previously seen in natural salt marshes[10].

Genotypes influence ecosystem structure and function

Long suspected but rarely tested, it is now clear that genetic differences within species can affect restoration outcomes. Seliskar[31] planted cordgrass (*Spartina alterniflora*) from Georgia, Delaware and Massachusetts (USA) into a tidal wetland restoration site in Delaware. The genotypes from different locations differed in stem density and height, belowground biomass and depth distribution, decomposition rate, and carbohydrate allocation; in addition, there were differences in the amount of edaphic chlorophyll and the presence of invertebrates in their respective localities[31]. The effect of introducing alternative strains of plants and animals to restoration sites deserves further research, to allow restorationists to make informed choices about whether genetic diversity should be manipulated (e.g. in reintroducing rare and endangered species).

These principles offer general guidance for wetland restoration, but practitioners will still experience surprise outcomes and an inability to explain them. The most promising antidote is to design the site as an experiment that tests alternative restoration approaches (see final section).

Restorability

Among the more interesting conclusions of recent research is that some degraded wetlands are not restorable. Three examples follow. In The Netherlands, drained fens resisted restoration of calciphilic plant species upon rewetting, even with surface water treatment to reduce nutrient loading and with calcium additions to reverse acidification[32]. Portnoy and Giblin[33] rewetted sediment cores from diked salt marshes and tracked changes in several biogeochemical attributes. They documented subsidence, increased sulfide concentrations and nutrient releases, and cautioned that restoration through dike breaching should be done slowly and carefully. Craft *et al.*[6] found that soil OM was lost readily but re-accumulated slowly. It is clear that restoring wetland soil is complicated; even if degraded soils can be restored, the time frame might be decades or even centuries.

Not all authors agree that wetlands can be engineered to match natural ecosystems. For example, LaSalle *et al.*[34] give salt marshes planted on dredge spoil deposits a positive assessment, whereas others[35,36] report shortcomings. Some disagreements are based on the use of different variables; thus, standard indicators of ecosystem function are needed. Animal species offer promise as indicators, and several are being used to model the hydrological restoration of the Kissimmee River[37] and the Everglades[19].

Whether biodiversity and function can be restored to levels observed in reference sites is particularly relevant to the policies and practices of mitigation (Box 1). Race and Fonseca's[38] review reaffirmed an earlier conclusion that both wetland area and function are lost in the process of restoring or constructing wetlands. The science base needs to be strengthened for this debate to be resolved.

Promising approaches for improving predictability

The desire to provide specific hydrological conditions (water quantity and quality) makes wetlands more difficult to restore than uplands (Table 2). Wetness especially affects biogeochemistry (e.g. acidification upon drainage is sometimes irreversible upon rewetting) and the importance of microtopography (e.g. subsidence or accretion of only 10 cm can shift composition to alternative plant assemblages). The effect of altering the timing, frequency, amplitude and duration of high water levels has not been adequately explored; thus, desired results cannot be guaranteed. At the same time, predictable results are much more necessary for wetlands, because mitigation requires that specific targets be met. To achieve predictability, we need bolder, more science-based approaches.

Table 2. Desirable wetland functions (services) and methods of facilitating their development in restoration sites[a]

Desired function (examples)	Potential actions (examples)
Nutrient removal	Position wetland appropriately, adjust water residence time, and for wastewater treatment wetlands, harvest plants to remove nutrients
Sediment removal	Slow water flow, and provide a basin to trap heavy sediments and allow clean-out
Shoreline-erosion control	Plant vegetation to anchor substrate
Flood-peak reduction	Position wetlands appropriately
Groundwater recharge	Provide sandy substrate and slow water flow

[a]The specific hydrological regime is crucial to the restoration of each function.

The design of restoration sites to incorporate experiments, such as the comparison of genotypes[31], offers great promise for advancing the science of wetland restoration. The idea has been extended to evaluate how many and which species to plant, and whether tidal creeks need to be excavated in a phased program of 'adaptive restoration' at Tijuana Estuary[10]. Future restoration sites could be designed to test other aspects of topographic heterogeneity, to compare methods of controlling exotic species, to test the ability of wetlands to maximize both biodiversity and functions, to explore the idea of using more southerly species or ecotypes in anticipation of global climate change, and to assess the costs and benefits of alternative restoration strategies. With experimentation should come greater predictability, at least among wetlands with a similar degradation history and similar restoration action[11].

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References

1 Costanza, R. *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature* 387, 253–259
2 National Research Council (1992) *Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy,* National Academy Press
3 Streever, W.J. (1999) Performance standards for wetland creation and restoration under Section 404. *National Wetlands Newsletter*, May–June, pp. 10–13
4 Ehrenfeld, J.G. (2000) Defining the limits of restoration: the need for realistic goals. *Restor. Ecol.* 8, 2–9
5 Zedler, J.B. and Callaway, J.C. Evaluating the progress of engineered tidal wetlands. *Ecol. Eng.* (in press)
6 Craft, C.B. *et al.* (1999) Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecol. Appl.* 9, 1405–1419
7 Dobson, A.P. *et al.* (1997) Hopes for the future: restoration ecology and conservation biology. *Science* 227, 515–522
8 Galatowitsch, S. and van der Valk, A. (1994) *Restoring Prairie Wetland: An Ecological Approach*, Iowa State University Press
9 Middleton, B. (1999) *Wetland Restoration, Flood Pulsing, and Disturbance Dynamics*, John Wiley & Sons
10 Zedler, J.B., ed. *Handbook for Restoring Tidal Wetlands (Marine Science Series)*, CRC Press (in press)
11 Zedler, J.B. (1999) The ecological restoration spectrum. In *An International Perspective on Wetland Rehabilitation* (Streever, W.R., ed.), pp. 301–318, Kluwer Academic Publishers
12 Brinson, M.M. (1993) *A Hydrogeomorphic Classification Of Wetlands*, Wetlands Research Program Technical Report WRP-DE-4 (U.S. Army Engineer Waterways Experiment Station), U.S. Army Corps of Engineers, Washington, DC
13 Bedford, B. (1999) Cumulative effects on wetland landscapes: links to wetland restoration in the United States and southern Canada. *Wetlands* 19, 775–788
14 Simenstad, C.A. and Thom, R. (1996) Functional equivalency trajectories of the restored Gog-Le-Hi-Te estuarine wetland. *Ecol. Appl.* 6, 38–56
15 Cole, C.A. (1999) Ecological theory and its role in the rehabilitation of wetlands. In *An International Perspective on Wetland Rehabilitation* (Streever, W.R., ed.), pp. 232–243, Kluwer Academic Publishers
16 Gwin, S. *et al.* (1999) Evaluating the effects of wetland regulation through hydrogeomorphic classification and landscape profiles. *Wetlands* 19, 477–489
17 Magee, T. *et al.* (1999) Floristic comparison of freshwater wetlands in an urbanizing environment. *Wetlands* 19, 517–534
18 Hunt, R.H. *et al.* (1999) Characterizing hydrology and the importance of ground water discharge in natural and constructed wetlands. *Wetlands* 19, 458–472
19 de Angelis, D.L. *et al.* (1998) Landscape modeling for Everglades ecosystem restoration. *Ecosystems* 1, 64–75
20 Shaffer, P. and Ernst, T. (1999) Distribution of soil organic matter in freshwater emergent/open water wetlands in the Portland, Oregon metropolitan area. *Wetlands* 19, 505–516
21 Wheeler, B.D. *et al.* (1995) *Restoration of Temperate Wetlands*, John Wiley & Sons
22 van der Hoek, D. and Braakhekke, W. (1998) Restoration of soil chemical conditions of fen-meadow plant communities by water management in The Netherlands. In *European Wet Grasslands: Biodiversity, Management and Restoration* (Joyce, C. and Wade, P., eds), pp. 265–275, John Wiley & Sons
23 Tallowin, J. *et al.* (1998) Residual effects of phosphorus fertilization on the restoration of floristic diversity to wet grassland. In *European Wet Grasslands: Biodiversity, Management and Restoration* (Joyce, C. and Wade, P., eds), pp. 249–263, John Wiley & Sons
24 Bakker, J.P. *et al.* (1997) Options for restoration and management of coastal salt marshes in Europe. In *Restoration Ecology and Sustainable Development* (Urbanska, K. *et al.*, eds), pp. 259–285, Cambridge University Press
25 Puurmann, E. and Ratas, U. (1998) The formation, vegetation and management of sea-shore grasslands. In *European Wet Grasslands: Biodiversity, Management and Restoration* (Joyce, C. and Wade, P., eds), pp. 97–110, John Wiley & Sons
26 Straskrabova, J. and Prach, K. (1998) Five years of restoration of alluvial meadows: a case study from Central Europe. In *European Wet Grasslands: Biodiversity, Management and Restoration* (Joyce, C. and Wade, P., eds), pp. 295–303, John Wiley & Sons
27 Galatowitsch, S. *et al.* (1999) Revegetation strategies for northern temperate glacial marshes and meadows. In *An International Perspective on Wetland Rehabilitation* (Streever, W., ed.), pp. 205–223, Kluwer Academic Publishers
28 Mitsch, W. *et al.* (1998) Creating and restoring wetlands. *Bioscience* 48, 1019–1030
29 van der Valk, A. (1998) Succession theory and restoration of wetland vegetation. In *Wetlands for the Future* (McComb, A.J. and Davis, J., eds), pp. 657–667, Gleneagles Publishing
30 Peterson, S.B. and Teal, J. (1998) The gap between social and ecological theory in wetland restoration. In *Wetlands for the Future* (McComb, A.J. and Davis, J., eds), pp. 669–678, Gleneagles Publishing
31 Seliskar, D. (1995) Exploiting plant genotypic diversity for coastal salt marsh creation and restoration. In *Biology of Salt-Tolerant Plants* (Khan, M.A. and Ungar, I.A., eds), pp. 407–416, Department of Botany, University of Karachi, Pakistan
32 van Duren, I.C. *et al.* (1998) A multidisciplinary evaluation of restoration measures in a degraded *Cirsio-Molinietum* fen meadow. *Appl. Veg. Sci.* 1, 115–130
33 Portnoy, J.W. and Giblin, A.E. (1997) Biogeochemical effects of seawater restoration to diked salt marshes. *Ecol. Appl.* 7, 1054–1063
34 LaSalle, M.W. *et al.* (1991) Evaluation of the flora and fauna of a *Spartina alterniflora* marsh established on dredged material in Winyah Bay, South Carolina. *Wetlands* 11, 91–208
35 Minello, T.J. and Webb, J.W. (1997) Use of natural and created *Spartina alterniflora* marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Mar. Ecol. Prog. Ser.* 151, 165–179
36 Melvin, S.L. and Webb, J.W. (1998) Differences in the avian communities of natural and created *Spartina alteriflora* salt marshes. *Wetlands* 18, 59–69
37 Dahm, C.N. *et al.* (1995) An ecosystem view of the restoration of the Kissimmee River. *Restor. Ecol.* 3, 225–238
38 Race, M. and Fonseca, M. (1996) Fixing compensatory mitigation: what will it take? *Ecol. Appl.* 6, 94–101
39 National Research Council (1996) *Wetlands Characteristics and Boundaries,* National Academy Press
40 Robb, J.G. (2000) *Indiana Wetland Compensatory Mitigation: Inventory,* Progress Report to US Environmental Protection Agency by Indiana Department of Environmental Management, Indianapolis
41 Barbour, M. *et al.* (1999) *Terrestrial Plant Ecology* (3rd edn), Addison Wesley Longman
42 Franklin, J.F. and MacMahon, J.A. (2000) Messages from a mountain. *Science* 288, 1183–1185