The Regional and Global Significance of Nitrogen Removal in Lakes and Reservoirs

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Abstract

Human activities have greatly increased the transport of biologically available N through watersheds to potentially sensitive coastal ecosystems. Lentic water bodies (lakes and reservoirs) have the potential to act as important sinks for this reactive N as it is transported across the landscape because they offer ideal conditions for N burial in sediments or permanent loss via denitrification. However, the patterns and controls on lentic N removal have not been explored in great detail at large regional to global scales. In this paper we describe, evaluate, and apply a new, spatially explicit, annual-scale, global model of lentic N removal called NiRReLa (**Ni**trogen **R**etention in **Re**servoirs and **La**kes). The NiRReLa model incorporates small lakes and reservoirs than have been included in previous global analyses, and also allows for separate treatment and analysis of reservoirs and natural lakes. Model runs for the mid-1990s indicate that lentic systems are indeed important sinks for N and are conservatively estimated to remove 19.7 Tg N yr^{-1} from watersheds globally. Small lakes ($< 50\ km^2$) were critical in the analysis, retaining almost half (9.3 Tg N yr^{-1}) of the global total. In model runs, capacity of lakes and reservoirs to remove watershed N varied substantially (0-100%) both as a function of climate and the density of lentic systems. Although reservoirs occupy just 6% of the global lentic surface area, we estimate they retain approximately 33% of the total N removed by lentic systems, due to a combination of higher drainage ratios (catchment surface area : lake or reservoir surface area), higher apparent settling velocities for N, and greater N loading rates in reservoirs than in lakes. Finally, a sensitivity analysis of NiRReLa suggests that, on-average, N removal within lentic systems will respond more strongly to changes in land use and N loading than to changes in climate at the global scale.

Introduction

Human activities such as fertilizer manufacturing, fossil fuel combustion, and cultivation of legume crops have more than doubled rates of reactive (non-N_2) N input to terrestrial ecosystems (Vitousek et al. 1997; Galloway et al., 2004). A substantial portion of this excess reactive N is exported from terrestrial ecosystems to aquatic ecosystems (Galloway et al. 2003; Green et al. 2004; Seitzinger et al. 2006; Seitzinger and Harrison, In Press), and a suite of environmental impacts have been attributed to N loading in coastal waters, including eutrophication, hypoxia leading to fish kills, and biodiversity loss, among others (Howarth et al. 1996; Vitousek et al. 1997; Carpenter et al. 1998).

The network of streams, lakes, and reservoirs that deliver N to coastal systems are not simple conduits, but rather play an important role in processing this excess N. A well-developed body of research has demonstrated that fluvial freshwater systems are important in mediating N export from watersheds (e.g. Alexander et al., 2000; Peterson et al., 2001; Seitzinger et al., 2002; Wollheim et al., 2006; Mulholland et al., 2008). However, comparatively little work has been done to evaluate the regional and global importance of lakes and reservoirs to the downstream transport of N. Once reactive N enters surface waters it has multiple potential fates, including permanent loss via denitrification, sediment burial, and temporary storage in biomass (Saunders and Kalff 2001). A number of system-specific and regional studies have shown that denitrification and N burial in freshwater aquatic systems (treated collectively hereafter as *N removal*: N_{in} minus N_{out}) can constitute an important sink for N within watersheds (Table 1). Indeed aquatic ecosystems are potential hot-spots for N loss given that denitrification is favored in sediments and hypoxic or anoxic bottom waters, particularly in systems with abundant organic carbon (C) and nitrate (Piña-Ochoa and Alvarez-Cobelas 2006; Seitzinger et al., 2006).

Due to their relatively long water residence time (compared with streams and rivers), and the resulting opportunity for enhanced particle settling and nutrient processing, lakes have long been recognized as systems where extensive denitrification and N burial can occur (Wetzel 2001). Hence, the presence of lakes or creation of impoundments and their placement in the landscape could play an important role in determining the biosphere's response to anthropogenically enhanced N loading not only at the watershed but at larger regional and global scales. Improved understanding of the role that lentic systems play in watershed N removal could contribute to the development of future N management strategies by elucidating how changing N sources, climate, and the placement of lakes and reservoirs within watersheds are likely to interact to affect N transport to downstream fresh and coastal waters.

In recent years, a number of local and regional field-based and modeling studies have investigated the controls on N removal within lakes and reservoirs. In general, N removal in lentic systems (kg N yr^{-1}) has been observed to correlate positively with N loading rates, and water residence time, and negatively with lake mean depth (Kelly et al., 1987; Dillon and Molot 1990; Molot and Dillon 1993; Windolf et al., 1996; Saunders and Kalff 2001).

Based on these relations, a number of models have been developed to predict lentic N removal at regional and, in one case, global scales (although the focus has been primarily on flowing waters and large lakes; Alexander et al., 2002; Seitzinger et al., 2002; Seitzinger et al., 2006). These models suggest that lakes and reservoirs can be important in determining the fate of N at regional scales, but that the importance of lakes can vary widely depending on the basin in question. For example Alexander et al. (2002) found that in New Zealand's Waikato Basin lakes and reservoirs were among the most statistically significant variables in a model predicting N transport, retaining 39-76% of N inputs to surface waters in the Waikato Basin and its sub-watersheds. Several lakes were estimated to retain over 50% of the N entering them with a maximum removal of 87% of N input. Conversely, Seitzinger et al. (2002) estimated that reservoirs account for very little N removal in watersheds of the Northeastern US.

Our goal was to develop a global-scale model that could account for such regional differences in lentic N removal, using relations that have been developed through observations of individual lakes and reservoirs. Previous attempts to scale up analyses of individual lentic systems in a spatially explicit manner to quantify regional- and global-scale patterns of lake and reservoir N removal have been limited to the large river basin scale and have not included the smallest lakes and reservoirs on the landscape (0.001-0.1 km^2; Seitzinger et al., 2006). In this paper, we describe, apply and evaluate a new, spatially explicit, annual-scale, global model of N removal in lakes and reservoirs called the **Ni**trogen **R**etention in **Re**servoirs and **La**kes (NiRReLa) model. The NiRReLa model moves beyond previous studies in several respects. First, the model is calibrated using a truly global dataset of N removal, comprised of information from 115 lakes and reservoirs, substantially more than any similar previous study. Furthermore, NiRReLa is the first attempt to incorporate small (down to 0.001 km^2 surface area) lakes and reservoirs into a global analysis of lentic N removal in a spatially explicit manner, and has a higher spatial resolution (half degree: ~2,500 km^2 at the equator) than any previous global models of lentic N removal. NiRReLa also allows model users to estimate the relative importance of lakes versus reservoirs on the landscape with respect to N removal, an analysis that has not previously been possible.

Methods

The NiRReLa Model Structure and Calibration

Model Structure

The NiRReLa model was formulated to estimate annual lentic N removal globally, in a spatially distributed fashion. In the NiRReLa model, N removal (N_{rem}; kg N yr^{-1}) for lakes and reservoirs is calculated as:

$$N_{rem} = R \times N_{in} \qquad (1)$$

where N_{in} is an estimate of N input to lake and reservoir surface waters, taken from Bouwman et al. (2005) and R is an estimate of the fraction of N retained within lakes and reservoirs. R is calculated in a manner similar to Wollheim et al. (2006) and Alexander et al. (2002), as:

$$R = 1 - \exp\frac{-V_f}{H_l} \qquad (2)$$

where V_f is the apparent settling velocity for N (m yr^{-1}) by lake or reservoir sediments, and H_l is the hydraulic load (m yr^{-1}) for a given lake, reservoir, or a series of tightly coupled reservoirs. Vf is essentially a piston velocity for N removal in lentic systems and accounts both for N removed via denitrification and for N removed via burial in sediments. Based on evaluation of existing studies (described below; Table 2), separate V_f values were assigned for lakes and reservoirs. H_l (m yr^{-1}) was calculated as:

$$H_l = \frac{1000 \times Q}{A} \tag{3}$$

where Q is water input to lakes and reservoirs (km^3 yr^{-1}) and A (km^2) is either surface area of individual lakes (for large lake analysis) or cumulative surface area of lakes in a given half-degree grid cell (for small lake analysis). H_l can be calculated either according to Eq. 3 or Eq. 5.

Model Calibration

The NiRReLa calibration dataset includes N removal data for 115 lakes and reservoirs (80 lakes and 35 reservoirs) from a range of sources. This dataset includes lakes from a broad range of size classes, and regions (Table 1). To avoid the potentially confounding influence of seasonal N uptake and storage, we limited our dataset to lakes and reservoirs for which at least a complete year of data during the ice-free period was available.

The fraction of N removed by lakes and reservoirs (R_{cal}; unit-less) was estimated as in Dillon and Molot (1990), as

$$R_{cal} = \frac{N_{in} - N_{out}}{N_{in}} \tag{4}$$

where N_{in} is the mass of N estimated to enter a lake or reservoir annually (kg N yr^{-1}) and N_{out} is the mass of N (kg N yr^{-1}) estimated to exit a lake or reservoir annually via surface water outlet(s).

For each lake and reservoir in our calibration dataset, an apparent settling velocity for N ($V_{f\text{-}cal}$) and hydraulic load ($H_{l\text{-}cal}$) were estimated. Hydraulic load ($H_{l\text{-}cal}$) was estimated as in Wollheim et al. (2006) as:

$$H_{l-cal} = \frac{z}{T} \tag{5}$$

where z is lake or reservoir average depth (m) and T is water residence time (yr: calculated as lake volume/water discharge). $V_{f\text{-}cal}$ was estimated as:

$$V_{f-cal} = -H_{l-cal} \times \ln(1 - R_{cal}) \tag{6}$$

where $H_{l\text{-}cal}$ is hydraulic load and $R_{\text{-}cal}$ is an estimate of the fraction of N retained within lakes and reservoirs (Eq. 4).

We also collected ancillary information for each system, including name, location (latitude and longitude), and surface area (Table 1). Lakes or reservoirs were considered to be tropical if they were located between the equator and 22.5° N or S, temperate if they fell between 22.5° and 55° N or S and boreal if they were above 55° N or S.

In the NiRReLa model development process, we tested whether there were any significant relations between lake or reservoir characteristics and apparent settling velocity (V_f) for N. We tested for relations using simple and multiple regression approaches as well as one-way ANOVAs. There were no significant correlations between V_f and system size, N concentrations (either as Total N or NO_3^-) or distance from the equator ($p>0.05$ in all cases). Therefore, these factors were not included in the NiRReLa model. However, V_f was significantly higher (by 1-Way ANOVA; Table 2) in reservoirs than in lakes (Table 2), both for the entire dataset and for subsets of the dataset divided into tropical, temperate, and boreal categories. In order to satisfy the assumptions of equal variances and normal distribution of the residuals of the ANOVA test, V_f data were log transformed. Based on this analysis, we incorporated the difference between lakes and reservoirs into the NiRReLa model by assigning reservoirs a higher V_f than lakes.

The values assigned were calculated as the median V_f values in the calibration dataset (4.6 m yr^{-1} and 9.1 m yr^{-1} for lakes and reservoirs, respectively).

Global Application of NiRReLa

Spatial Data

A number of spatial datasets were used in the global application of the NiRReLa model. These datasets all had a spatial resolution of 0.5° × 0.5° (approximately 50 km^2 × 50 km^2 at the equator) and were selected to represent conditions in 1995. Water runoff (m yr^{-1}), water discharge (km^3 yr^{-1}), and basin delineations for large rivers were taken from Fekete et al. (1999). Estimates of N loading to surface waters were from Bouwman et al. (2005) and a low estimate of N loading was derived from output of the **N**utrient **E**xport from **W**atershed**s** – **D**issolved **I**norganic **N**itrogen (NEWS-DIN) model (Dumont et al., 2005). Bouwman et al. (2005) estimate TN inputs to surface waters as a function of N loaded to the landscape (fertilizer N, manure N, atmospheric N deposition, N fixation, and point-source N inputs) and N removed from the landscape (N removal via crop harvest and export) coupled to a hydrologic model of N transport to surface waters. Lake locations and attributes were taken from Lehner and Döll (2004), currently the most comprehensive, global survey of lentic water bodies, containing 243,071 lakes and 822 reservoirs globally.

Though the general approach to estimating N removal within all lakes and reservoirs was similar across all system sizes, the availability of data required that N removal in large and small reservoirs be estimated somewhat differently. For example, information about watershed surface area was not readily available for small lakes and reservoirs, but this information was available for large lakes and reservoirs (Lehner and Döll 2004). In order to accommodate these differences in data availability for model calculations, lakes were divided into two size classes (large and small) where lakes and reservoirs with surface areas greater than 50 km^2 are referred to as "large" and those between 0.001-50 km^2 are referred to as "small". One-tenth of a hectare (0.001 km^2) was considered to be the smallest surface area for a perennial water body, as in Downing et al. (2006). Distribution of small lakes is described below.

NiRReLa and Small Lakes and Reservoirs

Small lakes and reservoirs are extremely numerous and constitute a substantial portion of the total surface area of lakes and reservoirs globally (approximately 31% for lakes < 0.1 km^2 according to Downing et al., 2006). Small lentic systems are important sites for biogeochemical processing (Wetzel 2001), but they are currently not included in any global models of N transport. As such, we deemed it important to include these small systems in NiRReLa. This presented a challenge, however, because currently there is no global database that includes water bodies smaller than 0.1 km^2. To overcome this limitation in the available global data, we assumed that the spatial distribution of the smallest lakes (<0.1 km^2) would scale in a linear fashion with the distribution of slightly larger (0.1-50 km^2) lakes. We then calculated the total global number and surface area of small lakes and reservoirs, assuming Pareto-type distributions for both lake and reservoir number and lake and reservoir surface area, as in Downing et al. (2006). The number, average surface area, and cumulative surface area of lakes and reservoirs within given size ranges were determined as in Downing et al. (2006), using identical coefficients.

Lakes and reservoirs were assumed to have a Pareto-type size distribution, as demonstrated by a recent analysis (Downing et al., 2006), and the shape of this distribution was determined by a coefficient *c*, describing the relative abundance of large versus small lakes.

Total global small lake and reservoir surface areas were then distributed on the global landscape. Small lake surface areas (A_{sm}) were distributed in direct proportion to the distribution of smaller lakes (0.1-50 km^2) in Lehner and Döll (2004) lakes database as:

$$A_{sm} = A_{sm-tot} \frac{A_{GLWD2-cell}}{A_{GLWD2-tot}} \qquad (7)$$

where A_{sm} is the total surface area of lakes 0.001 – 50 km^2 in each cell, A_{sm-tot} is the calculated global total surface area of lakes with individual surface areas between 0.001 and 50 km^2, $A_{GLWD2-cell}$ is the lake surface area of 0.1-50 km^2 lakes in a given cell as reported in Lehner and Döll (2004), and $A_{GLWD2-tot}$ is the global total lake surface area of 0.1-50 km^2 lakes as reported in Lehner and Döll (2004). Due to a general lack of data on global spatial distribution of small reservoirs, these systems were distributed uniformly across all grid cells between 55˚N and 55˚S. $\mathrm{A_{sm-tot}}$ was 2.55 x 10^6 km^2 for lakes and 9.83 x 10^4 km^2 for reservoirs. For comparison, the total small lake and reservoir surface area values in Lehner and Döll (2004) were 3.7 x 10^5 and 2.8 x 10^3, respectively, highlighting the importance of including the smallest lakes and reservoirs.

The fraction of N removed by small lakes and reservoirs (R_{sm}) was calculated as in Eq. 2 (See Wollheim et al., 2006 and Alexander et al., 2002), and N removal in small lakes and reservoirs was calculated as the product of R_{sm} and N load. Hydraulic load for small lakes and reservoirs (H_{l-sm}) was calculated as in Eq. 3. For small lakes and reservoirs, Q is total discharge ($km^3 yr^{-1}$) generated within each half-degree cell and A is the cumulative surface area of small (<50 km^2) lakes or reservoirs in a given half-degree cell. Water and N leaving terrestrial systems within each half-degree grid cell were assumed to enter a composite lake or reservoir made up of all small lakes or all small reservoirs before entering large lakes or reservoirs.

In NiRReLa, water and N are partitioned between small lakes and reservoirs in proportion to the relative surface areas of lakes and reservoirs within a given half-degree cell. For example, if 25% of the total lake and reservoir surface area within a cell is attributed to reservoirs, and the remainder is allocated to lakes, NiRReLa routes 25% of the water and N to reservoirs and the remainder to lakes.

NiRReLa and Large Lakes and Reservoirs

The spatial distribution of large lakes and reservoirs was taken from the global database of Lehner and Döll (2004), which contains 3067 of the largest lakes (area ≥ 50 km^2) and 654 of the largest reservoirs globally (storage capacity ≥ 0.5 km^3). Lakes in Lehner and Döll (2004) <50 km^2 (from GLWD2) are accounted for above. We estimated annual N removal (kg N yr^{-1}) in these large lakes and reservoirs (N_{large}) according to Eqns. 1 and 2, just as for small lakes and reservoirs. However, N_{in} and H_l are calculated somewhat differently for large lakes than for small lakes. For large lakes and reservoirs N_{in}, the amount of N estimated to enter a given large lake or reservoir annually, is calculated as:

$$N_{in} = W \times N_{surf} \tag{8}$$

where W represents the size of the watershed for a given large lake or reservoir (km^2) and N_{surf} is the area-weighted average rate of N loadings to surface waters (kg N km^{-2} yr^{-1}) within the large river watershed (Fekete et al., 1999) in which a large lake is located, as estimated by Bouwman et al. (2005). This approach is identical to that used by Seitzinger et al. (2006). Hydraulic load for large lakes and reservoirs (H_l) was calculated according to Eq. 3. Rather than being estimated at the grid-cell level as for small lakes and reservoirs, numerical values for Q and A for large systems were taken directly from Lehner and Döll (2004). To avoid double counting N removal by both large and small lakes, we assumed that small lakes and reservoirs processed N before it reached large lakes or reservoirs.

Model Sensitivity Analysis

A sensitivity analysis was performed in order to evaluate the response of NiRReLa model output to changes in various input parameters, including: rates of water runoff and N loading, the number, size and spatial distribution of lakes and reservoirs, and V_f within lakes and reservoirs. Water runoff and N loading were both halved and doubled. An additional low-end estimate of N loading was developed by taking predictions of DIN export from a river DIN export model (NEWS-DIN; Dumont et al., 2005) and using these estimates as inputs to the NiRReLa model. The NEWS-DIN model (Dumont et al., 2005) calculates DIN export from rivers to the coastal zone, and accounts for N removal within watersheds. Using NEWS-DIN model output as N input to the NiRReLa model results in a conservative estimate of lake and reservoir denitrification because: 1) before entering lakes and reservoirs, N exported from terrestrial landscapes has already been subject to removal in rivers before entering NiRReLa lakes and reservoirs, and 2) NEWS-DIN only estimates DIN, which is only a fraction of N.

We also evaluated NiRReLa sensitivity to the number, size and spatial distribution of lakes and reservoirs in several ways. First, we ran NiRReLa without any extrapolation to include the world's smallest lakes, including only lakes and reservoirs reported in a spatially explicit global dataset of small (0.1-50 km^2) lakes and reservoirs (GLWD2; Lehner and Döll 2002). In a second approach, we only extrapolated down to lakes with a surface area ≥ 0.01 km^2. In two additional experiments, we tested model sensitivity to assumptions about distribution of N and water between lakes versus reservoirs by varying distribution of N and water between small reservoirs and small lakes by ± 20% and further tested NiRReLa's sensitivity to changes in the number of small lakes and the shape of the Pareto distribution by varying the Pareto exponent (c in Eqns. 4, 5, and 10 in Downing et al., 2006) by ± 1 S.E.. Finally, sensitivity of NiRReLa predictions to changes in V_f was also evaluated by varying V_f from the 25th percentile value to the 75th percentile of all lakes and reservoirs in our calibration dataset, (2.20-7.56 m yr^{-1} and 3.15-19.41 m yr^{-1} for lakes and reservoirs, respectively).

Results and Discussion

Apparent Settling Velocities

As stated above in the section on model calibration, we did not detect any significant correlations between reservoir and lake characteristics and apparent settling velocities (V_f) in our global dataset. However, there was a significant difference in V_f

between lakes and reservoirs, with reservoirs demonstrating a higher V_f on average than lakes (mean $\underline{V_f}$ for lakes and reservoirs: 6.8 and 13.6 m yr^{-1}, respectively). The model V_f value for lakes is comparable to V_f values from a number of other studies (reviewed by Alexander et al., 2002) and is somewhat lower than V_f observed for rivers (Howarth et al., 1996; Alexander et al., Submitted, this volume). The NiRReLa V_f value for reservoirs is somewhat higher than V_f values observed in lakes, and is closer to V_f values observed for rivers (Wollheim et al., 2006), possibly because reservoirs function as hydrologic intermediates between rivers and lakes.

NiRReLa Model Performance

It was not feasible to test the results predicted by the entire NiRReLa model at the global scale since there currently is no global-scale validation data on N inputs to surface waters or large basin-scale data on N removal within lakes and reservoirs. However, we were able to evaluate the NiRReLa model's capacity to predict percent N removal within individual lakes and reservoirs by comparing measurement-based estimates of N removal in lakes and reservoirs (Eq. 4) with NiRReLa-modeled estimates of N removal (Eq. 2). In this test, the NiRReLa model performed reasonably well for both lakes and reservoirs (Figure 1). The root mean squared error for the NiRReLa model was 17% for both lakes and reservoirs, and 95% of the predictions fell within 43% of the measured removal rates for both lakes and reservoirs (41% and 44% for lakes and reservoirs, respectively). Neither the slope nor the intercept of the least-squares regression between measured and modeled TN removal ($r^2 = 0.54$ and $r^2 = 0.51$ for lakes and reservoirs, respectively) was significantly different from unity, suggesting a lack of systematic bias to the NiRReLa model. Thus, although a significant amount of variation remains unexplained, we were able to use the NiRReLa model to develop the first half-degree resolution maps of lake and reservoir N removal.

N Removal by Lakes and Reservoirs at Global Scale

Using the NiRReLa model, we estimate that globally, lentic aquatic systems larger than 0.001 km^2 remove 19.7 Tg N yr^{-1} from watershed flow paths (Table 3). This amount is slightly less than one third of the 65 Tg N yr^{-1} estimated to enter surface freshwaters globally (Bouwman et al., 2005), and is roughly equivalent to 7% of all land-based N sources (268 Tg N yr^{-1}; Seitzinger et al., 2006). The NiRReLa-estimated amount of N removal occurring in lakes and reservoirs globally is approximately 4 times the amount estimated to occur in estuaries (~5 Tg N yr^{-1}; Seitzinger et al., 2006), and comparable to the amount of N removal estimated to occur in rivers and streams (20-35 Tg yr^{-1}, based on different assumptions and databases; Seitzinger and Kroeze 1998, Green et al., 2004; Bouwman et al., 2005; Seitzinger et al., 2006). It should be noted that these existing estimates of river and stream N removal often include reservoir N removal. In fact, our analysis suggests that in many regions most of the N removal previously attributed to rivers and streams could be occurring primarily in lentic systems (Figure 2A).

Using NiRReLa we estimate that the area-specific rate of N removal by lentic systems globally is approximately 4,805 kg N km^{-2} yr^{-1} (Table 3), approximately half of a previous estimate by Seitzinger et al. (2006; 11,000 kg N km^{-2} yr^{-1}), but still well within measured denitrification rates for individual lakes (181- 38,263 kg km^{-2} yr^{-1} as compiled in Piña-Ochoa and Alvarez 2006). This discrepancy is in part due to our slightly lower global estimate of N removal by lakes and reservoirs of 19.7 Tg yr^{-1} relative to 31 Tg N yr^{-1}, but mostly due to the lower estimate of the global lake surface used in Seitzinger et al. (2006). Indeed, when we use the NiRReLa estimate of global lake and reservoir surface area, the values for area-specific N removal were comparable between the current analysis and the Seitzinger et al. (2006) estimate (Table 3).

Results from NiRReLa suggest that the inclusion of small lakes and reservoirs is crucial for predicting global N removal by lentic systems. NiRReLa model output indicates that small lakes remove more than twice as much N from watersheds as large lakes (9.3 Tg N yr^{-1} for small lakes versus 3.7 Tg N yr^{-1} for large lakes), and that small lakes (<50 km^2) account for almost half of the N removed by lentic systems (lakes and reservoirs combined) globally (Table 3). This important role of small lakes acting as biogeochemical sinks in the landscape was also observed in a similar analysis assessing the fate of carbon in freshwater aquatic ecosystems (Cole et al. 2007). On a per-unit area basis, small lakes also processed 16% more N than large lakes (Table 3). In interpreting these model results, it is important to remember that the NiRReLa model assumes that all N entering surface waters in each grid cell passes through a small lake, which is most likely not the case. Thus it is likely that NiRReLa somewhat overestimates the role of small lakes in removing N from the landscape. Nonetheless, these results underscore the potential importance of small lakes as sinks for N on the landscape. This analysis does not explicitly include N removal in stream reaches connecting lakes to each other.

Humans are actively increasing the number of "lakes" on the landscape via the creation of reservoirs (Takeuchi et al., 2000; Tomeszec and Kozelnick 2003). Therefore understanding the role of reservoirs in the processing of N at the landscape level is of critical importance. Despite the fact that the global abundance of lakes is almost two orders of magnitude greater than that of reservoirs (3.04×10^8 lakes versus 3.77×10^6 reservoirs greater than 0.001 km^2; Downing et al., 2006), NiRReLa estimated that reservoirs remove roughly 33% of the N removed by lentic systems, accounting for the removal of 6.6 Tg N yr^{-1}, an estimate similar to that made by an independent model of lake N removal (Wollheim et al., In Revision). Despite their comparatively low global surface area and numbers, large reservoirs appear to play as important a role in N removal as large lakes (Table 3). NiRReLa output suggests that approximately equal amounts of N are removed by large reservoirs and large lakes (3.6 Tg N yr^{-1} and 3.7 Tg N $yr^{-1}$for large reservoirs and large lakes, respectively; Table 3).

The parity of large lakes and large reservoirs with respect to N removal most likely results from the fact that reservoirs have large contributing watersheds, and thus relatively large N loading rates (kg N yr^{-1}) compared to large lakes, which generally (though not always) receive their water and N input from a more limited surface area and thereby receive less N input. In the large lake and reservoir dataset utilized for this study the mean drainage ratio (ratio of basin surface area to lake or reservoir surface area) for reservoirs was 83, whereas the ratio was 25 for lakes (Lehner and Döll 2004). The higher drainage ratio of reservoirs resulted in higher N loading to reservoirs than to lakes, on average. The higher V_f values observed for reservoirs in this study play a smaller, though still important, role as well. In reservoirs, flooding of previously terrestrial soils and ecosystems also may lead to an increased availability of highly labile organic matter

(Kelly et al., 1997) and bottom water anoxia which should favor denitrification. The greater frequency of reservoirs in areas with high N inputs may also contribute.

Regional Patterns of Lake and Reservoir N Retention

Considerable regional variability exists in the potential for lakes and reservoirs to act as sinks for N within watersheds (Figure 2). This spatial heterogeneity has heretofore gone largely un-quantified, in part, because there has not been a sufficiently high-resolution model to evaluate it (though see Wollheim et al., In Revision). NiRReLa output indicates that there are a number of regions globally where lakes and reservoirs have the capacity to filter virtually all N loaded to surface waters, whereas in other regions lakes have very little or no capacity to remove N input to the landscape. In general, areas where percent N removal approached or equaled 100% correspond to areas with large lake surface areas, low runoff rates, or both. Regions where lakes and reservoirs have the capacity to remove a large proportion of the N added to the landscape correspond to areas with high lake densities, including boreal regions in Canada, Northern Europe, and Russia, portions of the western US, Eastern Brazil, Sub-Saharan Africa, northern China, Eastern Europe, and Mongolia, and parts of Argentina. The predicted N removal efficiency of lentic systems in many parts of the world seems quite high. However, to the extent we were able to validate these regional patterns they are consistent with observations of watershed N export. For example, using Bouwman et al. (2005) estimates of N inputs to surface waters and measurements of N export at the mouths of rivers from Seitzinger and Harrison (In Press), we calculate that very small fractions of N inputs to surface waters are exported at basin mouths (0.7%, 6.0% and

~8.7% of N inputs to surface waters in the Churchill, Neva and St. Lawrence River Basins, respectively). This contrasts markedly with regions that exhibit relatively low predicted lentic N removal (as a fraction of N input) such as the Mississippi and Amazon Rivers, where much larger fractions are exported.

Regions with high estimated per-area rates of lake and reservoir N removal (kg N $km^{-2} yr^{-1}$; Figure 2B) are somewhat different than regions where N removal is estimated to approach 100% of the N applied to the landscape (Figure 2A). This pattern occurs because the lake and reservoir locations do not always correspond to regions of highest N input. For example, while a large fraction of N input to lakes and reservoirs is removed in Northern Canada, the rate of N removal is low because of low N inputs in this region. Basins with high rates of lentic N removal (kg N km^{-2} yr^{-1}) include the St. Lawrence, many of the river basins in southern Scandinavia, the Zambezi River, and several river basins in northeast China.

Sensitivity Analysis

A number of insights emerge from the sensitivity analysis described in the methods section, for which a summary of results is presented in Table 4. One of the principal insights resulting from this analysis is that while NiRReLa is relatively sensitive to changes in N loading rates, it is relatively insensitive to alterations in hydrology. Doubling global inputs of water to the landscape (and consequently cutting water residence time in individual systems in half) only decreased predicted lentic N removal (Tg N) by 11% . Decreasing water runoff by 50% resulted in a 15% increase in N removal (Tg N). In contrast to its relatively damped response to changes in hydrology, the NiRReLa model was quite sensitive to changes in N loading. As would be expected based on Eq. 1 above, doubling global inputs of N resulted in a doubling of N removal (Tg N), whereas cutting N inputs in half resulted in a halving of lake and reservoir N removal (Tg N). Using output from the NEWS-DIN model (Dumont et al., 2005) as input to the NiRReLa model resulted in a 23% decrease in estimated global lentic N removal (to 15.2 Tg N yr^{-1}), and this estimate can be considered to be quite conservative. Interactions between runoff and N loading were not explored in this sensitivity analysis, but could be important as one would expect N loading to increase with increasing runoff. Such a relation has been demonstrated for many watersheds globally (Dumont et al., 2005). Runoff dependence of N loading could make N removal either more or less sensitive to changes in hydrology. The net impact depends on the nature of the N loading response to increased runoff.

The observed difference in model response to changes in hydrologic and N-loading is a function of the relations between model inputs and model response variables. The relation between percent N removal and water residence time is log-linear (Eq. 2) whereas the relation between N load and N removal is linear. This suggests that the location of N inputs relative to the location of lakes and reservoirs is an important determinant of the effectiveness of lakes and reservoirs in removing N from surface waters (i.e. N inputs upstream from lakes and reservoirs will be subject to retention within lentic systems whereas N inputs downstream from those systems will not). This is also an uncertainty in the model worthy of future investigation. Taken together, these insights suggest that, in general, N removal within lentic systems will be more sensitive to land-use change than climate change at the global scale, though this is certain to vary substantially by region. Climate could also significantly alter N transfers to surface waters by altering the balance of runoff and evapotranspiration, but it is difficult to predict the magnitude, or even the direction, of this effect as increased runoff is likely to cause greater N inputs but lower water residence times.

In addition, in order to assess the NiRReLa model's sensitivity to uncertainty in V_f we ran the model using arithmetic mean V_f (6.8 and 13.6 m yr^{-1} for lakes and reservoirs, respectively), low V_f (25th percentile), and high V_f (75th percentile) values. Using mean V_f values for the NiRReLa model in place of median values increased global lentic TN retention by 3.4 Tg N yr^{-1}. This range of variation in V_f resulted in a variation in model output that ranged between 11.8 and 25 Tg N retained globally. Hence a 3.4-fold increase in V_f for lakes and a 6.2-fold increase in V_f for reservoirs resulted in an approximate doubling of global N removal in lakes and reservoirs. Hence, the NiRReLa model is less sensitive to variation in V_f than to changes in N loading.

We also examined how changes in the parameterization of the Pareto distribution of lakes and reservoirs affected N removal by varying the parameter "*c*" in equations 4, 5 and 10 in Downing et al. (2006) plus or minus one standard error. The change in model predictions resulting from this perturbation was minimal (Table 4). Finally, we examined the influence of the smallest lakes and reservoirs by excluding them from our analysis. Removing reservoirs smaller than 0.01 km^2 from the analysis decreased the N removal in lentic systems by 0.8%; removing lakes smaller than 0.01 km^2 decreased our estimate of small-lake N removal by 8.1%. Limiting our analysis to only lakes and reservoirs available in the most comprehensive global lake and reservoir database decreased our estimate of global lentic N removal by 9.8%, highlighting the importance of including the smallest lakes (0.001-0.1 km^2). If the surface area of small lakes is greater than we have estimated, then NiRReLa most likely underestimates TN retention by such systems.

Uncertainties and Future Directions

Here we have presented a higher resolution, spatially explicit, global analysis of lake and reservoir N removal than has previously been published. The NiRRela model is a promising new tool that provides insight into global rates and spatial organization of N removal within lentic systems. The model provides initial estimates of the relative importance of natural versus man-made lakes (reservoirs) and indicates factors to which N removal within lakes and reservoirs is likely to be sensitive.

Clearly a number of questions remain unanswered. For example the NiRReLa model does not distinguish between N removal via denitrification and N removal via other pathways such as sediment N burial or consumptive water use. Denitrification is clearly an important component of total lake N removal, and in many studies this process accounts for the majority of N removed from lake and reservoir waters (Jensen et al., 1990; Jensen et al., 1992; Saunders and Kalff 2001). However, it is likely that there are systems where sediment N burial, transient storage in macrophyte stands, and consumptive water use are important N sinks (e.g. Kelly 2001). A rough estimate using Cole et al. (2007) estimates of C burial along with an estimate of sediment C:N ratios (9-28; Brahney et al., 2006) suggests that sediment N burial could account for anywhere between 25-250% of the total NiRReLa-based estimate of N removal. A somewhat different approach using reported annual area-specific rates of denitrification in 21 lakes (1,760-45,080 kg N km^{-2} yr^{-1} mol N Piña-Ochoa and Álvarez-Cobelas 2006) and our estimate of global lake and reservoir surface area (4.05×10^6 km^2; Table 3) suggests that between 47 and 182 Tg N yr^{-1} (206-498% of the NiRReLa-based estimate of total N removal) could be denitrified in lakes and reservoirs. Though far from establishing the relative importance of different N removal pathways in lentic systems, and though even measurement-based estimates of N removal are quite uncertain, together, these rough calculations suggest that NiRReLa-based estimates of lentic N removal are quite conservative. Due to the high degree of uncertainty, these calculations also suggest that understanding lentic N removal is an important goal for future investigations.

In addition, the sensitivity of the NiRReLa model to N inputs raises the question whether there is a N-saturation threshold for lakes. This potential is not evident in our calibration dataset, but if such a threshold exists, it would have important implications for the capacity of lake and reservoir systems to act as buffers for N enrichment of surface waters on the landscape.

Given the general trend toward higher rates of biological and physical processing with increased temperatures in many systems, we were somewhat surprised not to find a significant relation between latitude and apparent settling velocity for N. However, this is consistent with a general lack of empirical evidence for a relation between latitude and denitrification rates (Piña-Ochoa Álvarez-Cobelas 2006). It may also be that differences in lake and reservoir mixing regimes at different latitudes (Lewis 1983) obscure a simple relation between temperature and lake and reservoir N apparent settling velocities.

The apparent relative importance of small (<0.1 km^2) reservoirs in controlling N removal along flow paths within watersheds suggests that an important area for future research is an improved understanding of the spatial distribution and biogeochemical role of such systems. Similarly, NiRReLa assumes a simple hydrologic linkage of small lakes with large lakes on the landscape. This simplistic view could certainly be improved in future models as appropriate data becomes available to support such enhancements. Other issues that merit further investigation and may result in substantial model improvements include lake and reservoir hydrology and mixing regimes, an improved representation of inflow seasonality, and an improved representation of N cycling, including the balance between nitrification, denitrification, sediment organic matter burial, and N mineralization in lentic systems.

Finally, this analysis should not be interpreted as an argument for the construction of dams as a mitigation strategy for coastal N delivery. Though reservoirs appear to be an important site for N removal within watersheds at regional and global scales, it is far from certain that the net impact of reservoir construction is a reduction in N transport to coastal systems. In part, the impact of reservoir construction on downstream N transport is a function of reservoir morphology, with narrow, deep reservoirs actually decreasing N removal compared to the original river reach. In addition, and probably more importantly, irrigation water made available by dams may increase the amount of land available for intensive agriculture and hence facilitate elevated rates of N application to the landscape. An improved understanding of the relation between reservoir operation and downstream N transport may lead to more effective N management strategies.

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Table and Figure Captions:

Table 1 : List of references, geographical location, and ranges of morphological and hydrological variables of the lakes and reservoirs used in the determination of different parameter estimates of the NiRReLa model.

Table 2. Comparison of average apparent settling velocities for N (V_f) among different system classifications. Values used in the NiRReLa model are italicized in bold. * denotes a significant difference among systems using a LSD-Tukey test in a 1-way ANOVA. All other comparisons were statistically not significantly different ($P>0.05$).

Table 3. Results of NiRReLa N removal estimates at the global scale for different aquatic system classes. Surface area represents the global surface as estimated by NiRReLa for small lakes and reservoirs (0.001-50 km^2) and large lakes and reservoirs (> 50 km^2). NiRReLa-based estimates of total surface area, total N removal, and per-area N removal are compared with estimates from Seitzinger et al. 2006.

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Table 1 : List of references, geographical location, and ranges of morphological and hydrological variables of the lakes and reservoirs used in the determination of different parameter estimates of the NiRReLa model.

Latitude	Lake or reservoir	n	Location	Surface Area (km^2)	mean Z[†] (m)	Residence Time (yr)	% N Removal	V_f	H_l[†] (m yr^{-1})	Reference
Boreal	lake	2	Switzerland	2.7 - 6.1	2.5 - 5.4	0.85 - 1.81	17.9 - 39.7	0.7 - 1.26	1.38 - 6.38	Ahlgren et al. 1994
Boreal	lake	6	Denmark	0.11 - 1.04	1.9 - 12	0.03 - 0.36	22.7 - 55.3	11.3 - 20.4	14 - 74.2	Andersen 1974
Boreal	lake	4	Denmark	0.16 - 23	1 - 2.6	0.05 - 1.75	41.4 - 54.4	0.61 - 16.9	1.08 - 21.9	Jeppesen et al. 1998
Boreal	lake	1	Estonia	270	2.8	0.88	53	2.41	3.18	Nõges et al. 1998
Boreal	lake	2*	Estonia	0.13	3.6	1.11 - 1.49	58 - 80	2.81 - 3.88	2.41 - 3.24	Nõges 2005
Boreal	lake	16	Denmark	N/A	0.9 - 5.6	0.02 - 0.69	11.0 - 57	2.7 - 12.8	4.2 - 100	Windolf et al. 1996
Boreal/ Temperate	lake	9	ON, Canada	0.12 - 0.71**	2.4 - 12.4	0.06 - 25	7.0 - 99	1.18 - 8.59	0.42 - 118	Kelly et al. 1987
Temperate	lake	1	US/ Canada	58016	84	100	66	0.91	0.84	Ayers 1970
Temperate	lake	1	Italy	1.81	45	4.7	40	4.89	9.57	Calderoni et al. 1978
Temperate	lake	4	ON, Canada	N/A	3.3 - 12.2	0.3 - 3.7	24 - 61	2.11 - 4.64	2.2 - 13.6	Dillon & Molot 1990
Temperate	lake	2	IA, US	1.09 - 14.68	1.5 - 2.9	0.4 - 1.6	50.2 - 82.2	2.62 - 3.13	1.81 - 3.75	J. Downing unpubl.
Temperate	lake	1	Germany	7.18	4.85	0.13	16.6	6.69	36.88	Dudel & Kohl 1992
Temperate	lake	2	Switzerland	5.2 - 38	33 - 84	4.1 - 14.1	78.8 - 87.4	12.3 - 1249	5.96 - 8.05	Mengis et al. 1997
Temperate	lake	7	ON, Canada	0.32 - 270	5 - 14.2	1.6 - 5.35	36 - 73	1.98 - 2.95	1.59 - 5.77	Molot & Dillon 1993
Temperate	lake	5	SK, Canada	7.7 - 20.20	6 - 14.4	0.4 - 1.3	41 - 80	4.52 – 19.3	8.57 - 20.5	Patoine et al. 2006 & Leavitt et al. 2007
Temperate	lake	8	QC, Canada	0.71 - 22.6	3 - 25.9	0.15 - 8.96	6.07 - 57.9	0.6 - 9.89	2.9 - 30.7	Y. Prairie unpubl.
Tropical	lake	9	Latin America/ Caribbean	1.11 - 1078.5	1.0 - 16	0.04 - 98.5	13.9 - 99.7	0.92 - 26.4	0.16 - 114	Salas & Martino 1991
Temperate	reservoir	2	IA, US	0.35 - 1.99	2.3 - 2.5	0.18 - 0.3	37.2 - 69.6	5.95 - 9.91	8.3 - 12.8	J. Downing unpubl.
Temperate	reservoir	6	France	21 - 48 **	3.5 - 8.9	0.03 - 0.62	12 - 54.5	7.2 - 19.2	12.26 - 150	Garnier et al. 1999
Temperate	reservoir	4	US	390 - 832	10 - 55	0.8 - 3.7	0 - 80	0 - 20.12	6.3 - 14.9	Kelly 2001
Temperate	reservoir	1	CA, US	104.4	17.26	0.01	0	0	1400	Teodoru & Wehrli 2005
Temperate	reservoir	4	SK, Canada	0.50 - 430	1.4 - 21.9	0.05 - 12.6	23 - 99	2.9 - 32.2	0.63 – 28	Patoine et al. 2006 & Leavitt et al. 2007
Tropical	reservoir	18	Latin America/ Caribbean	3.8 - 250	2.2 - 26.4	0.002 - 1.92	0.04 - 68.5	0.01 - 81	10.3 - 1250	Salas & Martino 1991

* same system 2 different years

** some data not available (N/A)

[†] Z is mean depth for a given lake or reservoir and H_l is hydraulic load.

Table 2. Comparison of average N apparent settling velocities (V_f) among different system classifications. Values used in the NiRReLa model are italicized in bold. * denotes a significant difference among systems using a Tukey test in a 1-way ANOVA on the log transformed data. All other comparisons were statistically not significantly different (P>0.05).

Axis of Comparison	**Systems Compared**	**n**	***Vf***	**SD**
Overall mean		115	8.91	10.27
System type	Lakes	80	***6.83****	5.8
	Reservoirs	35	***13.66****	15.5
N-form	Total N	89	9.92	11.15
	NO_3	24	5.66	5.34
Surface Area	>50 km^2	13	8.01	10.83
	<50 km^2	76	9.76	11.66
Latitude	Boreal	36	7.74	5.77
(Lakes only)	Temperate	35	5.13	4.63
	Tropical	9	9.81	8.38
Latitude	Temperate	17	9.35	8.36
(Reservoirs only)	Tropical	18	17.72	19.53

Table 3. Results of NiRReLa N removal estimates at the global scale for different aquatic system classes. Surface area represents the global surface as estimated by NiRReLa for small lakes and reservoirs (0.001-50 km^2) and large lakes and reservoirs (> 50 km^2). NiRReLa-based estimates of total surface area, total N removal, and per-area N removal are compared with estimates from Seitzinger et al. 2006.

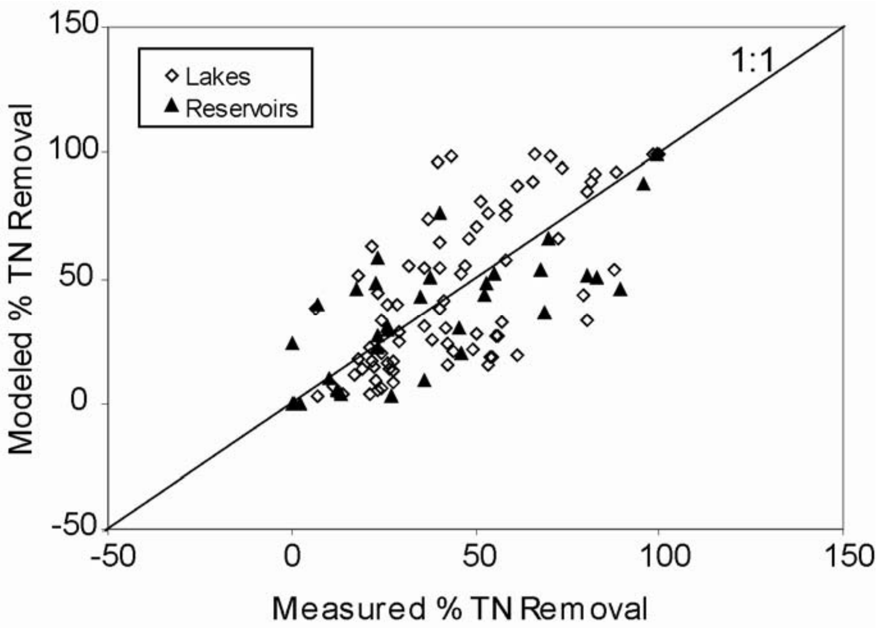
Waterbody Type	**Surface area (km^2)**	**N retained globally (Tg N yr^{-1})**	**N retained per unit area (kg N km^{-2} yr^{-1})**
Small Lakes	2.6×10^6	9.3	3,577
Large Lakes	1.2×10^6	3.7	3,083
All Lakes	3.8×10^6	13.0	3,421
Small Reservoirs	9.8×10^4	3.0	30,612
Large Reservoirs	1.5×10^5	3.6	24,000
All Reservoirs	2.5×10^5	6.6	26,400
Reservoirs and Lakes Combined	**4.1×10^6**	**19.7****	**4,805**
Other Lake Model			
Seitzinger et al. 2006	2.8×10^6	31 (19-43)	11,000
	4.1×10^6	31.0	7,660*

* per-area estimate determined using NiRReLa lentic surface area estimate

**does not sum because of rounding

Table 4. Results from a model sensitivity analysis. * signifies sensitivity analysis was only run on small lakes and reservoirs.

Parameter	**Δ Input**	**Δ Prediction(%)**	**Range of Predicted Lake & Reservoir N Retention (Tg yr^{-1})**
Runoff	Half-Double	-11% to +15%	17.5-22.7
N Inputs	Half-Double	-50% to +100%	9.85-39.4
V_f	25th percentile-75th percentile (2.2-7.56 m yr^{-1} and 3.15-19.41 m yr^{-1} for lakes and reservoirs, respectively)	-30% to +17%	13.7-25.1
c for lakes	± 1 S.E.	-0.1% to +0.1%	*12.3-12.4
c for reservoirs	± 1 S.E.	-1.6% to -1.6%	*12.1-12.4
Minimum Lake Area	Raised to 0.01 km^2	-8.1%	*11.3
Minimum Reservoir Area	Raised to 0.01 km^2	-0.8%	*12.2
Minimum Lake and Reservoir Area	Raised to 0.01 km^2	-9.8%	*11.1
Small Lake and Reservoir Cutoff	Used only documented lakes and reservoirs (>0.1 km^2)	-24.9%	14.8
N Inputs	Run with NEWS-DIN output	-22.8%	15.2



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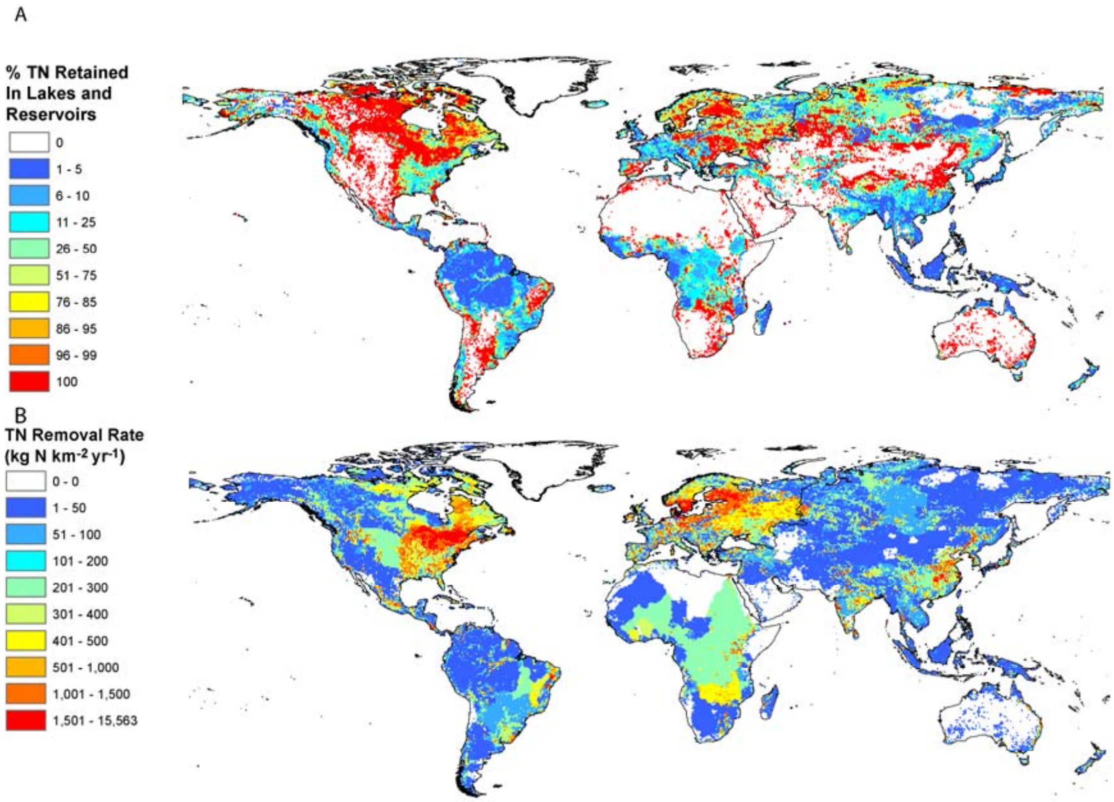

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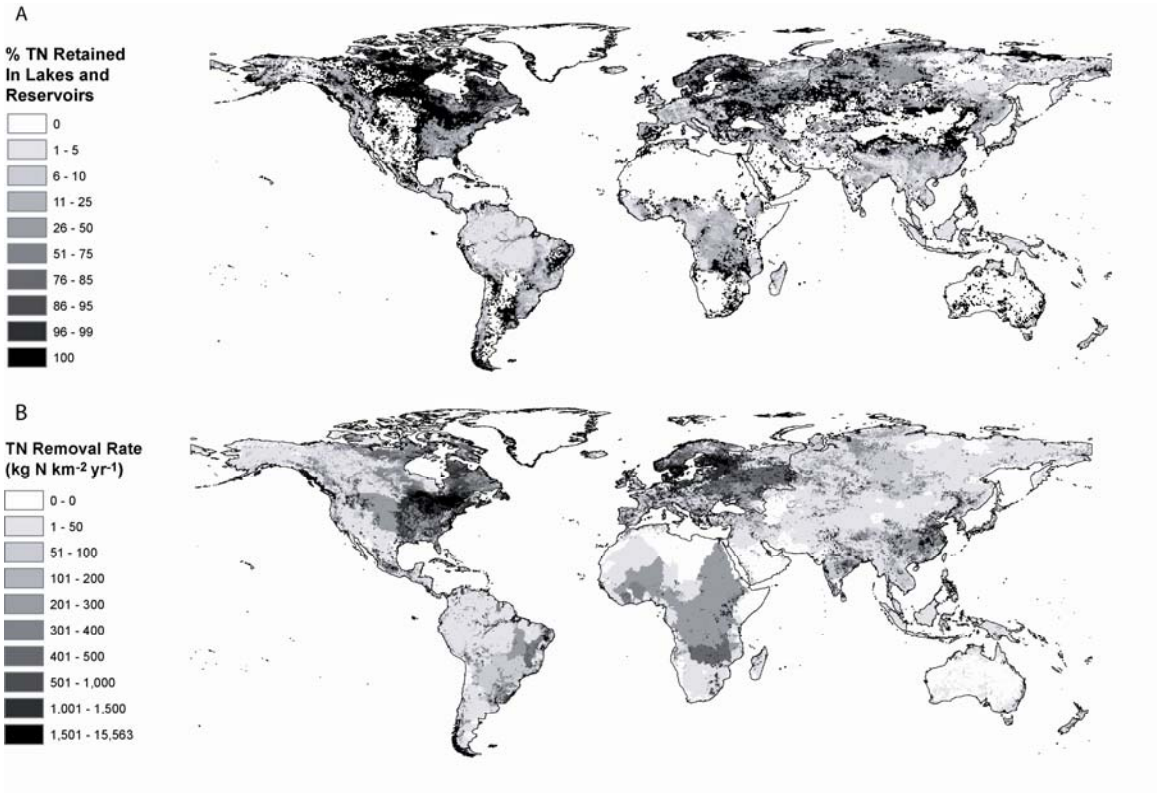

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