

Structural and Functional Loss in Restored Wetland Ecosystems

David Moreno-Mateos^{1,2*}, Mary E. Power¹, Francisco A. Comín³, Roxana Yockteng⁴

1 Integrative Biology Department, University of California at Berkeley, Berkeley, California, United States of America, **2** Jasper Ridge Biological Preserve, Stanford University, Woodside, California, United States of America, **3** Department of Conservation of Biodiversity and Ecosystem Restoration, Pyrenean Institute of Ecology – CSIC, Zaragoza, Spain, **4** UMR CNRS 7205, Muséum National d'Histoire Naturelle, Paris, France

Abstract

Wetlands are among the most productive and economically valuable ecosystems in the world. However, because of human activities, over half of the wetland ecosystems existing in North America, Europe, Australia, and China in the early 20th century have been lost. Ecological restoration to recover critical ecosystem services has been widely attempted, but the degree of actual recovery of ecosystem functioning and structure from these efforts remains uncertain. Our results from a meta-analysis of 621 wetland sites from throughout the world show that even a century after restoration efforts, biological structure (driven mostly by plant assemblages), and biogeochemical functioning (driven primarily by the storage of carbon in wetland soils), remained on average 26% and 23% lower, respectively, than in reference sites. Either recovery has been very slow, or postdisturbance systems have moved towards alternative states that differ from reference conditions. We also found significant effects of environmental settings on the rate and degree of recovery. Large wetland areas (>100 ha) and wetlands restored in warm (temperate and tropical) climates recovered more rapidly than smaller wetlands and wetlands restored in cold climates. Also, wetlands experiencing more (riverine and tidal) hydrologic exchange recovered more rapidly than depressional wetlands. Restoration performance is limited: current restoration practice fails to recover original levels of wetland ecosystem functions, even after many decades. If restoration as currently practiced is used to justify further degradation, global loss of wetland ecosystem function and structure will spread.

Citation: Moreno-Mateos D, Power ME, Comín FA, Yockteng R (2012) Structural and Functional Loss in Restored Wetland Ecosystems. *PLoS Biol* 10(1): e1001247. doi:10.1371/journal.pbio.1001247

Academic Editor: Michel Loreau, McGill University, Canada

Received: May 27, 2011; **Accepted:** December 8, 2011; **Published:** January 24, 2012

Copyright: © 2012 Moreno-Mateos et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: Support for this research came from Spanish Ministry for Innovation and Science (www.micinn.es) and Spanish Foundation for Science and Technology through the postdoctoral mobility grants program, and from the National Centre for Earth Surface Dynamics (nced.umn.edu), an NSF Science and Technology Center. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: davidmor@stanford.edu

Introduction

From tropical mangroves to boreal peatlands, wetlands are amongst the most productive and economically valuable ecosystems in the world [1]. They provide critical ecosystem goods and services, including carbon storage, biodiversity conservation, fish production, fuel production, water purification, flood and shoreline surge protection and erosion control, and recreation [1–3]. However, owing to human activities, over half of the wetland ecosystems existing in the early 20th century have been lost in North America, Europe, Australia, and China [2]. Over the last century, restoration of degraded wetlands and creation of new ones have been attempted, in efforts to recover physical, chemical, and biological processes and entities lost because of wetland destruction or degradation [4]. Frequently, however, this approach does not restore ecosystem structure and functions to preimpact levels [5–8]. In North America (including Canada, United States, and Mexico) alone, over US\$70 billion have been spent attempting to restore more than 3,000,000 ha of wetlands in the last 20 y (see Text S1) [9], but the recovery trajectories of structure and functions in restored wetlands have not yet been globally assessed [10,11].

After degradation or natural perturbation, ecosystem structure and functions recover towards reference levels [7,12], but recovery

rates might be affected by the physical characteristics of the ecosystem, the degrading activity, or the environmental setting [7,12]. Abiotic factors, such as size of restored ecosystems and climate, might affect recovery rates. It could be expected that intensely engineered small (few hectares) wetlands might recover faster than less manipulated, large wetlands (hundreds of hectares) to their original characteristics, but this prediction remains unconfirmed. Higher recovery rates could also be expected in warmer climates than in cold ones, because of accelerated ecosystem processes [7,13]. Restoration efforts during the recovery process may lead ecosystems to reference states or redirect them towards alternative states [14–16] that could also be initiated by prerecovery disturbance itself. If recovery is slow, it could be difficult to distinguish between these alternatives. We surveyed long-term (up to 100 y, available for some but not all of the studied variables) chronosequences of restored wetland ecosystems from 621 restored and created wetlands relative to 556 reference wetlands (Figure S1). Following Article 1.1 of the Ramsar Convention of Wetlands [17], we considered wetlands to be marshes, peatlands, floodplains, mangroves, depressional wetlands, and lacustrine wetlands—submerged permanently or periodically under flowing or still fresh, salty, or brackish water. We compared structure and function of 401 wetlands restored on sites where they had been previously degraded and 220 newly

Author Summary

Wetlands, which include tropical mangroves and boreal peatlands, are among the most valuable ecosystems in the world because they provide critical ecosystem goods and services, such as carbon storage, biodiversity conservation, fish production, water purification, and erosion control. As global change accelerates the loss of wetlands, attempts are increasing to restore this fragile habitat and its associated functioning. There has been no global evaluation, however, of how effective such restoration efforts have been. Here, we present a meta-analysis of the biological structure (driven mostly by plant communities) and biogeochemical functioning (driven primarily by the storage of carbon in wetland soils) of 621 wetland sites. Our analysis suggests that even a century after restoration efforts, these parameters remained on average 26% and 23% (respectively) lower in restored or created wetlands than in reference wetlands. Our results also indicate that ecosystem size and the environmental setting significantly affect the rate of recovery. Recovery may be more likely and more rapid if more than 100 contiguous hectares of habitat are restored. In warm climates, and in settings linked to riverine or tidal flows, recovery can also proceed more rapidly. In general, however, once disturbed, wetlands either recover very slowly or move towards alternative states that differ from reference conditions. Thus, current restoration practice and wetland mitigation policies will maintain and likely accelerate the global loss of wetland ecosystem functions.

created wetlands (wetland creation *de novo* is currently accepted for environmental mitigation [4]). We also examined how size of ecosystem and its environmental setting (climate regime and hydrologic connectivity) affected recovery. Using a standardized method (see Materials and Methods), we selected 124 studies (see Text S2) in which ecological responses were measured at known time intervals since restoration. From the selected studies, we extracted 1,501 data points (Tables 1, S1, and S2) comparing hydrologic, biological, and biogeochemical variables in restored or created and reference wetlands. Response ratios (see Materials and Methods) were calculated for each data point. Variables selected

from the same studies were not necessarily independent (see Materials and Methods), so statistical inferences must be interpreted cautiously.

We compared recovery trajectories of hydrologic, biological, and biogeochemical variables of restored and created wetlands to address three questions: (a) How fast are biological and biogeochemical components of restored ecosystems changing relative to less perturbed reference ecosystems?; (b) Do these changes trend towards or away from the predisturbed ecosystem or parallel control ecosystems?; and (c) Does wetland size or environmental setting (regional climate, hydrologic connectivity) affect recovery?

Results/Discussion

Hydrologic and Biological Recovery

Some hydrologic features can often be restored by manipulating local topography, soil permeability, surface and ground water flows—physical features that are usually engineered in wetland restoration projects. Hydrological features defined for these analyses (Table 1) appeared to be recovered immediately after restoration (Figure 1A), but see Cole [18], Hunt et al. [19], Ahn and Dee [20], and Kumar and Zhao [21] for deeper considerations of challenges to hydrologic restoration in wetlands (from factors like climate variation [20] or complex flow paths of water through heterogeneous vegetation and soils [21]). In addition, all hydrologic variables reported in studies we reviewed were followed only for 10 y to 15 y, so longer-term changes remain unknown.

In contrast to reported hydrologic performance, biological structure (as defined in Table 1) in restored or created wetlands, recovered to only 77% (on average) of reference values (Figure 1A and 1B; Table S3), even 100 y after restoration, when data on 14 taxa from two studies of three wetland sites are available [22,23]. Abundance, species richness, and diversity of native animals and plants in wetlands were severely reduced following degradation. After restoration, recovery proceeded at different rates, and trajectories plateaued at different levels. Vertebrate assemblages reached similar structural values to those in reference wetlands within 5 y (Figure 1B). Vertebrate richness recovered more slowly than abundance ($p=0.021$; Figure 2A), possibly reflecting responses by a few highly mobile vertebrate species [24,25] once

Table 1. Variables measured simultaneously in restored or created and reference wetlands to estimate wetland restoration performance over time.

Wetland Structure and Functions	n^a	Variables Measured
Hydrology	32	Water level, flooding regime, water storage
Biological components	809	
Vertebrates	166	Abundance, density, species richness, occupancy
Macroinvertebrates	161	Density, abundance, species richness
Plants	439	Plant cover, species richness, biomass, abundance
Biogeochemistry	692	
Carbon storage and cycling	103	Soil total and organic carbon, respiration rate, mineralization rate
Nitrogen storage and cycling	102	Soil total and organic nitrogen, denitrification, and nitrification
Phosphorus storage	103	Soil total and organic phosphorus, Ca-Fe-Al bounded phosphorus
Other elements storage	106	Salinity, soil Fe, Al, Ca, K, Mn, Mg, water dissolved oxygen
Organic matter accumulation	177	Soil organic matter, bulk density, soil texture, soil moisture

Only the most frequently measured variables were included (see Tables S1 and S2, for full description of the variables measuring restoration performance).

^a n = number of variables used to plot each chronosequence.

doi:10.1371/journal.pbio.1001247.t001

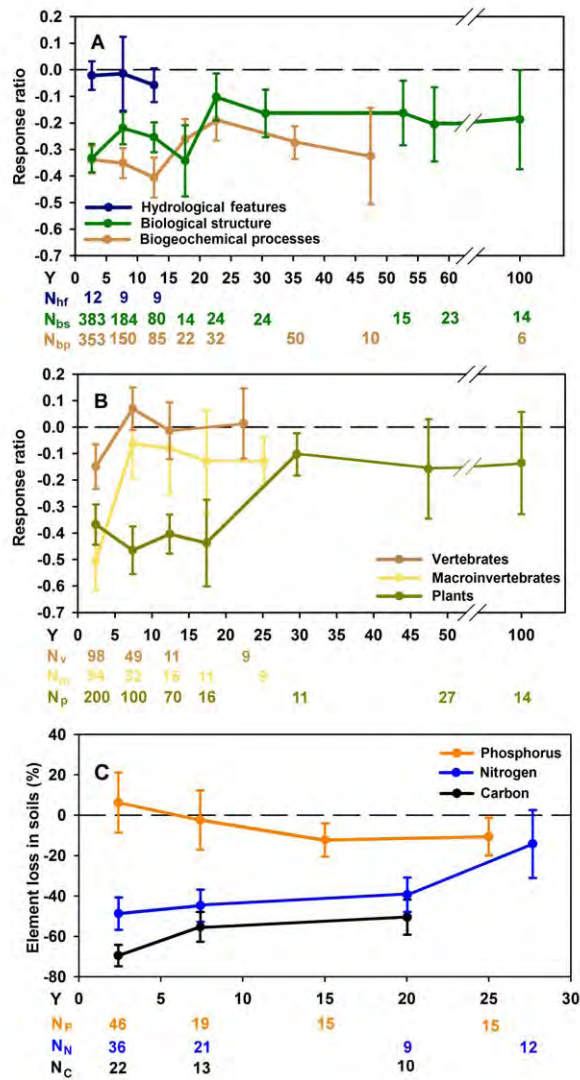


Figure 1. Recovery trajectories of created and restored wetlands. Chronosequences of the means (\pm standard error [SE]) of the response ratios (see Materials and Methods) of restored and created wetlands at successive age classes of 5 y or 10 consecutive y for hydrology, biological structure, and biogeochemical functions (A) and for the main biological structural components (B). Chronosequences of the means (\pm SE) of the element loss in soils of restored or created wetlands at successive age classes of 5 y or 10 consecutive y (C). The zero value dashed line represents reference wetlands. Only trend lines for those variables for which we had enough data points (see Materials and Methods) were plotted (N, number of data points used to calculate the mean [\pm SE] per age class; Y, years after restoration. Subscripts are as follows: bp, biogeochemical processes; bs, biological structure; C, carbon; hf, hydrological features; m, macroinvertebrates; N, nitrogen; p, plants; P, phosphorus; v, vertebrates). doi:10.1371/journal.pbio.1001247.g001

hydrological connectivity was restored. Macroinvertebrates (64% noninsects) took 5 y to 10 y to statistically converge with reference assemblages in restored and created wetlands (Figure 1B), and average values never reached absolute reference levels. Many macroinvertebrates cannot recolonize new or restored wetlands by themselves, but are carried in by flowing water or other organisms [26,27]; however, their short life cycles (often annual or semi-

annual) could accelerate population recovery after they arrive [28,29].

Plant assemblages in restored and created wetlands were slowest to recover. Plants took on average 30 y to converge statistically with reference states; although again, absolute average values of structural features of plant assemblages remained lower than reference levels even after 100 y following restoration (Figures 1B and 2B). The slow and incomplete recovery of plant assemblage might be due to dispersal limitation, vulnerable early life history stages, or sensitivity of any life stage to altered conditions (e.g., reduced organic content of soils, discussed below) during early succession following disturbance [30,31]. Other factors, such as exotic colonists, subsequent disturbance or altered disturbance regimes, priority effects (historical legacies), and nonlinear interactions may also lead to delayed recovery or persistent differences between restored biota and those in reference wetlands [6,31,32].

Biogeochemical Recovery

Four biogeochemical responses were sufficiently well documented in some studies we reviewed to examine trends over time: these were the storage of carbon, nitrogen, and phosphorus (Figure 1C) (see also storage and cycling combined for carbon and nitrogen in Figure S2A), and the accumulation of organic matter in soil (Figure S2B). The storage and cycling of carbon and nitrogen were drastically reduced from preimpact levels after degradation. In contrast, phosphorus storage seemed unaffected. After restoration, responses were variable. Initially, carbon storage increased slightly but then plateaued below reference levels; nitrogen storage and cycling increased slowly but continuously; and phosphorus storage remained unaffected. Wetland degradation notoriously oxidizes stores of accumulated organic carbon and releases CO_2 to the atmosphere, as aerobic conditions accelerate microbial respiration [2,33]. After wetland hydrologic regimes are recovered, more anaerobic conditions allow stores of organic carbon to slowly reaccumulate in the soil. After 20 y, however, carbon storage in restored and created wetland soils was still significantly lower (by 50%; $p = 0.008$) than in reference wetlands (Figure 1C; Table S3; Text S1; data from six studies of 21 wetlands). Organic matter accumulated slowly [34,35], so that average values remained only 62% of the value at the reference wetlands 20–30 y following restoration (Figure S2B; data from seven studies of 21 wetlands).

Aerobic conditions in degraded wetlands also perturb nitrogen storage and cycling, allowing mineralization of organic N and transformation of ammonium to nitrate [2]. Nitrate is quickly processed by microorganisms and plants, leaving the original pool of nitrogen in the soil depleted or unavailable. Nitrogen storage remained significantly lower in restored wetlands for 30 y after the wetlands were restored or created (Figure 1C; Table S3). Depleted or unavailable soil nitrogen can limit wetland productivity, retarding carbon storage [33,36]. In contrast, total phosphorus decreased only slightly in restored or created wetlands and did not show significant differences with reference wetlands (Figure 1C). Although, phosphorus chemical fractions could change in representation, the amount of total phosphorus did not change significantly [37]. This lack of variation in phosphorus might be explained because of the more conservative cycling by phosphorus (lack of exchange with the atmosphere) [38]. In addition, without extrinsic inputs, phosphorus levels would be geologically determined.

After 50 y to 100 y, restored wetlands recovered only to an average of 74% of their biogeochemical functioning relative to reference wetlands (Figure 1A; data from two studies of seven wetlands; data of wetlands recovering for more than 50 y after

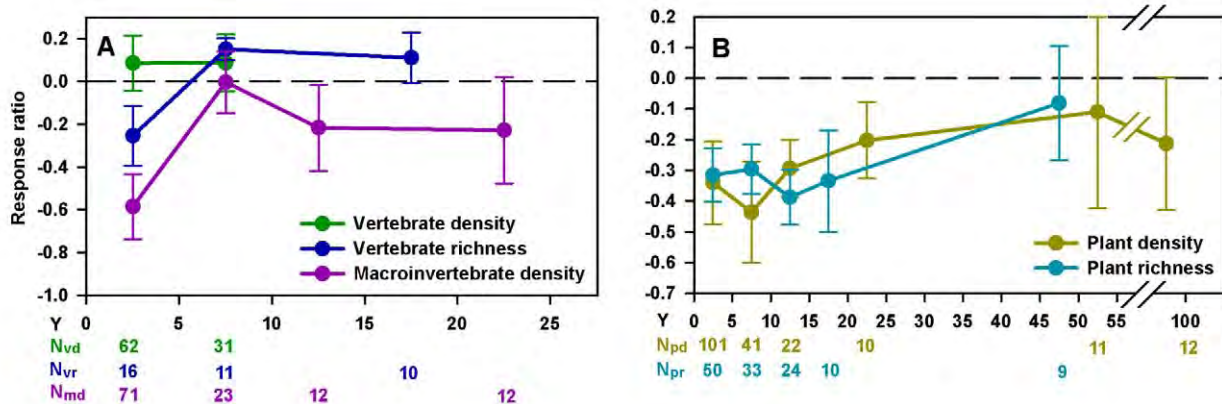


Figure 2. Recovery trajectories of animal and plant richness and density. Chronosequences of the means (\pm standard error [SE]) of the response ratios (see Materials and Methods) of restored or created wetlands at successive age classes of 5 y or 10 consecutive y for vertebrates and macroinvertebrates density and richness (A) and for plant density and richness (B). Insufficient data points meeting our plotting criteria (see Materials and Methods) were available to plot for macroinvertebrate richness. The zero value dashed line represents reference wetlands (N, number of data points used to calculate the mean (\pm SE) per age class; Y, years after restoration). Subscripts are as follows: md, macroinvertebrates density; pd, plant density; pr, plant richness; vd, vertebrate density; vr, vertebrates richness). doi:10.1371/journal.pbio.1001247.g002

restoration were not plotted in Figure 1A because the sample size did not meet our criteria for average points, see Materials and Methods section, on this graph). Since phosphorus storage appeared only slightly changed, the overall lack of recovery of biogeochemical functioning may have been driven largely by the low recovery of the carbon storage and the low accumulation of soil organic matter (see Text S1).

Effects of Size and Environmental Setting

Comparing wetland recovery trajectories under different conditions may shed light on factors that impede or facilitate recovery. Although biogeochemical responses in both restored and created wetlands were similar, biological structure in created wetlands approached reference conditions more quickly (Figure S3A and S3B; Table S5). Created wetlands may have been engineered to force the initial system towards defined reference conditions [39].

Ecosystem size and local and regional context affect wetland recovery. Large wetlands (>100 ha) appeared to recover their biological structure and biogeochemical functions sooner after restoration or creation than smaller wetlands (Figures 3 and S4; Table S4; data from 13 studies of 25 wetlands). This differential recovery suggests that small wetlands may not provide adequate local resources or connectivity for local biota to restore preimpact functioning. Restored and created wetlands, particularly if small, may have become more isolated and surrounded by more fragmented landscapes than they had been before impact [40]. Also, small wetlands would only be able to support a limited number of individuals, and thus, will not be able to support all the species, particularly taxa with large body sizes, formerly capable of occupying the area [41].

Regional climate had a strong effect on the sequence and rate of wetland recovery following restoration. As expected, warm temperatures accelerate ecosystem processes [7,13,42], including those mediating biological and biogeochemical recovery after wetland restoration or creation. In tropical and summer-warm temperate climates, wetlands approached reference conditions relatively rapidly, while wetlands restored in cold climates had not recovered to reference conditions after 50 y (Figure 4A and 4B; Tables S3 and S5). In tropical climates only, biogeochemical

variables recovered to reference levels before biological structure did (data from eight studies of eight wetlands). Whether this difference in recovery sequence is a real aspect of tropical wetlands, or an artifact of small sample size, remains to be seen. In a much larger sample of studies from temperate climates this sequence was reversed, and biogeochemical recovery was slower. Biological structural variables appeared recovered 5 y after restoration, while even 30 y after restoration, biogeochemical functions had only recovered to 79% of reference levels (data from 83 studies of 302 wetlands). In cold climates, corresponding biogeochemical recovery was only 53% 50 y after restoration; both biogeochemical functions and biological structure variables

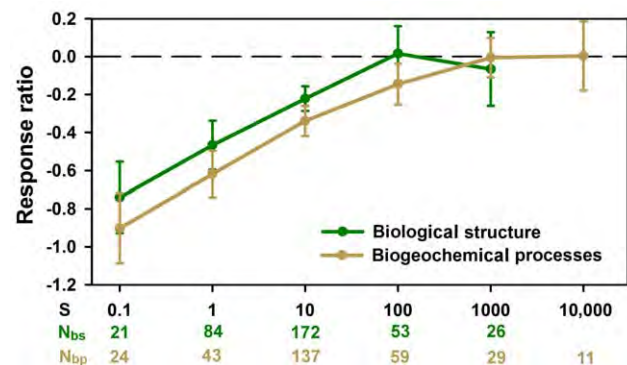


Figure 3. Effect of size on wetland recovery. Evolution of the mean (\pm standard error [SE]) of the response ratios (see Materials and Methods) of restored or created wetlands at successive size categories for wetlands between 0 y to 5 y after restoration or creation. The zero value dashed line represents reference wetlands. Mean (\pm SE) at 0.1 ha was estimated for wetlands with sizes \leq 0.1 ha. Means (\pm SE) at 1 ha were estimated for wetlands in which sizes ranged between 0.1 ha and 1 ha. The same approach was used to estimate the means (\pm SE) at 10, 100, 1,000, and 10,000 ha (N, number of data points used to calculate the mean (\pm SE) per age class; size, size in hectares of the restored wetlands. Subscripts are as follows: bp, biogeochemical processes; bs, biological structure). doi:10.1371/journal.pbio.1001247.g003

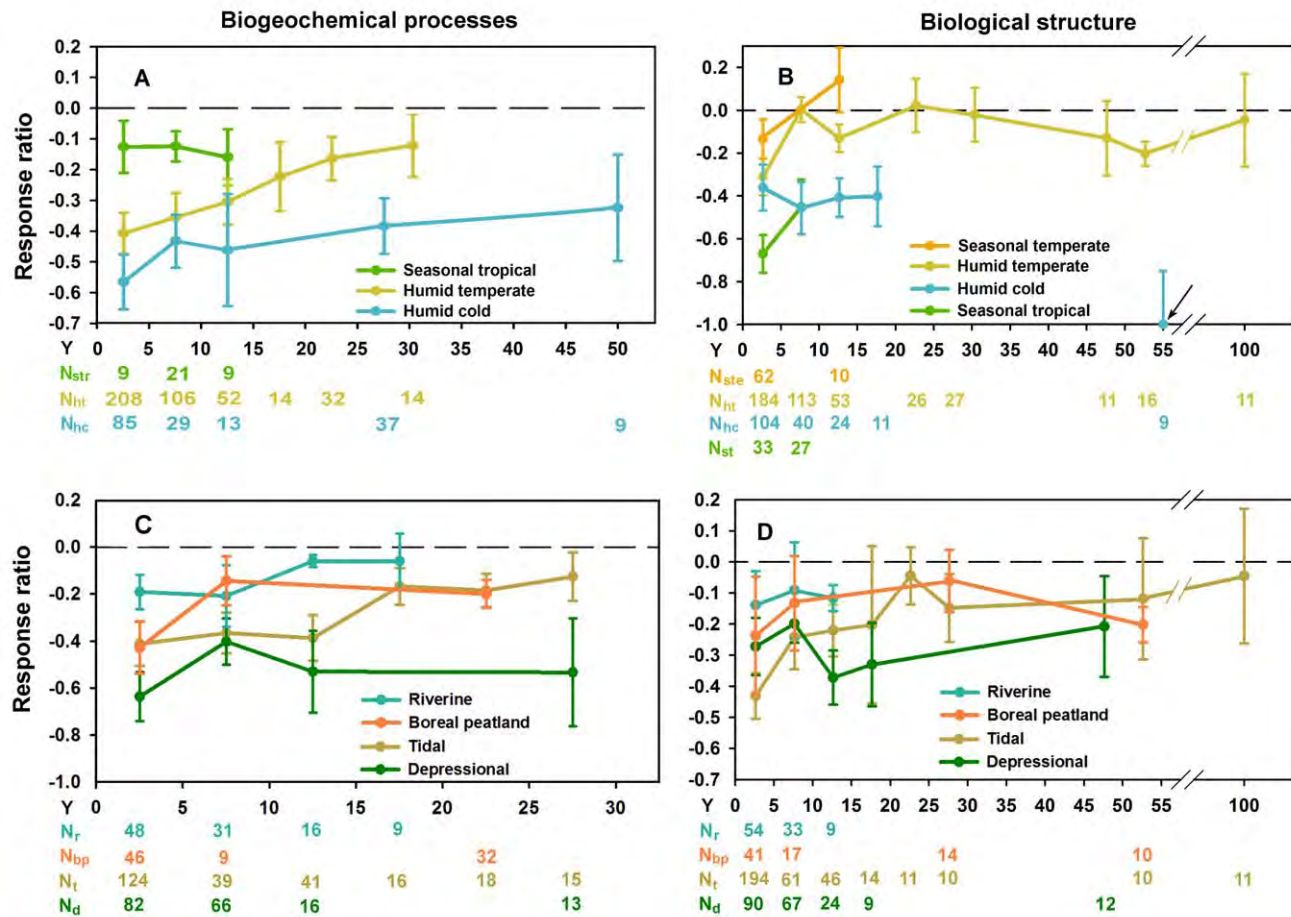


Figure 4. Effects of climate and hydrology on wetland recovery trajectories. Chronosequences of the means (\pm standard error [SE]) of the response ratios (see Materials and Methods) of restored and created wetlands at successive age classes of 5 y or 10 consecutive y for biogeochemical functions and for biological structures under contrasting climates (A and B), and under different hydrologic connectivity (C and D) [31]. The zero value dashed line represents reference wetlands. The arrow (B) indicates the outlier mean value of two restoration studies with extremely low recovery rates (N, number of data points used to calculate the mean (\pm SE) per age class; Y, years after restoration). Subscripts are as follows: bp, boreal peatland; d, depression; hc, humid cold; ht, humid temperate; r, riverine; str, seasonal tropical; ste, seasonal temperate; t, tidal). doi:10.1371/journal.pbio.1001247.g004

remained statistically distinct from reference conditions for the entire (50-y) chronosequence (Figure 4A and 4B; Tables S3 and S5; data from 33 studies of 311 wetlands).

Hydrologic setting [43] also affected recovery (Figure 4C and 4D; Tables S3 and S5). Riverine and tidal wetlands, linked to larger hydrologic regimes by natural flow variation, recovered biogeochemical functions and biological structure after 20 y and 30 y, respectively (data from 73 studies of 210 wetlands). These results are similar to those (15 y to 25 y to recover the original biotic composition and diversity) found by Borja et al. [8] in 51 globally distributed estuarine and coastal ecosystems. In contrast, wetlands in inland depressions that were watered by precipitation or groundwater flow had not recovered to reference conditions even after 50 y following restoration (data from 36 studies of 358 wetlands). Peatlands (usually only the upper layer [<1 m] of peat was removed) recovered biological structure immediately, but 30 y after restoration, biogeochemical functioning in peatlands remained statistically lower than in reference wetlands (data from 11 studies of 18 wetlands).

Slow Recovery or Alternative States?

Two hypotheses could explain the lag in biological and biogeochemical recovery of the biological structure and biogeo-

chemical functioning. First, the chronosequences we examined may be too short (<30 y) for full recovery, especially of carbon and nitrogen storage [44]. Second, restored wetlands may have shifted to alternative states, different from their condition before degradation [14,15]. The subreference plateaus of soil organic accumulation, carbon storage, and general biogeochemical functioning could support the second hypothesis of alternative states in restored systems. Slow recovery of plant density and richness might be linked to lags in carbon storage. Mutualist symbionts critical for plant productivity (e.g., N-fixing bacteria [2] or mycorrhizal fungi [45]) may be absent in recently (<50 y) restored wetland soils. Alternatively, fast-growing, early successional terrestrial plants, and potentially also wetland plants, usually allocate most of their carbon to photosynthetically active structures of low density and high nutrient content, which are easily grazed or rapidly decomposed, retarding local storage of carbon [46,47].

Comparison with Other Findings

Two other studies have assessed recovery rates of large scale natural ecosystems following disturbance or perturbations [7,12]. Both of these studies examined a broad range of ecosystem types (terrestrial, freshwater, and marine), including wetlands. Jones and

Schmitz [12] found that across ecosystems and perturbation types (natural and human-caused), about half of the tracked response variables were considered by original authors to have recovered to preimpact states. Jones and Schmitz computed averaged recovery times for the subsamples of variables and cases that primary authors considered to have recovered over the course of their studies. These recovery times ranged from about 10 y to 40 y, and were longer for forests, and following human-caused, rather than natural perturbations. To assess whether systems had recovered or not, Jones and Schmitz used authors' expert opinion, return to historic initial conditions, or approach to parallel reference states (our study evaluated recovery only for studies using the last of these criteria). Given the narrower scope of our study (assessing wetlands only), and our different analysis approach, estimated recovery times from these two reviews are surprisingly similar. Rey Benayas et al. [7] studied recovery across a wide range of human-perturbed ecosystems, including wetlands. Using (as we did) the response ratio of restored to reference ecosystems, Benayas et al. found biodiversity and selected ecosystem services to be 86% and 80% recovered in a sample of 89 cases pooled over all age categories since perturbation. Interestingly, they reported slightly (6%) higher recovery in biological variables compared to ecosystem services (nutrient cycling; primary production; provisioning of timber, fish, and food crops; and regulation of climate, water supply, and soil). These ecosystem services overlap in part with categories of biogeochemical variables in our study (e.g., carbon and nutrient storage and cycling). The similarity between their results and our finding (that biological variables were 9% more recovered than these biogeochemical responses) suggests that structural recovery might often be necessary to achieve functional recovery.

Conclusions

Our meta-analysis suggests that recovery of wetlands following restoration as currently practiced is often slow and incomplete. In warm climates, and in settings linked to riverine or tidal flows, recovery may proceed more rapidly. Recovery may also be more likely and more rapid if >100 contiguous ha are restored. In many wetlands, however, ecosystem services may not be fully recovered even when wetlands appear to be biologically restored. If markets for ecosystem services and mitigation offsets from restored or created wetlands are used to justify further wetland degradation, net loss of global wetland services will continue and likely accelerate (see also Race and Fonseca [48]). We join other wetland ecologists and restoration scientists in calling for better scientific understanding of biotic and abiotic factors that constrain ecosystem restoration. For our common future, we need more realistic, long-term evaluations to find better ways to alleviate constraints limiting the recovery of wetland ecosystems.

Materials and Methods

Literature Search

On the 22nd of December 2010 a reference search was done in the scientific database ISI Web of Science – SCI-Expanded. The terms used were “(wetland* or floodplain* or peatland* or marsh* or mangrove*) same (restor* or creat* or re-creat* or rehabilit*)”. We used these terms to cover a wide variety of wetlands as defined in the Article 1.1 of the Ramsar Convention text [7]. For this analysis, we considered restored wetlands to be wetlands recreated on sites where wetlands had formerly existed but been drained or otherwise severely degraded. Created wetlands were described by authors as wetlands built on sites that lacked previous wetland history. We selected studies of wetlands under natural hydrological regimes, planted with native species, and in which no allochtho-

nous substrates were imported during the restoration or creation activities. For this reason, the term “construct*” was not included in the search terms, because we found in an independent search that >99% of the studies of constructed wetlands were of highly artificial systems not maintained under natural conditions. The search produced 2,959 selected articles. We applied the general selection criterion: “Articles must compare measurements of structural components and biogeochemical processes in restored or created and reference wetlands at a known age.” Under this criterion we selected 172 articles. These articles were read, and those in which data were averaged over time intervals larger than 5 y, those in which sizes differing by more than one order of magnitude were averaged, and those lacking reliable measurements or comparable restored and reference conditions were discarded, leaving 124 articles (see Text S2). Reference wetlands were usually adjacent to restored or created wetlands, although in some cases they were separated by several kilometers (maximum distance found was ~100 km). In all cases, restored or created wetlands were of the same wetland hydrogeomorphic type [17] as reference wetlands with which they were compared. From the selected articles, six were carried out on experimental wetlands, the rest were carried out on wetland restoration or creation projects. Studies either described measurements at a known age after wetlands were restored or created, or a chronosequence of the progression during the wetland restoration process. Restored and created wetlands were located in 12 countries and totaled >21,294 ha in area and reference wetlands >19,694 ha. The exact total area is not known because it was not reported in 23 out of the 124 selected studies.

Data Extraction

Measurements of structural components and biogeochemical processes were extracted from the main text, tables, and figures of the articles. When abundance of one species was measured at different life stages, only the adult abundance of each species was selected. Variables describing hydrological structure, biological structure, element storage and cycling, and organic matter accumulation were classified as structural components or biogeochemical processes according to wetland functions described by Smith et al. [42], and as ecosystem services described in the Millennium Ecosystem Assessment (MEA) (organic matter accumulation was sometimes designated as “soil formation” in the MEA but not in other soil science references) [49].

Element storage and cycling variables measured processes (mineralization or denitrification) and concentration of elements in different pools (total content in soil, organic content in soil, or content in roots), which suggest how nutrients are moving between pools through biotic and abiotic processes (Tables S1 and S2). The studies presented enough data points to plot recovery of storage of carbon, nitrogen, and phosphorus.

Response Ratio Calculation

To standardize and compare data, we used standard response ratios used in meta-analysis, $\ln(X_{rest}+1/X_{ref}+1)$ [3], where X_{rest} is the value of the measured variable in the restored or created wetland and X_{ref} is the value of the measured variable in the reference wetland. To avoid the value “0” in the natural logarithm of the equation, “1” was added to both values in restored or created and reference wetlands. The effect of adding “1” to the values in the response ratio equation has been demonstrated to have little effect on conclusions [50]. The effect size was not weighted because variance was reported for only 64% of the variables. Differences between weighted and unweighted meta-analysis statistics are generally small [7].

As variables depicting structural components and biogeochemical processes in restored or created wetlands converged to values in the reference wetlands, recovery of function was generally enhanced. But for some variables, such as soil bulk density [51,52], or proportions of exotic species [53,54], higher values are associated with lower levels of wetland recovery. In some cases, the specific context of a study made variables negative for recovery of a particular restored wetland, e.g., the presence of woody species where none had occurred in the reference wetlands [55,56]. In these cases (11% of the collected variables), we changed the sign to reverse the value of the response ratio.

Data Classification

For each variable we recorded the age of the restored or created wetland, the wetland hydrogeomorphic type, the number of restored or created and reference wetlands considered in a given study, the size (ha) of the restored or created and reference wetlands, the initial condition (restored or created), the geographic location, and the climate. Most data (49%) were from wetlands that had been restored or created for less than 5 y (Figure S1). If data from several wetlands of different sizes were averaged in the study, then we also averaged the sizes for our analysis. The geographic location was registered as the latitude and longitude in degrees of the center of the wetland or group of wetlands. The climate was classified according to the last revision of the Köppen-Geiger climate classification [57]. We used the name humid temperate climate for Cf climate, humid cold climate for Df climate, seasonal temperate climate for Cs climate (with dry summer), and seasonal tropical for A climates. Two of our sampled studies were done in seasonal temperate climate with dry winter (Köppen-Geiger climate classification Cw), and were not considered in our climate study. Wetland hydrogeomorphic type was classified according to Brinson [58] and Smith et al. [42] as depressional, riverine, tidal, peatland, lacustrine, and seeping slope. Only three studies were on lacustrine wetlands and one on seeping slope wetlands, so these types were not considered in our study of differences among wetland types.

In studies where more than one wetland was studied and data were available for each individual wetland, data were collected for each wetland. In 27 studies, more than one wetland was compared with the same reference wetland, and in 11 studies, restored or created wetlands were compared with more than one reference wetland. All studies where more reference rather than restored or created wetlands were studied provided only averaged data for both groups of wetlands. We calculated contingency tables between the wetland size, the initial conditions (created versus restored), and the covariates included in the environmental setting section (climate and wetland hydrogeomorphic type), using contingency coefficients (C), to test for independence between them. Wetland type showed relevant degrees of association with the climate ($C=0.63$) and wetland size ($C=0.58$), the rest of variables had coefficients below 0.5, indicating low degree of association. These associations may be explained by the influence of the climate on wetland types, e.g., peatlands are usually associated to cold climates, and mangroves to tropical climates. Also, peatlands usually extend over vast surfaces (hundreds or thousands of hectares) and depressional wetlands are usually small basins (less than 10 ha or few tens of hectares).

Statistical Analysis

Because data were non-normally distributed (according to the Kolmogorov-Smirnoff test for normality), we used Wilcoxon signed rank tests to test for significant deviations from zero (no

difference from reference conditions) for each estimated mean of the response ratios for variables at each age interval of a restored or created wetland. To test for differences between the same variable measured under two different environmental settings at a given recovery time, we used Kruskal-Wallis tests.

Chronosequences Plotting

To plot the temporal trends, the mean values and the standard error of each variable with every age class of 5 y (0–4.9, 5–9.9, etc) were used. The criterion for a mean for a certain age class to be used in the plot was that it must have been derived from at least nine different data points obtained from at least two different studies. When this criterion was not fulfilled, the mean values and standard error of age classes of 10 y (e.g., 10–19.9, or 20–30) were used. Temporal trend lines were fitted when enough data to calculate means for two or more age classes were available.

Supporting Information

Figure S1 Distribution of wetland sizes across wetland ages for the 654 restored and created wetlands considered in the study.

(TIF)

Figure S2 Chronosequences for the storage and cycling of carbon and nitrogen (A), and for the accumulation of organic matter in soils (B).

(TIF)

Figure S3 Chronosequences for biogeochemical processes (A) and for biological structures (B) under contrasting initial conditions (restored wetlands versus wetlands created de novo in dry lands).

(TIF)

Figure S4 Evolution of the response ratios of restored or created wetlands at successive size categories for wetlands between 5 y to 15 y after restoration or creation.

(TIF)

Table S1 Variables measuring structural components.

(DOC)

Table S2 Variables measuring biogeochemical processes.

(DOC)

Table S3 Statistical significance of differences between the means of the response ratios in restored or created versus reference wetlands.

(DOC)

Table S4 Statistical significance of differences between the means of the response ratios in restored or created versus reference wetlands at each size interval.

(DOC)

Table S5 Statistical significance of differences between the response ratios in restored or created wetlands under different environmental settings.

(DOC)

Text S1 Wetland restoration investment and carbon storage calculation.

(DOC)

Text S2 References used in the meta-analysis.

(DOC)

Acknowledgments

We acknowledge the comments from Joy B. Zedler, Oswald Schmidt, J.M. Rey Benayas, William E. Dietrich, Andrea Swei, and one anonymous reviewer on earlier versions of the manuscript, and the collaboration of Maribel Vara Rodriguez.

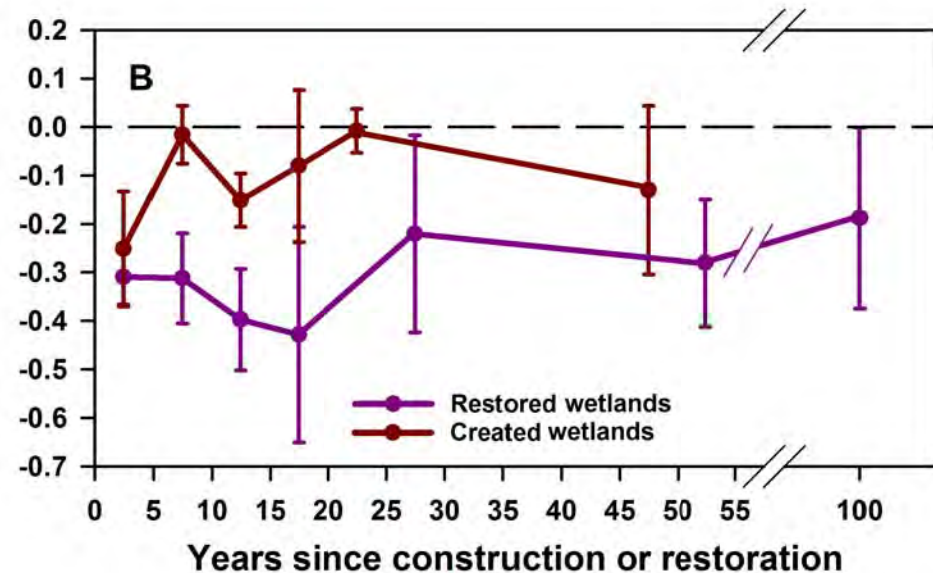
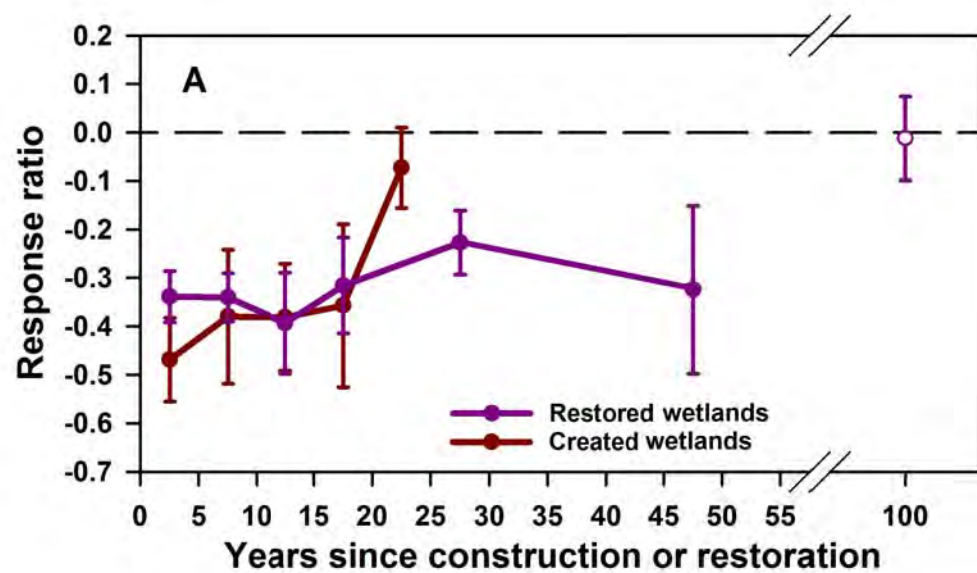
References

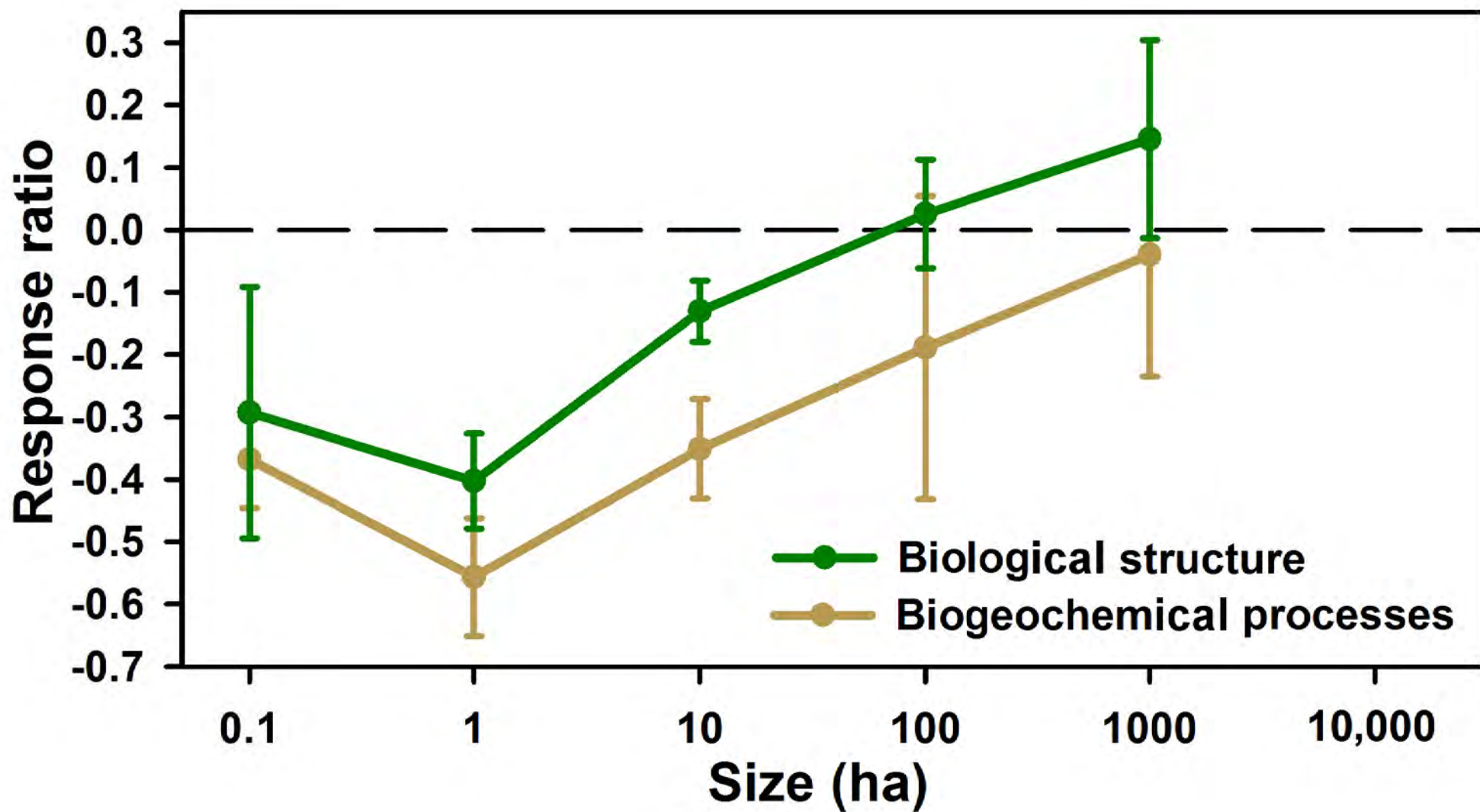
- Costanza R, d'Arge R, deGroot R, Farber S, Grasso M, et al. (1997) The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Mitsch WJ, Gosselink JG (2007) *Wetlands*. Hoboken (New Jersey): John Wiley & Sons, Inc. pp 177–183.
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: wetlands and water*. Washington (D.C.): World Resources Institute.
- Palmer MA (2009) Reforming watershed restoration: science in need of application and applications in need of science. *Estuaries Coasts* 32: 1–17.
- Matthews JW, Endress AG (2008) Performance criteria, compliance success, and vegetation development in compensatory mitigation wetlands. *Environ Manage* 41: 130–141.
- Zedler JB, West JM (2008) Declining diversity in natural and restored salt marshes: a 30-year study of Tijuana Estuary. *Restor Ecol* 16: 249–262.
- Rey Benayas JM, Newton AC, Diaz A, Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325: 1121–1124.
- Borja A, Dauer DM, Elliott M, Simenstad CA (2010) Medium- and long-term recovery of estuarine and coastal ecosystems: patterns, rates and restoration effectiveness. *Estuaries Coasts* 33: 1249–1260.
- Copeland C (2010) *Wetlands: an overview of issues*. Washington (D.C.): Congressional Research Service. RL33483.
- Palmer MA, Filoso S (2009) Restoration of ecosystem services for environmental markets. *Science* 325: 575–576.
- Zedler JB (2000) Progress in wetland restoration ecology. *Trends Ecol Evol* 15: 402–407.
- Jones HP, Schmitz OJ (2009) Rapid recovery of damaged ecosystems. *Plos One* 4: e5653. doi:10.1371/journal.pone.0005653.
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, et al. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol Evol* 24: 599–605.
- Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* 19: 46–53.
- Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* 24: 271–279.
- Ramsar Convention Secretariat (2006) *The Ramsar Convention Manual: a guide to the Convention on Wetlands (Ramsar, Iran, 1971)*, 4th edition. Gland, Switzerland: Ramsar Convention Secretariat.
- Cole CA (1999) *Ecological theory and its role in the rehabilitation of wetlands*. Streever WR, ed. An international perspective on wetland rehabilitation. Dordrecht, The Netherlands: Kluwer Academic Publishers. pp 232–243.
- Hunt RJ, Walker J, Krabbenhoft D (1999) Characterizing hydrology and the importance of ground-water discharge in natural and constructed wetlands. *Wetlands* 19: 458–472.
- Ahn C, Dee S (2011) Early development of plant community in a created mitigation wetland as affected by introduced hydrologic design elements. *Ecol Eng* 37: 1324–1333.
- Kumar JLG, Zhao YQ (2011) A review on numerous modeling approaches for effective, economical and ecological treatment wetlands. *J Environ Manage* 92: 400–406.
- Collins BD, Montgomery DR (2002) Forest development, wood jams, and restoration of floodplain rivers in the Puget Lowland, Washington. *Restor Ecol* 10: 237–247.
- Crooks S, Schutten J, Sheern GD, Pye K, Davy AJ (2002) Drainage and Elevation as Factors in the Restoration of Salt Marsh in Britain. *Restor Ecol* 10: 591–602.
- Lesbarreres D, Fowler MS, Pagano A, Lode T (2010) Recovery of anuran community diversity following habitat replacement. *J Appl Ecol* 47: 148–156.
- 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.
- Levin LA, Talley TS (2002) Natural and manipulated sources of heterogeneity controlling early faunal development of a salt marsh. *Ecol Appl* 12: 1785–1802.
- Figuerola J, Green AJ, Michot TC (2005) Invertebrate eggs can fly: evidence of waterfowl-mediated gene flow in aquatic invertebrates. *Am Nat* 165: 274–280.
- Badosa A, Frisch D, Arechederra A, Serrano L, Green AJ (2010) Recovery of zooplankton diversity in a restored Mediterranean temporary marsh in Doñana National Park (SW Spain). *Hydrobiologia* 654: 67–82.

Author Contributions

The author(s) have made the following declarations about their contributions: Conceived and designed the experiments: DMM MEP. Analyzed the data: DMM. Wrote the paper: DMM MEP. Performed the meta-analysis: DMM RY. Interpreted and discussed results from the meta-analysis: DMM MEP FAC.

- Meyer CK, Whiles MR (2008) Macroinvertebrate communities in restored and natural Platte River slough wetlands. *J N Am Benthol Soc* 27: 626–639.
- Donath TW, Holzel N, Otte A (2003) The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Appl Veg Sci* 6: 13–22.
- Matthews JW, Endress AG (2010) Rate of succession in restored wetlands and the role of site context. *Appl Veg Sci* 13: 346–355.
- Zedler JB, Callaway JC (1999) Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restor Ecol* 7: 69–73.
- Knops JMH, Tilman D (2000) Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81: 88–98.
- Ballantine K, Schneider R (2009) Fifty-five years of soil development in restored freshwater depressional wetlands. *Ecol Appl* 19: 1467–1480.
- Bechtold JS, Naiman RJ (2009) A quantitative model of soil organic matter accumulation during floodplain primary succession. *Ecosystems* 12: 1352–1368.
- van Groenigen KJ, Six J, Hungate BA, de Graaff MA, van Breemen N, et al. (2006) Element interactions limit soil carbon storage. *Proc Natl Acad Sci U S A* 103: 6571–6574.
- Lawrence D, Schlesinger WH (2001) Changes in soil phosphorus during 200 years of shifting cultivation in Indonesia. *Ecology* 82: 2769–2780.
- Smil V (2000) Phosphorus in the environment: natural flows and human interferences. *Annu Rev Energ Env* 25: 53–88.
- Korfel CA, Mitsch WJ, Hetherington TE, Mack JJ (2010) Hydrology, physiochemistry, and amphibians in natural and created vernal pool wetlands. *Restor Ecol* 18: 843–854.
- Maurer BA (2006) *Ecological restoration from a macroscopic perspective*. Falk DA, Palmer MA, Zedler JD, eds. Foundations of restoration ecology. Washington (D.C.): Island Press.
- Whittaker RJ (2006) *Island biogeography: ecology, evolution, and conservation*. Oxford, UK: Oxford University Press.
- Anderson-Teixeira KJ, Vitousek PM, Brown JH (2008) Amplified temperature dependence in ecosystems developing on the lava flows of Mauna Loa, Hawai'i. *Proc Natl Acad Sci U S A* 105: 228–233.
- Brinson MM (1993) A hydrogeomorphic classification for wetlands. Washington (D.C.): US Army Corps of Engineers. WRP-DE-4. 103 p.
- Craft C, Magonigal P, Broome S, Stevenson J, Freese R, et al. (2003) The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecol Appl* 13: 1417–1432.
- Dolinar N, Gaberscik A (2010) Mycorrhizal colonization and growth of *Phragmites australis* in an intermittent wetland. *Aquat Bot* 93: 93–98.
- Kardol P, Wardle DA (2010) How understanding aboveground belowground linkages can assist restoration ecology. *Trends Ecol Evol* 25: 670–679.
- De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol Lett* 11: 516–531.
- Race MS, Fonseca MS (1996) Fixing compensatory mitigation: what will it take? *Ecol Appl* 6: 94–101.
- Smith RD, Ammann A, Bartoldus C, Brinson MM (1995) An approach for assessing wetland functions using hydrogeomorphic classification, reference wetlands, and functional indices. Washington (D.C.): US Army Corps of Engineers.
- Scheiner SM, Gurevitch J (2001) *Design and analysis of ecological experiments*. Cary/North Carolina: Oxford University Press, Incorporated.
- Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, et al. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989–992.
- Marvier M, McCreedy C, Regetz J, Kareiva P (2007) A meta-analysis of effects of Bt cotton and maize on nontarget invertebrates. *Science* 316: 1475–1477.
- Craft C, Broome S, Campbell C (2002) Fifteen years of vegetation and soil development after brackish-water marsh creation. *Restor Ecol* 10: 248–258.
- Ballantine K, Schneider R (2009) Fifty-five years of soil development in restored freshwater depressional wetlands. *Ecol Appl* 19: 1467–1480.
- Gutrich JJ, Taylor KJ, Fennessy MS (2009) Restoration of vegetation communities of created depressional marshes in Ohio and Colorado (USA): the importance of initial effort for mitigation success. *Ecol Eng* 35: 351–368.
- Parikh A, Gale N (1998) Vegetation monitoring of created dune swale wetlands, Vandenberg Air Force Base, California. *Restor Ecol* 6: 83–93.
- Zampella RA, Laidig KJ (2003) Functional equivalency of natural and excavated coastal plain ponds. *Wetlands* 23: 860–876.
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15: 259–263.





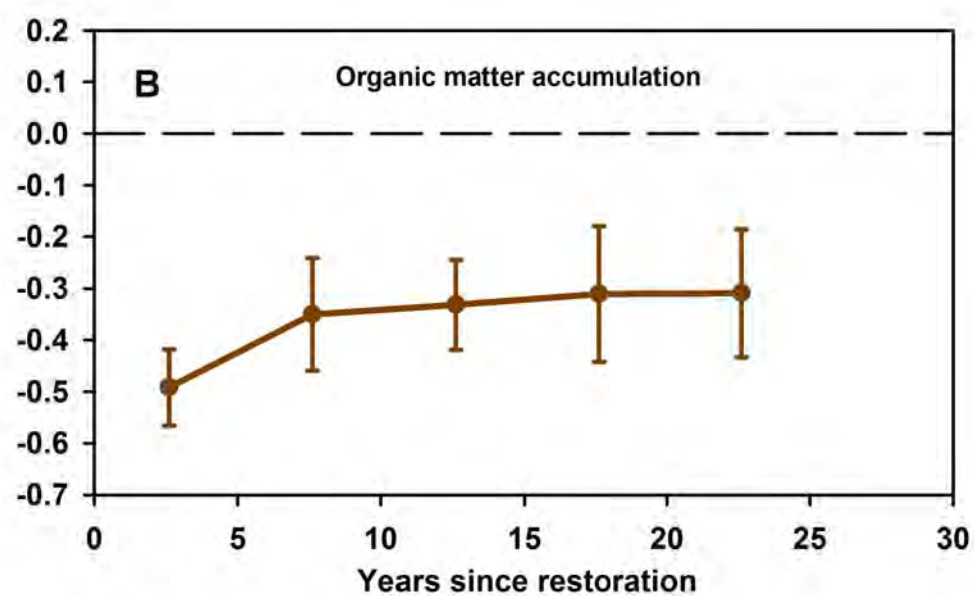
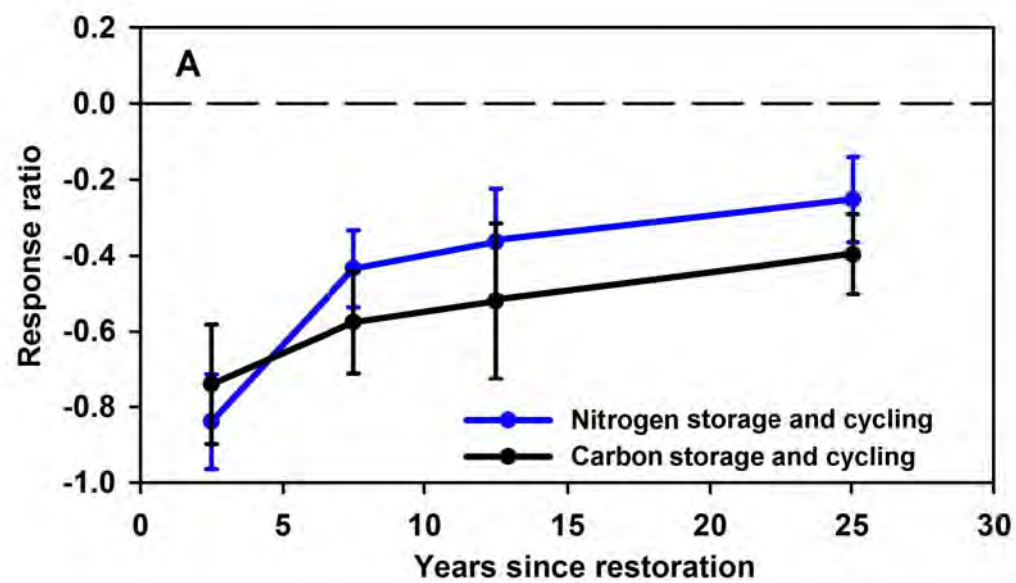


Table S1. Variables measuring structural components (n=809) simultaneously in restored or created and reference wetlands to estimate wetland restoration performance along a 100-years chronosequence. The last column (n) indicates the number of variables used in the analysis representing more than 5% of the total number of variables (N=number of variables used to plot the chronosequence).

Hydrological structure (N=34)	Units	n
Water level	m	12
Flooding regime	unitless index	10
Water storage	unitless index	6
Biological structure (N=775)		
Vertebrates (N=166)		
Density	individuals/area or sample unit	42
Abundance	individuals/wetland	41
Absolute species richness	no. spp/wetland	29
Relative abundance	% spp of a functional or taxonomical group	18
Occupancy	% of ecosystem units occupied by one species	11
Diversity	Shannon-Wiener index	10
Species richness per area unit	no. spp/area	6
Macroinvertebrates (N=161)		
Density	Individuals/area or sample unit	102
Relative abundance	% spp of a functional or taxonomical group	24
Absolute species richness	no. spp/wetland	12
Abundance	individuals/wetland	9
Species richness per sample or area unit	no. spp/sample or area	8
Diversity	Shannon-Wiener index	5
Plants (N=439)		
Plant cover	%	141
Plant species richness	no. spp/wetland	87
Plant biomass	g/m ²	75
Abundance	stems or individuals/area	19
Diversity	Shannon-Wiener index	15
Stem height	m	15
Basal area	m ² /ha	11
Seed density	seeds/m ² of soil	7
Species richness per area or sample unit	no. spp/sample or area	6

Table S2. Variables measuring biogeochemical functions (n=692) simultaneously in restored or created and reference wetlands to estimate wetland restoration performance along a 100-year chronosequence. The last column (n) indicates the number of variables used in the analysis representing more than 5% of the total number of variables. (N=number of variables used to plot the chronosequence).

Elements storage and cycling (N=471)	Units	n
Carbon storage and cycling (N=103)		
Soil organic C	mg C/g soil or g C/m ² soil or %	23
Soil total C	mg C/g soil or g C/m ² soil or %	23
Soil C:N	wt (g):wt (g)	16
Respiration	gC/g soil or m ² /time	15
C mineralization rate	μmol CO ₂ /g soil/s or g/m ² ·day	10
Root C content	g C/m ² soil	5
Nitrogen storage and cycling (N=102)		
Soil total N	mg N/g soil or g N/m ² soil or %	47
Soil organic NO ₃ and NH ₄	μg/cm ³ or μg/g	29
Denitrification and nitrification	ng CO ₂ /cm ³ ·hr	11
Phosphorus storage (N=103)		
Soil total P	mg P/g soil or μg P/cm ³ or g P/m ² soil or %	53
Soil PO ₄	mg P/g soil or μg P/cm ³	16
Soil organic P	μg P/cm ³ or mg P/g soil	16
Soil Ca, Fe, Al bounded P	μg P/cm ³ or mg P/g soil	9
Other elements storage (N=106)		
Salinity and conductivity	‰ or % or μg	19
Several forms of soil Fe	kg/ha or kmol/ha	14
Several forms of soil Ca	mg/kg	13
Dissolved oxygen	mg/L	12
Several forms of soil K	mg/kg	12
Several forms of soil Al	kg/ha or kmol/ha	11
Several forms of soil Mg	mg/kg	9
Several forms of soil Mn	kmol/ha or mg/kg	7
Organic matter accumulation (N=177)		
Soil organic matter	g C/m ² soil or %	64
Bulk density	g/cm ³	35
Soil texture	%	21
Soil moisture	g/cm ³	13
Soil porosity	%	6

Table S3. Statistical significance of differences between the means of the response ratios in restored or created versus reference wetlands at each age class in years (Wilcoxon ranked sign test)(nd = no data available, Proc.= processes, * this age class comprises 10 years starting at the beginning of the interval and ending at the end of the interval of the next age class)

Figure	Described variable	Years since restoration or creation (<i>p</i> values)									
		0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	50-55	55.1-60	100
1A	Biogeochemical proc.	0.000	0.000	0.000	0.001	0.011	nd	0.000*	0.023	nd	nd
1A	Biological structure	0.000	0.000	0.000	0.023	0.324	0.052*	nd	0.054	0.009	0.255
1A	Hydrological structure	0.395	0.500	0.155	nd	nd	nd	nd	nd	nd	nd
1B	Macroinvertebrate assemblage	0.000	0.233	0.139	0.249	0.062*	nd	nd	nd	nd	nd
1B	Plant assemblage	0.000	0.000	0.000	0.010	nd	0.221*	nd	0.096	nd	0.377
1B	Vertebrate assemblage	0.186	0.268	0.288	0.444	nd	nd	nd	nd	nd	nd
1C	Carbon storage	0.000	0.001	nd	0.008*	nd	nd	nd	nd	nd	nd
1C	Nitrogen storage	0.001	0.001	nd	0.008*	nd	0.440	nd	nd	nd	nd
1C	Phosphorus storage	0.249	0.687	0.125*	nd	nd	0.345*	nd	nd	nd	nd
3A	Biogeochemical proc. seasonal tropical	0.057	0.020	0.046	nd	nd	nd	nd	nd	nd	nd
3A	Biogeochemical proc. humid temperate	0.000	0.000	0.000	0.025	0.000	0.181*	nd	nd	nd	nd
3A	Biogeochemical proc. humid cold	0.00	0.000	0.037	nd	nd	0.000	nd	0.043	nd	nd
3B	Biological structure seasonal tropical	0.000	0.001	nd	nd	nd	nd	nd	nd	nd	nd
3B	Biological structure seasonal temperate	0.118	nd	0.124	nd	nd	nd	nd	nd	nd	nd
3B	Biological structure humid temperate	0.000	0.340	0.004	nd	0.424	0.281*	nd	0.297	0.002	0.464
3B	Biological structure. humid cold	0.000	0.000	0.000	0.010	nd	nd	nd	nd	nd	nd
3C	Biogeochemical depressionnal	0.000	0.000	0.004	nd	nd	0.014	nd	nd	nd	nd
3C	Biogeochemical riverine	0.002	0.058	0.007	0.249	nd	nd	nd	nd	nd	nd
3C	Biogeochemical tidal	0.000	0.000	0.000	0.018	0.016	0.276	nd	nd	nd	nd
3C	Biogeochemical peatland	0.000	nd	nd	nd	nd	0.000	nd	nd	nd	nd
3D	Biological structure depressionnal	0.000	0.010	0.000	0.018	nd	nd	nd	nd	nd	nd
3D	Biological structure riverine	0.160	0.459	0.010	nd	nd	nd	nd	nd	nd	nd
3D	Biological structure tidal	0.000	0.010	0.002	0.172	0.429	0.107	nd	0.254	nd	0.464
3D	Biological structure peatland	0.107	0.230	nd	nd	0.285	nd	nd	0.018	nd	nd
S2A	Carbon storage and cycling	0.000	0.000	0.009	nd	0.002*	nd	nd	nd	nd	nd
S2A	Nitrogen storage and cycling	0.000	0.000	0.003	nd	0.015*	nd	nd	nd	nd	nd
S2A	Phosphorus storage	0.123	0.326	0.032	nd	0.050*	nd	nd	nd	nd	nd

Figure	Described variable	Years since restoration or creation (<i>p</i> values)									
		0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	50-55	55.1-60	100
S2B	Accumulation organic matter	0.000	0.000	0.000	0.021	0.010	nd	nd	nd	nd	nd
S4A	Biogeochemical proc. restored	0.000	0.000	0.000	0.000	nd	0.000	nd	0.014	nd	nd
S4A	Biogeochemical proc. created	0.000	0.001	0.000	0.014	0.036	nd	nd	nd	nd	nd
S4B	Biological structure restored	0.000	0.000	0.000	0.019	nd	0.081	nd	0.002	nd	0.256
S4B	Biological structure created	0.004	0.449	0.003	0.297	0.500	nd	nd	0.254	nd	nd

Table S4. Statistical significance of differences between the means of the response ratios in restored or created versus reference wetlands at each size interval (Wilcoxon ranked sign test)(nd = no data available)

Figure	Described variable	Area (ha) (<i>p</i> values)					
		0-0.1	0.11-1	1.1-10	10.1-100	101-1000	1001-10,000
2	Biogeochemical processes	0.000	0.000	0.000	0.034	0.185	0.395
2	Biological structure	0.000	0.000	0.000	0.218	0.116	nd
S3	Biogeochemical processes	0.000	0.000	0.000	0.058	0.399	nd
S3	Biological structure	0.000	0.000	0.024	0.347	0.276	nd

Table S5. Statistical significance of differences between the means of the response ratios in restored or created wetlands under different environmental settings at each age class in years (Kruskal-Wallis test)(nd = no data available, Biol. Struct. = Biological structures, Biogeo. = Biogeochemical processes, * this age class comprises 10 years starting at the beginning of the interval and ending at the end of the interval of the next age class).

Figure	Described variable	Years since restoration or creation (<i>p</i> values)							
		0-5	5.1-10	10.1-15	15.1-20	20.1-25	25.1-30	30.1-35	50-55
3A	Biogeo. seasonal tropical vs. humid temp.	0.203	0.040	0.620	nd	nd	nd	nd	nd
3A	Biogeo. seasonal tropical vs. humid cold	0.064	0.012	0.316	nd	nd	nd	nd	nd
3A	Biogeo. humid temp. vs. humid cold	0.097	0.351	0.269	nd	nd	0.270	nd	nd
3B	Biol. struct. seasonal tropical vs. humid temp.	0.002	0.000	nd	nd	nd	nd	nd	nd
3B	Biol. struct. seasonal tropical vs. humid cold	0.009	0.351	nd	nd	nd	nd	nd	nd
3B	Biol. struct. seasonal tropical vs. seasonal temp.	0.000	nd	nd	nd	nd	nd	nd	nd
3B	Biol. struct. humid temp. vs. humid cold	0.292	0.000	0.021	nd	0.037*	nd	nd	0.006
3B	Biol. struct. humid temp. vs. seasonal temp.	0.197	nd	0.100	nd	nd	nd	nd	nd
3B	Biol. struct. seasonal temp vs. humid cold	0.029	nd	0.009	nd	nd	nd	nd	nd
3C	Biogeo. depressional vs. tidal	0.016	0.188	0.591	nd	nd	0.334	nd	nd
3C	Biogeo. depressional vs. peatland	0.129	nd	nd	nd	nd	0.339	nd	nd
3C	Biogeo. depressional vs. riverine	0.003	0.028	0.007	nd	nd	nd	nd	nd
3C	Biogeo. riverine vs. peatland	0.271	nd	nd	nd	nd	nd	nd	nd
3C	Biogeo. riverine vs. tidal	0.371	0.214	0.009	0.378	nd	nd	nd	nd
3C	Biogeo. tidal vs. peatland	0.491	nd	nd	nd	nd	0.564	nd	nd
3C	Biol. struct. depressional vs. peatland	0.886	0.913	nd	nd	nd	nd	nd	0.504
3C	Biol. struct. depressional vs. riverine	0.050	0.559	0.082	nd	nd	nd	nd	nd
3C	Biol. struct. depressional vs. tidal	0.509	0.564	0.224	0.867	nd	nd	nd	0.391
3C	Biol. struct. riverine vs. peatland	0.475	0.722	nd	nd	nd	nd	nd	nd
3C	Biol. struct. riverine vs. tidal	0.014	0.293	0.465	nd	nd	nd	nd	nd
3C	Biol. struct. tidal vs. peatland	0.454	0.608	nd	nd	nd	0.542	nd	0.320
S3A	Biogeo. restored vs. created	0.060	0.789	0.363	0.529	0.760	nd	nd	nd
S3B	Biol. struct. restored vs. created	0.749	0.005	0.010	0.103	nd	0.205	nd	0.950

Text S1

Wetland restoration investment

To estimate total wetland restoration costs, an estimate of the areal proportion of each type (riverine, tidal, and depressional) of restored and created wetlands was calculated from our data-set. These proportions were multiplied by a conservative estimation of the total amount of restored wetlands in North America in the last 20 years (3,000,000 ha)[1], then multiplied by the average price for that type of wetland provided by Zentner et al. 2003 [2]. These cost estimates were updated for 2010 with a 3% annual increase.

Carbon storage calculation

From our data-set, we selected only measurements of carbon accumulation (in g C/m², g/cm³, g/kg, or % of carbon in soil by weight) in the soil of restored or created and reference wetlands (n=47) excluding restored peatlands. All restored peatlands in our selected studies were not exploited until the mineral soil, thus, maintaining contents of carbon in superficial layers (<20 cm from the soil surface) similar to those in non-impacted reference peatlands. This specific situation would bias our results towards an apparent but unreal recovery. After, we calculated the percentage of carbon lost from the soil by dividing the values at restored and created wetland by the amount of carbon in reference wetland soils. We calculated the average of this value for zero to five years, 5.1 to 10 years, and 10.1 to 25 years after restoration, according with the availability of data-points. Carbon loss of restored and created wetlands was 69% compared to reference wetlands after zero to five years, and 56% after five to 10 years of restoration.

Text S2

References used in the meta-analysis

1. Copeland C, A. Zinn J (2008) Wetlands: An Overview of Issues. Washington, DC: Congressional Research Service. RL33483.
2. Zentner J, Glaspy J, Schenk D (2003) Wetland and Riparian Woodland Restoration Costs. *Ecol Restor* 21: 166-173.
3. Aldous A, McCormick P, Ferguson C, Graham S, Craft C (2005) Hydrologic regime controls soil phosphorus fluxes in restoration and undisturbed wetlands. *Restor Ecol* 13: 341-347.
4. Armitage AR, Fong P (2004) Gastropod colonization of a created coastal wetland: Potential influences of habitat suitability and dispersal ability. *Restor Ecol* 12: 391-400.
5. Armitage AR, Jensen SM, Yoon JE, Ambrose RF (2007) Wintering shorebird assemblages and behavior in restored tidal wetlands in southern California. *Restor Ecol* 15: 139-148.
6. Aronson MFJ, Galatowitsch S (2008) Long-term vegetation development of restored prairie potholes wetlands. *Wetlands* 28: 883-895.
7. Ashworth SM (1997) Comparison between restored and reference sedge meadow wetlands in south-central Wisconsin. *Wetlands* 17: 518-527.
8. Balcombe CK, Anderson JT, Fortney RH, Kordek WS (2005) Wildlife use of mitigation and reference wetlands in West Virginia. *Ecol Eng* 25: 85-99.
9. Balcombe CK, Anderson JT, Fortney RH, Rentch JS, Grafton WN, et al. (2005) A comparison of plant communities in mitigation and reference wetlands in the mid-appalachians. *Wetlands* 25: 130-142.
10. Ballantine K, Schneider R (2009) Fifty-five years of soil development in restored freshwater depressional wetlands. *Ecol Appl* 19: 1467-1480.
11. BishelMachung L, Brooks RP, Yates SS, Hoover KL (1996) Soil properties of reference wetlands and wetland creation projects in Pennsylvania. *Wetlands* 16: 532-541.
12. Brawley AH, Warren RS, Askins RA (1998) Bird use of restoration and reference marshes within the Barn Island Wildlife Management Area, Stonington, Connecticut, USA. *Environ Manage* 22: 625-633.
13. Brown SC (1998) Remnant seed banks and vegetation as predictors of restored marsh vegetation. *Canadian Journal of Botany-Revue Canadienne De Botanique* 76: 620-629.
14. Brown SC (1999) Vegetation similarity and avifaunal food value of restored and natural marshes in northern New York. *Restor Ecol* 7: 56-68.
15. Brown SC, Smith CR (1998) Breeding season bird use of recently restored versus natural wetlands in New York. *J Wildl Manage* 62: 1480-1491.
16. Bruland GL, Richardson CJ, Whalen SC (2006) Spatial variability of denitrification potential and related soil properties in created, restored, and paired natural wetlands. *Wetlands* 26: 1042-1056.

17. Buchsbaum RN, Catena J, Hutchins E, James-Pirri MJ (2006) Changes in salt marsh vegetation, *Phragmites australis*, and nekton in response to increased tidal flushing in a new England salt marsh. *Wetlands* 26: 544-557.
18. Castillo JM, Leira-Doce P, Rubio-Casal AE, Figueroa E (2008) Spatial and temporal variations in aboveground and belowground biomass of *Spartina maritima* (small cordgrass) in created and natural marshes. *Estuarine Coastal and Shelf Science* 78: 819-826.
19. Cole CA, Brooks RP (2000) A comparison of the hydrologic characteristics of natural and created mainstem floodplain wetlands in Pennsylvania. *Ecological Engineering* 14: 221-231.
20. Cole CA, Urban CA, Russo P, Murray J, Hoyt D, et al. (2006) Comparison of the long-term water levels of created and natural reference wetlands in northern New York, USA. *Ecol Eng* 27: 166-172.
21. Cooper DS (2008) The use of historical data in the restoration of the avifauna of the Ballona Wetlands, Los Angeles County, California. *Nat Areas J* 28: 83-90.
22. Craft C, Broome S, Campbell C (2002) Fifteen years of vegetation and soil development after brackish-water marsh creation. *Restor Ecol* 10: 248-258.
23. 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: 1417-1432.
24. Craft C, Reader J, Sacco JN, Broome SW (1999) Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications* 9: 1405-1419.
25. Craft CB, Seneca ED, Broome SW (1991) Porewater chemistry of natural and created marsh soils. *J Exp Mar Biol Ecol* 152: 187-200.
26. Dawe NK, Bradfield GE, Boyd WS, Trethewey DEC, Zolbrod AN (2000) Marsh creation in a northern Pacific estuary: Is thirteen years of monitoring vegetation dynamics enough? *Conserv Ecol* 4.
27. Delphrey PJ, Dinsmore JJ (1993) Breeding bird communities of recently restored and natural prairie potholes. *Wetlands* 13: 200-206.
28. Desrochers DW, Keagy JC, Cristol DA (2008) Created versus natural wetlands: Avian communities in Virginia salt marshes. *Ecoscience* 15: 36-43.
29. Dodson SI, Lillie RA (2001) Zooplankton communities of restored depressional wetlands in Wisconsin, USA. *Wetlands* 21: 292-300.
30. Edwards KR, Proffitt CE (2003) Comparison of wetland structural characteristics between created and natural salt marshes in southwest Louisiana, USA. *Wetlands* 23: 344-356.
31. Fennessy MS, Rokosch A, Mack JJ (2008) Patterns of plant decomposition and nutrient cycling in natural and created wetlands. *Wetlands* 28: 300-310.
32. Galatowitsch SM (2006) Restoring prairie pothole wetlands: does the species pool concept offer decision-making guidance for re-vegetation? *Applied Vegetation Science* 9: 261-270.
33. Galatowitsch SM, vanderValk AG (1996) Vegetation and environmental conditions in recently restored wetlands in the prairie pothole region of the USA. *Vegetatio* 126: 89-99.

34. Galatowitsch SM, vanderValk AG (1996) The vegetation of restored and natural prairie wetlands. *Ecol Appl* 6: 102-112.
35. Gleason RA, Euliss NH, Hubbard DE, Duffy WG (2004) Invertebrate egg banks of restored, natural, and drained wetlands in the prairie pothole region of the United States. *Wetlands* 24: 562-572.
36. Graham SA, Craft CB, McCormick PV, Aldous A (2005) Forms and accumulation of soil P in natural and recently restored peatlands - Upper Klamath Lake, Oregon, USA. *Wetlands* 25: 594-606.
37. Gutrich JJ, Taylor KJ, Fennessy MS (2009) Restoration of vegetation communities of created depressional marshes in Ohio and Colorado (USA): The importance of initial effort for mitigation success. *Ecol Eng* 35: 351-368.
38. Hampel H, Cattijse A, Vincx M (2003) Habitat value of a developing estuarine brackish marsh for fish and macrocrustaceans. *ICES J Mar Sci* 60: 278-289.
39. Hartzell D, Bidwell JR, Davis CA (2007) A comparison of natural and created depressional wetlands in central Oklahoma using metrics from indices of biological integrity. *Wetlands* 27: 794-805.
40. Heaven JB, Gross FE, Gannon AT (2003) Vegetation comparison of a natural and a created emergent marsh wetland. *Southeast Nat* 2: 195-206.
41. Hoeltje SM, Cole CA (2009) Comparison of Function of Created Wetlands of Two Age Classes in Central Pennsylvania. *Environ Manage* 43: 597-608.
42. Hogan DM, Jordan TE, Walbridge MR (2004) Phosphorus retention and soil organic carbon in restored and natural freshwater wetlands. *Wetlands* 24: 573-585.
43. Hunter RG, Faulkner SP, Gibson KA (2008) The importance of hydrology in restoration of bottomland hardwood wetland functions. *Wetlands* 28: 605-615.
44. Janousek CN, Currin CA, Levin LA (2007) Succession of microphytobenthos in a restored coastal wetland. *Estuaries and Coasts* 30: 265-276.
45. Kellogg CH, Bridgham SD (2002) Colonization during early succession of restored freshwater marshes. *Canadian Journal of Botany-Revue Canadienne De Botanique* 80: 176-185.
46. Kimball ME, Able KW (2007) Tidal utilization of nekton in Delaware bay restored and reference intertidal salt marsh creeks. *Estuaries and Coasts* 30: 1075-1087.
47. Lehtinen RM, Galatowitsch SM (2001) Colonization of restored wetlands by amphibians in Minnesota. *American Midland Naturalist* 145: 388-396.
48. Levin LA, Talley TS (2002) Natural and manipulated sources of heterogeneity controlling early faunal development of a salt marsh. *Ecological Applications* 12: 1785-1802.
49. Lu JW, Wang HJ, Wang WD, Yin CQ (2007) Vegetation and soil properties in restored wetlands near Lake Taihu, China. *Hydrobiologia* 581: 151-159.
50. McKenna JE (2003) Community metabolism during early development of a restored wetland. *Wetlands* 23: 35-50.
51. Melvin SL, Webb JW (1998) Differences in the avian communities of natural and created *Spartina alterniflora* salt marshes. *Wetlands* 18: 59-69.
52. Menzel JM, Menzel MA, Kilgo JC, Ford WM, Edwards JW (2005) Bat response to Carolina bays and wetland restoration in the southeastern US Coastal Plain. *Wetlands* 25: 542-550.

- 1 53. Meyer CK, Baer SG, Whiles MR (2008) Ecosystem recovery across a
2 chronosequence of restored wetlands in the platte river valley. *Ecosystems* 11:
3 193-208.
- 4 54. Meyer CK, Whiles MR (2008) Macroinvertebrate communities in restored and
5 natural Platte River slough wetlands. *J N Am Benthol Soc* 27: 626-639.
- 6 55. Moseman SM, Levin LA, Currin C, Forder C (2004) Colonization, succession, and
7 nutrition of macrobenthic assemblages in a restored wetland at Tijuana Estuary,
8 California. *Estuarine Coastal and Shelf Science* 60: 755-770.
- 9 56. Moser K, Ahn C, Noe G (2007) Characterization of microtopography and its
10 influence on vegetation patterns in created wetlands. *Wetlands* 27: 1081-1097.
- 11 57. Moser KF, Ahn C, Noe GB (2009) The Influence of Microtopography on Soil
12 Nutrients in Created Mitigation Wetlands. *Restor Ecol* 17: 641-651.
- 13 58. Moy LD, Levin LA (1991) Are spartina marshes a replicable resource? - A functional
14 approach to evaluation of marsh creation efforts. *Estuaries* 14: 1-16.
- 15 59. Nair VD, Graetz DA, Reddy KR, Olila OG (2001) Soil development in phosphate-
16 mined created wetlands of Florida, USA. *Wetlands* 21: 232-239.
- 17 60. Neff KP, Rusello K, Baldwin AH (2009) Rapid Seed Bank Development in Restored
18 Tidal Freshwater Wetlands. *Restor Ecol* 17: 539-548.
- 19 61. Paller MH, Reichert MJM, Dean JM, Seigle JC (2000) Use of fish community data to
20 evaluate restoration success of a riparian stream. *Ecol Eng* 15: S171-S187.
- 21 62. Parikh A, Gale N (1998) Vegetation monitoring of created dune swale wetlands,
22 Vandenberg Air Force Base, California. *Restor Ecol* 6: 83-93.
- 23 63. Parkinson RW, DeLaune RR, Hutcherson CT, Stewart J (2006) Tuning surface
24 water management and wetland restoration programs with historic sediment
25 accumulation rates: Merritt Island National Wildlife Refuge, East-Central Florida,
26 USA. *J Coast Res* 22: 1268-1277.
- 27 64. Pechmann JHK, Estes RA, Scott DE, Gibbons JW (2001) Amphibian colonization
28 and use of ponds created for trial mitigation of wetland loss. *Wetlands* 21: 93-
29 111.
- 30 65. Petranka JW, Harp EM, Holbrook CT, Hamel JA (2007) Long-term persistence of
31 amphibian populations in a restored wetland complex. *Biol Conserv* 138: 371-
32 380.
- 33 66. Petranka JW, Kennedy CA, Murray SS (2003) Response of amphibians to
34 restoration of a southern appalachian wetland: A long-term analysis of
35 community dynamics. *Wetlands* 23: 1030-1042.
- 36 67. Petranka JW, Murray SS, Kennedy CA (2003) Responses of amphibians to
37 restoration of a southern appalachian wetland: Perturbations confound post-
38 restoration assessment. *Wetlands* 23: 278-290.
- 39 68. Poach ME, Faulkner SP (1998) Soil phosphorus characteristics of created and
40 natural wetlands in the Atchafalaya Delta, LA. *Estuarine Coastal and Shelf*
41 *Science* 46: 195-203.
- 42 69. Ratti JT, Rocklage AM, Giudice JH, Garton EO, Golner DP (2001) Comparison of
43 avian communities on restored and natural wetlands in North and South Dakota.
44 *J Wildl Manage* 65: 676-684.
- 45 70. Rozas LP, Minello TJ (2001) Marsh terracing as a wetland restoration tool for
46 creating fishery habitat. *Wetlands* 21: 327-341.

- 1 71. Seabloom EW, van der Valk AG (2003) Plant diversity, composition, and invasion of
2 restored and natural prairie pothole wetlands: Implications for restoration.
3 Wetlands 23: 1-12.
- 4 72. Sidle WC, Roose DL, Yzerman VT (2000) Isotope evaluation of nitrate attenuation in
5 restored and native riparian zones in the Kankakee watershed, Indiana.
6 Wetlands 20: 333-345.
- 7 73. Stanczak M, Keiper JB (2004) Benthic invertebrates in adjacent created and natural
8 wetlands in northeastern Ohio, USA. Wetlands 24: 212-218.
- 9 74. Stevens CE, Diamond AW, Gabor TS (2002) Anuran call surveys on small wetlands
10 in Prince Edward Island, Canada restored by dredging of sediments. Wetlands
11 22: 90-99.
- 12 75. Stevens CE, Gabor TS, Diamond AW (2003) Use of restored small wetlands by
13 breeding waterfowl in Prince Edward Island, Canada. Restor Ecol 11: 3-12.
- 14 76. Stolt MH, Genthner MH, Daniels WL, Groover VA, Nagle S, et al. (2000)
15 Comparison of soil and other environmental conditions in constructed and
16 adjacent palustrine reference wetlands. Wetlands 20: 671-683.
- 17 77. Streever WJ, Portier KM, Crisman TL (1996) A comparison of dipterans from ten
18 created and ten natural wetlands. Wetlands 16: 416-428.
- 19 78. Watts CH, Clarkson BR, Didham RK (2008) Rapid beetle community convergence
20 following experimental habitat restoration in a mined peat bog. Biol Conserv 141:
21 568-579.
- 22 79. Williams GD, Zedler JB (1999) Fish assemblage composition in constructed and
23 natural tidal marshes of San Diego Bay: Relative influence of channel
24 morphology and restoration history. Estuaries 22: 702-716.
- 25 80. Zampella RA, Laidig KJ (2003) Functional equivalency of natural and excavated
26 coastal plain ponds. Wetlands 23: 860-876.
- 27 81. Zheng L, Stevenson RJ, Craft C (2004) Changes in benthic algal attributes during
28 salt marsh restoration. Wetlands 24: 309-323.
- 29 82. Able K, Nemerson D (2004) Evaluating salt marsh restoration in Delaware Bay:
30 analysis of fish response at former salt hay farms. Estuaries and Coasts 27: 58-
31 69.
- 32 83. Andersen R, Francez a, Rochefort L (2006) The physicochemical and
33 microbiological status of a restored bog in Québec: Identification of relevant
34 criteria to monitor success. Soil Biol Biochem 38: 1375-1387.
- 35 84. Andersen R, Grasset L, Thormann MN, Rochefort L, Francez A-J (2010) Changes in
36 microbial community structure and function following Sphagnum peatland
37 restoration. Soil Biol Biochem 42: 291-301.
- 38 85. Bosire JO, Dahdouh-Guebas F, Kairo JG, Koedam N (2003) Colonization of non-
39 planted mangrove species into restored mangrove stands in Gazi Bay, Kenya.
40 Aquat Bot 76: 267-279.
- 41 86. Boyer KE, Callaway JC, Zedler JB (2000) Evaluating the Progress of Restored
42 Cordgrass (*Spartina foliosa*) Marshes: Belowground Biomass and Tissue
43 Nitrogen. Estuaries 23: 711-721.
- 44 87. Byers SE, Chmura GL (2007) Salt Marsh Vegetation Recovery on the Bay of Fundy.
45 Estuaries and coasts 30: 869-877.

- 1 88. Card SM, Quideau Sa (2010) Microbial community structure in restored riparian
2 soils of the Canadian prairie pothole region. *Soil Biol Biochem* 42: 1463-1471.
- 3 89. Card SM, Quideau Sa, Oh S-W (2010) Carbon Characteristics in Restored and
4 Reference Riparian Soils. *Soil Sci Soc Am J* 74: 1834.
- 5 90. Chamberlain RH, Beach WP, Barnhart RA (1993) Early Use by Fish of a Mitigation
6 Salt Marsh, Humboldt Bay, California. *Estuaries* 16: 769-783.
- 7 91. Collins BD, Montgomery DR (2002) Forest development, wood jams, and
8 restoration of floodplain rivers in the Puget Lowland, Washington. *Restor Ecol* 10:
9 237-247.
- 10 92. Elsey-Quirk T, Middleton Ba, Proffitt CE (2009) Seed Dispersal and Seedling
11 Emergence in a Created and a Natural Salt Marsh on the Gulf of Mexico Coast in
12 Southwest Louisiana, U.S.A. *Restor Ecol* 17: 422-432.
- 13 93. Erfanzadeh R, Garbutt A, Pétilion J, Maelfait J-P, Hoffmann M (2009) Factors
14 affecting the success of early salt-marsh colonizers: seed availability rather than
15 site suitability and dispersal traits. *Plant Ecol* 206: 335-347.
- 16 94. Fearnley S (2008) The Soil Physical and Chemical Properties of Restored and
17 Natural Back-Barrier Salt Marsh on Isles Dernieres, Louisiana. *J Coast Res* 241:
18 84-94.
- 19 95. Fell PE, Murphy KA, Peck MA, Recchia ML (1991) Re-establishment of *Melampus*
20 *bidentatus* (Say) and other macroinvertebrates on a restored impounded tidal
21 marsh: comparison of populations above and below the impoundment dike. *J*
22 *Exp Mar Biol Ecol* 152: 33-48.
- 23 96. Glatzel S (2003) Dissolved organic matter properties and their relationship to carbon
24 dioxide efflux from restored peat bogs. *Geoderma* 113: 397-411.
- 25 97. Hagan SM, Brown SA, Able KW (2007) Production of mummichog (*Fundulus*
26 *heteroclitus*): response in marshes treated for common reed (*Phragmites*
27 *australis*) removal. *Wetlands* 27: 54-67.
- 28 98. Howe E, Simenstad C (2007) Restoration trajectories and food web linkages in San
29 Francisco Bay's estuarine marshes: a manipulative translocation experiment.
30 *Mar Ecol Prog Ser* 351: 65-76.
- 31 99. James-Pirri M (2001) Diet Composition of Mummichogs, *Fundulus heteroclitus*, from
32 Restoring and Unrestricted Regions of a New England (U.S.A.) Salt Marsh.
33 *Estuar Coast Shelf Sci* 53: 205-213.
- 34 100. Kimball ME, Able KW, Grothues TM (2010) Evaluation of Long-Term Response of
35 Intertidal Creek Nekton to *Phragmites australis* (Common Reed) Removal in
36 Oligohaline Delaware Bay Salt Marshes. *Restor Ecol* 18: 772-779.
- 37 101. Laggoun-Défarge F, Mitchell E, Gilbert D, Disnar J-R, Comont L, et al. (2008) Cut-
38 over peatland regeneration assessment using organic matter and microbial
39 indicators (bacteria and testate amoebae). *J Appl Ecol* 45: 716-727.
- 40 102. Levin LA, Talley D, Thayer G (1996) Succession of macrobenthos in a created salt
41 marsh. *Mar Ecol Prog Ser* 141: 67-82.
- 42 103. Llanso RJ, Bell SS, Vose FE (1998) Food habits of red drum and spotted seatrout
43 in a restored mangrove impoundment. *Estuaries* 21: 294-306.
- 44 104. Luo ZK, Sun OJ, Xu HL (2010) A comparison of species composition and stand
45 structure between planted and natural mangrove forests in Shenzhen Bay, South
46 China. *Journal of Plant Ecology-Uk* 3: 165-174.

- 1 105. Macintosh DJ, Ashton EC, Havanon S (2002) Mangrove rehabilitation and intertidal
2 biodiversity: A study in the Ranong mangrove ecosystem, Thailand. *Estuarine*
3 *Coastal and Shelf Science* 55: 331-345.
- 4 106. Marchetti MP, Garr M, Smith ANH (2008) Evaluating Wetland Restoration Success
5 Using Aquatic Macroinvertebrate Assemblages in the Sacramento Valley,
6 California. *Restor Ecol* 18: 457-466.
- 7 107. McKee KL, Faulkner PL (2000) Restoration of biogeochemical function in
8 mangrove forests. *Restor Ecol* 8: 247-259.
- 9 108. Meyer CK, Whiles MR, Baer SG (2010) Plant Community Recovery following
10 Restoration in Temporally Variable Riparian Wetlands. *Restor Ecol* 18: 52-64.
- 11 109. Miller MJ, Able KW (2004) Movements and growth of tagged young-of-the-year
12 Atlantic croaker (*Micropogonias undulatus* L .) in restored and reference marsh
13 creeks in Delaware. *J Exp Mar Biol Ecol* 267: 15 - 33.
- 14 110. Minello TJ, Zimmerman RJ (1992) Utilization of natural and transplanted Texas salt
15 marshes by fish and decapod crustaceans. *Mar Ecol Prog Ser* 90: 273-285.
- 16 111. Peck MA, Fell PE, Allen EA, Gieg JA, Guthke CR, et al. (1994) Evaluation of tidal
17 marsh restoration: comparison of selected macroinvertebrate populations on a
18 restored impounded valley marsh and an unimpounded valley marsh within the
19 same salt marsh system in Connecticut, USA. *Environ Manage* 18: 283-293.
- 20 112. Piehler MF, Currin CA, Cassanova R, Paerl HW (1998) Development and N₂-
21 Fixing Activity of the Benthic Microbial Community in Transplanted *Spartina*
22 *alterniflora* Marshes in. *Restor Ecol* 6: 290-296.
- 23 113. Raposa K (2002) Early Responses of Fishes and Crustaceans to Restoration of a
24 Tidally Restricted New England Salt Marsh. *Restor Ecol* 10: 665-676.
- 25 114. Raposa KB (2008) Early Ecological Responses to Hydrologic Restoration of a
26 Tidal Pond and Salt Marsh Complex in Narragansett Bay , Rhode Island. *J Coast*
27 *Res* 55: 180-192.
- 28 115. Ren H, Jian SG, Lu HF, Zhang QM, Shen WJ, et al. (2008) Restoration of
29 mangrove plantations and colonisation by native species in Leizhou bay, South
30 China. *Ecol Res* 23: 401-407.
- 31 116. Rozas L, Minello T (2009) Using nekton growth as a metric for assessing habitat
32 restoration by marsh terracing. *Mar Ecol Prog Ser* 394: 179-193.
- 33 117. Rozas LP, Minello TJ (2007) Restoring coastal habitat using marsh terracing: the
34 effect of cell size on nekton use. *Wetlands* 27: 595-609.
- 35 118. Rozas LP, Minello TJ, Zimmerman RJ, Caldwell P (2007) Nekton populations,
36 long-term wetland loss, and the effect of recent habitat restoration in Galveston
37 Bay, Texas, USA. *Marine Ecology-Progress Series* 344: 119-130.
- 38 119. Teo S (2003) Growth and production of the mummichog (*Fundulus heteroclitus*) in
39 a restored salt marsh. *Estuaries and Coasts* 26: 51-63.
- 40 120. Thompson SP, Paerl HW, Go MC (1995) Seasonal patterns of nitrification and
41 denitrification in a natural and a restored salt marsh. *Estuaries* 18: 399-408.
- 42 121. Tupper M, Able KW (2000) Movements and food habits of striped bass (*Morone*
43 *saxatilis*) in Delaware Bay (USA) salt marshes : comparison of a restored and a
44 reference marsh. *Mar Biol*: 1049-1058.

- 1 122. Vose FE, Bell SS (1994) Resident fishes and macrobenthos in mangrove-rimmed
2 habitats: Evaluation of habitat restoration by hydrological modification. *Estuaries*
3 17: 585-596.
- 4 123. Waddington JM, Warner KD (2001) Atmospheric CO₂ sequestration in restored
5 mined peatlands. *Ecoscience* 8: 359.
- 6 124. Walton ME, Le Vay L, Lebata JH, Binas J, Primavera JH (2007) Assessment of the
7 effectiveness of mangrove rehabilitation using exploited and non-exploited
8 indicator species. *Biol Conserv* 138: 180-188.
- 9

1 Carbon storage and organic matter accumulation are likely correlated variables;
2 however, statistical tests could not be performed because only five studies reported
3 simultaneous measurements of both variables.

4 *References*

- 5 1. Zeug S, Shervette V, Hoeinghaus D, Davisiii S (2007) Nekton assemblage structure
6 in natural and created marsh-edge habitats of the Guadalupe Estuary, Texas,
7 USA. Estuar Coast Shelf Sci 71: 457-466.
- 8 2. Matthews JW, Endress AG (2010) Rate of succession in restored wetlands and the
9 role of site context. Applied Vegetation Science: 346-355.