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Wetlands as Sinks for Reactive Nitrogen at Continental and Global Scales: A Meta-Analysis

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Abstract

Wetlands support physical and ecological functions that result in valuable services to society, including removal of reactive nitrogen (Nr) from surface water and groundwater. We compiled published data from wetland studies worldwide to estimate total Nr removal and to evaluate factors that influence removal rates. Over several orders of magnitude in wetland area and Nr loading rates, there is a positive, near-linear relationship between Nr removal and Nr loading. The linear model (null hypothesis) explains the data better than either a model of declining Nr removal efficiency with increasing Nr loading, or a Michaelis–Menten (saturation) model. We estimate that total Nr removal by major classes of wetlands in the conterminous U.S. is approximately 20–21% of the total anthropogenic load of Nr to the region. Worldwide, Nr removal by wetlands is roughly 17% of anthropogenic Nr inputs. Historical loss of 50% of native wetland area suggests an equivalent loss of Nr removal capacity. Expanded protection and large-scale restoration of wetlands should be considered in strategies to re-balance the global nitrogen cycle and mitigate the negative consequences of excess Nr loading.

Key words: nitrogen; reactive nitrogen; wetlands; denitrification; nitrogen removal; nitrogen loading.

Introduction

Wetlands are, or once were, dominant features of coastal plains, river valleys, and other landscapes in many parts of the world. Salt marshes, mangrove forests, tidal freshwater marshes, forested swamps, and riverine flood plain wetlands perform physical and ecological functions that can result in valuable services to society and human well-being (Murray and others 2009). Many wetland systems have been constructed specifically to perform one or more of these functions (Spieles and Mitsch 2000). Removal of reactive nitrogen (Nr) from surface water and groundwater is an important service of many wetland systems, a matter of investigation for at least the past several decades (for example, Valiela and others 1973; Richardson and others 1975). This service is a benefit to society where excess amounts of Nr otherwise would contribute to (a) eutrophication in rivers, lakes, estuaries, and coastal waters (Dodds and others 2009; Howarth and Marino 2006; Pinckney and others 2006) or (b) contamination of surface water and groundwater

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with nitrate (NO_3^-), nitrite (NO_2^-), or ammonium (NH_4^+) in concentrations harmful to humans and aquatic life (Townsend and Howarth 2010).

Some aquatic ecosystems are contaminated by excess amounts of Nr, mostly as NO_3^-, NO_2^-, and NH_4^+, delivered from shallow groundwater, the atmosphere, and direct discharges. These proximal sources receive Nr from upstream municipal and industrial point-source discharges, as well as diffuse agricultural (AG), urban, and atmospheric sources. Despite major efforts in some regions to reduce Nr discharges, reductions generally have been insufficient to meet policy goals and water quality criteria because of increasing inputs of Nr to the environment, the high costs and low efficiencies of treatment and control methods, and long lag times between non-point-source controls and system responses (STAC 2005). Moreover, continuing population growth, especially in coastal watersheds, combined with AG expansion and intensification, will increase anthropogenic fluxes of Nr (Galloway and others 2004) and hence, the potential for Nr contamination of aquatic systems. These effects could be magnified by climate change as water temperatures increase (Hagy and others 2004). Because wetlands are known to be sinks for anthropogenic Nr, natural, modified, restored, and newly created wetlands should be expected to have increasing importance in controlling Nr, thus contributing to water quality management and the sustainability of aquatic ecosystem services.

Hypothetically, Nr removal in the types of wetlands considered here might be expected to increase asymptotically with increasing inputs of Nr up to a saturation point, or where concentrations are not so high as to cause degradation of the wetland biome and its functions. Atmospheric Nr deposition has been associated with nitrogen saturation and ecological degradation in forests (Aber and others 1989). Nonetheless, exceptions to this principle and substantial variability between wetlands are recognized (Bedford and others 1999). Brin and others (2010) found that a New England salt marsh continued to remove Nr efficiently in response to increased Nr loading, even though the marsh had experienced decades of Nr enrichment. O'Brien and others (2007) did not find evidence for saturation of Nr processing (Michaelis–Menten model) in mid-western streams over a wide gradient of NO_3^- concentrations, and offered alternative models: a linear model in which Nr processing increased monotonically with Nr concentrations, and a ''declining efficiency'' model in which Nr removal increases with Nr loading, but the proportion of the Nr load removed declines. The pattern described by the declining efficiency model has been observed in wetlands and other aquatic systems by many authors (for example, Mitsch and others 2005; Mulholland and others 2008). Wetlands process Nr through a variety of biological, chemical, and physical mechanisms, supporting most or all of the natural transformations of N, which are mediated largely by biochemical mechanisms in plants, animals, and microorganisms. Close coupling of aerobic and anaerobic regimes in wetland soils, in combination with high rates of plant productivity and organic matter processing, supply favorable environments for conversion of Nr to N_2 by microbial enzymatic processes (principally denitrification). Conditions favorable for denitrification favor sequestration of Nr in biomass and buried soils, but also may contribute to emissions of N_2O, an important greenhouse gas and product of partial denitrification, to the atmosphere. Even though most wetlands, under appropriate environmental conditions, are valuable sinks for Nr, this service is not universal. Wetland plant-microbial communities can fix nitrogen (convert N_2 to Nr), and wetlands receive Nr from the atmosphere, so that some wetlands are net exporters of Nr to surface waters (Morris 1991). Plant productivity in most wetlands is limited by Nr availability (especially coastal wetlands, but also freshwater systems), whereas productivity in some wetlands is limited by phosphorus (Morris 1991). Along with organic carbon, interactions of these nutrients with the ecological functions of wetlands are complex and not fully explored.

Because of the complexity of the nitrogen cycle, an initial simplification would treat nitrogen dynamics in wetlands as an input–output, or black box problem (Figure 1). In this formulation, the inputs are loads of Nr from water inflows and the atmosphere; the outputs are discharges of Nr to water, groundwater, and the atmosphere. By difference, we obtain the net quantity of nitrogen either recycled to the atmosphere as N_2 or sequestered within wetland biomes and soils. The aggregate of Nr removal and sequestration in this scheme is a function of the inputs, in combination with easily observed covariates (wetland class, vegetative and soil condition, hydrology, climate) rather than the multitude of interacting biogeochemical processes within the wetland. At the simplest level, the difference between inputs and outputs of Nr, integrated over an appropriate time period and wetland area, equals the nitrogen removal service in mass per area per time, for example, $g\ N\ m^{-2}\ y^{-1}$. A caveat is that black box observations of nutrient removal in wetlands could

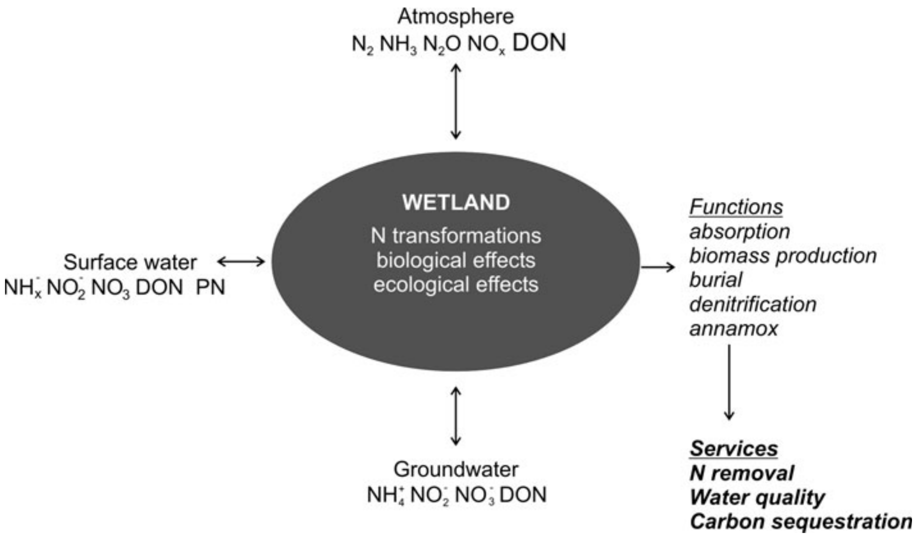

Figure 1. Conceptual input–output model of the interactions of nitrogen with wetlands.

be biased if all flows are not accounted for. Where only surface-water inflow and outflow concentrations are measured, inflows of low-nutrient groundwater may dilute high-nutrient inflows, giving the appearance of nutrient removal even in its absence (Howard-Williams 1985); conversely, inflows of high-nutrient groundwater could be falsely interpreted as the result of N fixation.

The science of Nr dynamics in wetlands is incomplete—fully detailed analysis of the processes involved for many wetlands, wetland types, or complexes of wetlands in landscapes will not be feasible in the near future. In this paper we synthesize existing information, with its considerable uncertainties, to support predictions of the magnitude of Nr removal by wetlands at various scales. Such predictions should be useful for *prima facie* evaluations of scenarios at national and large regional scales for wetland gains, losses, and modifications. Our specific objectives were to: (1) quantify the rates of Nr removal in various classes of wetlands, (2) explore correlations of Nr removal rates with Nr loading and other environmental factors, and (3) to estimate the role of wetlands in nitrogen cycling at the largest spatial scales. To our knowledge, the meta-analysis presented here is unprecedented, in terms of geographic scope, the ranges of wetland types, sizes, distribution, and Nr loading rates.

Methods

An initial literature search covered the databases Greenfile, APIRS, Agricola, Biosis, CAB Abstracts, Energy Science and Technology, General Science Abstracts, NTIS, and Waternet; the keywords nitrogen, wetlands, marshes, mangroves, nitrate, ammonia, and denitrification; and the years 2000–2008. The search was extended by ad hoc internet queries to a large amount of additional literature reaching back to the 1970s (Supplemental Material). In addition to quantitative Nr loading rates coupled with removal, output, or efficiency rates, the final criteria for retaining data required a basis for computing these values by area (m^{-2}) and annually. Studies that reported Nr only as concentrations without volumetric flow measures, or could not be annually averaged, were not included. Each record was classified into one of five wetland types, loosely based on the Cowardin and others (1979) classification: AG, estuarine emergent (EE), palustrine emergent (PE), palustrine forested (PF), or other (OT: experimental wetlands, those with a few data points, for example, palustrine shrub wetlands, mixed wetlands). The few useful observations from mangroves were included in class EE, along with salt marshes. Ancillary environmental data were selected for relevance and availability: absolute values of latitude, wetland area, volumetric flow rate, tidal regime (whether the wetland was in a tidal or non-tidal environment), and wetland origin (natural or constructed). Because few reports included temperature data that could be applied on an annual basis, absolute latitude was used as a surrogate for mean annual temperature. Where not given in the literature, we calculated the variables hydraulic loading rate (volumetric flow rate divided by wetland area: m/y), and percent efficiency of Nr removal (100 · (Nr removal rate/Nr loading rate)).

Data were analyzed by linear and non-linear regression, analysis of covariance, random resampling to estimate robustness of regression slopes and efficiency estimates, and graphical methods, using SAS version 9.1. Variables were log-transformed as necessary to improve homogeneity of variances and normality of residual distributions.

We compiled a dataset of 190 observations with sufficient information for spatially and temporally normalized input–output models of Nr reduction by wetlands. For the majority of these observations, hydrologic flow rate, wetland total area, and latitude could be identified; species of Nr included NO_3^-, total reactive N (TN), and dissolved inorganic N (DIN). The analysis was limited to these variables and their derivatives (Nr removal efficiency and hydraulic loading rate). In many cases, Nr removal efficiency rather than mass removal was reported, so Nr removal was calculated as the fraction of the Nr load removed. All data and sources are tabulated in Supplemental Material.

Results

Nr Loading to Wetlands

The statistical distribution of Nr loads to wetlands showed strong positive skewness, that is, there were many observations of low to moderate loads, and fewer observations of very high loads. The range was from 0.002 to 9048 gN m^{-2} y^{-1}, median 53.03 gN m^{-2} y^{-1}. The skewed distribution was illustrated by the large difference between the geometric mean of 42.2 gN m^{-2} y^{-1} and the arithmetic mean (241.2 gN m^{-2} y^{-1}). Log-transformed Nr load data more closely approximated a normal frequency distribution than untransformed data, with moderate negative skewness. Based on a two-way ANOVA with wetland class and constructed versus natural as main effects, mean loads of Nr varied significantly ($P = 0.0211$) between wetland classes, with the greatest loads to classes PE and AG (least squares means with Tukey adjustment for multiple comparisons; Figure 2). Many of the wetlands in these classes were constructed specifically for water quality management or experimental purposes; geometric mean Nr loads to constructed wetlands (90.1 g m^{-2} y^{-1}) were significantly larger ($P = 0.0008$) than to natural wetlands (13.8 g m^{-2} y^{-1}).

Nr Removal as a Function of Nr Load and Other Variables

Similar to Nr loading rates, Nr removal rates varied over more than four orders of magnitude, with an approximately log-normal frequency distribution. Therefore, Nr removal rates were $\log_{10}$ transformed for statistical analysis. Regardless of wetland class and other potentially modifying variables, there was a positive, nearly linear relationship between

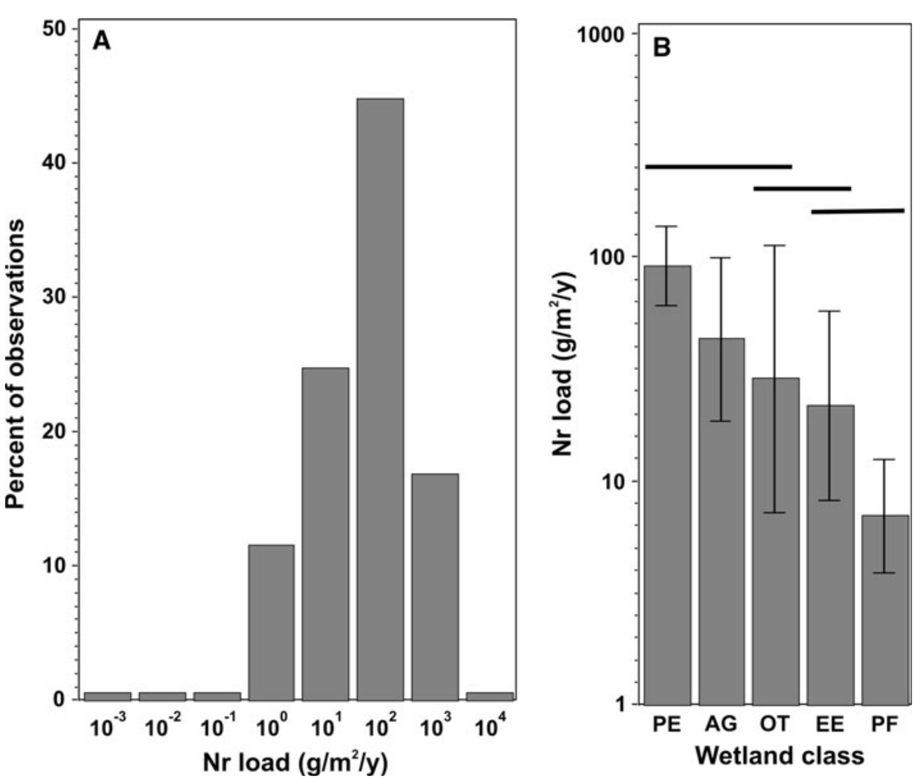

Figure 2. **A** Frequency distribution of Nr load; all data. **B** Mean Nr load for five classes of wetlands; *error bars* are within-class 95% confidence limits. *AG* agricultural, *EE* estuarine emergent (salt marshes), *OT* other, *PE* palustrine emergent, *PF* palustrine forested. The heavy *horizontal bars* indicate means that are not significantly different ($P > 0.05$, based on one-way ANOVA, least squares means with Tukey adjustment for multiple comparisons).

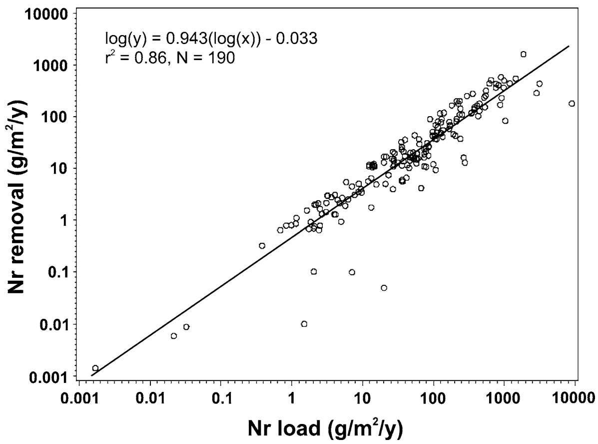

Figure 3. Nr removal by wetlands as a function of Nr load; all data (linear regression).

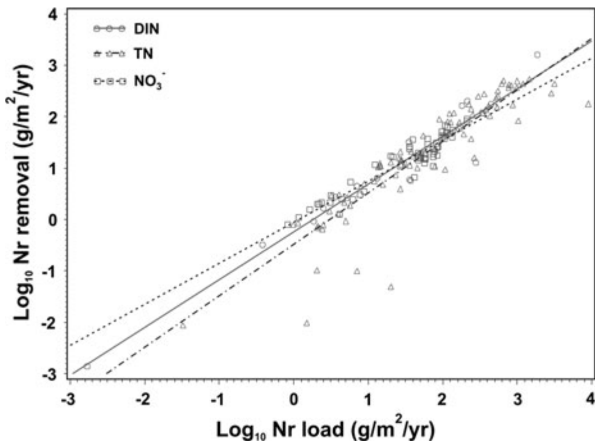

Figure 4. Nr removal as a function of Nr load for three forms of Nr. *DIN* dissolved inorganic N; *TN* total [reactive] N. Regression for DIN: $\log_{10}(y) = 0.93 \cdot \log_{10}(x) - 0.24$, $r^2 = 0.94$; for TN $\log_{10}(y) = 0.99 \cdot \log_{10}(x) - 0.46$, $r^2 = 0.82$; for NO_3^- $\log_{10}(y) = 0.81 \cdot \log_{10}(x) - 0.06$, $r^2 = 0.91$. The slopes differ significantly (linear regression with dummy variable to represent Nr form; $P = 0.019$ for the hypothesis that the interaction term, $\log_{10}$ Nr load × wetland class, =0).

the logarithms of Nr loading and Nr removal expressed as gN m^{-2} y^{-1} (Figure 3). Estimates of the slope of Nr removal on Nr input from regression analysis of 500 random samples (30 observations each) from the data set ranged from 0.65 to 1.24, with a mean of 0.93 (bootstrap standard error = 0.08); 90% of the slope estimates were between 0.80 and 1.09.

Nitrogen removal had significant positive relationships with Nr loading for each of the five classes of wetlands, for constructed and natural wetlands, and for both tidal and non-tidal systems. Among wetland classes, the strongest relationships, judging by the adjusted r^2 statistic, were for classes PE and AG. The weakest relationships were for EE (salt marshes and mangroves) and PF (swamps and riparian forests). Class PE, which included many constructed wetlands, had the steepest slope (indicating relatively high efficiency for Nr removal), whereas OT had the shallowest slope. The positive relationship between Nr load and Nr removal was not affected to a large extent by the forms of Nr reported, whether DIN, NO_3^-, or TN (Figure 4), although the slopes differed significantly.

The simultaneous relationships of all independent variables to Nr removal were explored by analysis of covariance (ANCOVA). Only Nr load was significant at $P < 0.05$, dominating the other variables in terms of variance accounted for (Table 1). Including the interaction of wetland class with Nr load (test for difference between slopes of Nr removal on Nr load) did not have a significant effect on the results. Without Nr load in the analysis, however, only wetland origin (constructed or natural) and latitude were not significant at $P < 0.05$. It is clear that HLR, and possibly other variables, were confounded with Nr load; both Nr load and HLR are functions of wetland area and volumetric flow.

Efficiency of Nr Removal

Efficiency is the proportion of the Nr load removed within the wetland, or y/x where y is mass of Nr removed per area per time, and x is the input of Nr in the same units (here we express efficiency as percentage, that is, $100 \cdot (y/x)$. Overall efficiency ranged from 0.25 to 99.6%, with a mean of 46.7%. Among wetland classes, mean efficiency ranged from 32.9% for EE to 62.7% for PF (Figure 5). Mean efficiency of Nr removal was significantly higher (t test, $P = 0.033$) for non-tidal wetlands (48.6%) than for tidal systems (38.5%). The difference between mean efficiency for constructed (45.7%) and natural wetlands (48.2%) was not significant (t test, $P = 0.51$). The absolute value of latitude was negatively correlated with efficiency ($r = -0.30$, $P < 0.0001$). The combined effects of independent variables on efficiency were analyzed with ANCOVA. Only latitude and wetland class were significantly associated with efficiency (Table 2). Mean Nr removal efficiency was 25% at latitudes of 50° or greater and 59% at latitudes of 30° or less, compared to mid-latitude and overall mean efficiency of 47%. Estimates of mean efficiency from an analysis of 500 random samples (30 observations each) were 35–62%, with an overall

Table 1. Analysis of Covariance for Nr Removal (g m^{-2} y^{-1}; $\log_{10}$) With and Without Nr Load as a Variable

Variable	df	With Nr load		Without Nr load	
		F	*P*	*F*	*P*
Nr load	1	452.79	<0.0001		
Absolute latitude	1	3.02	0.0847	0.26	0.6099
HLR (m/y; $\log_{10}$)	1	0.74	0.3912	41.53	<0.0001
Wetland class	4	1.28	0.2806	3.55	0.0088
Constructed (Y/N)	1	0.02	0.8991	2.61	0.1086
Tidal (Y/N)	1	3.85	0.0521	7.56	0.0068
N species	3	0.26	0.8535	3.53	0.0168
Nr load × wetland class	4	1.35	0.2571		

Statistics are based on Type III sums of squares. With Nr load overall R^2 = 0.93; without Nr load overall R^2 = 0.53. df = degrees of freedom; HLR = hydraulic loading rate (m/y, $\log_{10}$); Nr species are DIN, TN, NO_3^-, other; N = 139.

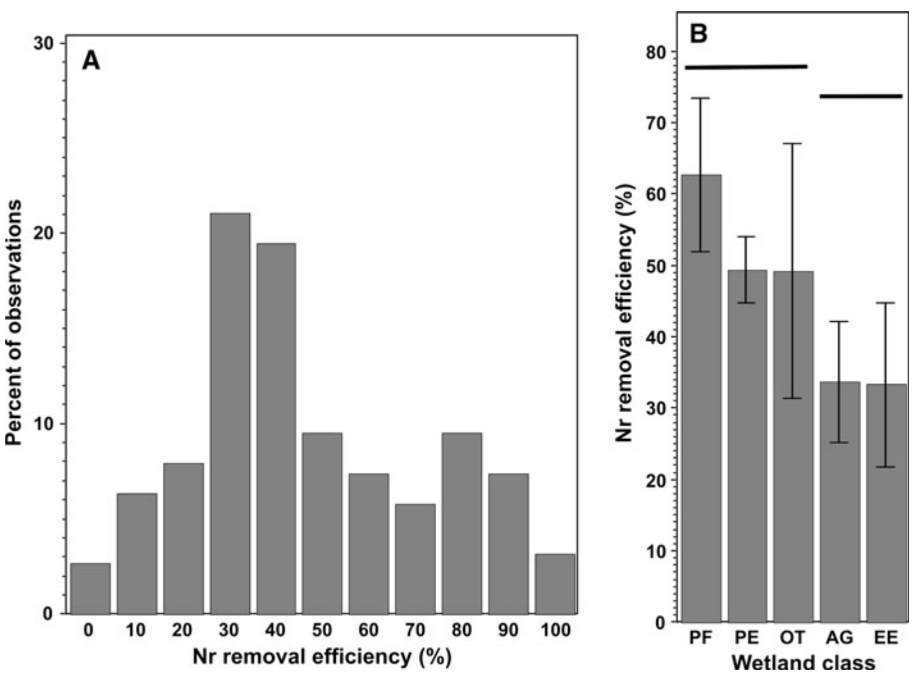

Figure 5. **A** Frequency distribution of Nr removal efficiency. **B** Mean efficiency of Nr removal for six classes of wetlands. *Error bars* are within-class 95% confidence limits. *AG* agricultural, *EE* estuarine emergent, *OT* other, *PE* palustrine emergent, *PF* palustrine forested. The heavy *horizontal bars* indicate means that are not significantly different ($P > 0.05$, based on one-way ANOVA, least squares means with Tukey adjustment for multiple comparisons).

Table 2. Analysis of Covariance for Nr Removal Percent Efficiency

Variable	df	*F*	*P*
Absolute latitude	1	7.11	0.0087
HLR	1	3.03	0.0841
Wetland class	4	2.46	0.0485
Constructed (Y/N)	1	1.09	0.2983
Tidal (Y/N)	1	2.65	0.1061
Nr species	3	1.31	0.2745

Statistics are based on Type III sums of squares. Overall R^2 = 0.26; df = degrees of freedom; HLR = hydraulic loading rate (m/y, $\log_{10}$); Nr species are DIN, TN, NO_3^- other; N = 138.

mean and median of 47.3% (bootstrap standard error = 4.8%); 90% of the estimates were between 40 and 56%.

Discussion

This meta-analysis has demonstrated that Nr removal in wetlands is directly proportional to Nr loading over a wide range of environmental conditions, with an average removal rate of approximately 47%. We have focused on two aspects of Nr removal in wetland ecosystems: mass removal per time, and efficiency of Nr removal. These variables share inherent correlations with Nr loading, because both removal and efficiency are functions of loading. For removal, a positive linear correlation (removal = load − output) is expected, as observed in our results. For efficiency, the expected relationship is a negative exponential (efficiency = output · load^{-1}). Therefore, these inherent relationships serve as default models, or null hypotheses, against which other models may be tested. Alternative hypotheses include (1) an inhibition model, where the slope of Nr removal on load is less than 1; (2) a model in which removal is stimulated by increasing loading rates, where the slope of efficiency on load is about 0, as opposed to the default ''declining efficiency'' model; and (3) a Michaelis–Menten relationship between efficiency and load, that is, a saturation model. Several studies (among them Crumpton and others 2006; Mulholland and others 2008; Valiela and Cole 2002; Mitsch and Day 2006) have evaluated mass removal or efficiency as functions of loading, without noting the inherent correlations.

A preliminary dataset included several observations of net Nr export (negative Nr removal), but none of these studies met our final criteria for inclusion; they either were incomplete budgets, short-term, or involved other ambiguities. Wetlands with long-term net exports of Nr are uncommon, apparently, and under steady-state conditions this dynamic should occur only where internal N fixation exceeds losses to denitrification, burial, and sequestration (Morris 1991). In the non-steady-state case of wetlands undergoing degradation for reasons such as coastal erosion or water diversions, Nr export has been observed (Childers and Day 1990; DeLaune and others 1989).

Some reports from salt marsh and mangrove wetlands show net Nr exports (Abd Aziz and Nedwell 1986; Woodwell and others 1979; Axelrad and others 1976). In tidal systems, outwelling of particulate N in detrital matter or dissolved organic and inorganic Nr from sediment pore waters could account for net exports on tidal or longer sub-annual time scales, for example, large seasonal variations in Nr import and export were observed in a New England salt marsh by Valiela and others (1978), but it seems unlikely that long-term net exports could be sustained except where N fixation is a major internal source of Nr. The balance may depend on the magnitude of external sources of Nr. In an early study, Valiela and others (1973) found that fertilized salt marsh plots retained 80–94% of the Nr added.

The anaerobic ammonia oxidation (annamox) process is hindered by salinity more so than denitrification (Koop-Jacobsen and Giblin 2009), so this route to Nr removal should be less important in estuarine wetlands than in freshwater wetlands. Nr removal in saline wetlands is a function of sequestration in sediments and plant biomass, as well as denitrification, but the overall role of tidal wetlands in Nr removal is not fully resolved. Estimating reliable N input–output budgets for salt marsh and mangrove systems can be exceedingly difficult because of diffuse inflow and outflow paths and oscillating tidal fluxes, which can be orders of magnitude larger than long-term net fluxes.

Factors Affecting Nr Removal

Secondary to Nr loading, latitude was significantly associated with Nr removal rates and removal efficiency (but latitude was not a significant predictor of Nr removal when Nr load was removed from the model). Denitrification, and Nr removal rates more generally, increase with temperature, and hence should have an inverse relationship with latitude. Spieles and Mitsch (2000) applied a temperature function of $1.1^{(T-20)}$, where T is temperature (°C), in a model of NO_3^- removal in constructed wetlands. We observed the expected negative correlation of Nr removal efficiency with absolute latitude. Latitude, as a surrogate for annual mean temperature, should be associated not only with the rates of microbial biochemical processes that remove Nr, but also with Nr uptake by wetland plants, which have shorter growing seasons at higher latitudes, even though summer temperatures may match those of more tropical areas.

Among wetland classes, PF had the highest mean efficiency. Much of the data for Class PF (forested swamps) came from subtropical areas in the lower Mississippi River floodplain. These swamps are at relatively low latitudes, implying higher efficiency, and class PF also had the lowest mean HLR, implying greater water residence times. Classes AG and EE had the lowest efficiencies. AG wetlands would be expected to have some degree of disturbance from AG activities and to lack a natural complement of wetland plant species. Also, some AG wetlands have artificial drainage systems (ditches or tile drains) which would reduce residence times and contact of Nr-loaded water with wetland soils. Moreover, these types of wetlands typically experience dry periods, which would reduce denitrification rates temporarily, although nitrification would continue to supply nitrate that could be denitrified upon the return of saturated conditions (Crumpton and Goldsborough 1998). Tidal wetlands should be expected to have lower Nr removal efficiency for the same reasons that they have lower mean Nr removal rates than other wetland classes (discussed above).

Part of the reason for the strong relationship between Nr loading and removal could be that as loads increase, available NO_3^- generally increases (most of the larger loading rates are dominated by NO_3^-), thereby facilitating denitrification. Nonetheless, increasing inputs of NH_x to a constructed wetland system without increasing NO_3^- also increased Nr removal rates proportionately (Jing and Lin 2004). Whether the NH_x was removed through the nitrification–denitrification pathway, annamox reaction, or other processes was not determined. As further evidence of the insensitivity of Nr removal to the forms of Nr involved, our analysis showed only minor differences in the loading-removal relationships for NO_3^-, DIN, and TN. A concern is that dissolved inorganic N (DON), included only in the TN data, can be a significant component of Nr loads to wetlands (Morris 1991). Thus, studies in which DON is not measured could be biased accordingly.

We have not considered the successional status of wetlands in this analysis, but all wetlands undergo succession over various time scales (Howard-Williams 1985). Newly created wetlands generally do not remove Nr effectively until plant communities have become established. When the plants are grasses, succession to a quasi-steady-state with effective Nr removal requires only weeks or months, whereas newly established forested wetlands show a more gradual progression in Nr removal capacity, over periods of years as the trees and soils mature (Aber and others 1989).

Synthesis

Syntheses of Nr removal in wetlands have been conducted regionally, and for specific classes of wetlands. Crumpton and others (2006) tabulated 34 examples of NO_3^- removal by wetlands in the upper Mississippi and Ohio River basins from several sources (Figure 6); the range of removal was from 27 to 93% of the inflow load, with a mean of 46% (loads of other forms of Nr were minor compared to NO_3^- in these systems). Valiela and Cole (2002) reported on the potential for Nr removal in salt marsh and mangrove systems, ranging over several orders of magnitude in area and Nr loads, from published and unpublished studies (Figure 7). Their data, extrapolated over the spatial areas of various estuarine wetlands from published denitrification and Nr burial rates, reinforced the pattern of linear increase in Nr removal with increasing load. A strong positive correlation between nitrate concentrations and mass Nr removal has been observed in prairie potholes of the U.S. Midwest (Crumpton and Goldsborough 1998).

At the expansive scale of this synthesis, wetlands are important sinks for Nr, in near-linear propor-

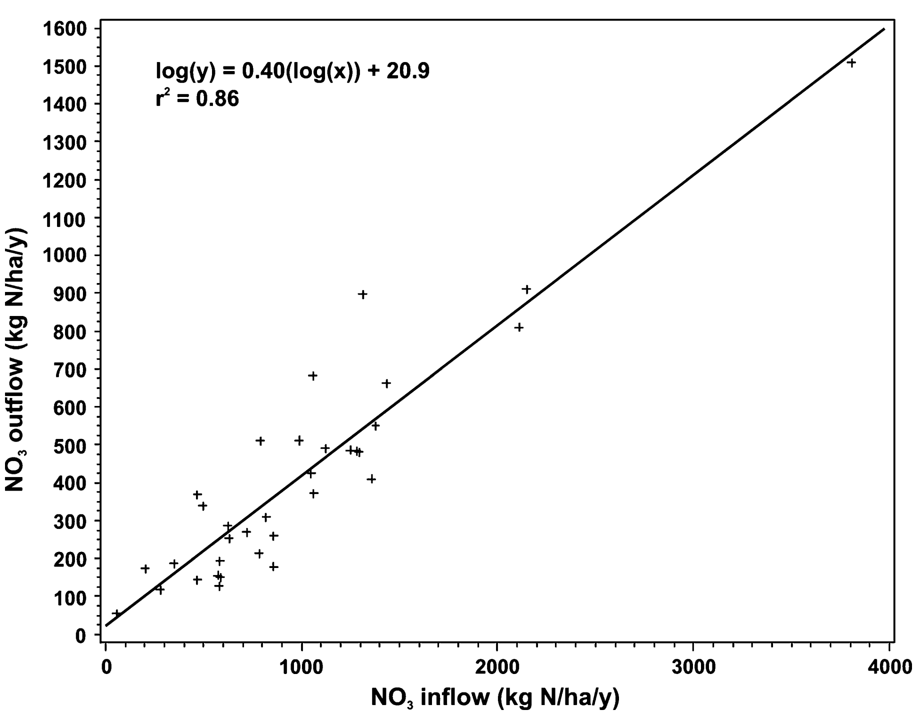

Figure 6. Nr removal as a function of Nr load for wetlands in the upper Mississippi River drainage, from data compiled by Crumpton and others (2006; Table 2).

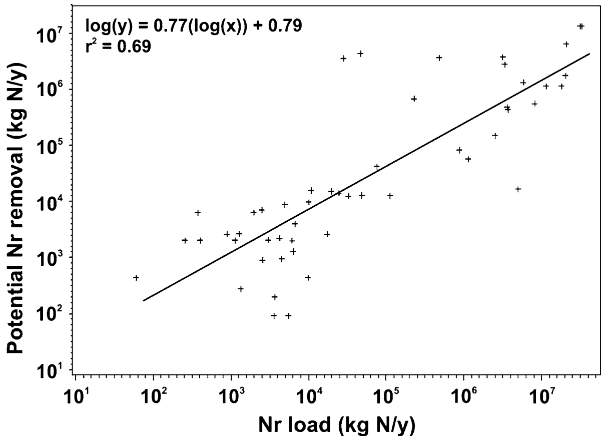

Figure 7. Potential for Nr removal from salt marsh and mangrove wetland systems, from data compiled by Valiela and Cole (2002).

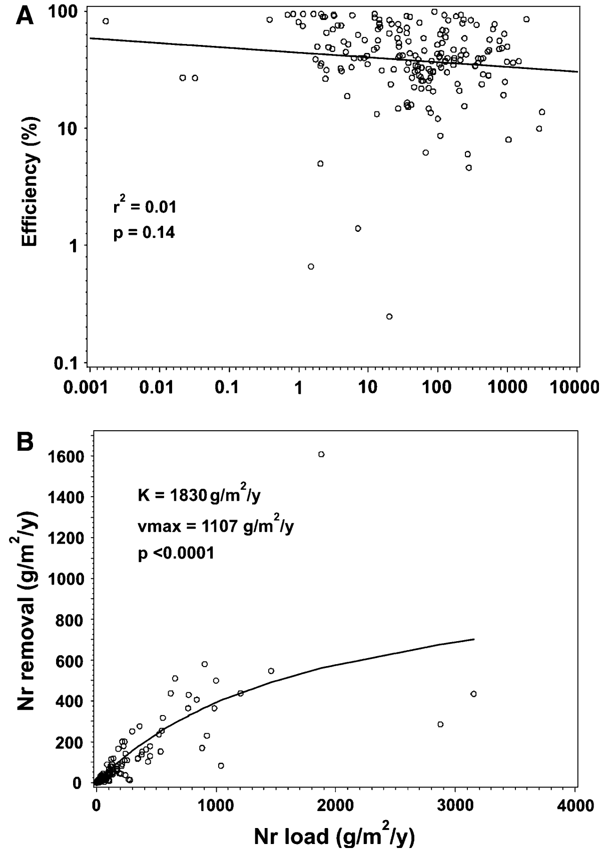

Figure 8. Alternatives to a linear model of the functional relationship between Nr loading and Nr removal. **A** Declining efficiency model, fit by linear regression. **B** Michaelis–Menten (saturation) model, fit by non-linear regression; N = 189. One highly influential outlying observation was omitted from the data for both models; this was from an agricultural wetland in Sweden with an exceptionally high Nr load (>9000 g m^{-2} y^{-1}) and short residence time (Supplemental Material, reference 2).

tion to Nr loading rates, which alone account for 86% of the variation in Nr removal. The analysis, and this principal finding, is not greatly sensitive to the type of wetland (within the subset of classes included) or any of the variables considered other than Nr loading rate. We have shown through random resampling of the data that the major findings of this analysis are insensitive to inclusion or deletion of blocks of data. The narrow distributions of regression coefficients and mean efficiency estimates generated from random subsets of data suggest that an unbiased data set would give similar results. Moreover, other studies that have compiled data on Nr removal in various types of wetlands generated results quantitatively similar to those reported here (Poach and others 2004; Valiela and Cole 2002; Crumpton and Goldsborough 1998).

Meta-analysis in general is subject to a particular bias, in that studies without positive results tend not to be published. Therefore, we expect that our dataset is censored to some extent. If additional observations with negligible or negative Nr removal were included, the principal effect might be to increase the variance of the estimates. In a simulation, we added 10% (19) random log-normal values of Nr loading and Nr removal to the dataset. To simulate negligible rates of N removal, the mean and standard deviation of random Nr removal values were set at 1% of those derived from the meta-analysis. As expected, the simulation increased the variance of the relationship (r^2 = 0.64 vs. 0.86). The slope of Nr removal on Nr loading decreased (0.87 vs. 0.94), but remained significant ($P < 0.0001$).

Of the three models describing the functional relationship between Nr loading and Nr removal discussed by O'Brien and others (2007), the linear model was the best fit to the data in our study, based upon linear and non-linear (Michaelis–Menten model) regression analysis. The alternatives, that is, declining efficiency and Michaelis–Menten models, are plotted against the data, with descriptive statistics, in Figure 8 (Figure 3 is the linear model). The Michaelis–Menten model indicates a saturation effect at very high Nr loading rates that is not apparent in the linear model; the slope of the declining efficiency model is close to zero, as predicted by the linear model.

The relationships derived here allow an estimate of total Nr removal for selected wetland classes throughout the contiguous United States, based on the total areas of these classes of wetlands in 2004 (Dahl 2006). Multiplying geometric mean loads for the major classes EE, PE, and PF by mean

Table 3. Estimated Total Nr Removal by Selected Classes of Wetlands in the United States

Class	Area (km^2)	Mean Nr load	Mean efficiency	Total Nr removal
EE	18,501	17.75	0.333	133,550
PE	105,813	98.65	0.493	4,746,098
PF	210,564	8.62	0.627	923,493
Total	406,270			5,803,140

Nr loads are geometric means in gN m^2 y^{-1}. Total Nr removal is in metric tons (1 × 10^6 g) per year.

efficiencies and areas gives a grand total of 5.8 Tg of Nr removed per year (Table 3). Although we had insufficient data to tabulate mean Nr load and efficiency for palustrine shrub wetlands, the sparse data suggest that an additional 0.3 Tg N/y would be removed by this class. The lower estimate is 91% of the amount of Nr produced by natural processes in the contiguous U.S. (6.4 Tg N/y), 20% of the total anthropogenic contribution of 29 Tg N/y, and 16% of total U.S. Nr production (U.S. EPA, unpublished data). Whatever the uncertainties in these estimates, it is clear that removal in wetlands is a significant sink for Nr, especially considering that wetlands represent a small fraction of the overall U.S. landscape. At the global scale, estimates of the total extent of freshwater swamps and marshes (Spiers 2001), plus an assumption that the combined area of salt marshes and mangroves globally is proportional to that in the U.S, yields a rough estimate of 26 Tg/y Nr removed. Denitrification in wetlands globally has been estimated at 18 Tg/y (Armentano and Verhoeven 1990), including a large contribution from rice fields, but excluding other removal processes. Compared with estimates of global Nr inputs (Galloway and others 2003), the amount of Nr removed is 11% of natural Nr inputs, 17% of anthropogenic inputs, or 8% of total inputs. These estimates likely would be considerably larger if more complete data on wetland areas were available (Spiers 2001). Given the several uncertainties, we suggest that this global estimate is a lower bound on Nr removal by wetlands.

Considering that at least 50% of native wetlands have been lost over the past century (Spiers 2001), great potential for Nr removal has been lost, along with other benefits of these resources. The present analysis implies that the mass of Nr removed by wetlands is primarily a function of wetland area and Nr loading rate, with no apparent upper limit. Preservation of existing wetlands, large-scale restoration of wetlands (Mitsch and Day 2006), and diversion of Nr sources from waterways to wetlands should be considered as major components of regional, national, and global strategies to mitigate the negative effects of the nitrogen cascade (Galloway and others 2003). In fact, this may be the only practical strategy that can achieve the necessary scale of mitigation for diffuse sources of Nr. Maintaining services and values of wetlands such as biodiversity, flood reduction, water supply, esthetics, recreational opportunities, and so on (Dodds and others 2008; Keddy and others 2009) that could be diminished by excessive Nr loads would be an important consideration in such strategies, as would the potential for additional contributions of N_2O to greenhouse gas emissions.

Estimates of Nr removal by wetlands at all spatial scales could be improved by coordinated research focusing on natural wetlands—the volume of available literature is dominated by studies of constructed systems. Relevant studies from tropical and boreal wetlands are sparse in the scientific literature, a minor matter for the contiguous U.S., but a major one at the global scale. More comprehensive estimates of nutrient removal by tidal wetlands are needed; this is a difficult area of research that could benefit from advanced techniques such as stable isotope tracers and remote sensing. In 2011, the U.S. Environmental Protection Agency, with the states, will undertake the first national survey of the ecological condition of wetlands (http://www.epa.gov/owow/wetlands/survey/). Although Nr removal will not be measured directly, several relevant indicators (for example, standing stocks of organic C and C:N:P ratios in soils; above- and below-ground plant biomass) will be measured. From these indicators, it may be possible to generate independent (indirect) estimates of Nr removal at the continental scale for comparison with the results reported here.

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