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RESEARCH ARTICLE

Evaluating the effects of upstream lakes and wetlands on lake phosphorus concentrations using a spatially-explicit model

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Abstract Lake phosphorus concentrations are strongly influenced by the surrounding landscape that generates phosphorus loads and water inflow to lakes, and the physical characteristics of the lake that determine the fate of these inputs. In addition, the presence, connectivity, and configuration of upstream lakes and wetlands likely affect downstream lake phosphorus concentrations. These freshwater landscape features have only sometimes been incorporated into phosphorus loading models, perhaps because of the need for spatially-explicit approaches that account for their location and hydrologic configuration. In this paper, we developed a lake phosphorus concentration model that includes three modules to estimate phosphorus loading, water inflow, and phosphorus retention, respectively. In modeling phosphorus loading and water inflow, we used a spatially-explicit approach to address their export at sources and their attenuation along flow-paths. We used 161 headwater lakes for model calibration and 28 headwater lakes for model validation. Using the calibrated model, we examined the effects of upstream lakes and wetlands on downstream lake phosphorus concentrations. To examine the effects of upstream lakes, we compared the output of the calibrated model for three additional datasets (208 lakes in total) that contained increasing area of upstream lakes. To examine the effect of upstream wetlands, we used the calibrated model to compare flow-path cell series that contained wetlands and those that did not. In addition, we simulated catchments in which all wetlands were converted to forest and recalculated downstream lake phosphorus concentrations. We found that upstream lakes decreased the phosphorus concentrations in downstream lakes; and, counter-intuitively, we found that wetlands increased phosphorus concentrations in most downstream lakes. The latter result was due to the fact that although wetlands reduced phosphorus loads to downstream lakes, they also reduced water inflow to downstream lakes and thus increased the phosphorus concentration

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of inflows to lakes. Our results suggest that when modeling lake phosphorus concentrations, freshwater features of the landscape and their spatial arrangement should be taken into account.

Keywords Lake phosphorus concentration · Spatially-explicit modeling · Wetland · Upstream lake · Flow-path · Distance-attenuation effect

Introduction

Nutrient concentrations in freshwater ecosystems are strongly influenced by two categories of factors: the surrounding landscape that generates nutrient and water inflow, and the physical characteristics of the water body that determine the fate of these inputs. For lakes, the latter factor has been effectively incorporated into empirical models that predict lake nutrient concentrations as a function of water depth, hydraulic residence times, and nutrient loads (Vollenweider 1976; Reckhow and Chapra 1983). However, for lakes, the effect of the surrounding landscape on nutrient and water inflow has been less effectively modeled, in part because of the large amount of spatial complexity that influences nutrient and water transport to them. This spatial complexity results in several challenges in modeling landscape effects on lake nutrient concentrations. First, incorporating greater spatial complexity in models requires large amounts of calibration data, which often are not available, as has been recognized in several reviews of the topic (e.g., Grayson et al. 1992; Breuer et al. 2008). Second, choosing which of the many land-based catchment features, such as soils, topography, and land use/land cover (LULC) types, to include in a spatially-explicit manner is often not clear. Third, a challenge that has received far less attention is the need to account for the composition and spatial configuration of the freshwater landscape, such as the presence of upstream lakes and wetlands and the hydrologic connections among them (Soranno et al. 2010). It is notable that researchers modeling nutrient flow to waterbodies have incorporated spatial complexity of the land-based elements of the landscape much more than they have incorporated the presence or spatial configuration of connected, with a few exceptions (e.g., Marcarelli and Wurtsbaugh 2007; Goodman et al. 2010; Powers et al. 2012).

There is much evidence to suggest that upstream waterbodies play an important role when modeling nutrient transport from catchments to lakes. For example, wetlands can be important sinks for nutrients originating from agricultural and urban lands and they may play a significant role in improving water quality of downstream aquatic ecosystems (Baker 1992; Zedler and Kercher 2005; Verhoeven et al. 2006). However, the evidences for the specific effects of wetlands on lake phosphorus concentration, in particular, are equivocal. For example, studies have shown wetland cover to be positively related to downstream waterbody phosphorus concentrations in some settings (Devito et al. 2000; Fergus et al. 2011), but negatively related to downstream waterbody phosphorus concentrations in other settings (Detenbeck et al. 1993; Fergus et al. 2011). In addition, for upstream lakes, we would expect them to be negatively related to downstream lake nutrient concentrations because of sedimentation and uptake within lakes that typically results in lower outflow phosphorus concentrations compared to inflow phosphorus concentrations (Ahlgren et al. 1988; Malmaeus et al. 2006; Bryhn and Håkanson 2007; Brett and Benjamin 2008). The fact that most detailed studies of nutrient transport from land to lakes are conducted on headwater lakes (i.e., lakes without upstream lakes and few connected wetlands) shows that the important role of connected waterbodies has been recognized, but avoided due to the complexity of modeling such connections. Therefore, studies are needed that quantify the effects of both upstream lakes and wetlands on downstream lakes so that phosphorus concentrations in larger catchments containing upstream waterbodies can be better estimated.

Related to the above issues is the overall consideration of the trade-offs between complexity and simplicity in models. In response to these trade-offs, a wide range of models with different levels of spatial complexity have been developed, from non-spatial empirical regression models to complex physically-based and spatially-explicit models. Non-spatial regression modeling uses simple landscape metrics as predictors of nutrient loading to, or concentrations of, waterbodies (e.g., Jones et al. 2001; Prepas et al. 2001; Brett et al. 2005). These landscape metrics attempt to capture relevant aspects of spatial pattern related to nutrient transport. For modeling lake nutrients, such indices can be divided into ones that characterize landscape composition (e.g., percent agricultural land in a lake catchment), or ones that characterize landscape configuration (e.g., contagion index of a lake catchment) (Gémesi et al. 2011). This approach can be used to explore and test the possible linkages between landscape characteristics and nutrient dynamics and allows one to easily include a large number of lakes because minimal input data are needed. However, simple landscape metrics may not capture the complexity of nutrient flow from land to water. This fact makes it difficult to infer the underlying hydrological processes that the models are intended to represent.

At the other end of the complexity spectrum are physically-based and spatially-explicit models that have spatially-distributed variables and parameters. This approach has become widely used to estimate nutrient loading, as reviewed by Grayson et al. (1992), Bouraoui (1994), Borah and Bera (2003, 2004), and Breuer et al. (2008). These models are very useful for understanding nutrient and water transport and they help improve fine-scale management practices (Borah and Bera 2004). However, some practical difficulties prevent these complex spatially-explicit models from being widely and successfully used to estimate lake phosphorus concentrations. First, these models often require detailed measurements of hydrology and nutrients that are not typically available for most streams and lakes. Second, some complex spatially-explicit models are computationally intensive. Applying them in heterogeneous and large catchments can be extremely time-consuming. Third, the spatio-temporal scales adopted in many spatially-explicit models are not suitable for many questions related to nutrient transport. For example, some models use an hourly or daily time step, which is too fine of a scale to examine processes that occur across large catchments, while other models aggregate a catchment into hydrological response units that are too coarse to examine many questions related to spatial heterogeneity of nutrient and water flow. Finally, because many of these complex models have large numbers of parameters, they tend to over-fit the calibration data and may not have good predictive power for other catchments (Grayson et al. 1992; Sivapalan 2003). In sum, both the simple landscape metrics models and the most complex spatially-explicit models have limitations for modeling lake phosphorus. It is not clear from the literature what level of spatial detail is needed to address the landscape heterogeneity of catchments and the complexity of hydrological processes for modeling phosphorus concentration in lakes.

Our two objectives in this study were to: (1) develop a spatially-explicit lake phosphorus concentration model that is intermediate in complexity, requires only publically available data as inputs, and is not computation-prohibitive when applied to a large number of lake catchments; and (2) examine the effects of upstream lakes and wetlands on modeled downstream lake phosphorus concentrations. For Objective 1, we developed a model (called the flow-path attenuation model) that has three modules that estimate phosphorus loading, water inflow, and phosphorus retention. For the phosphorus loading and water inflow modules, we used a spatially-explicit approach that modeled the export of phosphorus and water at sources and their attenuation along flow-paths. For the phosphorus retention module, we used the Vollenweider model to estimate lake phosphorus concentration change from lake's inflow. For Objective 2, we examined the effects of upstream lakes on downstream lake phosphorus concentrations by comparing the outputs of the calibrated model from three additional datasets that contained increasing area of upstream lakes. In this step, we predicted that for lakes within increasing area of upstream lakes, the phosphorus concentrations would be increasingly overestimated, suggesting trapping effects of upstream lakes on downstream lake phosphorus concentrations. We also examined the effects of upstream wetlands on downstream lake phosphorus concentrations at two scales. First, we compared the transport of phosphorus and water between flow-path cell series that contained wetlands and those that did not. Second, at the catchment scale, we simulated a landscape in which all wetland cells were converted to forest cells and calculated downstream lake phosphorus concentrations. Unlike upstream lakes, for which we had clear expectations of their effects on downstream lake phosphorus concentrations, we expected that upstream wetlands would have complex effects on the phosphorus concentration of downstream lakes that would be difficult to predict in advance.

Methods

Study region and lake data

We studied 397 lakes that are distributed throughout the state of Michigan (Fig. 1). Most lakes in Michigan have been shaped by glaciers and glacial meltwater.

Fig. 1 Study lakes and their catchments in the state of Michigan. From **a–e**, the lakes are for calibration, validation, and Evaluations 1–3, respectively

We excluded lakes that were considered to be reservoirs or that contained sewage treatment plants in their catchments because the effects of both situations on water inflow or phosphorus loads were difficult to quantify with available data. The lakes span two orders of magnitude in size and their catchments also vary greatly in size and LULC composition (Table 1).

Within the 397 study lakes, there were 189 headwater lakes that did not have sizable upstream lakes (defined as having a cumulative upstream lake area <15 ha). We randomly selected 161 lakes from

Table 1 Characteristics of the study lakes and their catchments

Lake sets	Calibration ($N = 161$)			Validation ($N = 28$)			Evaluation 1 ($N = 71$)			Evaluation 2 ($N = 68$)			Evaluation 3 ($N = 69$)		
	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med	Min	Max	Med
Lake area (km^2)	0.2	41	0.5	0.1	40	1.1	0.2	19	0.8	0.2	35	1.0	0.2	70	1.3
Lake depth (m)	1	16	4	2	22	4.6	1	17	4.4	1.3	13	5.0	0.8	21	4.5
Catchment area (km^2)	0.5	113	4	0.7	116	10	1.3	224	16	2.6	362	20	9.5	7,068	105
TP (μg L^{-1})	4	91	14	4	48	15	4	62	14	2	41	13	1	58	13
% Agriculture	0	69	7	0	57	16	0	70	19	0	58	18	0	55	22
% Urban	1	79	10	2	26	12	2	38	9	1	53	10	2	43	9
% Forest	2	86	38	12	77	43	6	78	39	3	78	36	15	85	43
% Wetland	1	46	13	3	53	11	5	61	17	4	57	19	6	49	21

The minimum, maximum, and median values are listed

these headwater lakes to calibrate our model, and we used the other 28 lakes to validate the model (Fig. 1a, b; Objective 1). We divided the remaining 208 lakes into three datasets for evaluating the effects of upstream lakes on modeled downstream phosphorus concentrations (see below; Objective 2).

We used lake phosphorus concentration data, specifically that sampled during spring turnover when lake water is well mixed, collected by the USGS from 2001 to 2008 through the Lake Water Quality Assessment monitoring program (Fuller and Minnerick 2008). Our subset of data represents sampling during April (81 %) as well as late March and early May (19 %).

Landscape and climate data

We delineated lake catchments for each of the 397 lakes using 1:24,000 stream data and 30 m flow direction grid data as input of the Hydrology Tools in ESRI ArcGIS 9.3. The stream data were from the USGS National Hydrography Dataset (NHD) and the flow direction grid data were from the USGS NHDPlus dataset. The flow direction data were a hydrologic derivative product of HydroDEM, which is a modified digital elevation model produced using drainage enforcement techniques (e.g., stream burning and DEM filling techniques) on the National Elevation Dataset and the National Hydrography Dataset (refer to ftp://ftp.horizon-systems.com/NHDPlus/documentation/NHDPLUS_UserGuide.pdf for more details about the data processing of NHDPlus dataset). The catchment of a lake includes all of the grids that drain into the lake or its upstream lakes and streams. Hereafter, the final recipient lake of a catchment is called the “focal lake” and the other lakes in its catchment are called “upstream lakes”.

We obtained 2007 LULC data from the USDA Cropland Data Layer (CDL) for the state of Michigan (http://www.nass.usda.gov/research/Cropland/SARS1a.htm). We aggregated the CDL data into six LULC types: pasture, row crop, forest, urban, wetland (which includes both wetlands and small lakes), and focal lakes. We aggregated LULC types to minimize the number of parameters that were fit in the calibration step and because rare LULC types could not be fit to the data. To calculate the annual precipitation in each lake catchment, we summed the monthly precipitation for the 12 months prior to the lake phosphorus concentration sampling. The monthly precipitation data were from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) datasets (http://www.prism.oregonstate.edu/products/). The spatial resolution of the precipitation data is approximately 4 km, which is much coarser than the other geographic data included in our model, but matches the characteristics of smooth spatial variation for annual precipitation.

Model approach

The complexity level of our flow-path attenuation model falls between the simple multivariable regression models and the process-based models. The model is spatially explicit but does not contain detailed physical processes. Our flow-path attenuation model contains three modules: phosphorus loading to lakes, water inflow to lakes, and lake phosphorus retention.

Phosphorus loading is defined as the amount of phosphorus transported from land to a lake in a year. Water inflow is the volume of incoming water to a lake in a year. These two modules were used to calculate the inflow phosphorus concentrations. Finally, we calculated lake phosphorus concentrations using the inflow phosphorus concentration and the third module, the lake phosphorus retention module.

The phosphorus load module adopts the basic concept of an export coefficient model. An export coefficient is an estimate of the mass of a pollutant exported from a unit area of a particular LULC type in a year. Unlike the traditional export coefficient model that ignores spatial heterogeneities of other factors that govern nutrient export and delivery processes, our module takes into consideration two important spatially-explicit factors: precipitation and nutrient attenuation. For the source cells, we included annual precipitation, which is positively correlated with nutrient export from a source area (Vanni et al. 2001; Wang and Choi 2005). For the grid cells along flow-paths, we used delivery ratios to quantify the attenuation effects on the nutrient flowing through these cells. Delivery ratio of a grid cell is the fraction of nutrient that is not trapped in that grid cell. We distinguished terrestrial cells from wetland cells to address their different delivery effects on phosphorus. Thus, the effective phosphorus load from a source cell to a lake is the product of the exported phosphorus at the source cell and the cumulative delivery ratio of the cells in its flow-path:

$$l = p \cdot E \cdot r_1 \cdot r_2 \cdot \cdots = p \cdot E \cdot R \tag{1}$$

where l is the effective phosphorus load from a source cell (kg year^{-1}); p is the normalized annual precipitation factor of that source cell (normalized by the average precipitation of the study area); E is its phosphorus export coefficient (kg year^{-1}); and R is the cumulative delivery ratio of phosphorus, or the product of delivery ratios (r_i) of the cells along the flow-path. Here, although different terrestrial or wetland cell types may differ in their effectiveness at trapping phosphorus (Detenbeck et al. 1993; Abu-Zreig et al. 2003; Diebel et al. 2009), we did not further distinguish them into subtypes because our sample size was too small to do so and we did not have good information on wetland types.

The total phosphorus load to a lake (L) is:

$$L = \sum_{j=1}^{6} \sum_{i=1}^{n_j} p_{ij} \cdot E_j \cdot R_{ij} \tag{2}$$

where j refers to the LULC type and n_j is the number of grid cells of j type in the catchment. Besides the five LULC types in the catchment, the focal lake is regarded as a special LULC type with the cumulative delivery ratio (R) of one because the direct phosphorus load to a lake cell (e.g., the atmospheric load and internal load) contributes entirely to the load.

The module of water inflow to lakes is similar in concept to the module of phosphorus loads to lakes. Water yield from a source grid cell is not only affected by its LULC type but also is proportional to its annual precipitation. Water will decrease as passing through a grid cell, and the fraction of delivered water is different between terrestrial and wetland cells. Thus, the annual water inflow to a lake (Q, in m^3 year^{-1}) is:

$$Q = A_{cell} \cdot \sum_{j=1}^{6} \sum_{i=1}^{n_j} P_{ij} \cdot w_j \cdot S_{ij} \tag{3}$$

where A_{cell} is the area of a grid cell (m^2); P is the annual precipitation depth at each cell (m year^{-1}); w is a factor that compensates for other anthropogenic or natural water losses or gains (e.g., evapotranspiration, irrigation, groundwater discharges/recharges); and S is the cumulative delivery ratio of water along the flow-path. With L and Q, phosphorus concentration of inflow (μ L^{-1}) is given by:

$$TP_{in} = \frac{L}{Q} \times 10^6 \tag{4}$$

where 10^6 is the coefficient for unit conversion. Equation (3) is a coarse model for estimating water yield from the landscape, especially in the Great Lakes region where hydrological routing and base flow are broadly affected by glacial geology and groundwater characteristics (Winter 1999; Neff et al. 2005). However, simulating water flow in a more accurate way for nearly 400 ungauged catchments that span the state of Michigan requires introducing many additional parameters and unavailable data. We developed this simpler model to keep the parameters few enough to make calibration feasible with our sample size.

For the lake phosphorus retention module, we tested several models and adopted the widely-used Vollenweider model (Vollenweider 1976) because it had the best performance as measured by R^2 (Zhang, unpublished data). The Vollenweider model can be rewritten as (Brett and Benjamin 2008):

$$TP = \frac{TP_{in}}{1 + \sigma\tau} \tag{5}$$

where TP is the lake phosphorus concentration (μg L^{-1}); σ is the first-order rate coefficient for phosphorus loss from the lake ($year^{-1}$); and τ is the mean hydraulic residence time (year), which is given by:

$$\tau = \frac{V_{lake}}{Q} = \frac{A_{lake} \cdot D_{lake}}{Q} \tag{6}$$

where V_{lake}, A_{lake}, and D_{lake} are the lake volume (m^3), lake area (m^2), and lake mean depth (m), respectively.

Model calibration and validation

To calibrate the model, we used a simulated annealing optimization method (Kirkpatrick et al. 1983) to determine the parameter estimates that minimized the root of mean squared error (RMSE) between observed and predicted lake phosphorus concentrations. We then applied the calibrated model in the validation dataset and evaluated the predictive performance of the calibrated model. We quantified several metrics to evaluate the calibration and validation results. For calibration, the three metrics were Nash-Sutcliffe model Efficiency coefficient (NSE), R^2, and RMSE. For validation, the four metrics were NSE, R^2, RMSE, and the percent bias (PBIAS). NSE indicates how well the plot of predicted versus observed data fits the 1:1 line and PBIAS measures the average tendency of the simulated data to be larger or smaller than their observed counterparts (Moriasi et al. 2007).

Assessing the effects of upstream lakes and wetlands on lake phosphorus concentrations

For our second objective, we divided the 208 lakes that had upstream lakes in their catchments into three datasets with increasing amounts of upstream lake area as measured by two metrics: (1) total upstream lake area (A_{up} in ha) and (2) the lake areal ratio, defined as the ratio between the upstream lakes and the focal lake (A_{up}/A_{focal}, unitless). Including lake areal ratio in this criterion is consistent with using the lake influence index (Snelder and Biggs 2002) to estimate the effect of upstream lakes on controlling downstream flow and sediment regimes. The definition of these three datasets is in Table 2 and the locations of these lakes and their catchments are shown in Fig. 1c–e. For convenience, we hereafter call the three datasets Evaluations 1–3. We quantified the performance of the flow-path attenuation model for these three evaluation datasets to study the effect of increasing upstream lake prevalence on predicting lake phosphorus concentrations. We compared their PBIAS values to determine whether increasing amounts of upstream lakes result in increased bias in the model's prediction.

We evaluated the effects of catchment wetlands on focal lake phosphorus concentrations at two scales. First, at the scale of the flow-path cell-series, we compared the change of phosphorus load and concentration between a cell-series with only terrestrial LULC types and a cell-series that starts with terrestrial cells and ends with wetland cells. Then, at the scale of the catchment, we reran the flow-path attenuation model using the calibration lake dataset but with a simulated landscape within which all existing wetlands were converted to terrestrial land (i.e., forest land) and compared the differences in predicted phosphorus loading to the focal lakes between the two scenarios.

Results

Spatially-explicit phosphorus concentration model

The calibration and validation results implied that our spatially-explicit flow-path attenuation model

Table 2 Definition of the datasets used to evaluate the effect of upstream lakes

Name	N	Definition
Evaluation 1	71	$(A_{up} < 60\,\text{ha}) \cap (A_{up}/A_{focal} < 0.5)$
Evaluation 2	68	$(A_{up} < 200\,\text{ha}) \cap (A_{up}/A_{focal} < 2) - \text{Evaluation1}$
Evaluation 3	69	$(A_{up} > 200\,\text{ha}) \cup (A_{up}/A_{focal} > 2)$

A_{up} means the total upstream lake area and A_{focal} means the area of focal lake. N is the number of lakes in each dataset

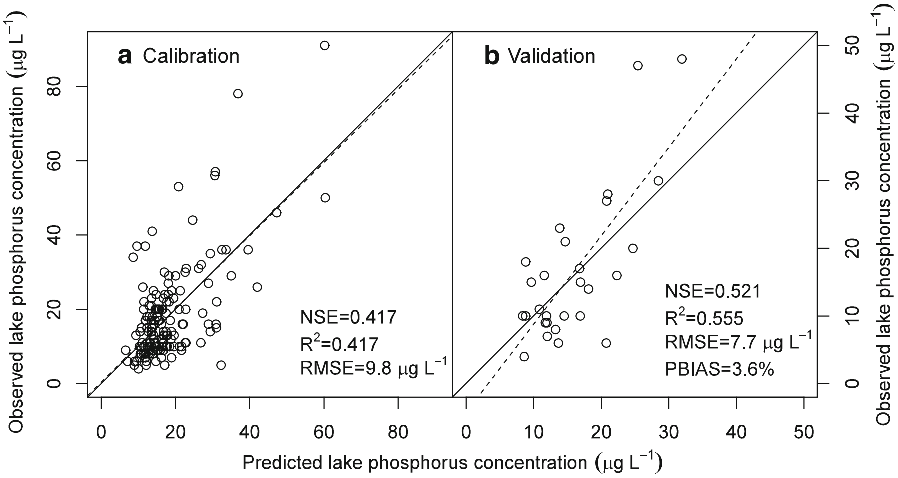

Fig. 2 The predicted versus observed plots for the calibration (**a**) and validation (**b**) of the flow-path attenuation model. Each data point is a lake. The *solid lines* are 1:1 lines. The *dashed lines* are regression lines between predicted phosphorus concentrations and observed phosphorus concentrations

performed fairly well when estimating lake phosphorus concentration for headwater lakes (Fig. 2). For calibration, the NSE and R^2 values were 0.417. In validation, the NSE value was 0.521 and the R^2 value was 0.555. The PBIAS value was 3.6 %, indicating that the model did not overestimate or underestimate lake phosphorus concentrations.

The parameter estimation results of the flow-path attenuation model are summarized in Table 3. Agricultural land use was the most important source of phosphorus in our calibrated flow-path attenuation model (Table 3). The phosphorus export coefficients of pasture and row crop were 0.946 and 0.601 kg year^{-1} ha^{-1}, respectively. A possible reason that our estimated pasture export coefficient was higher than that of crop may be because intensive animal feeding operations may have made the pasture plots a very important source of phosphorus (Beckert et al. 2011). In contrast, the phosphorus export coefficient of wetlands was only 0.121 kg year^{-1} ha^{-1}, which is lower than all terrestrial LULC types. Lakes also had a small positive phosphorus export coefficient (0.060 kg year^{-1} ha^{-1}). This result is consistent with the fact that during spring turnover season, oxygenated water is often introduced to a previously anoxic hypolimnion and injects sediment-bound phosphorus into the water column. For the flow-path attenuation effects, the half-decay distance of phosphorus and water in terrestrial LULC types were 227 m and 932 m, respectively. In contrast, the half-decay distance for phosphorus and water in wetlands was only about 30 m.

Effects of upstream lakes and wetlands on downstream lake phosphorus concentrations

When examining the effects of upstream lakes on focal lake phosphorus concentrations, we found a trend of increasing bias towards the overestimation of phosphorus concentration in the evaluation datasets. PBIAS values were −17.9 %, −40.8 %, and −67.7 %, respectively for Evaluation 1, Evaluation 2, and Evaluation 3 datasets (Fig. 3). Accordingly, the paired *t* test for the observed and predicted phosphorus concentrations showed that the prediction bias became significant in Evaluation 2 and 3 ($p < 0.01$ with a confidence level of 0.95). Therefore, in our flow-path attenuation model, lake phosphorus concentration was increasingly overestimated in the evaluation datasets when upstream lakes were not included in the model. This was especially notable when we compared these values to those PBIAS calculated for the validation dataset (3.6 %) that contained no, or very minor amounts of, upstream lakes (Fig. 2b). This model result implies that as upstream lake area and its ratio to focal lake area increases, the phosphorus concentrations in downstream lakes decreases. This result is consistent with the lake phosphorus retention module (i.e., the Vollenweider model) that shows that lakes with large volume have high phosphorus retention and thus reduce the phosphorus flowing to their downstream lakes.

For the effects of wetlands on downstream lake phosphorus concentrations, as mentioned above, wetlands have a phosphorus export efficient lower than

Table 3 Model parameter calibration results

Parameter	Terrestrial				Wetland	Lake
	Pasture	Rowcrop	Forest	Urban		
Phosphorus export coefficient	0.946 (0.103)	0.601 (0.118)	0.400 (0.047)	0.272 (0.065)	0.121 (0.059)	0.060 (0.016)
Water yield depth	0.017 (0.155)	1.091 (0.174)	1.969 (0.163)	0.765 (0.223)	0.001 (0.275)	0.761 (0.091)
Phosphorus delivery ratio	0.737 (<0.034)				0.100 (<0.059)	–
Water delivery ratio	0.928 (<0.019)				0.100 (<0.059)	–
Phosphorus loss rate in lake	1.09×10^{-2} (3.68×10^{-2})					

Phosphorus export coefficients are in the unit of kg ha^{-1} year^{-1} and water yield depths are in the unit of m year^{-1}. They are the estimations in the condition of annual precipitation of 0.851 m. Phosphorus and water delivery ratios are unitless and are ratios over a flow length of 100 m. Phosphorus loss rates in lake are in the unit of year^{-1}. Their approximate standard deviation values are given in the parentheses under the condition that the covariances among parameters are ignored

the export coefficient of any terrestrial land use type. We also found that wetlands were more effective at trapping phosphorus and water than other terrestrial LULC types. Because phosphorus is attenuated quickly in wetlands, wetlands often act as important sinks for phosphorus accumulated in upslope landscapes. However, because phosphorus concentration is affected not only by the phosphorus loads, but also by the water inflow, the overall impact of wetlands on their downstream lake phosphorus concentrations may be complex.

We explored the influence of wetlands on phosphorus concentration at two scales: the scale of flow-path cell-series and the scale of catchment. In the flow-path cell-series analysis in which we compared terrestrial versus wetland flow-paths, the cumulative phosphorus loading increased consistently through the terrestrial-only cell series, whereas the loading sharply declined at wetland cells in the terrestrial-wetland cell series (Fig. 4a). However, because wetlands cells were sinks for both phosphorus and water, they did not necessarily reduce the inflow phosphorus concentration to lakes (Fig. 4b). On the contrary, phosphorus concentrations in the wetland cells were higher than those in the terrestrial cells because the rate of water loss from the wetland cell was higher than the rate of phosphorus attenuation.

When we simulated the conversion of wetland to forest cover at the catchment scale, we found that phosphorus loads and water inflow to focal lakes increased and lake hydraulic residence time decreased in most cases (Fig. 5a–c). The effect of increased water inflow dominated the effect of increased phosphorus loads in most lakes, resulting in a lower inflow phosphorus concentration in the converted landscape than in the original landscape that contained wetlands. The increased water inflow rate reduced the lake phosphorus retention effect. In sum, the net result of converting wetlands to forest in this simulation was a decrease in phosphorus concentrations in most downstream focal lakes (Fig. 5d) despite the fact that phosphorus loads increased.

Discussion and conclusions

Our results lend support to the importance of including spatially-explicit factors related to both terrestrial and freshwater features when modeling lake phosphorus concentrations. Specifically, we demonstrated the potential importance of upstream lakes and catchment wetlands for modeling and understanding variation in lake phosphorus concentrations. Our model results suggest that upstream lakes decrease the phosphorus concentrations in downstream lakes, whereas upstream wetlands increase phosphorus concentrations in a large portion of downstream lakes. According to our simulation results, this seemingly counterintuitive effect of upstream wetlands is likely related to the complex effects of upstream wetlands on both phosphorus loads and water inflow (which collectively determine inflow phosphorus concentration), as well as the hydraulic residence time of the downstream lake. However, wetlands are temporally and spatially heterogeneous in their vegetation, hydrology, and biogeochemistry (Bowden 1987;

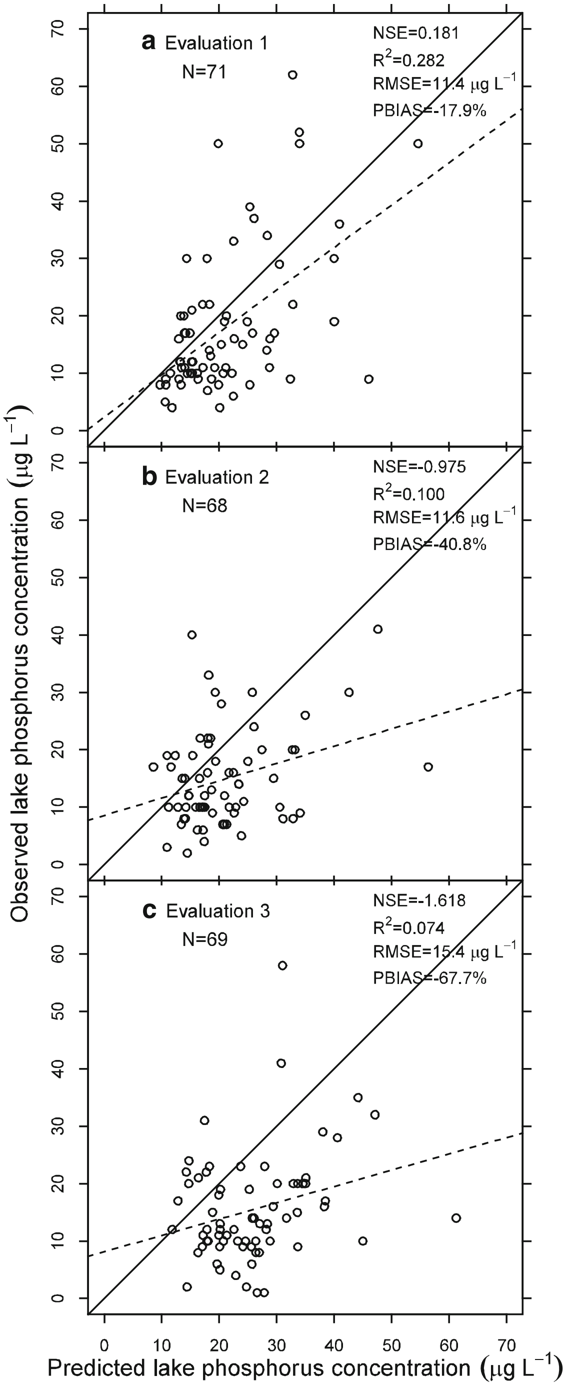

Fig. 3 The evaluation results of the flow-path attenuation model for each of the datasets that contain increasing amounts of upstream lakes area (Evaluations 1–3). Each data point is a lake. The *solid lines* are 1:1 lines. The *dashed lines* are the regression lines between predicted phosphorus concentrations and observed phosphorus concentrations

Detenbeck et al. 1996; Tompkins et al. 1997; Bedford et al. 1999; Reddy and DeLaune 2008). In our flow-path attenuation model, we did not consider the heterogeneity of those factors. Therefore, further research that includes such wetland heterogeneity should improve our ability to infer the complex effects of wetlands on lake phosphorus conditions.

Modeling lake phosphorus concentrations is more complicated than modeling lake phosphorus loads because of the need to estimate water inflow. Water inflow estimation plays an important role in quantifying lake phosphorus concentrations because it not only relates to the calculation of inflow phosphorus concentrations, but also affects the simulation of in-lake phosphorus retention (Imboden 1974; Ahlgren et al. 1988). Our module for estimating water inflow is not a detailed process-based hydrological model. Rather, it is simple in concept, easy to apply, and does not require data from gauged streams. As a result, we have provided an approach to model lake phosphorus concentrations that will be useful for quantifying the effects of certain landscape composition and configuration properties on lake phosphorus concentrations across a wide variety of lakes.

Effects of upstream lakes on lake phosphorus concentrations

Under steady state conditions, phosphorus retention in the form of lake sedimentation makes lake phosphorus concentrations lower than input phosphorus concentrations, as implied in the Vollenweider model that we adopted in our lake phosphorus retention module (Eq. (5)). Consequently, the phosphorus load transferred from an upstream lake to a downstream lake is usually lower than the phosphorus load to the upstream lake. If water inflow to a lake is constant, reducing phosphorus loading to a lake should result in a proportional reduction in lake phosphorus concentrations (Brett and Benjamin 2008). Therefore, it is expected that if all other things are equal, a lake with upstream lakes will have a lower phosphorus concentration than a lake without upstream lake. The trend we found of increasing overestimation bias for lake phosphorus concentrations in Evaluations 1–3 is consistent with this hypothesis that upstream lakes reduce the phosphorus concentrations of downstream lakes and that larger upstream lake area will result in a larger reduction of downstream phosphorus concentrations.

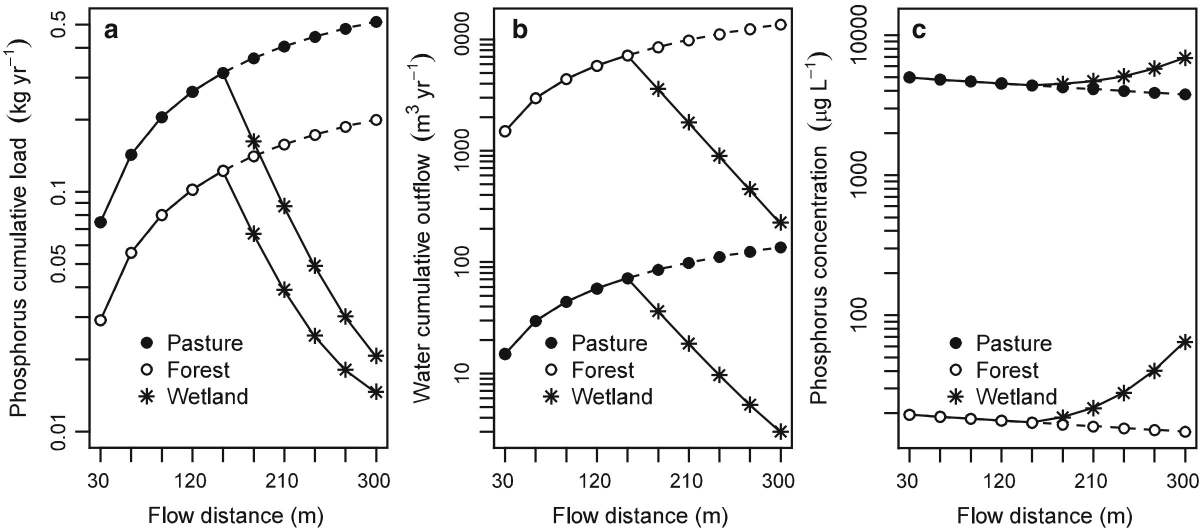

Fig. 4 Plots of phosphorus cumulative loads (**a**), water cumulative outflow (**b**), and phosphorus concentration (**c**) versus flow distance of a flow-path for terrestrial-wetland cell series (*solid*) and terrestrial-only cell series (*dashed*). In the case of the terrestrial-wetland cell series, the wetland cells begin at the fifth cell (150 m) and continue from there. Only two terrestrial LULC types (pasture and forest) are presented because the patterns are similar for all terrestrial types

Although these results make ecological sense, one may argue that the above results might be due to other variables that are correlated to upstream lake area. The most likely candidate for such a confounding relationship is focal lake catchment area. In our dataset, we did find that the rank of focal lake catchment area is significantly correlated with the rank of two upstream lake area metrics ($\rho = 0.79$ and 0.76 for the total area of upstream lakes and the maximum lake area respectively, $p < 0.001$). Because others have suggested that catchment area can influence nutrient transport over land (Prairie and Kalff 1986; Alexander et al. 2002; Smith et al. 2003a), we evaluated the potential effects of focal lake catchment area on our PBIAS results using two methods. First, we compared catchment areas across all four datasets, and, although there is a trend of increasing focal lake catchment area across the four datasets, there are large overlaps in the catchment areas among them (Table 1). Because of these overlaps, it is likely that the interpretation of the PBIAS trend across the validation and evaluation datasets has more to do with the larger differences in upstream lake area than the smaller differences in catchment area across these datasets. Second, to assess whether the continuously increasing overestimation bias across the four datasets was due to increasing catchment area instead of increasing upstream lake area, we re-classified the lakes into evaluation and validation datasets using catchment area instead of upstream lake area. For these new groups, the PBIAS values (from low to high catchment areas) are −18.4 %, −10.6 %, −40.8 %, and −66.3 %. Thus, the PBIAS values for the validation datasets using catchment area did not increase as smoothly with increasing values of catchment area as did for increasing values of upstream lake area. However, the two validation datasets with the largest catchment areas clearly have the highest PBIAS, which suggests that increasing catchment area likely contributes to the lack of model fit in addition to increasing upstream lake area. Unfortunately, due to the co-linearity of these two variables, we could not fully tease apart the effects of each on the observed PBIAS trend across the four datasets.

The effect of upstream lakes on the phosphorus concentrations of their downstream lakes likely depends on several other factors in addition to the area of upstream lakes. For example, the depth of upstream lakes should also affect phosphorus concentrations of downstream lakes. As Eq. (5) shows, the ratio between input phosphorus concentration and lake phosphorus concentration is largely determined by lake hydraulic residence time, which is inversely proportional to lake area and mean depth (Eq. (6)). Therefore, a deeper upstream lake should result in a

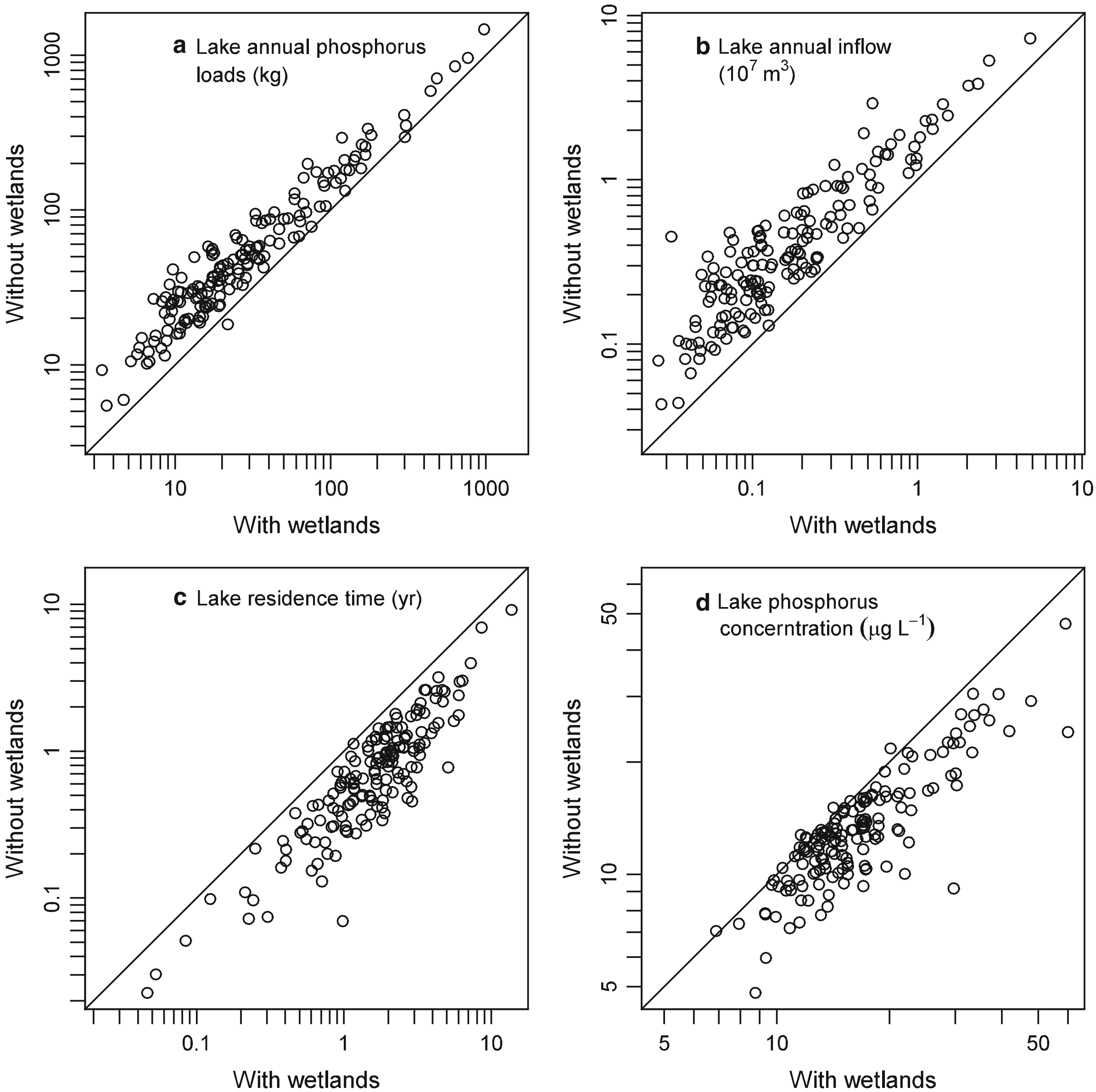

Fig. 5 Comparisons between two different landscapes: a landscape with wetlands as in the calibration dataset (X axis) and a simulated landscape in which wetlands have been converted to forested land (Y axis) for lake phosphorus loads (**a**), lake annual inflow (**b**), lake hydraulic residence time (**c**), and lake phosphorus concentration (**d**). Each data point is a lake. The *solid lines* are 1:1 lines. In the converted landscape, the lake phosphorus concentration is decreased despite the loading increases in most cases

lower phosphorus load to its downstream lakes than a shallow upstream lake, given the same area of the two upstream lakes and the same phosphorus and water input to them. Different types of lakes may also have different impacts on their downstream lakes. A seepage lake has no or little downstream phosphorus loss through surface runoff. Therefore, we expect that seepage lakes would retain phosphorus more effectively than drainage lakes. If a focal lake has a seepage lake within its catchment, the focal lake's phosphorus loading should be less than if there was a drainage lake upstream or no lake upstream. However, because seepage lakes usually retrain both more water and more phosphorus than drainage lakes, the phosphorus concentration of the focal lake with a seepage lake in its catchment would not necessarily be lower than the same focal lake with a drainage lake upstream.

Effects of upstream wetlands on lake phosphorus concentrations

In our modeling scenario, wetlands had a complex role in altering lake phosphorus concentrations. The simulation results of our flow-path attenuation model imply that wetlands have three main effects on lake phosphorus concentrations. First, wetlands can retain a large amount of phosphorus from their inflow water (Fig. 5a), as reviewed by Johnston (1991), Reddy et al. (1999), and Fisher and Acreman (2004). Second, wetlands can retain a large amount of their inflowing water (Fig. 5b), which also has been demonstrated with field studies quantifying water yield from wetlands. For example, studies have found that during spring, wetlands may yield less runoff than upland cover types because of their large hydraulic storage capacity, extensive evapotranspiration of plants, or other factors (Taylor and Pierson 1985; Devito 1997; Tompkins et al. 1997; Smerdon et al. 2007). Third, because of wetlands' effects of reducing water inflow to downstream lakes, upstream wetlands can increase the hydraulic residence time in downstream lakes (Fig. 5c) and thus result in more phosphorus being retained in lakes. Among these three effects, the effects of retaining phosphorus in wetlands and increasing the residence time in downstream lakes tend to reduce lake phosphorus concentration, whereas the mechanism of retaining water in wetlands tends to increase the lake phosphorus concentration.

Whether the overall effect of wetlands is to increase or decrease lake phosphorus concentration depends on the relative magnitude of the above three effects under the specific landscape setting of the lake catchment. Our flow-path attenuation model suggests that at the scale of a flow-path cell-series, the water reduction effect of wetland cells should exceed their phosphorus retention effect and thus predicts that the presence of wetland cells will result in higher phosphorus concentration at the end of the flow-path (Fig. 4b). Similar patterns have been found in field studies of wetlands (e.g., Kadlec and Bevis 1990; White and Bayley 2001). In our model, this effect of wetlands makes the phosphorus concentrations lower for most lakes in the simulated landscape with wetlands converted to forested land (Fig. 5d). However, in that simulation, there were a few lakes whose predicted phosphorus concentrations were higher than those in the unconverted landscape (Fig. 5d). The increased hydraulic residence time mentioned above may have offset the increase of phosphorus concentration in the wetland-related flow-paths in these cases. The specific landscape composition and configuration of the catchments may be another factor mediating wetland effects on downstream lake phosphorus concentrations. For example, Woltemade (2000) found that the performance of constructed wetlands that receive crop field drainage water varied considerably with the wetland size relative to the drainage area and the wetland location in the focal lake catchment. In addition, Prepas et al. (2001) found that in wetland-dominated catchments, lake phosphorus concentration was positively correlated with percent wetland cover in the catchment whereas in upland-dominated catchments there was no such relationship between percent wetland cover and lake phosphorus concentrations.

The complex effects of wetlands described above may help explain two paradoxes that exist in the literature. The first is the varied response of phosphorus concentrations within wetlands. High phosphorus concentrations usually have been found to decline within constructed treatment wetlands along the flow direction, but increased phosphorus concentrations have also been observed in some wetlands and in some seasons or for some phosphorus forms (e.g., Kadlec and Bevis 1990; White and Bayley 2001; Ontkean et al. 2003; Reinhardt et al. 2005). This inconsistency may be due to differences in inflow phosphorus concentrations between constructed treatment wetlands and natural headwater wetlands. When inflow phosphorus concentration of a wetland is very high, it is likely that the wetland's effect on phosphorus retention exceeds its effect on consuming water and thus makes the phosphorus concentration lower at the outlet of wetland. It is also possible that other factors such as internal loading may contribute to the increase of phosphorus concentration in some wetlands.

Second, although wetlands often remove phosphorus, the percent wetland in the catchment and lake phosphorus concentrations are sometimes paradoxically positively correlated (e.g., Detenbeck et al. 1993; Devito et al. 2000; Prepas et al. 2001; Zedler 2003; Verhoeven et al. 2006; Fergus et al.. 2011). In this study, we also observed a positive correlation between percent wetland and lake phosphorus concentrations (Zhang, unpublished data). This paradox may be partly explained by incorporating the effect of water retention in wetlands. Although wetlands are important phosphorus sinks and reduce a large amount of phosphorus loading for their downstream lakes, our results imply that their net effect on downstream lake phosphorus concentrations is more complex due to their effects on water flow as well. Understanding the implications of wetlands on downstream lake phosphorus concentration requires detailed landscape and hydrological information about the catchments of individual wetland units (Tompkins et al. 1997).

Advantages and limitations of our modeling approach

Although our model results and simulations have shown some complex effects of upstream lakes and wetlands on downstream lake phosphorus concentrations, the true effects of these freshwater systems are much more complex than described above. Our simulation approaches are highly-simplified and do not model the actual processes occurring in these complex ecosystems. For example, we adopted coarse LULC types to ensure the feasibility of calibration with our limited sample size. For the same reason, we did not distinguish among different wetland types which may have different hydrological and biochemical functions in nutrient loading. We assumed that phosphorus export and water yield were both linearly correlated with precipitation. In addition, we were not able to include a wide range of factors that could potentially affect the production and transportation of phosphorus and water, such as catchment slope, soil, vegetation, livestock, geology, and groundwater characteristics. The lake phosphorus retention module (Vollenweider model) was also a highly-simplified model that does not consider many specific factors in lake phosphorus dynamics (such as wind, temperature, and lake profile). All of these limitations affect the performance of our models and contribute to the moderate predicative power we attained. Finally, because there are no measurement of phosphorus loads and lake inflow, we had to simultaneously fit the three modules (phosphorus loading to lakes, water inflow to lakes, and lake phosphorus retention). Thus, there was no chance to evaluate the performance of the modules individually.

Despite the limitations mentioned above, our flow-path attenuation model can be used to provide insights into the spatially-explicit modeling of nonpoint source pollution to lakes. This model is located at an intermediate level of complexity between simple regression models and complex process-based models, and we show that the effects of upstream lakes and wetlands are fairly complex but potentially predictable, and should be studied further. When exploring the relationship between catchment LULC characteristics and nutrient loading in waterbodies, such models may prove to be useful prior to engaging in exhaustive, process-based modeling (Baker et al. 2006).

Empirical modeling has been found to be a useful method to study the roles of landscape composition and configuration patterns in nonpoint source nutrient loading (e.g., Johnson et al. 2001; Jones et al. 2001; Smith et al. 2003b; Weller et al. 2003; Cifaldi et al. 2004; Soranno et al. 2008; Gémesi et al. 2011; Fergus et al. 2011). However, consideration of more theoretical simulation-type models such as ours has the potential to serve as another way to study the importance of spatial configuration and composition on ecosystem processes such as nutrient dynamics (e.g., Levine 1992; Hunsaker and Levine 1995; Soranno et al. 1996; Weller et al. 1998; Giasson et al. 2002; Canham et al. 2004; Gergel 2005; Zhang 2011). These studies on landscape-scale nutrient dynamics have shed light on the possibility of exploring and testing the relationships among specific landscape metrics and nutrient loading through simulations of simple theoretical models. Coupling the two approaches should further our understanding about these relationships. On one hand, patterns observed in model simulation results can facilitate the design of new landscape metrics that can be applied broadly. On the other hand, the landscape metrics that have been identified to govern nutrient loading in an empirical study can be further verified in models such as ours by comparing their roles on nutrient loading in different simulated scenarios.

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References

Abu-Zreig M, Rudra RP, Whiteley HR, Lalonde MN, Kaushik NK (2003) Phosphorus removal in vegetated filter strips. J Environ Qual 32:613–619

Ahlgren I, Frisk T, Kamp-Nielsen L (1988) Empirical and theoretical models of phosphorus loading, retention and concentration vs. lake trophic state. Hydrobiologia 170:285–303

Alexander RB, Elliott AH, Shankar U, McBride GB (2002) Estimating the sources and transport of nutrients in the Waikato River Basin, New Zealand. Water Resour Res 38:1268. doi:10.1029/2001WR000878

Baker LA (1992) Introduction to nonpoint source pollution in the United States and propects for wetland use. Ecol Eng 1:1–26

Baker ME, Weller DE, Jordan TE (2006) Improved methods for quantifying potential nutrient interception by riparian buffers. Landscape Ecol 21:1327–1345

Beckert KA, Fisher TR, O'Neil JM, Jesien RV (2011) Characterization and comparison of stream nutrients, land use, and loading patterns in Maryland coastal bay watersheds. Water Air Soil Pollut 221:255–273

Bedford BL, Walbridge MR, Aldous A (1999) Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–2169

Borah DK, Bera M (2003) Watershed-scale hydrologic and nonpoint-source pollution models: review of mathematical bases. Trans ASAE 46:1553–1566

Borah DK, Bera M (2004) Watershed-scale hydrologic and nonpoint-source pollution models: review of applications. Trans ASAE 47:789–803

Bouraoui F (1994) *Development of a continuous, physically-based, distributed parameter, nonpoint source model*. Virginia Polytechnic Institute and State University, Dissertation

Bowden WB (1987) The biogeochemistry of nitrogen in freshwater wetlands. Biogeochemistry 4:313–348

Brett MT, Benjamin MM (2008) A review and reassessment of lake phosphorus retention and the nutrient loading concept. Freshw Biol 53:194–211

Brett MT, Arhonditsis GB, Mueller SE, Hartley DM, Frodge JD, Funke DE (2005) Non-point-source impacts on stream nutrient concentrations along a forest to urban gradient. Environ Manage 35:330–342

Breuer L, Vaché KB, Julich S, Frede H-G (2008) Current concepts in nitrogen dynamics for mesoscale catchments. Hydrol Sci J 53:1059–1074

Bryhn AC, Håkanson L (2007) A comparison of predictive phosphorus load-concentration models for lakes. Ecosystems 10:1084–1099

Canham CD, Pace ML, Papaik MJ, Primack AGB, Roy KM, Maranger RJ, Curran RP, Spada DM (2004) A spatially-explicit watershed-scale analysis of dissolved organic carbon in Adirondack lakes. Ecol Appl 14:839–854

Cifaldi RL, Allan JD, Duh JD, Brown DG (2004) Spatial patterns in land cover of exurbanizing watersheds in southeastern Michigan. Landsc Urban Plan 66:107–123

Detenbeck NE, Johnston CA, Niemi GJ (1993) Wetland effects on lake water quality in the Minneapolis/St. Paul metropolitan area. Landscape Ecol 8:39–61

Detenbeck NE, Taylor DL, Lima A, Hagley C (1996) Temporal and spatial variability in water quality of wetlands in the Minneapolis/St. Paul, MN metropolitan area: implications for monitoring strategies and designs. Environ Monit Assess 40:11–40

Devito KJ (1997) Flow reversals in peatlands influenced by local groundwater systems. Hydrol Process 11:103–110

Devito KJ, Creed IF, Rothwell RL, Prepas EE (2000) Landscape controls on phosphorus loading to boreal lakes: implications for the potential impacts of forest harvesting. Can J Fish Aquat Sci 57:1977–1984

Diebel MW, Maxted JT, Robertson DM, Han S, Vander Zanden MJ (2009) Landscape planning for agricultural nonpoint source pollution reduction III: assessing phosphorus and sediment reduction potential. Environ Manage 43:69–83

Fergus CE, Soranno PA, Spence Cheruvelil K, Bremigan MT (2011) Multiscale landscape and wetland drivers of lake total phosphorus and color. Limnol Oceanogr 56: 2127–2146

Fisher J, Acreman MC (2004) Wetland nutrient removal: a review of the evidence. Hydrol Earth Syst Sci 8:673–685

Fuller LM, Minnerick RJ (2008) State and regional water quality characteristics and trophic conditions of MI's inland lakes, 2001–2005. Scientific Investigations Report 2008–5188, U.S. Geological Survey

Gémesi Z, Downing JA, Cruse RM, Anderson PF (2011) Effects of watershed configuration and composition on downstream lake water quality. J Environ Qual 40:517–527

Gergel SE (2005) Spatial and non-spatial factors: when do they affect landscape indicators of watershed loading? Landscape Ecol 20:177–189

Giasson E, Bryant RB, DeGloria SD (2002) GIS-based spatial indices for identification of potential phosphorous export at watershed scale. J Soil Water Conserv 57:373–381

Goodman KJ, Baker MA, Wurtsbaugh WA (2010) Mountain lakes increase organic matter decomposition rates in streams. J N Am Benthol Soc 29:521–529

Grayson RB, Moore ID, McMahon TA (1992) Physically based hydrologic modeling: 2. Is the concept realistic? Water Resour Res 26:2659–2666

Hunsaker CT, Levine DA (1995) Hierarchical approaches to the study of water quality in rivers. Bioscience 45:193–203

Imboden DM (1974) Phosphorus model of lake eutrophication. Limnol Oceanogr 19:297–304

Johnson GD, Myers WL, Patil GP (2001) Predictability of surface water pollution loading in Pennsylvania using watershed-based landscape measurements. J Am Water Resour Assoc 37:821–835

Johnston CA (1991) Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. Crit Rev Environ Sci Technol 21:491–565

Jones KB, Neale AC, Nash MS, Van Remortel RD, Wickham JD, Riitters KH, O'Neill RV (2001) Predicting nutrient and sediment loadings to streams from landscape metrics: a multiple watershed study from the United States Mid-Atlantic Region. Landscape Ecol 16:301–312

Kadlec RH, Bevis FB (1990) Wetlands and wastewater: Kinross, Michigan. Wetlands 10:77–92

Kirkpatrick S, Gelatt CD Jr, Vecchi MP (1983) Optimization by simulated annealing. Science 220:671–680
Levine DA (1992) A geographic information system approach to modeling nutrient and sediment transport. Indiana University, Bloomington, Indiana, PhD dissertation
Malmaeus JM, Blenckner T, Markensten H, Persson I (2006) Lake phosphorus dynamics and climate warming: a mechanistic model approach. Ecol Model 190:1–14
Marcarelli AM, Wurtsbaugh WA (2007) Effects of upstream lakes and nutrient limitation on periphytic biomass and nitrogen fixation in oligotrophic, subalpine streams. Freshw Biol 52:2211–2225
Moriasi DN, Arnold JG, Van Liew MW, Bingner RL, Harmel RD, Veith TL (2007) Model evaluation guidelines for systematic quantification of accuracy in watershed simulations. Trans ASABE 50:885–900
Neff BP, Day SM, Piggott AR, Fuller LM (2005) Base flow in the Great Lakes Basin. Scientific Investigations Report 2005–5217, U.S. Geological Survey
Ontkean GR, Chanasyk DS, Riemersma S, Bennett DR, Brunen JM (2003) Enhanced prairie wetland effects on surface water quality in Crowfoot Creek, Alberta. Water Qual Res J Can 38:335–359
Powers SM, Johnson RA, Stanley EH (2012) Nutrient retention and the problem of hydrologic disconnection in streams and wetlands. Ecosystems. doi:10.1007/s10021-012-9520-8
Prairie YT, Kalff J (1986) Effect of catchment size on phosphorus export. Water Resour Bull 22:465–470
Prepas EE, Planas D, Gibson JJ, Vitt DH, Prowse TD, Dinsmore WP, Halsey LA, McEachern PM, Paquet S, Scrimgeour GJ, Tonn WM, Paszkowski CA, Wolfstein K (2001) Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments. Can J Fish Aquat Sci 58:1286–1299
Reckhow KH, Chapra SC (1983) Engineering approaches for lake management, volume 1: data analysis and empirical modeling. Butterworth Publisher, Boston
Reddy KR, DeLaune RD (2008) Biogeochemistry of wetlands: science and applications, chapter 3: biogeochemical characteristics. CRC Press, Boca Raton, pp 27–65
Reddy KR, Kadlec RH, Flaig E, Gale PM (1999) Phosphorus retention in streams and wetlands: a review. Crit Rev Environ Sci Technol 29:83–146
Reinhardt M, Gächter R, Wehrli B, Müller B (2005) Phosphorus retention in small constructed wetlands treating agricultural drainage water. J Environ Qual 34:1251–1259
Sivapalan M (2003) Prediction in ungauged basins: a grand challenge for theoretical hydrology. Hydrol Process 17: 3163–3170
Smerdon BD, Mendoza CA, Devito KJ (2007) Simulations of fully coupled lake-groundwater exchange in a subhumid climate with an integrated hydrologic model. Water Resour Res 43:W01416. doi:10.1029/2006WR005137
Smith RA, Alexander RB, Schwarz GE (2003a) Natural background concentrations of nutrients in streams and rivers of the conterminous United States. Environ Sci Technol 37: 3039–3047
Smith SV, Swaney DP, Talaue-Mcmanus L, Bartley JD, Sandhei PT, McLaughlin CJ, Dupra VC, Crossland CJ, Buddemeier RW, Maxwell BA, Wulff F (2003b) Humans, hydrology, and the distribution of inorganic nutrient loading to the ocean. Bioscience 53:235–245
Snelder TH, Biggs BJF (2002) Multiscale river environment classification for water resources management. J Am Water Resour Assoc 38:1225–1239
Soranno PA, Hubler SL, Carpenter SR, Lathrop RC (1996) Phosphorus loads to surface waters: a simple model to account for spatial pattern of land use. Ecol Appl 6:865–878
Soranno PA, Spence Cheruvelil K, Stevenson RJ, Rollins SL, Holden SW, Heaton S, Torng EK (2008) A framework for developing ecosystem-specific nutrient criteria: integrating biological thresholds with predictive modeling. Limnol Oceanogr 53:773–787
Soranno PA, Spence Cheruvelil K, Webster KE, Bremigan MT, Wagner T, Stow CA (2010) Using landscape limnology to classify freshwater ecosystems for multi-ecosystem management and conservation. Bioscience 60:440–454
Taylor CH, Pierson DC (1985) The effect of a small wetland on runoff response during spring snowmelt. Atmos Ocean 23:137–154
Tompkins TM, Whipps WW, Manor LJ, Wiley MJ, Radcliffe CW, Majewski DM (1997) Wetland effects on hydrological and water quality characteristics of a mid-Michigan river system. In: Trettin CC, Jurgensen MF, Grigal DF, Gale MR, Jeglum JK (eds) Northern forested wetlands: ecology and management. CRC Press, Boca Raton, pp 273–285
Vanni MJ, Renwick WH, Headworth JL, Auch JD, Schaus MH (2001) Dissolved and particulate nutrient flux from three adjacent agricultural watersheds: a five-year study. Biogeochemistry 54:85–114
Verhoeven JTA, Arheimer B, Yin C, Hefting MM (2006) Regional and global concerns over wetlands and water quality. Trends Ecol Evol 21:96–103
Vollenweider RA (1976) Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Istituto Italiano di Idrobiologia 33:53–83
Wang Y, Choi W (2005) Long-term impacts of land-use change on non-point source pollutant loads for the St. Louis metropolitan area, USA. Environ Manage 35:194–205
Weller DE, Jordan TE, Correll DL (1998) Heuristic models for material discharge from landscapes with riparian buffers. Ecol Appl 8:1156–1169
Weller DE, Jordan TE, Correll DL, Liu Z (2003) Effects of land-use change on nutrient discharges from the Patuxent River Watershed. Estuaries 26:244–266
White JS, Bayley SE (2001) Nutrient retention in a northern prairie marsh (Frank Lake, Alberta) receiving municipal and agro-industrial wastewater. Water Air Soil Pollut 126:63–81
Winter TC (1999) Relation of streams, lakes, and wetlands to groundwater flow systems. Hydrogeol J 7:28–45
Woltemade CJ (2000) Ability of restored wetlands to reduce nitrogen and phosphorus concentrations in agricultural drainage water. J Soil Water Conserv 55:303–309
Zedler JB (2003) Wetlands at your service: reducing impacts of agriculture at the watershed scale. Front Ecol Environ 1:65–72
Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. Ann Rev Environ Resour 30:39–74
Zhang T (2011) Distance-decay patterns of nutrient loading at watershed scale: regression modeling with a special spatial aggregation strategy. J Hydrol 402:239–249