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Effects of Damming on River Nitrogen Fluxes: A Global Analysis

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Key Points:
- Globally, denitrification and burial in reservoirs exceed N fixation, hence causing a reduction in riverine N export to the coastal ocean
- Damming increases riverine N:P ratios, thus reducing the degree of N limitation in downstream water bodies
- In the coming decades, the largest changes in in-reservoir N fixation, N burial, and denitrification fluxes will happen in Asia

Supporting Information:
- Supporting Information S1

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Abstract Damming creates biogeochemical hotspots along rivers that modify the riverine flow of nutrients, including nitrogen (N). Here, we quantify the impact of dams on global riverine N fluxes using a reservoir N mass balance model. In-reservoir processes represented in the model include primary production, mineralization of organic N, denitrification, and sedimentary burial. In addition, we explicitly account for N fixation as a source of N, assuming that the N to phosphorus (P) ratio of the inflow regulates the magnitude of N fixation in reservoirs. The model is scaled up via a Monte Carlo analysis that yields global relationships between N elimination in reservoirs, either by denitrification or burial, and the hydraulic residence time. These relationships are then combined with N loads to the world's dam reservoirs generated by the Global-NEWS model and the estimated N fixation fluxes. According to the results, in year 2000, worldwide N fixation in reservoirs was on the order of 70 Gmol yr^{-1}, while denitrification and burial in reservoirs eliminated around 270 Gmol yr^{-1}, equal to 7% of N loading to the global river network. The latter is predicted to double to 14% by 2030, mainly as a result of the current boom in dam building. The results further imply that, largely due to N fixation in reservoirs, damming causes a global upward shift in riverine N:P ratios, thus lessening N limitation in receiving water bodies.

1. Introduction

Humans have altered the flow of nitrogen (N) transported by rivers from land to sea, not only by increasing N loading to rivers from nonpoint sources and wastewater discharges (Wollheim et al., 2008) but also through the building of dams (Van Cappellen & Maavara, 2016). We are currently in the midst of the second-largest boom in dam construction since the 1950s. The number of large hydroelectric dams, which currently represent about 20% of dams worldwide, is expected to double following the completion of dams currently under construction or planned (Zarfl et al., 2015). Upon dam closure, the water residence time in the section of river that is transformed into the reservoir increases, while turbulence decreases. These conditions promote the in-reservoir biogeochemical cycling of N, with removal of particulate N by burial in sediments accumulating in the reservoir and by gaseous emissions to the atmosphere. Thus, the growing fragmentation of river networks by dams is expected to increasingly affect the magnitude and speciation of N fluxes delivered to receiving lakes and nearshore marine environments (Harrison et al., 2009; Van Cappellen & Maavara, 2016).

Because of burial and denitrification, dams are generally assumed to lower riverine fluxes of total N (Harrison et al., 2009). However, N fixation can also act as a source of N to reservoirs (Cook et al., 2010; Horváth et al., 2013; Howarth et al., 1988; Jankowski et al., 2012). Hence, N fixation can be a confounding factor when assessing the overall role of reservoirs on riverine N fluxes along the land to ocean aquatic continuum. Multiple factors regulate N fixation in freshwater systems (Forbes et al., 2008). Among these, it is widely accepted that a low external input of N, relative to that of P, stimulates N fixation in lakes and reservoirs (Pinto & Litchman, 2010; Levine & Schindler, 1999; Nõges et al., 2008; Schindler et al., 2008; Vrede et al., 2009). However, there are few data or estimates available to quantify the global contribution of N fixation to reservoir N budgets.

The elimination of N in a reservoir is usually estimated as the difference between the annual flux of N carried with the river inflow and the flux of N flowing out through the dam (Garnier et al., 1999; Hansen et al., 2016; Tomaszek & Koszelnik, 2003). Using this approach, Harrison et al. (2009) proposed that in the mid-1990s, lakes and reservoirs eliminated 1,407 Gmol N yr^{-1} globally, with reservoirs responsible for 33% of this

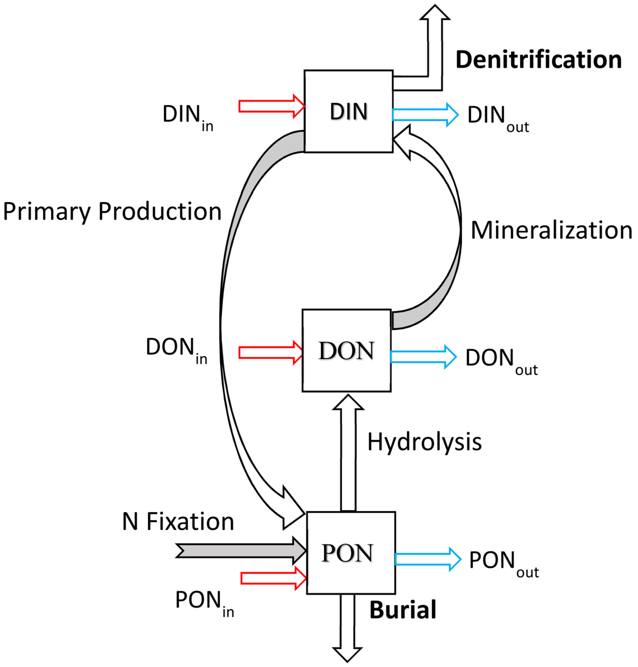

Figure 1. Reservoir nitrogen mass balance model with three pools (DIN = dissolved inorganic N; DON = dissolved organic N; PON = particulate organic N). Red arrows and blue arrows represent inflow into and outflow from the reservoir, respectively.

value (464 Gmol N yr^{-1}). These authors calculated elimination as a fraction of the N input, based on the apparent settling velocity in the lake or reservoir and the hydraulic load. Their model was calibrated using a data set of 80 lakes and 35 reservoirs, and the resulting empirical relationship was then extrapolated worldwide using the data set of the global lake and reservoir surface area (Lehner & Döll, 2004). More recently, Beusen et al. (2016) estimated that, at the end of the twentieth century, 1,929 Gmol N yr^{-1} were being eliminated in river systems, with 24% taking place in reservoirs (463 Gmol N yr^{-1}). The latter authors used the IMAGE-GNM model, which calculates N elimination as a function of the nutrient N uptake velocity, temperature, and N concentration in the aquatic system. Both these model studies report total removal of N in reservoirs, but do not distinguish between denitrification and burial. Moreover, neither studies account for N fixation in dam reservoirs.

In the present study, we expand on the earlier work by (1) estimating global N fixation in reservoirs; (2) differentiating between the two main reservoir sinks of N, sediment burial, and denitrification; and (3) providing these results in a spatially explicit format. In addition, we perform our analyses for three time points: the years 1970, 2000, and 2030. We scale up a process-based model that represents the biogeochemical processes controlling in-reservoir N cycling, following the general approach developed by Maavara et al. (2014, 2015, 2017) and applied previously to estimate the modifications of the global riverine fluxes of nutrient silicon (Si), phosphorus (P), and organic carbon (C_{org}) by damming. We further distinguish between gross and net elimination of N by dams. Gross elimination is defined here as the sum of the denitrification and burial fluxes in a reservoir; net N elimination is defined as gross N elimination minus N fixation.

2. Material and Methods

2.1. Model Concept

A process-based model computes the in-reservoir biogeochemical N transformations (Figure 1). The model represents three pools of reactive N: dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), and particulate organic nitrogen (PON). Total N (TN) refers to the sum of DIN, DON, and PON. The pools include both the water column and the upper, active portion of the reservoir sediments. The model computes annually averaged pool sizes and fluxes. At a yearly timescale, reservoirs are assumed to be well mixed. Reservoir processes represented are N fixation, denitrification, primary production, mineralization, and hydrolysis (Figure 1). Denitrification and burial of PON below the active upper sediment layer permanently remove N from the aquatic system, while N fixation acts as an additional source of N to the reservoir. Each N pool is also supplied by riverine input and discharges downstream through the dam. Note that the inputs of N by atmospheric deposition and groundwater discharge are assumed to be negligible, relative to the riverine supply.

The mathematical formulations used to compute the fluxes associated with the in-reservoir N processes are reviewed in section 2.2. Probability density functions (PDFs) are assigned to the parameters in these formulations. The PDFs account for the ranges and global variability of the parameters; they are based on an extensive search of the literature (Table 1). River discharge, reservoir volume, TN concentration of the river inflow, and the relative proportions of DIN, DON, and PON in the inflow are similarly assigned PDFs derived from observational data for flowing and lentic freshwater environments. The PDFs imposed in the modeling are listed in the Supporting Information in Table S1.

The PDFs are combined with Monte Carlo simulations to generate a large set of virtual reservoirs that are assumed to exhibit statistical properties approaching those of actual reservoirs worldwide. The virtual reservoir database is used to extract globally representative equations for N burial and denitrification. These

Table 1
Summary of References Used for Parameterization and Comparison of the Model Results with the Literature Data

	References
Model parameters and inputs	
Mineralization first-order rate coefficients	(Bruce et al., 2006; Chung et al., 2014; Cui et al., 2016; Doan et al., 2015; Imteaz et al., 2003; Marcé et al., 2010; Özkundakci et al., 2011; Romero et al., 2004; Schladow & Hamilton, 1997)
Burial first-order rate coefficients	(Grantz et al., 2014; Knoll et al., 2014; Kunz, Wüest, et al., 2011)
Hydrolysis first-order rate coefficients	(Bruce et al., 2006; Chung et al., 2014; Imteaz et al., 2003; Marcé et al., 2010; Özkundakci et al., 2011; Schladow & Hamilton, 1997)
Inflowing TN concentrations	(Bhat et al., 2014; Boyer, 2008; Chen et al., 2017; Edwards et al., 2000; Goolsby & Battaglin, 2001; Gurung, 2007; Hur & Cho, 2012; Jarvie et al., 1998; Judd, 2008; Lévesque & Page, 2011; Policht-latawiec, 2013; Ren et al., 2015; Sprague et al., 2002; Sun et al., 2013; Vandermeulen & Gemza, 1991; Windolf et al., 1996)
Proportions of DIN, DON, and PON in inflowing TN	(Berner & Berner, 1995; Meybeck, 1982; Seitzinger et al., 2005)
Nitrogen fixation rates	(Ashton, 1981; Bartoszek & Koszelnik, 2016; Findlay et al., 1994; Gondwe et al., 2008; Grantz et al., 2014; Howarth et al., 1988; Levine & Lewis, 1984; Mugidde, 2001; Persson, 2003; Toetz & McFarland, 1987)
Empirical coefficient (K_{DEN}) of denitrification	(Akbarzadeh et al., 2018; Canavan et al., 2006; Han et al., 2014; Jones & Simon, 1981; McCarthy et al., 2007; Seitzinger, 1994)
Comparison of the model results	
Apparent elimination efficiencies	(Donald et al., 2015; Garnier et al., 1999; Knoll et al., 2014; Némery et al., 2016; Powers et al., 2015; Ran et al., 2017; Yang et al., 2018)
Areal denitrification rates	(David et al., 2006; Gardner et al., 1987; Gibson et al., 1992; Grantz et al., 2012; Koszelnik et al., 2007; Mengis et al., 1997; Messer & Brezonik, 1983; Molot & Dillon, 1993; Noges et al., 1998; Saunders & Kalff, 2001; Tomaszek & Czerwieniec, 2000)
Areal burial rates	(Brenner et al., 2001; Höhener & Gächter, 1993; Huang et al., 2018; Jensen et al., 1992; Knoll et al., 2014; Mengis et al., 1997; Yu et al., 2018)

Note. DIN = dissolved inorganic nitrogen; DON = dissolved organic nitrogen; PON = particulate organic nitrogen; TN = total nitrogen.

equations are applied to databases of existing and future reservoirs (Lehner et al., 2011; Zarfl et al., 2015), together with nutrient loads estimated with the Global-NEWS model (Mayorga et al., 2010), plus N fixation fluxes calculated from the degree of N limitation of the river inflow. Aggregated estimates of N fixation, denitrification, and N burial in the reservoirs are then presented for the world's river basins at the different time points. The estimates for 2030 are based on the Millennium Ecosystem Assessment (MEA) scenarios (Alcamo et al., 2006), implemented in Global-NEWS.

2.2. In-Reservoir Processes

The model calculations account for the major biogeochemical processes controlling the fate of N in lentic systems. Mineralization, hydrolysis and burial fluxes are modeled with first-order kinetics:

$$F = k \times M \tag{1}$$

where F is the flux in mol N yr^{-1}, k is an apparent first-order rate coefficient per year, and M is the molar mass of N in the pool from which the flux originates. The PDFs for the first-order rate coefficients describing in-reservoir mineralization, hydrolysis, and burial are given in Table S1. For N elimination by burial, a uniform distribution is assigned to the first-order rate constant, k_{bur}. The range of k_{bur} is adjusted by trial and error, until the average molar TN:TP ratio of buried material in the virtual reservoir data set generated by the Monte Carlo simulations (Figure S1) matches that of sedimentary material of lentic systems reported in the literature (n = 17, median TN:TP = 7.3). The computed total P (TP) concentrations of buried material are those obtained with our previous P mass balance model for reservoirs (Maavara et al., 2015); TP comprises particulate organic P (POP), exchangeable P (EP), and unreactive particulate P (UPP), as defined in Maavara et al. (2015).

The outflow fluxes through a dam of the different N species are also calculated using equation (1) where the rate coefficient is set equal to the inverse of the water residence time (τ_r), that is, the flushing rate of the reservoir (Maavara et al., 2015). The inflow fluxes to reservoirs in the Monte Carlo analysis are based on PDFs describing river discharge, TN concentrations, and the proportions of the different species that make up the inflow TN concentration (Table S1). The global distributions of reservoir volume and discharge are fitted to Pareto distributions obtained from the Global Reservoirs and Dams (GRanD) database Version 1.01 (Lehner et al., 2011) (Table S1).

The flux of N added to the reservoir by N fixation is calculated using an empirical relationship that links the relative contribution of N fixation (N_{fix}) to the relative supply of N and P via the riverine inflow. The relationship, shown in Figure S2, builds on 30 data points from reservoirs and lakes for which the annual mean TN:TP ratio of the river inflow and the corresponding fraction of N fixation are either directly reported or can be calculated from the data provided (Table S2). As expected, the highest N_{fix} values are observed for the lower TN:TP input ratios, that is, when primary production in the reservoir tends to be N limited. The data fit shown in Figure S2 yields:

$$N_{fix}(\%) = \frac{\alpha}{(1 + \exp(0.5 \times TN : TP + \beta))} \tag{2}$$

where the values of the dimensionless parameters α and β are 37.2 and −6.877, respectively.

Equation (2) is further modified to account for the effect of the hydraulic residence time in the reservoir on N fixation. Natural algal communities require time to establish themselves, and, therefore, the water residence time needs to be long enough to avoid the algae from being flushed out (Paerl & Tucker, 1995; Søballe & Kimmel, 1987; Straškraba et al., 1993). This is particularly true for N fixing bacteria, due to their relatively slow growth rates (Maberly et al., 2002). That is, at short water residence times, the doubling time can become a more important limiting factor than nutrient availability (Straškraba et al., 1993). This is represented by introducing a unitless rate multiplier (μ):

$$N_{fix}(\%) = \mu \times \frac{\alpha}{(1 + \exp(0.5 \times TN : TP + \beta))} \tag{3}$$

For N-fixing algae, the minimum water residence time is estimated to be on the order of 10 days, while the organisms function at their maximum capacity when the residence time exceeds 60 days (Straškraba et al., 1993). The relationship between μ and the water residence time (τ_r) is accordingly expressed as (Figure S3):

$$\mu = \text{erf}\left(\frac{\tau_r - 0.028}{0.04}\right) \tag{4}$$

where τ_r is in years. To account for uncertainties in the N_{fix} estimates, we assume a normal distribution with a standard deviation of ±10% around the N_{fix} values predicted by equation (3). For consistency, the N demand of primary productivity in a given reservoir, that is, the N uptake flux associated with photosynthesis, is imposed as the upper limit for the N fixation flux.

Estimations of the N fluxes associated with primary production and denitrification are derived from the corresponding carbon (C) fluxes obtained with the previously developed organic carbon (C_{org}) mass balance model for reservoirs (Maavara et al., 2017). Thus, the N uptake flux by primary production ($mol \cdot N \cdot yr^{-1}$) is given by:

$$F_{up} = R_{up} \times \frac{TDP}{TDP + K_{sp}} \times \frac{16}{106} \tag{5}$$

where R_{up} is the maximum photosynthesis rate in mol C yr^{-1}, TDP is the total dissolved P concentration in the reservoir (mol km^{-3}), K_{sp} is the half-saturation TDP concentration (mol km^{-3}), and the fraction 16:106 is the Redfield ratio for algal biomass production that converts C moles into N moles. Values of R_{up} are from Maavara et al. (2017): they are computed as the product of the annual chlorophyll concentration in the reservoir and the maximum chlorophyll-specific carbon fixation rate. The chlorophyll concentration in turn depends on the photosynthetically active radiation and its attenuation with depth below the water surface. Correction factors further account for the effects of water temperature and the yearly fraction of ice-free days. The second term on the RHS of equation (5) assumes that the availability of P is the ultimate limiting nutrient for annual primary production (Schindler, 1977; Schindler et al., 2008). In other words, we assume that, on an annual basis, N fixation balances any N deficit of the nutrient supply to a given reservoir. The values of TDP and K_{sp} are those calculated with the reservoir P mass balance model of Maavara et al. (2015).

Denitrification fluxes (F_{den} in mol N yr^{-1}) are calculated as fractions of the corresponding C_{org} mineralization fluxes (F_{minC} in mol C yr^{-1}) in Maavara et al. (2017). Assuming the idealized stoichiometry of denitrification, where four nitrate ions are consumed per 5 C_{org} mineralized (Akbarzadeh et al., 2018), the denitrification fluxes are given by:

$$F_{den} = 0.8 \times F_{minC} \times \frac{[DIN]}{[DIN] + K_{DEN}} \tag{6}$$

where DIN is the concentration of DIN in mol mol N L^{-1} and K_{DEN} is an empirical coefficient (mol N L^{-1}). The last term on the RHS corresponds to the fraction of the C_{org} mineralization flux that is coupled to nitrate reduction. Equation (6) is applied to the in-reservoir decomposition of allochthonous (i.e., supplied from the upstream catchment) and autochthonous C_{org} (i.e., produced in the reservoir), as well as the C_{org} of the soil organic matter and biomass flooded upon closure of the dam (see Maavara et al., 2017, for details). Because of slightly improved fits to the Monte Carlo output, the calculated reservoir DIN concentration is used in equation (6) in the case of the allochthonous and autochthonous C_{org} pools, while the river inflow DIN concentration is used in the case of flooded C_{org}.

The value of K_{DEN} in equation (6) is an independently constrained fitting parameter calibrated using literature data for sediments for which both the depth-integrated C_{org} decomposition rate and the depth-integrated denitrification rate are reported (Figure S4 and Table S3). In a number of instances, the sediment oxygen demand serves as a measure of the depth-integrated rate of C_{org} decomposition (Canfield et al., 1993; Van Cappellen & Gaillard, 1996). The resulting value of K_{DEN} is fairly large (115 μmol L^{-1}), implying that in most reservoirs, except those receiving very high nitrate loadings, denitrification is responsible for a relatively small fraction of the total C_{org} oxidation. The same value of K_{DEN} is applied to all three C_{org} pools.

2.3. Scaling Up

The N mass balance model is run 6,000 times, each time randomly selecting parameter values from the predefined PDFs in Table S1. The ensemble of Monte Carlo simulations yields a database of hypothetical N cycling in virtual reservoirs. The key assumption is that the N dynamics in this virtual set of reservoirs are representative of those of real reservoirs. From the virtual data set, we then extract global relationships that express the relative importance of N burial and denitrification as a function of a reservoir's water residence time, τ_r (Figure S5). Following Maavara et al. (2015, 2017), we fit the Monte Carlo data to:

$$f_i = a_i - \frac{b_i}{1 + c_i \times \tau_r} \tag{7}$$

where f_i is the fraction of the total TN input (i.e., river input plus N fixation) to the reservoir that is eliminated either by sediment burial or denitrification and a_i, b_i, and c_i are the parameters fitted to the mean values of f_i in the virtual database. Separate parameter sets apply to burial and denitrification (Table S4). The parameter values also differ for the different MEA scenarios for the years 2030, because of the effect of variable air temperatures associated with the different MEA scenarios (Fekete et al., 2010).

For the year 1970 and 2000 simulations, the global relationships (i.e., equation [(7)]) are applied to the reservoirs built before 1970 and 2000, respectively, that are compiled in the GRanD database Version 1.01 (Lehner et al., 2011). The database accounts for at least 76% of the actual global volume of reservoirs at the end of the twentieth century (Lehner et al., 2011). For the 2030 scenarios, the year 2000 GRanD reservoirs (V1.01) are augmented with the beta version of the Future Hydropower Reservoirs and Dams Database (FHReD, Zarfl et al., 2015), which comprises hydroelectric dams that are currently under construction or planned to be in operation by 2030 (Grill et al., 2015).

For any given reservoir, the riverine inputs of N and P are those generated using (1) the undammed catchment area of the reservoir, extracted from Lehner et al. (2011); (2) the areal yields for that catchment area of dissolved inorganic N and P (DIN and DIP), dissolved organic N and P (DON and DOP) and particulate N and P (PN and PP) predicted by Global-NEWS, and for cascading dams; (3) also the export fluxes of N and P from the upstream reservoir(s). This routing procedure is the same as described in detail in Maavara et al. (2017). For the future scenarios (year 2030), Global-NEWS yields spatially explicit riverine nutrient yields for the four MEA scenarios based on prescribed changes in social, economic, cultural, and political drivers (Alcamo et al., 2006; Seitzinger et al., 2010). Therefore, the effects of climate change are reflected in the 2030 riverine influxes of N and P. The increases in temperature from 2000 to 2030 in the four MEA scenarios are in the range of 0.91–1.09 °C (Fekete et al., 2010). For further details on the scaling up, the reader is referred to Maavara et al. (2015, 2017).

2.4. Comparison to Observational Data

A full validation of global-scale biogeochemical models is rarely possible. In the present case, there is no comprehensive data based on reservoir N budgets that is globally representative. This data limitation is partially overcome by combining process knowledge of N cycling in freshwater systems with a stochastic reservoir modeling approach. A comparison with available observational data helps assess whether the model outcomes are reasonable. Below we provide such comparisons for the rates of denitrification and N burial in reservoirs and the apparent net N elimination efficiencies by dams.

Areal rates of denitrification and N sediment burial (in $gN{\cdot}m^{-2}{\cdot}yr^{-1}$) are calculated with the model for the reservoirs in the GRanD database in year 2000 (Figures S6 and S7). These rates are then compared to areal rates of denitrification ($n = 26$, Table S5) and N burial ($n = 11$, Table S6) reported in the literature for reservoirs and lakes. Note that for denitrification, we only include literature studies that either report annual rates directly or provide enough measured rates across different seasons to estimate yearly averaged denitrification fluxes. In the case of N burial, the data in the literature are more limited; hence, all rate values that could be found are considered.

The model-predicted median and mean denitrification rates in dam reservoirs of 7.8 and 19.8 $gN{\cdot}m^{-2}{\cdot}yr^{-1}$ are very close to the corresponding literature values of 7.8 and 21.4 $gN{\cdot}m^{-2}{\cdot}yr^{-1}$. For nitrogen burial, the median and mean rates predicted by the model, 5.5 and 16 $gN{\cdot}m^{-2}{\cdot}yr^{-1}$, are within a factor of two of the median (4.1 $gN{\cdot}m^{-2}{\cdot}yr^{-1}$) and mean (8.6 $gN{\cdot}m^{-2}{\cdot}yr^{-1}$) literature values. While these comparisons are based on relatively small numbers of observational data, they indicate that the model yields annual N elimination fluxes associated with damming that are within the expected orders of magnitude.

We also assembled literature data for dams for which the average water residence time and apparent net N elimination efficiency are given or can be derived. The apparent net N elimination is defined as the fractional difference between the annual flux of N carried with the river inflow and the flux of N flowing out through the dam. Thus, an apparent elimination efficiency of 0.5 means that N flowing out of the dam is 50% less than flowing in. For most of the selected reservoirs, the apparent elimination is based on measured TN concentrations in river inflow and dam outflow. In some cases, however, the elimination efficiencies of specific N species are reported, or N input via precipitation is added to the N inflow, for instance, for the reservoirs in the Lake Winnipeg watershed in Canada (Figure 2 and Table S7). The assembled data set includes 36 reservoirs worldwide (Table S7). Note that for these reservoirs, N fixation is not included as part of the N input, either because N fixation was shown not to be important or the data are not available. Also note that only reservoirs with measurements of inflows and outflows collected over at least 1 year are included.

The apparent elimination efficiencies in the data set (Table S7) are compared in Figure 2 to those of the virtual reservoirs (i.e., generated via the Monte Carlo simulations) calculated from the model-predicted TN inflows and outflows. The values obtained from the literature are generally consistent with the overall trend and spread obtained with the virtual reservoirs, although they tend to be somewhat higher than the average model trend. Three agricultural reservoirs in the Midwestern United States show the largest deviations from the model-predicted trend (see also section 2.6). The very high apparent N elimination efficiencies of these three reservoirs may be linked to the very high nitrate loads entering the reservoirs, which in turn cause very high rates of denitrification (Powers et al., 2015; Vanni et al., 2011).

2.5. Parameter Sensitivity

A bootstrapping method is used to evaluate the sensitivity of the model output to the model parameters. First, we generate 6,000 runs for year 2000, referred to as the virtual dam data set, from which 5000 samples with replacement are selected randomly. The observed N fixation fluxes ($\widehat{y}_i$) of the 30 data points from reservoirs and lakes used to generate Figure S2 are then compared to those model simulated fluxes (y_i) that have

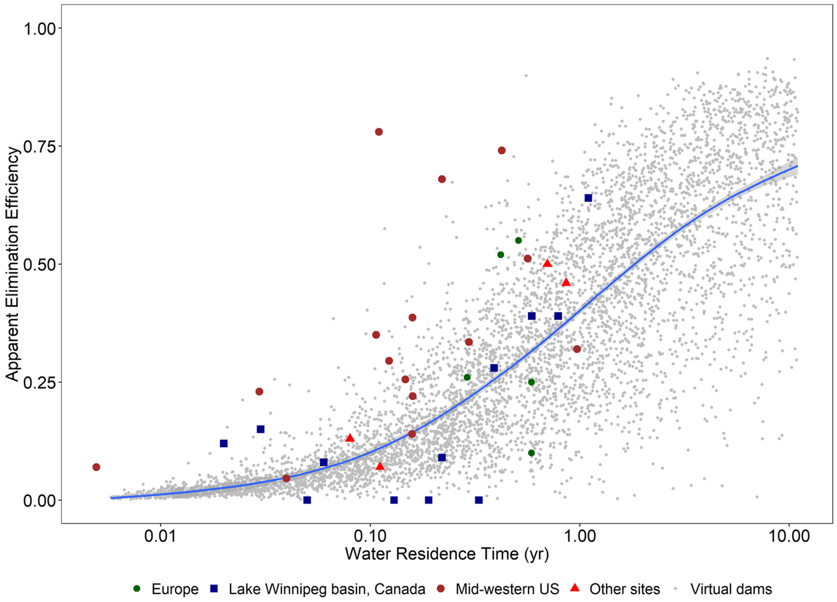

Figure 2. The relationship between water residence time and apparent N elimination efficiency for the virtual data set of dams. The blue line represents the average trend of the apparent elimination efficiency in the virtual data set of dams. Other symbols display data collected from the literature for individual reservoirs. The apparent elimination is defined as the difference between the annual flux of N carried with the river inflow and the flux of N flowing out through the dam.

the same corresponding TN:TP ratios in the river inflow. The average sum of squared prediction errors (SSPE) is computed as:

$$\mathrm{SSPE} = \frac{1}{n}\sum_{i=1}^{n}\left(y_i - \hat{y}_i\right)^2 \tag{8}$$

where n is the number of observations (here n = 30). The entire process is repeated 5,000 times, and, each time, the new virtual data set is fitted to equation (2), and a new SSPE is calculated. The resulting 5,000 SSPE values (Figure S8) are symmetrically distributed around the value of SSPE for the virtual data set of dams (dashed line in Figure S8), hence, showing low sensitivity of the model results to the random sampling process. The standard deviations of the parameters α and β in equation (2) are 0.007 and 0.162, respectively, which translate in a ±11% standard deviation for the estimated global N fixation in reservoirs in year 2000.

The same procedure is repeated for N burial and denitrification: values for the parameters a, b, and c in equation (7) are estimated based on 5,000 iterations for N burial and denitrification separately. Standard deviations of the parameter values are presented in Table S8. For the global flux estimates, this translates into standard deviations of ±11% and ±8% for N burial and denitrification in reservoirs in year 2000.

2.6. Model Uncertainty

The box model calculations in this study provide a simplified representation of the aquatic N cycle. While box models are conceptually straightforward, they do not account for the spatial heterogeneity of the physical and biogeochemical processes affecting the fate of N along reservoirs. Adding complexity to the model system to improve its structural realism, however, leads to more parameters and may add to the potential uncertainty. The N reservoir model further runs on an annual scale; therefore, it cannot account for the variability associated with processes that operate at shorter timescales (e.g., daily to seasonal variations in biological activity and short-lived hydrological events).

Another source of uncertainty is the catchment-specific nutrient yields predicted by the Global-NEWS model. The magnitudes of the predicted global scale N transformations in reservoirs, burial, denitrification, and N fixation, reported in this study, strongly depend on the inputs of N, P, and C to rivers that ultimately derived from these yields. The burial and denitrification sinks are a function of the riverine flow and

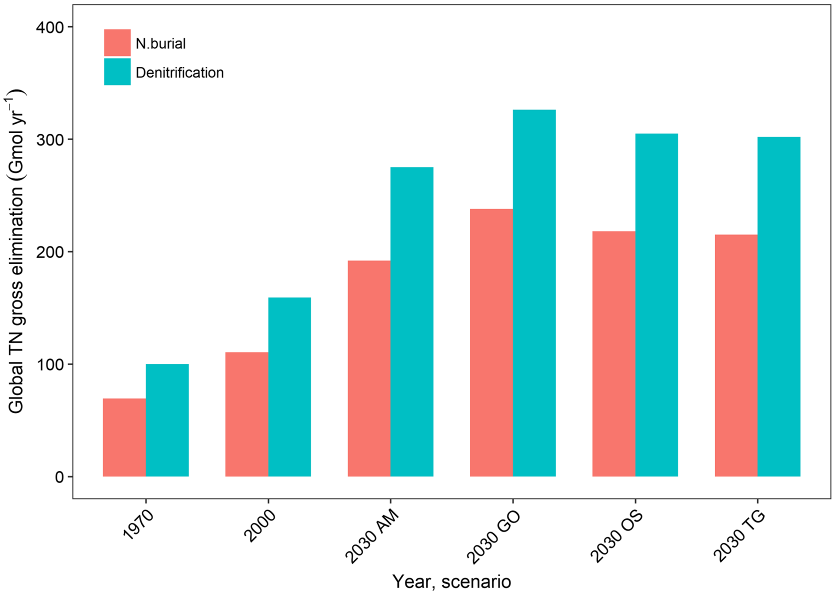

Figure 3. Global TN elimination via denitrification and N burial for years 1970, 2000, and 2030. The Millennium Ecosystem Assessment scenarios are identified in the caption of Table 2. AM = adaptive mosaic; GO = global orchestration; N = nitrogen; OS = order from strength; TG = TechnoGarden; TN = total N.

speciation of N into the reservoirs and, in the case of denitrification, also on the riverine supply of C_{org}. The TN:TP ratio of reservoir inflow in turn is the key driver determining the amount of N fixation estimated with the model. As nutrient delivery fluxes to rivers are updated, or additional future scenarios are proposed, it will be possible to recalculate the dam-related changes to riverine N fluxes.

Overall, the results presented here should be viewed as minimum estimates of the global impacts of dams on riverine N fluxes. This is because at each of the selected time points (years 1970, 2000, and 2030), the existing dam databases only cover a fraction of the total number of existing dams, with a focus on the larger dams. Further work will therefore be needed to account for the effects of the many smaller dams and reservoirs along the world's waterways. In addition, as shown in Figure 2, the majority of net N elimination efficiencies extracted from the literature lie above the average model trend, further suggesting that the model may underestimate the global reduction in riverine N fluxes by dams.

3. Results

3.1. Hindcasting: 1970 and 2000

For 1970, the model predicts a global TN gross elimination in dam reservoirs of 169 Gmol yr^{-1}, 69 and 100 Gmol yr^{-1} via N burial and denitrification, respectively (Figure 3; Table 2). This gross elimination (denitrification plus burial) represents 34% of the global input of TN (river inflow plus N fixation) into reservoirs in 1970 and 5.7% of the total N loading to river systems (which includes N that does not pass through any dam). Note that denitrification associated with the oxidation of C_{org} of soil organic matter and biomass flooded upon closure of dams are reported separately in Table 2 but are not considered in the gross and net N elimination calculations. In 1970, global N fixation in reservoirs estimated at 38 Gmol yr^{-1} or 7.6% of the TN input to reservoirs. The five top river basins in 1970 with the highest gross elimination of TN in reservoirs are, in order of decreasing importance, Mississippi, Zambezi, Volga, Niger, and Saint Lawrence (Table 3; Figure 4). The five top river basins for N fixation are Volga, Mississippi, Saint Lawrence, Columbia (North America) and Ganges-Brahmaputra (Table 4).

For year 2000, the model-estimated TN elimination fluxes via N burial and denitrification are 110 and 159 Gmol yr^{-1}, respectively, or a total gross elimination of 269 Gmol yr^{-1}, which represents a 59% increase relative to 1970. In 2000, 35.5% of the TN input to reservoirs is eliminated, equivalent to 7.4% of total N loading to the world's rivers. Global N fixation in reservoirs increases to 70 Gmol yr^{-1}, nearly a doubling compared to

Table 2
Global Effects of Dams on Riverine N Fluxes in Years 1970, 2000, and 2030

Global estimations	1970	2000	2030 AM	2030 GO	2030 OS	2030 TG
River N loading, Gmol yr^{-1}	2,973	3,631	3,411	3,778	3,632	3,512
N fixation in reservoirs, Gmol yr^{-1}	38	70	179	244	219	248
TN input to reservoirs (including N fixation), Gmol yr^{-1}	498	757	1,473	1,862	1,760	1,629
TN buried, Gmol yr^{-1}	69	110	192	239	218	215
TN denitrified, Gmol yr^{-1}	100	159	275	327	305	302
TN gross elimination, Gmol yr^{-1}	169	269	467	566	523	517
TN denitrified by flooded Corg, Gmol yr^{-1}	996	544	480	520	509	492
N uptake by primary production, Gmol yr^{-1}	85	149	404	616	556	591
Fraction of global TN riverine load eliminated (gross elimination), %	5.7	7.4	13.7	15.0	14.4	14.7
N fixation as a fraction of global TN riverine load, %	1.3	1.9	5.2	6.5	6.0	7.1
Fraction of global TN riverine load eliminated (net elimination), %	4.4	5.5	8.4	8.5	8.4	7.6
Fraction of global TN input to reservoirs eliminated (gross elimination), %	33.9	35.5	31.7	30.4	29.7	31.7
N fixation as a fraction of global TN input to reservoirs, %	7.6	9.2	12.1	13.1	12.4	15.2
Number of reservoirs	4,393	6,846	10,547	10,547	10,547	10,547
Total reservoir volume (km^3)	3,573	6,191	8,503	8,503	8,503	8,503

Note. The 2030 projections are based on the four Millennium Ecosystem Assessment (MEA) scenarios: AM = adaptive mosaic; GO = global orchestration; OS = order from strength; TG = TechnoGarden. Denitrification coupled to mineralization of organic carbon flooded upon dam closure is not considered in the calculations of global N elimination in reservoirs.
N = nitrogen; TN = total N.

1970. Similar to 1970, the basins of the Mississippi and Zambezi Rivers remain the top two watersheds eliminating most TN behind dams in 2000. However, major contributions are now also seen for the basins of the Paraná River (70 dams), the Chang Jiang (Yangtze River, 353 dams), and the Tocantins River in South America (4 dams). The shifts in the geographical distributions of TN elimination and N fixation in reservoirs between 1970 and 2000 are illustrated in Figures 4 and 5.

3.2. Forecasting: 2030

Global gross N elimination by dams rises from 269 Gmol yr^{-1} in 2000 to 566 Gmol yr^{-1} in the 2030 GO (Global Orchestration) scenario (an increase of 110%) (Table 2 and Figure 3). Even in the most environmentally favorable scenario (AM, Adapting Mosaic), gross N elimination increases by 74% from 2000 to 2030. Based on these projections, in 2030, dam reservoirs eliminate between 30% (GO scenario) and 32% (AM scenario) of the TN influx to reservoirs by denitrification plus N burial. Relative to 2000, global N fixation in 2030 is projected to grow by at least 155% (179 Gmol yr^{-1}, AM scenario) and up to 254% (248 Gmol yr^{-1}, TechnoGarden or TG scenario). The 2030 results highlight the major role of ongoing dam construction in Southeast Asia and to a lesser extent South America (Figures 4, 5, and 6). From 2000 to 2030, the largest changes in in-reservoir N fixation, N burial, and denitrification fluxes are predicted to happen in Asia, where both the number of dams and TN loading to rivers will experience large increases (Seitzinger et al., 2010; Zarfl et al., 2015). In the 2030 simulations, one single watershed, that of the Chang Jiang (Yangtze), accounts for 15% of the total global gross elimination of N in reservoirs. In this watershed, TN loading to reservoirs is estimated to increase by 41% between 2000 and 2030 (from 106 Gmol yr^{-1} to 149 Gmol yr^{-1} under the GO scenario), while at the same time, the number of dams will increase from 353 to 495. Additionally, in 2030, 32% of the total global N fixation in reservoirs will occur in three river basins in Southeast Asia: Chang Jiang (Yangtze), Ganges-Brahmaputra, and Mekong.

4. Discussion

4.1. Nutrient Elimination by Dams

The damming of rivers creates new biogeochemical reactors along the aquatic continuum. The cycling of bioactive elements in dam reservoirs significantly changes their fluxes and chemical speciation (Van Cappellen & Maavara, 2016). It is generally assumed that the presence of dams reduces the net fluxes of nutrients along river systems. This is the case for P and silicon (Si), which are retained by burial of particle-associated P and Si in sediments accumulating in reservoirs (Maavara et al., 2014, 2015). The key difference between N and the nutrient elements P and Si, however, is that the latter two nutrient elements have

Table 3
Top 10 Watersheds Ranked According to Annual Mass of N Eliminated by Denitrification Plus Burial in Dam Reservoirs, for Years 1970, 2000, and 2030 (GO Scenario)

Rank	Watershed	TN gross elimination	Riverine TN load into watershed*	N fixation in reservoirs of watershed	No. of reservoirs	TN gross elimination as % of TN input**
1970						
1	Mississippi	28.5	79.7	2.9	552	35
2	Zambezi	12.1	34.5	0.5	25	35
3	Volga	11.8	21.4	3.3	17	48
4	Niger	9.8	28.9	0.4	27	33
5	Saint Lawrence	8.0	42.1	1.6	162	18
6	Ganges-Brahmaputra	7.6	155.2	1.4	59	4.9
7	Yenisei	7.0	23.3	0.4	3	30
8	Nile	5.7	7.1	0.8	11	72
9	Dnieper	4.4	7.9	1.0	5	49
10	Columbia	4.1	18.8	1.6	114	20
2000						
1	Mississippi	26.1	70.8	1.5	703	36
2	Zambezi	19.8	38.5	3.4	49	47
3	Niger	13.3	32.4	0.8	52	40
4	Paraná	11.5	65.0	3.4	70	17
5	Volga	10.2	50.3	3.1	17	19
6	Chang Jiang (Yangtze)	9.0	105.7	3.8	353	8.2
7	Ganges-Brahmaputra	8.7	226.0	2.4	86	3.8
8	Yenisei	8.2	25.0	0.9	7	32
9	Saint Lawrence	8.0	44.1	0.8	182	18
10	Tocantins	5.3	31.8	1.2	4	16
2030 (GO scenario)						
1	Chang Jiang (Yangtze)	82.5	148.7	42.6	495	43
2	Ganges-Brahmaputra	43.6	239.4	19.4	486	17
3	Mekong	28.2	56.8	15.9	138	39
4	Mississippi	27.8	71.9	3.9	703	37
5	Amazon	25.5	275.7	11.0	191	8.9
6	Zambezi	22.0	40.0	4.1	64	50
7	Paraná	18.0	65.4	11.9	418	23
8	Niger	15.6	34.5	1.7	74	43
9	Salween	12.7	18.9	4.7	26	54
10	Volga	12.3	24.4	5.5	17	41

Note. All units are Gmol N yr^{-1}.
*Note that not all the riverine TN load into a watershed necessarily passes through a dam. **TN input = riverine TN load into a given watershed plus N fixation in the reservoirs of that watershed.

no natural gas phase forms. Elimination (or retention) of P and Si by a given dam can therefore be obtained directly from the difference between the inflow into the reservoir of the dissolved and particulate species of the elements and their outflow through the dam, typically integrated over an annual timescale.

The same inflow-outflow mass balance method has been used to quantify N elimination in reservoirs. That is, the difference between the TN river load to a reservoir and the TN outflow through the dam is attributed to TN elimination by burial and denitrification in the reservoir (Némery et al., 2016; Tomaszek & Koszelnik, 2003). In some cases, the inflow-outflow mass balance calculations are combined with measurements of denitrification rates (David et al., 2006; Garnier et al., 1999; Koszelnik et al., 2007) and N sedimentation rates (Vanni et al., 2011). The role of N fixation is usually neglected in existing N budgets of reservoirs. However, because N fixation is a source of new N to reservoirs, ignoring N fixation can underestimate the efficiency of N elimination, particularly in N-limited reservoirs.

4.2. Nitrogen Fixation

The balance of N fixation versus N burial plus denitrification (i.e., versus gross elimination) controls whether the presence of a dam increases or decreases the riverine N flux. Until now, only a few studies have included N fixation in mass balance calculations of N elimination in reservoirs (Kunz, Wüest, et al., 2011; Ramírez-Zierold et al., 2010). Based on our results, in year 2000, N fixation added 70 Gmol N to reservoirs worldwide

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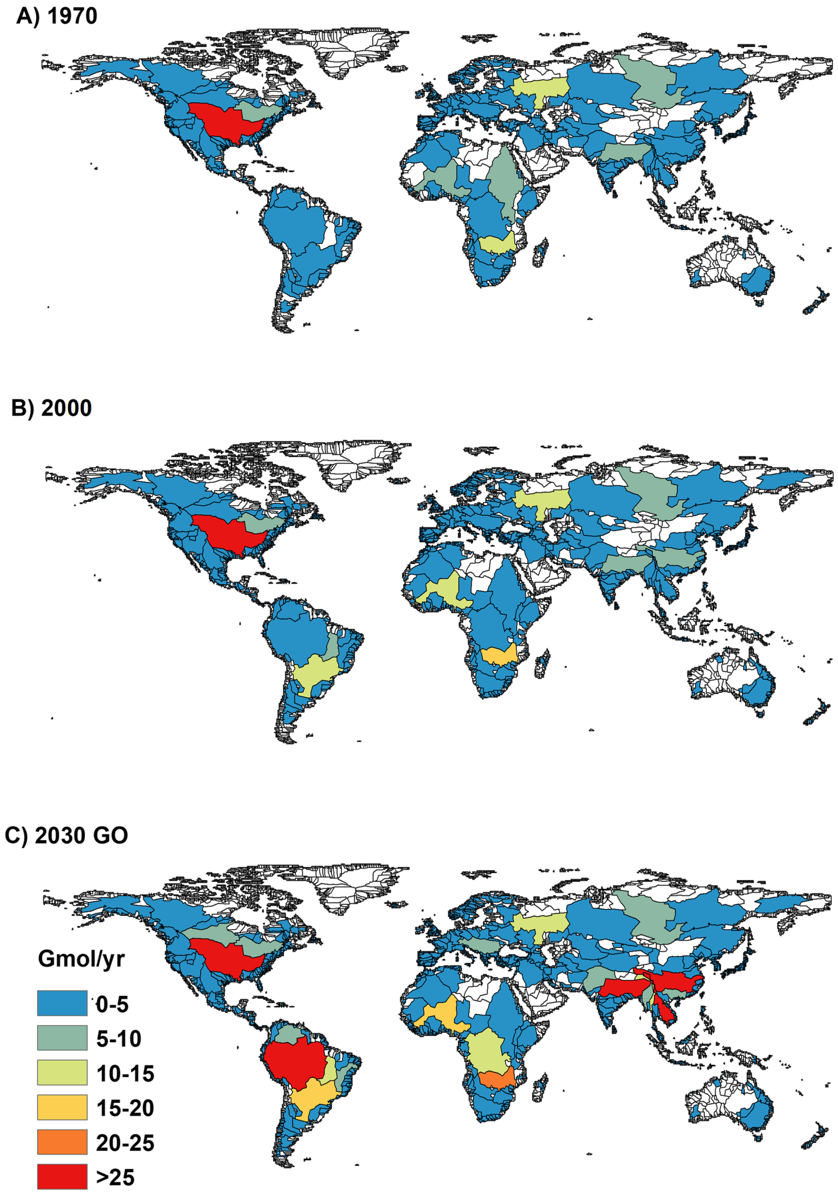

Figure 4. Total gross N elimination (denitrification plus burial) in individual watersheds in 1970 (A), 2000 (B), and 2030 (C) under GO scenario. GO = global orchestration.

(Table 2). At the same time, gross elimination by dams equaled 269 Gmol N, which represents 35% of the total TN input to reservoirs (i.e., river inflow plus N fixation). When neglecting N fixation as a source of N to reservoirs, the inflow-outflow method predicts that elimination in year 2000 amounts to only 199 Gmol N yr^{-1}, or 29% of the TN river inflow (687 Gmol yr^{-1}). These calculations illustrate that accounting for N fixation or not has a non-negligible impact on the assessment of the N elimination efficiency of dam reservoirs.

The changes in global N fixation in reservoirs with time are driven by changes in the number, geographical location, and hydraulic residence time distribution of dams, as well as changes in the absolute and relative supplies of N and P to the reservoirs. Between 1970 and 2030, global in-reservoir N fixation is predicted to increase more than fivefold (Table 2). This large increase is caused primarily by the rising number of dams but also by the increase in the relative loading of reactive P to reservoirs (Seitzinger et al., 2010), which in turn increases the demand for N fixation in N limited reservoirs. For instance, N fixation is estimated to

Table 4
Top 10 Watersheds Ranked According to Annual Mass of N Fixed in Dam Reservoirs, for 1970, 2000, and 2030 (GO Scenario)

Rank	Watershed	N fixation in reservoirs of watershed	Riverine TN load into watershed	No. of reservoirs	Fixation as % of TN input
1970					
1	Volga	3.3	21.4	17	13
2	Mississippi	2.9	79.7	552	3.5
3	Saint Lawrence	1.6	42.1	162	3.7
4	Columbia	1.6	18.8	114	7.8
5	Ganges-Brahmaputra	1.4	155.2	59	0.9
6	Dnieper	1.0	7.9	5	11
7	Chang Jiang (Yangtze)	0.8	58.5	225	1.3
8	Nelson	0.7	9.8	76	6.7
9	Balsas	0.6	3.1	9	16
10	Trinity	0.5	2.0	18	20
2000					
1	Chang Jiang (Yangtze)	3.8	105.7	353	3.5
2	Paraná	3.3	65.0	70	4.8
3	Volga	3.1	50.3	17	5.8
4	Ganges- Brahmaputra	2.4	226.0	86	1.1
5	Columbia	1.7	18.5	130	8.4
6	Balsas	1.5	5.5	12	21
7	Mississippi	1.5	70.8	703	2.1
8	Dnieper	1.3	12.8	6	9.2
9	Zhujiang	1.2	32.7	50	3.5
10	Tocantins	1.2	31.8	4	3.6
2030 (GO scenario)					
1	Chang Jiang (Yangtze)	42.6	148.7	495	22
2	Ganges- Brahmaputra	19.4	239.4	486	7.5
3	Mekong	15.9	56.8	138	22
4	Paraná	11.9	65.4	418	15
5	Amazon	11.0	275.7	191	3.8
6	Volga	5.5	24.4	17	18
7	Salween	4.7	18.9	26	20
8	Zambezi	4.1	40.0	64	9.3
9	Tocantins	3.9	32.6	88	11
10	Mississippi	3.8	71.9	703	5.0

Note. GO = global orchestration; N = nitrogen; TN = total N.

be highest for the TG scenario although the global TDP inflow to reservoirs is lower for the TG than GO scenario. The latter, however, also has a higher TN inflow that leads to a lower N fixation demand. As a result of the combination of the various drivers, the model calculations predict that the contribution of N fixation to the global TN input to reservoirs increases from around 8% in 1970 to 12–15% in 2030.

A significant number of studies have highlighted the role of N fixation in sustaining primary production in lakes (Howarth et al., 1988). However, the fraction of the N input to lentic systems supplied by N fixation varies greatly, from 0 to 99.5% (Horne & Galat, 1985; Horváth et al., 2013; Mugidde et al., 2003; Schindler, 2012). According to our results, the global contribution of N fixation to the annual N demand of primary production in reservoirs ranges between 39 and 47% for the different time points and future scenarios considered. This relatively small range implies that the large increase in absolute N fixation in reservoirs in the period 1970–2030 mostly reflects the increasing amount of in-reservoir primary productivity, which in terms of N demand grows from 85 Gmol yr^{-1} in 1970 to 616 Gmol yr^{-1} in 2030 (GO scenario).

4.3. Denitrification and Burial

Together, global reservoir denitrification plus N burial (i.e., gross elimination) exceeds N fixation under all conditions considered (Table 2). Thus, globally, dams reduce the flow of TN carried by rivers. At the start of the 21st century, 7.4% of the riverine N load was eliminated via N burial and denitrification behind dams. Taking into account N fixation in reservoirs, net elimination in year 2000 amounts to 5.5% of the

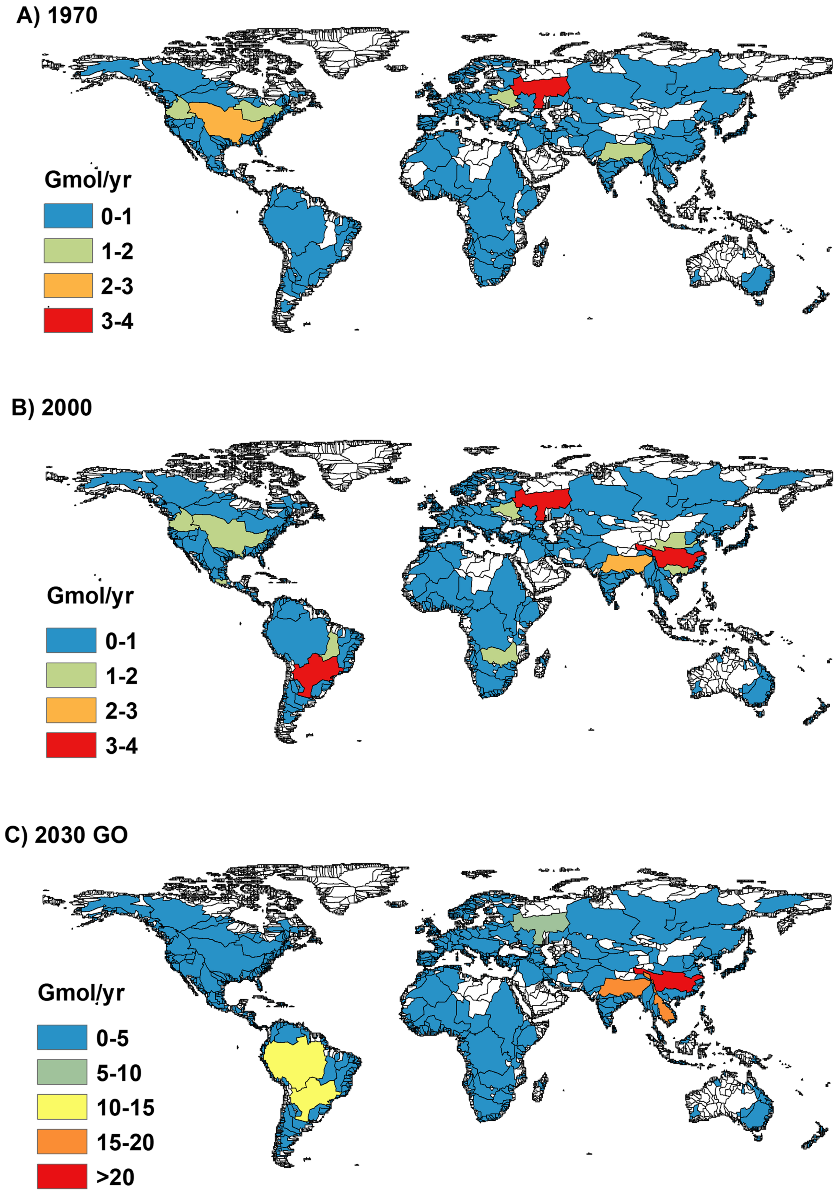

Figure 5. N fixation in individual watersheds in 1970 (A), 2000 (B), and 2030 (C) under GO scenario. GO = global orchestration.

riverine N load. With the world's growing number of dams, reservoirs are expected to become an even larger sink of N by 2030, and denitrification and burial could be eliminating as much as 15% of the riverine N load.

Most published studies that report estimates of global N elimination in lakes and reservoirs do not distinguish between denitrification and sedimentary burial (Beusen et al., 2016; Harrison et al., 2009; Wollheim et al., 2008). Here, we explicitly separate the two elimination mechanisms (Figure 1). Our results for year 2000 imply that denitrification eliminated 21% (159 Gmol yr^{-1}) of the TN input to reservoirs (river inflow plus N fixation), while burial accounted for 14% (110 Gmol yr^{-1}). The model calculations thus point to denitrification as the larger N elimination mechanism in reservoirs; its contribution to gross elimination varies between 58% and 59% in the model calculations. This finding is consistent with other studies that conclude on a dominant role for denitrification in TN elimination in lakes and reservoirs (Cook et al., 2010; Grantz et al., 2014; Kunz, Anselmetti, et al., 2011).

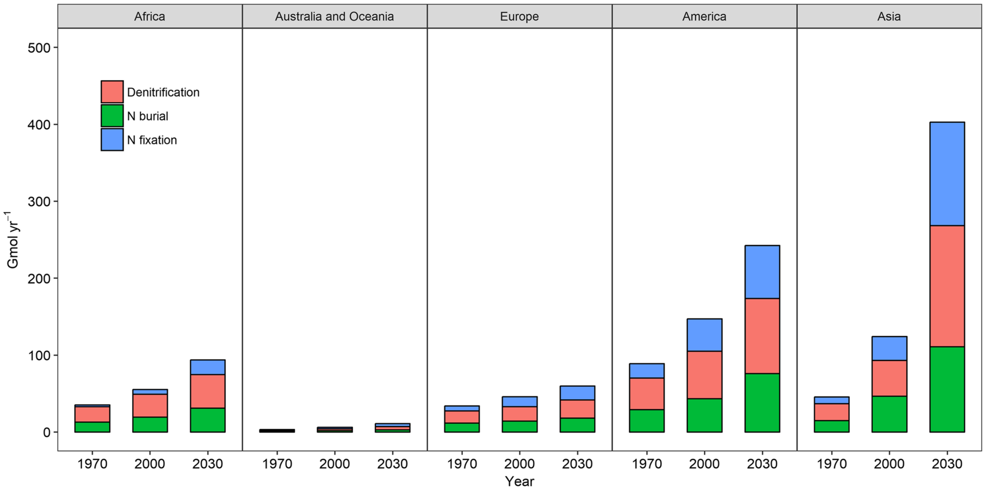

Figure 6. Denitrification, N burial, and N fixation per continent for years 1970, 2000, and 2030 (GO scenario).

Global gross N elimination in reservoirs by denitrification and burial decreases from 35% in 2000 to 30 ± 2% in 2030. This relative drop is due the fact that our 2030 projections account for the construction of the 3,700 new hydroelectric dams with capacity ≥1 MW that are reported by Zarfl et al. (2015) to be under construction or planned to be operational by 2030 (Grill et al., 2015). Hydroelectric dams have relatively short water residence times, which lower their elimination efficiencies. As shown in Figure S9, the average water residence time of reservoirs decreases from year 2000 to 2030 across all continents (except Antarctica where there are no dams). The most significant reduction in water residence time occurs in South America, where a more than fivefold increase in the number of large hydroelectric dams is expected (from 300 dams in 2000 to 1,598 dams in 2030). Consequently, in 2030, 50% of the reservoirs in South America will have a hydraulic residence time lower than 0.1 yr.

The results of the 2030 model calculations only represent the effects of dams included in the published survey of large hydroelectric dams (Zarfl et al., 2015). Evidence suggests that many more dams, in particular smaller ones, are being or will be built in the coming decades (Berg et al., 2016). These unreported dams will likely cause departures from the results presented here, including the water residence time distributions shown in Figure S9. Thus, to more reliably assess, the effects of damming on the continental cycles of N and other nutrient elements will require further, internationally coordinated, efforts to generate a comprehensive inventory of all existing and future dams.

4.4. N:P Ratios

The comparative analysis of the results obtained here with the N mass balance model and those of an earlier P mass balance model (Maavara et al., 2015) implies that the average global molar TN to TP ratios delivered to reservoirs are on the order of 12–13 (Figure 7). That is, on average, reservoirs are slightly N limited, which in turn drives in-reservoir N fixation. The input TN:TP values are a function of the nutrient loadings in watersheds predicted by the Global-NEWS model and, in the case of dam cascades, also the effects of upstream dams. The relatively small temporal changes in the average input TN:TP ratios to reservoirs are modulated by multiple factors, including changes in land use, agricultural practices, water treatment, and atmospheric N inputs. For example, the increase in median values of the input TN:TP ratio from 12.4 to 13.2 between 1970 and 2000 likely reflects more restrictive policies on P use in fertilizers and detergents and increased wastewater treatment (Bouwman et al., 2009; Mackenzie et al., 2002).

The differences between inflow and outflow TN:TP ratios in Figure 7 are the result of the in-reservoir processes affecting both nutrient elements. As can be seen in the figure, the median TN:TP ratios of dam outflows are predicted to be systematically higher than those of reservoir inflows across all three time points considered. The upward shift in TN:TP ratios is primarily the result of N fixation in N-limited reservoirs coupled to the relatively more efficient P removal by burial in reservoir sediments (Maavara et al., 2015).

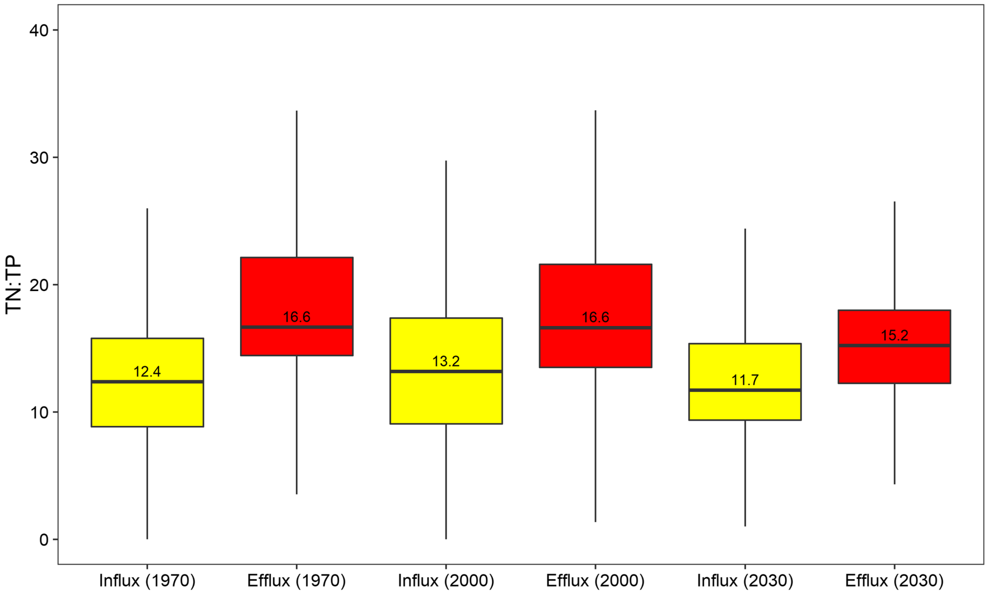

Figure 7. Global TN:TP ratios of river inflow (in yellow) and dam outflow (in red) of reservoirs in 1970, 2000, and 2030 (global orchestration scenario). In each box plot, the central mark is the median; the edges of the box are the 25th and 75th percentiles; and the whiskers extend to the most extreme data points not considered outliers. The values of the medians are indicated in the boxes. Note that the numbers of reservoirs included in the analysis differ for years 1970 (4393 dams), 2000 (6847 dams), and 2030 (10547 dams). TN = total nitrogen; TP = total phosphorus.

Because of in-reservoir processes, the outflow from reservoirs approaches the theoretical Redfield ratio of 16:1 for phytoplankton production.

An upward shift in the TN:TP ratio of outflow, relative to the inflow, has been reported for over 30 reservoirs (Ashton, 1981; Burford et al., 2012; Cook et al., 2010; Gasparini et al., 2011; Grantz et al., 2014; Hart et al., 2002; Molisani et al., 2013; Ramírez-Zierold et al., 2010; Vanni et al., 2011; Wagner, 2010). A good example is provided by the dammed rivers that feed into Lake Winnipeg, Canada. For the 28 large reservoirs and lakes along the river network of the Lake Winnipeg watershed, Donald et al. (2015) show that P is generally eliminated more efficiently than N, based on 3 years of monitoring with data collected once or twice a month, both upstream and downstream from the reservoirs and lakes. We note, however, that it is sometimes difficult to interpret long-term trends in TN:TP ratios in rivers, because they are affected not only by changes due to damming but also by changes in nutrient loading. For example, in a study of eleven cascading dams, Yang et al. (2018) found that, in the lower reaches of the Lancang Jiang River basin, changes in N and P inputs from anthropogenic sources balanced the effects of dams on the river TN:TP ratios.

The decrease in median TN:TP ratios between inflow and outflow is less pronounced in the 2030 projections than in earlier years. Again, this reflects the ongoing boom in hydroelectric dam construction, which leads to a downward shift in the reservoir water residence time distributions (Figure S9) and therefore a lower extent of in-reservoir processing of the nutrient elements. Overall, however, damming of rivers is predicted to reduce the degree of N limitation of primary production in receiving freshwater and coastal marine ecosystems.

5. Conclusions

Damming creates hotspots of biogeochemical activity in river networks. In-reservoir N fixation, denitrification, and sediment burial modify the flows of dissolved and particulate forms of N carried by rivers. Globally, dam reservoirs act as a sink of N, because denitrification and burial (i.e., gross elimination) exceed N fixation. According to our results, at the start of this century, dams globally eliminated 7.4% of N loading to river networks, but this could rise to 15% by 2030 as a result of the rapid building of new dams, particularly in South

America and Southeast Asia. The findings of our study further suggest that dams increase the N:P ratio of riverine discharge, principally due to in-reservoir N fixation, thereby reducing N limitation of primary production in receiving lentic and coastal marine environments. Damming therefore has important implications for managing the impacts of cultural eutrophication.

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