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Multiscale landscape and wetland drivers of lake total phosphorus and water color

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Abstract

We quantified relationships between local wetland cover in the riparian lake buffer and lake total phosphorus (TP) and water color (color) using multilevel mixed-effects models that also incorporate landscape features such as hydrogeomorphology and land use at broad regional scales to determine the following: (1) Within regions, are local wetland relationships with TP and color affected by interactions with local land use or hydrogeomorphic variables? (2) Across regions, are local wetland relationships with TP and color different? And if so, (3) Are differences in local wetland relationships with TP and color a result of cross-scale interactions? We answered these questions by analyzing TP, color, and multiscaled landscape data for 1790 north temperate lakes. Local wetland–TP and wetland–color relationships were not affected by local-scale interactions. However, these same relationships were different when compared across regions, and these differences were related to cross-scale interactions with regional landscape characteristics. For example, regional human land use affected local wetland–TP relationships such that in regions with high amounts of agriculture, local wetlands were associated with decreased lake TP. However, in regions with low amounts of agriculture, local wetlands were associated with increased lake TP. In contrast, regional hydrogeomorphic characteristics influenced local wetland–color relationships such that in regions with high groundwater contribution, the strength of local wetland relationships were weak. Regional landscape setting influences local wetland relationships with TP and color through cross-scale interactions, and lake TP and color are controlled by both local-scale wetland extent and regional-scale landscape variables.

Lake water chemistry is affected by lake morphometry and landscape features in the surrounding catchment. In particular, total phosphorus (TP) and dissolved organic carbon (DOC) are related to hydrogeomorphic (HGM) variables including lake and catchment morphometry and natural land cover (Rasmussen et al. 1989; D'Arcy and Carignan 1997; Prepas et al. 2001). Because lake TP and DOC are positively correlated to one another (Detenbeck et al. 1993; Dillon and Molot 1997), they may be controlled by similar landscape features. For example, both lake TP and DOC are negatively correlated to lake depth (Rasmussen et al. 1989; Webster et al. 2008) and positively correlated to drainage ratio (the catchment area : lake area ratio [Prepas et al. 2001; Mullholland 2003]). However, few studies have examined and compared landscape controls of lake TP and DOC together (but *see* Webster et al. 2008). Because both TP and DOC are important predictors of lake productivity or trophic status (Williamson et al. 1999), it is important to understand their underlying heterogeneity.

Many studies relate lake water chemistry to landscape variables quantified at the lake catchment scale, ignoring the portions of the landscape that fall outside the catchment lines. However, nutrient and material transport between terrestrial and aquatic systems likely operate at multiple spatial scales (Gergel et al. 1999; Sliva and Williams 2001). It has been suggested that catchment boundaries may not capture important regional-scale processes that affect lake water chemistry, such as groundwater flow (Devito et al. 2005). In addition, studies have shown that lake TP and DOC exhibit regional variation, and that broad-scale variables such as elevation and climate may explain these regional patterns (D'Arcy and Carignan 1997; Xenopoulos et al. 2003; Sobek et al. 2007). Together these studies indicate that features of the regional landscape may be important drivers of lake water chemistry. However, few comparative studies have been performed across multiple geographic regions that attempt to explain the regional differences, and few studies have quantified landscape variables at the regional scale. These limitations have restricted our ability to integrate and apply findings from studies conducted at the catchment scale to regional scales.

Cross-scale interactions, defined as ecological processes operating at one spatial scale interacting with processes at another spatial scale (Peters et al. 2007), can lead to unexpected relationships between ecosystem variables across different geographic regions. Traditional hierarchy theory suggests that broad-scale processes act uniformly on ecological response variables. However, processes at different scales may interact (i.e., cross-scale interactions) and result in context-specific patterns (Peters et al. 2007). There is great potential for cross-scale interactions affecting freshwater ecosystems, but they have rarely been quantified (but *see* Qian et al. 2010). This gap may be attributed to the challenge of gathering data for lakes distributed across different regions and quantifying landscape characteristics at multiple spatial scales.

Possible candidates for cross-scale interactions involve the effects of wetlands on lake chemistry. Wetlands are considered to be influential landscape modifiers of lake and stream water chemistry (Johnston et al. 1990; Mitsch and

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Gosselink 2007), and are typically quantified at the catchment or riparian spatial scale (i.e., the local scale). But, wetland effects on surface-water chemistry are not always consistent from region to region, suggesting that these relationships may be influenced by cross-scale interactions. For example, a cross-scale interaction could exist between wetlands quantified at the local scale and regional hydrology, such that local wetlands affect lake chemistry differently in regions with different hydrologic characteristics. This cross-scale interaction means that wetland–lake chemistry relationships would be substantially different for lakes with the same proportion of wetlands in the local catchment but with different regional hydrology. Specifically, there is evidence of large regional differences in wetland effects on both lake TP and DOC. Wetland relationships with lake TP show both positive and negative correlations across studies (Detenbeck et al. 1993; Devito et al. 2000; Diebel et al. 2009). In contrast, wetlands are typically positively correlated with lake DOC and water color (the humic colored portion of DOC) for lakes in a wide range of regional settings (Gergel et al. 1999; Canham et al. 2004). However, the magnitude of the wetland–lake-DOC relationships is variable across geographic regions (Xenopoulos et al. 2003). Thus, wetland–lake-water chemistry relationships may be better understood by quantitatively accounting for the regional setting and the potential of cross-scale interactions.

Wetlands can be found in diverse regional HGM and human land-use settings, and these different settings may affect wetland relationships with surface-water chemistry (Cole et al. 2002). For lake TP in north temperate regions with moderate to high agriculture and urban land use, wetland extent in a lake or stream catchment has been associated with decreased TP concentrations (Detenbeck et al. 1993; Weller et al. 1996; Diebel et al. 2009). Wetlands in these disturbed catchments may act as nutrient modifiers by intercepting some of the excess phosphorus from agriculture and urban activities and water flow from receiving surface waters (Moustafa 1999). However, in regions with low human land use, wetland extent in a catchment has been associated with increased lake TP concentrations, suggesting that these wetlands are sources of phosphorus to lakes (Dillon and Molot 1997; Devito et al. 2000). For lake DOC, differences in the regional HGM setting, as opposed to land use, may account for differences in wetland relationships with DOC. Because hydrologic features such as runoff and groundwater contribution are related to lake DOC (Jordan et al. 1997; Canham et al. 2004), regional amounts of these features may constrain wetland–DOC relationships. Therefore, wetlands could interact with regional land use and hydrology to affect lake TP and DOC.

One obstacle to assessing multiscaled landscape effects on surface-water chemistry is the limitation of traditional statistical approaches. Classical regression models are often inappropriate for regional analyses because they either pool observations across regions (i.e., ignore regional variation) and violate assumptions of statistical independence or separate observations into regional groups that can lead to inflated variance estimates within each region (Gelman and Hill 2007). Although classical regression approaches are appropriate when regional variation is not significant, in many cases these approaches do not account for significant sources of hierarchical–spatial variance. Statistical approaches such as multilevel mixed-effects models can account for multiscaled drivers of lake chemistry by modeling variation in chemistry attributed to features at both the catchment (i.e., local) and ecoregion (i.e., regional) scales. Mixed-effects models have not been widely used in freshwater land-use and land-cover studies (but *see* Taranu and Gregory-Eaves 2008), but are highly relevant to the hierarchical structure of freshwater ecosystems and ecological processes (Wagner et al. 2006).

In our study, we used multilevel mixed-effect models to examine local wetland relationships with lake TP and color that explicitly considered both local and regional HGM and human land-use variables. Our specific research questions were as follows: (1) Within regions, are local wetland relationships with lake TP and water color affected by local interactions? (2) Across regions, are local wetland relationships with lake TP and water color different? And if so, (3) Are differences in local wetland relationships with lake TP and water color related to cross-scale interactions? To address these questions, we compiled lake-water chemistry and landscape data for lakes distributed across 23 regions in four states in the United States of America: Maine, New Hampshire, Michigan, and Wisconsin. We took an information theoretic approach to answer our research questions by comparing and ranking six candidate models based on hypothesized mechanisms from the literature. These candidate models tested specific hypotheses about how local wetlands and local and regional landscape-context variables, both independently (i.e., direct effects) and together (i.e., cross-scale interactions), influence lake TP and color (Table 1).

Methods

Study lakes and lake data—We compiled existing landscape, hydrologic, and lake-water chemistry data for 1790 lakes in Maine (ME), New Hampshire (NH), Michigan (MI), and Wisconsin (WI; Fig. 1). These data were collected and obtained from state agencies that sampled the lakes as part of state water-quality monitoring programs. We included lakes with surface area > 0.01 km^2 and maximum depths > 2 m. *See* Webster et al. (2008) for a complete description of the compiled database. Although a large portion of the data set overlaps with a data set used in Webster et al. (2008), the research questions and analyses described in this paper are entirely different. In this paper, we quantified HGM and land use and land cover variables at the regional spatial scale to model relationships between wetlands and TP and color using multiscaled landscape variables and quantify cross-scale interactions to understand regional patterns in lake TP and color. In contrast, the analysis in Webster et al. focused on lake and local–landscape relationships with lake TP and color. For this study, we analyzed two lake data sets. The first data set includes all 1790 lakes that have TP data (*see* below). The second data set is a subset of this TP data set that includes

Table 1. Candidate models (1a, 1b, 1c, 2, 3a, 3b) to test hypothesized relationships between local and regional landscape variables, with total phosphorous (TP) and color analyzed at each individual scale and for cross-scale interaction. Landscape variables were grouped into prediction type classes: hydrogeomorphic variables (HGM), wetlands (WET), human land use (LU), local wetland and human land use interactive effects ($WET_L \times LU_L$), random local wetland effects across regions ($WET_{L\ Random}$), and cross-scale interactive effects ($WET_L \times X_R$). Variables excluded from the models are denoted by '—'. Positive relationships (pos.), negative relationships (neg.), and nonsignificant relationships (ns) between landscape variables and TP and color are noted. Variables with the same hypothesized relationship as the previous model are symbolized by '*'. Regional landscape-context variables are italicized.

	Scale of predictor variables:	Local			Local and regional		
	Scale of interaction:			Local			Regional
Lake response	Landscape-context variable	1a. HGM_L + WET_L	1b. HGM_L + WET_L + LU_L	1c. HGM_L + WET_L + LU_L ($WET_L \times LU_L$)	2. Top local + $WET_{L\ Random}$	3a. Top local + regional + $WET_{L\ Random}$	3b. Top local + regional + $WET_{L\ Random}$ ($WET_L \times X_R$)
TP	Lake depth	neg.[1]	*	*	*	*	*
	Drainage ratio	pos.[2]	*	*	*	*	*
	Baseflow	neg.[3]	*	*	*	*	*
	Wetland	ns[3,4]	*	*	*	*	*
	Agriculture	—	pos.[4]	*	*	*	*
	Urban	—	pos.[5]	*	*	*	*
	$WET_L \times LU_L$	—	—	neg. interact.[4]	*	*	*
	$WET_{L\ Random}$	—	—	—	random	*	*
	Agriculture$_{Regional}$	—	—	—	—	*pos.*	*
	Agriculture$_R \times WET_L$	—	—	—	—	—	*neg. interact.*
Color	Lake depth	neg.[6]	*	*	*	*	*
	Drainage ratio	pos.[7]	*	*	*	*	*
	Baseflow	neg.[8]	*	*	*	*	*
	Wetland	pos.[6]	*	*	*	*	*
	Agriculture	—	ns[9]	*	—	—	—
	Urban	—	—	ns	—	—	—
	$WET_L \times Baseflow_L$	—	—	neg. interact.	—	—	—
	$WET_{L\ Random}$	—	—	—	random[10]	*	*
	Baseflow$_{Regional}$	—	—	—	—	*neg.*	*
	Baseflow$_R \times WET_L$	—	—	—	—	—	*neg. interact.*

[1] Canfield and Bachmann 1981.
[2] Prepas et al. 2001.
[3] Devito et al. 2000.
[4] Detenbeck et al. 1993.
[5] Soranno et al. 1996.
[6] Rasmussen et al. 1989.
[7] D'Arcy and Carignan 1997.
[8] Jordan et al. 1997.
[9] Wilson and Xenopoulos 2008.
[10] Xenopoulos et al. 2003.

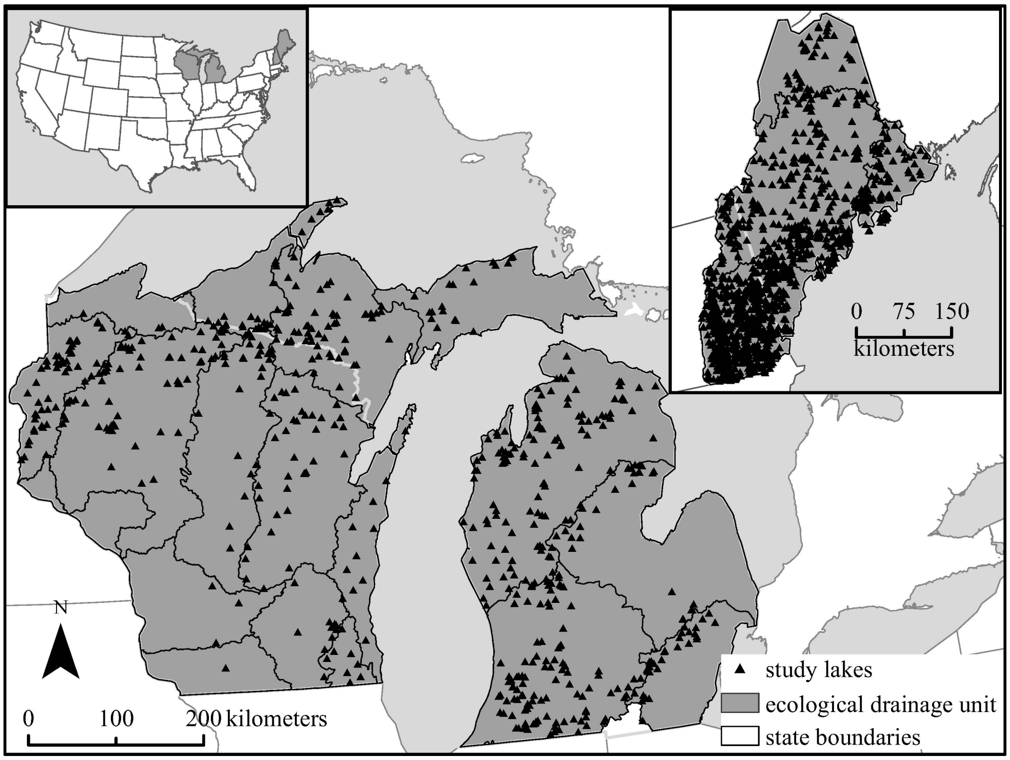

Fig. 1. Study lakes (n = 1790) within the 23 regions (Ecological Drainage Units).

the lakes for which we have color data (n = 1527 lakes). The data set is available in the Dryad Repository: doi:10.5061/dryad.4v2m5.

State agencies collected the majority of water chemistry measurements during 1990–2003, and they followed standardized field and laboratory procedures. These procedures included colorimetric analyses with persulfate digestion for TP and visual comparators in platinum cobalt units for water color. Lakes had either true color estimates, measured from filtered samples, or apparent color estimates (unfiltered). To correct for the positive bias attributed to apparent color measures, Webster et al. (2008) developed a regression equation to convert apparent color to true color (R^2_{adj} = 0.96, eq. $\text{Color}_{\text{True}} = 0.827 \times \text{Color}_{\text{Apparent}}$). We restricted water chemistry measurements to single samples collected from the epilimnion from June–September when summer stratification was likely to occur. The study lakes captured a wide range of TP and color, although in general, the lakes tended toward oligotrophic (Tables 2, 3).

All of the geographic data for measuring HGM, wetlands, and land use around lakes came from national geographic information systems (GIS) databases so that all data would be standardized across states. HGM variables in the models were: lake depth, lake drainage ratio, and baseflow. We compiled measures of lake depth (maximum and mean) and total catchment area from state databases. We quantified lake surface area using state GIS data at 1 : 24,000 resolution. We calculated lake drainage ratio by dividing the catchment area by lake surface area, which is a morphometric measure related to water residence time and allochthonous sources of material to recipient waters. We quantified baseflow, the proportion of streamflow from groundwater discharge, using a baseflow raster coverage developed by the United States Geological Survey (USGS) for the conterminous United States that interpolated baseflow index point values estimated from available stream gage data across the United States. (Wolock 2003). We quantified baseflow for each lake as the average baseflow value for each cell within the local and regional extents.

We obtained land use and land cover (LULC) and wetland data from the 1992 National Land Cover Dataset (NLCD; http://landcover.usgs.gov/natllandcover.php). We chose the 1992 LULC data for our analyses because (1) it is close to the median year (1989) of lake sampling in our data set, (2) LULC data were not available for each year lakes were sampled, and (3) it is unclear which time period is best to measure land use effects on lakes. Thus, we assume that LULC measured during 1992 will be strongly correlated to LULC within a 15-yr time span around 1992. We defined two human land-use variables as agriculture (including both pasture and row cropping) and urban land uses. Although there are other human disturbances that affect lakes, we use agriculture and urban land uses as indicators of many of the major human effects that influence water chemistry (Morrice et al. 2007).

With the exception of lake depth and drainage ratio, we quantified all of the landscape-context variables at two spatial scales: local and regional. Local landscape variables in this paper were quantified within a 500-m buffer surrounding lakes. Although using the 500-m buffer is likely not as effective as using lake catchments to quantify landscape variables, true lake catchments have not been

Table 2. Summary statistics of local and regional landscape variables used to predict total phosphorous (TP; $n = 1790$ lakes, $N = 23$ regions). HGM is hydrogeomorphic variables, WET is wetland cover, and LU is human land use. Regional variables are italicized.

			TP data set		
Prediction type	Scale	Variable	Median	SD	Range
LAKE		TP (μg L^{-1})	11	14	1–193
		Color (PtCo)	14	19	1–140
HGM	Local	Catchment area (km^2)	7	192	0.09–1974
		Lake area (km^2)	0.5	7	0.01–180
		Drainage ratio	13	191	1–2800
		Mean depth (m)	4	3	0.3–26
		Max. depth (m)	10	9	2–68
		% Baseflow	54	10	34–89
		% Forest	78	22	4–100
WET		% Wetland	3	9	0–66
LU		% Agriculture	4	17	0–90
		% Urban	1	0.9	0–93
HGM	Regional	*Regional area (km^2)*	15,250	11,524	2830–48,950
		% Baseflow	53	8	46–78
		% Forest	76	20	9–86
WET		*% Wetland*	3	6	1–35
LU		*% Agriculture*	7	19	1–78
		% Urban	2	3	0–20

delineated for the majority of the United States, as it has been for stream catchments, and it is very difficult to do so. The 500-m buffer is used as an indicator of the catchment values of land use. For example, correlation analyses using a subset of our study lakes (461 lakes in MI) showed that LULC proportions in the 500-m lake buffer were correlated (% agriculture, $r = 0.79$; % forest cover, $r = 0.86$; and % wetland cover, $r = 0.64$) with LULC proportions in the lake catchment, which was defined as the area of land that includes streams that drain into the lake (P. Soranno unpubl.). In addition, wetlands quantified in the riparian buffers around several WI lakes were as good a predictor of lake DOC as wetlands quantified for the whole catchments (Gergel et al. 1999). Therefore, this cost-effective method to obtain data for broad geographic areas can capture ecologically relevant features at the local scale that are related to lake nutrient and carbon dynamics. Although using the 500-m buffer to approximate catchment-scale estimates of landscape variables should produce conservative relationships (i.e., quantifying LULC at the lake catchment scale would likely yield stronger relationships between local wetlands and lake-water chemistry vari-

Table 3. Summary statistics of local and regional landscape-context variables used to predict color ($n = 1527$ lakes, $N = 21$ regions). TP is total phosphorous, HGM is hydrogeomorphic variables, WET is wetland cover, and LU is human land use. Regional variables are italicized.

			Color data set		
Prediction type	Scale	Variable	Median	SD	Range
LAKE		TP (μg L^{-1})	10	11	1–155
		Color (PtCo)	14	19	1–140
HGM	Local	Catchment area (km^2)	7	195	0.9–197
		Lake area (km^2)	0.5	7	1–180
		Drainage ratio	14	200	1–2800
		Mean depth (m)	4	3	1–26
		Max. depth (m)	9	9	2–68
		% Baseflow	53	10	36–89
		% Forest	80	21	4–100
WET		% Wetland	3	9	0–66
LU		% Agriculture	4	15	0–88
		% Urban	4	9	0–93
HGM	Regional	*Regional area (km^2)*	15,250	12,020	2830–48,950
		% Baseflow	55	8	46–78
		% Forest	70	18	9–86
WET		*% Wetland*	6	6	2–35
LU		*% Agriculture*	13	17	1–78
		% Urban	3	3	0–20

ables), future research should explore the use of other landscape metrics and the development of national lake-catchment coverages. We tested a suite of wetland vegetation classes to determine the best single wetland vegetation class for the analyses. We explored univariate relationships between local wetlands and TP and color for three wetland vegetation classes that were based on NLCD classification: forested, emergent, and total wetlands. We found that forested wetlands had the strongest relationship with both TP and color. In addition forested wetland extent was highly correlated with total wetland extent ($r = 0.97$); therefore, we included only forested wetlands in the model-building procedure.

Regional landscape variables in this paper were quantified within Ecological Drainage Units (EDU; Higgins et al. 2005). EDUs are part of a hierarchical ecoregion framework that was developed to classify freshwater ecosystems for aquatic biodiversity conservation using landscape features, such as climate and landform. The Nature Conservancy delineated EDU boundaries by grouping eight-digit USGS Hydrologic Unit watersheds that share common physiographic and climatic characteristics (Higgins et al. 2005). We chose this framework because it has been shown to capture more variation in lake-water chemistry variables, on average, than other ecoregion frameworks (Cheruvelil et al. 2008). For the TP data set, there were 23 EDUs within our study area, containing (on average) 78 lakes per EDU (range from 1 lake to 542 lakes per region). For the color data set, there were 21 EDUs, containing (on average) 73 lakes per EDU (range from 1 lake to 528 lakes per region). For each EDU, we quantified the proportion of agricultural land, urban land, forested wetlands, and baseflow.

Both lake and landscape features were very diverse in our study area (Tables 2, 3). For example, at the local scale, agricultural land use surrounding lakes ranged from 0% to 93%, although most of the lakes were dominated by forest cover (median 78%) with low agricultural (median 4%) and urban (median 1%) land use. In addition, the EDUs were composed of diverse climatic, hydrologic, and landscape characteristics. Regional agriculture and urban land use ranged from 1% to 78% and 0% to 20%, respectively. Hydrogeomorphic characteristics varied among EDUs, with regional baseflow ranging from 46% to 78% and regional wetland cover ranging from 1% to 35%. Several regional variables were highly correlated to one another and, thus, we included only agriculture and baseflow as the regional variables for the candidate models (Table 4).

Statistical analyses—We developed six candidate models based on hypothesized relationships between multiscaled landscape variables and lake TP and color (Table 1). These models were developed to quantify the local and regional drivers of lake TP and color across broad geographical regions, to identify underlying relationships to infer possible ecological mechanisms, but not to predict TP and color. We quantified and compared the supporting evidence for each candidate model to provide insight into the multiscaled landscape drivers of lake water chemistry.

Table 4. Correlations between the proportions of regional landscape variables ($N = 23$ regions). All correlations were significant ($\alpha < 0.05$).

	Baseflow	Wetland	Forest	Agriculture	Urban
Baseflow	1	—	—	—	—
Wetland	0.71	1	—	—	—
Forest	−0.51	−0.42	1	—	—
Agriculture	0.35	0.16	−0.94	1	—
Urban	−0.22	−0.40	−0.15	0.18	1

We addressed our first research question with candidate Models 1a, 1b, and 1c, which included direct effects and interactions between wetlands and human land use or baseflow at the local scale. We tested our second research question with Model 2, which allowed for local wetland relationships with lake TP or water color to vary among regions. We addressed our third and final question with Models 3a and 3b, which included regional variables and cross-scale interactions between local wetlands and regional agriculture or baseflow to determine whether regional-scale features could explain regional differences in wetland–lake chemistry relationships.

To meet statistical assumptions of normality, we natural-log–transformed lake TP and color and lake and catchment morphometry variables, and we arcsine-square-root–transformed LULC proportions. Local predictor variables were group-mean centered $(X_{ij} - X_{.j})$ by subtracting the mean EDU value from individual observations within that EDU to control for among-region differences and reduce correlations with regional predictors (Enders and Tofighi 2007). Regional variables were grand-mean–centered by subtracting the overall mean value from each individual observation $(X_{ij} - \bar{X}_{..})$ to reduce correlations between intercept estimates across regions. Multilevel mixed-effects analyses were performed using Statistical Analysis Software mixed linear procedure (SAS MIXED), version 9.2 of the SAS System for Windows (Copyright© 2002–2008 by SAS Institute). The SAS codes for the analyses used in this paper are posted as metadata with the data set in the Dryad Repository: doi:10.5061/dryad.4v2m5.

Mixed-effects model-building process—We outline the mixed-effect analyses below using lake TP as an example, but we applied the same steps to the color models. Prior to testing our candidate models, we determined whether there was significant regional-scale variation in TP by developing an unconditional model that had no predictor variables, but allowed TP to vary by region (random intercept). This preliminary analysis partitioned the total variation in TP into two variance components: σ^2, within region (local variation) and τ_{00}, among region (regional variation). From these variance components, we calculated the intra-class correlation coefficient (ICC, ρ) that measures the proportion of TP variance that is among regions:

$$\rho = \tau_{00} / \left(\tau_{00} + \sigma^2\right) \tag{1}$$

The ICC provides an estimate of the extent to which individual lake TP concentrations in a region are correlated to one another. The ICC value was used to evaluate whether a mixed-effect model approach was needed or whether regional variation was sufficiently low that ordinary least-squares regression models were appropriate.

Question 1: Local wetland–lake chemistry relationships and local land use and HGM interactions [Models 1a,b,c]: To address research question 1, we modeled within-region (local) TP variation using a priori local landscape-context variables hypothesized to affect TP (Models 1a,b,c in Table 1, *see* description of Model 3b for model equation). Local predictor variables that were correlated to one another ($r > 0.5$) were not included in the same model to avoid problems of collinearity. Local landscape variables were treated as fixed effects across regions. Model parameters were derived using full maximum-likelihood estimation to maximize the likelihood of the parameters given the data, as opposed to the ordinary least-squares method of minimizing the model residual error (Gelman and Hill 2007). We used $\alpha = 0.1$ as the value to determine statistical significance of parameter estimates.

The proportion of variance explained by the landscape variables was calculated at each spatial scale. Below is an example of the variance explained by local predictor variables,

$$Var_{\text{local}} = \left(\sigma^2_{\text{unconditional}} - \sigma^2_{\text{current model}}\right) / \sigma^2_{\text{unconditional}} \quad (2)$$

where Var_{local} is the within-region TP variation explained by the local model; $\sigma^2_{\text{unconditional}}$ is the local variation in the unconditional random intercept model, and $\sigma^2_{\text{current model}}$ is the local variation in the models conditioned with predictor variables. Local predictor variables that reduced the within-region variation (σ^2) were retained in the model-building process.

Question 2: Regional differences in local wetland–lake chemistry relationships [Model 2]: Local wetlands were treated as random effects to determine whether wetland relationships with TP were different among regions (i.e., random wetland slopes; Model 2, Table 1). Among-region differences in wetland slopes were represented by the variance term (τ_{11}). Models were evaluated using an alpha of 0.10 to determine whether wetlands should be treated as random effects or fixed effects across all regions.

Question 3: Cross-scale interactions between regional landscape predictors and local wetland–lake chemistry relationships [Model 3a,b]: Regional landscape-context variables were added to the best ranked local model to explain TP variation among regions (Model 3a, Table 1). Regional variables that reduced among-region variation (τ_{00}) were retained in the model. We explained regional variation in wetland–TP slopes by including cross-scale interaction terms between local wetlands and regional landscape-context variables (Model 3b, Table 1). A decrease in τ_{11} indicated that the cross-scale interaction reduced variation in wetland–TP regression slopes among regions.

Table 5. Unconditional multilevel mixed-effect models for total phosphorous (TP) and color with random intercepts and no predictor variables. Variance estimates for within-region (σ^2) and between-region (τ_{00}) are provided. *See* text for description of calculations.

Lake data set	n (N for regions)	Intercept estimate	σ^2	τ_{00}	% ICC*
TP	1790(23)	2.66	0.42	0.19	31
Color	1527(21)	2.55	0.67	0.10	13

* ICC = intra-class correlation coefficient.

Below is an example of a full model that includes local- and regional-scale fixed effects, random local wetland slopes, and cross-scale interactions. All models used in the analyses are simplified variations of this model.

$$\begin{aligned} Y_{ij} = {} & \beta_{0j} + \beta_{1j}\left(\text{Depth}_{ij}\right) + \beta_{2j}\left(\text{Wet}_{ij}\right) \\ & + \beta_{3j}\left(\text{Wet}_{ij} \times \textit{Regional Agric.}\right) + r_{ij} \end{aligned} \quad (3)$$

$$\beta_{0j} = \gamma_{00} + \gamma_{01}(\textit{Regional Agric.})_j + u_{0j}$$

$$\beta_{1j} = \gamma_{10}$$

$$\beta_{2j} = \gamma_{20} + u_{2j}$$

$$\beta_{3j} = \gamma_{21}$$

where $r_{ij} \sim N(0,\sigma^2)$ and $\begin{pmatrix} u_{0j} \\ u_{2j} \end{pmatrix} \sim N\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \tau_{00}\tau_{01} \\ \tau_{10}\tau_{11} \end{pmatrix}\right]$

In this model, TP (Y_{ij} for lake i in region j) is a function of the overall intercept (γ_{00}), the main effect of regional agriculture (γ_{01}), fixed effect of lake depth (γ_{10}), random effect of local wetlands (γ_{20}), and the cross-scale interaction between local wetlands and regional agriculture (γ_{21}). Both the intercept and local wetland slope are allowed to vary among regions by including the error terms u_{0j} and u_{2j}, where u_{0j} is the regional intercept error for region j and τ_{00} represents the among-region variability in TP after controlling for regional agriculture; u_{2j} is the regional error to the slope associated with region j and τ_{11} represents the among-region local wetland effect variability; and τ_{01} is the covariance between u_{0j} and u_{2j}. The residual error (r_{ij}) is considered to be normally distributed (N) with a mean of zero and variance σ^2.

Model evaluation using information criteria: All candidate models were evaluated using weight-of-evidence approaches and ranked based on Akaike Information Criteria values (AIC) and Akaike weights (w_i). Candidate models for each data set were compared based on differences in AIC values (Δ_i), where lower AIC values indicate better model fits for the data. The Akaike weights quantify the evidence for empirical support of that model (Anderson and Burnham 2002).

Results

Regional variation in lake chemistry: unconditional models with random intercepts—Lake TP and color were different among regions (Table 5). For the TP data set, the intraclass correlation coefficient (ICC) was 31%, which indicated that 31% of the total variation in TP was attributed to across-region differences and 69% was attributed to within-region lake differences. For the color data set, 13% of the total variation in color was attributed to across-region differences and 87% was attributed to within-region lake differences (Table 5). The unconditional models showed that lakes within the same region have more similar TP and color concentrations than lakes from other regions, although to different degrees, and to treat lakes as independent observations would violate statistical assumptions of independence. Thus, all remaining analyses were multilevel mixed-effects models in which we accounted for this regional variation in TP and color by allowing for random intercepts among regions.

Local wetland–lake chemistry relationships and local land use and HGM interactions (Question 1)—Landscape variables quantified at the local scale accounted for a portion of the variation in lake TP and color within regions. The TP and color relationships with HGM variables followed expectations from the literature. Both TP and color had negative relationships with lake depth and baseflow, and positive relationships with lake drainage ratio (Tables 6, 7). Different lake-depth measures were used for the TP and color candidate models: maximum lake depth was more strongly related to TP, and mean lake depth was more strongly related to color. Local wetlands were not significantly related to lake TP when treated as fixed effects among regions (Model 1a in Table 6). Local agriculture and urban lands were positively related to TP, but local-scale interactions between human land use and wetlands did not significantly improve model fit for TP (Model 1c in Table 6). In contrast, local wetlands had positive relationships with lake color when treated as a fixed effect among regions (Model 1a in Table 7). Including human land use or local-scale interactions between baseflow and local wetlands did not lower the AIC value nor improve the model fit to predict color (Models 1b and 1c in Table 7). The top-performing local-scale model for TP (Model 1b) accounted for 21% of the variation in lake TP attributed to the local scale, and the top-performing local-scale color model (Model 1a) accounted for 32% of the variation in color attributed to the local scale.

After accounting for local landscape variables, there was significant regional TP and color variation remaining. We calculated the deviation of regional mean TP and color from the grand mean, referred to as best linear unbiased predictors (BLUPs; Robinson 1991), and plotted the BLUPs in Figs. 2A, 3A (region codes are described in Table 8). On average, regions in the Great Lakes (MI and WI) had higher TP compared to lakes in the Northeast (ME and NH; Fig. 4A). Color had less obvious regional spatial patterns (Fig. 5A). This suggests that TP concentrations may be more related to regional landscape characteristics than color.

Regional differences in local wetland–lake chemistry relationships (Question 2)—Local wetland relationships with lake TP and color were different among regions, and allowing for random wetland regression slopes among regions (Model 2), lowered AIC values and improved model fit as compared to models that treated local wetlands as fixed effects. For TP, variation in the random local wetland–lake TP effect was different from zero ($\tau_{11} = 0.37$, $\alpha < 0.10$) and lowered the AIC values by 23 units from top-performing local–TP model (Model 1b) that included a fixed-wetland effect across regions (Table 6). For color, variation in the random local wetland–lake color effect was different from zero ($\tau_{11} = 0.50$, $\alpha < 0.10$) and lowered the AIC values by 11 units from top-performing local-color model (Model 1a) that included a fixed-wetland effect across regions (Table 7).We plotted the deviation in regional mean local wetland–lake chemistry (TP and color) relationships from the grand-mean local wetland–lake chemistry relationships (Figs. 2B, 3B). Some of these deviations were not different from the overall local wetland effect (i.e., the grand mean), but local wetland effects were larger than the grand mean in some regions and smaller than the grand mean in other regions. On average, local wetland relationships with TP were positive in NH and ME regions and negative in a region in southwestern WI (Fig. 4B). Local wetland relationships with color were, on average, greater than the grand mean in northwestern WI and southern NH regions and lower than the grand mean in northwestern MI regions (Fig. 5B).

The slopes and intercepts of the regions were related to each other, but to different degrees for TP and color. Regional TP intercepts were negatively related to wetland–lake TP regression slopes ($R^2 = 0.85$; $p < 0.0001$). Regional color intercepts were related to increased wetland–lake color regression slopes ($R^2 = 0.18$; $p = 0.06$). These results suggest that the regional context may not only drive differences in lake TP and color within regions, but also differences in the local wetland relationships with lake TP and color within regions.

Cross-scale interactions between regional landscape predictors and local wetland–lake chemistry relationships (Question 3)—The addition of regional landscape context variables to the best local models reduced lake TP and color variation among regions (τ_{00}) and improved the model fit for both data sets (Model 3a in Tables 6, 7). For lake TP, the proportion of agriculture within the region was positively associated with region-average TP concentrations and explained about 22% of the regional TP variation (Table 6). Lakes within regions with high agricultural land use tended to have higher TP concentrations compared to lakes from regions with low agricultural land use (Fig. 6A; $p < 0.0001$). For lake color, the proportion of baseflow in the region accounted for 4% of the regional color variation (Table 7). Regions with high baseflow tended to have less colored lakes as compared to regions with low baseflow (Fig. 6B; $p = 0.05$).

The top-ranked lake TP and color models included cross-scale interaction terms between local wetlands and regional landscape variables (Model 3b in Tables 6, 7).

Table 6. Mixed-effects models predicting total phosphorous (TP; $n = 1790$ lakes, $N = 23$ regions). Variance components were estimated for within-region lake TP (σ^2), between-region intercept (τ_{00}), and between-region wetland slopes (τ_{11}). Models (1a, 1b, 1c, 2, 3a, 3b) were compared using Akaike Information Criteria (AIC) by taking the difference in AIC values with the lowest AIC model (Δ_i) and calculating Akaike weights (w_i). Agriculture (AGR), urban (URB), and wetlands (WET) were quantified at the local scale ($_L$) and regional scale ($_R$). Parameters and interactions not included in the models were noted with an em-dash (—). HGM is hydrogeomorphic variables, WET is wetland cover, and LU is human land use; regional landscape-context variables are italicized.

	Scale of predictor variables:	Local			Local and regional		
	Scale of interaction:	—	—	Local	—	—	Regional
Category	Landscape-context variable	1a. HGM_L + WET_L	1b. HGM_L + WET_L + LU_L	1c. HGM_L + WET_L + LU_L + ($WET_L \times LU_L$)	2. Top local + $WET_{L\ Random}$	3a. Top local + regional + $WET_{L\ Random}$	3b. Top local + regional + $WET_{L\ Random}$ + ($WET_L \times LU_R$)
HGM_L	Maximum depth	−0.43***	−0.43***	−0.43***	−0.43***	−0.43***	−0.43***
	Drainage ratio	0.08***	0.06***	0.06***	0.06***	0.06***	0.06***
	Baseflow	−0.008**	−0.008**	−0.008**	−0.008**	−0.008**	−0.008**
WET_L	Wetland	ns	ns	ns	ns	ns	ns
LU_L	Agriculture	—	0.76***	0.74***	0.70***	0.72***	0.70***
	Urban	—	0.42***	0.46***	0.38***	0.38***	0.38***
$WET_L \times LU_L$	$WET_L \times AGR_L$	—	—	ns	—	—	—
	$WET_L \times URB_L$	—	—	ns	—	—	—
LU_R	*Agriculture*$_R$	—	—	—	—	*1.21****	*1.20****
$WET_L \times LU_R$	$AGR_R \times WET_L$	—	—	—	—	—	*−1.60****
	Intercept	2.68***	2.69***	2.69***	2.69***	2.44***	2.44***
Variance components	σ^2	0.31***	0.29***	0.29***	0.29***	0.29***	0.29***
	τ_{00}	0.21**	0.22**	0.22**	0.22**	0.06**	0.06**
	τ_{11}	—	—	—	0.37*	0.22*	0.07^{ns}
Variation explained	Within region	18%	21%	21%	22%	22%	22%
	Between region	—	—	—	—	22%	22%
Model selection	AIC	3085	2954	2956	2945	2928	2922
	Δ_i	163	32	34	23	6	0
	w_i	0.001	<0.001	<0.001	<0.001	0.04	0.95

* $p < 0.1$; ** $p < 0.05$; *** $p < 0.001$.

Table 7. Mixed-effects models predicting color (n = 1527 lakes, N = 21 regions). Variance components are estimated for within-region color (σ^2), between-region intercept (τ_{00}), and between-region wetland slopes (τ_{11}). Models (1a, 1b, 1c, 2, 3a, 3b) were compared using Akaike Information Criteria (AIC) by taking the difference in AIC values with the lowest AIC model (Δ_i) and calculating Akaike weights (w_i). Wetlands (WET) and baseflow were quantified at the local scale ($_L$) and regional scale ($_R$). Parameters and interactions not included in the models were noted with an em-dash (—). HGM is hydrogeomorphic variables, WET is wetland cover, and LU is human land use; regional landscape-context variables are italicized.

	Scale of predictor variables:	Local			Local and regional		
	Scale of interaction:	—	—	Local	—	—	Regional
Category	Landscape-context variables	1a. HGM_L + WET_L	1b. HGM_L + WET_L + LU_L	1c. HGM_L + WET_L + (WET_L × $baseflow_L$)	2. Top local + $WET_{L\ Random}$	3a. Top local + regional + $WET_{L\ Random}$	3b. Top local + regional + $WET_{L\ Random}$ + (WET_L × $baseflow_R$)
HGM	Mean depth	−0.47***	−0.47***	−0.47***	−0.46***	−0.46***	−0.46***
	Drainage ratio	0.20***	0.20***	0.20***	0.20***	0.20***	0.20***
	Baseflow	−0.02***	−0.02***	−0.02***	−0.02***	−0.02***	−0.02***
WET	Wetland	1.45***	1.46***	1.45***	1.38***	1.38***	1.63***
LU	Agriculture	—	ns	—	—	—	—
	Urban	—	ns	—	—	—	—
Interaction	WET_L×$baseflow_L$	—	—	ns	—	—	—
Regional	*$baseflow_R$*	—	—	—	—	*−0.02***	*−0.02***
	$baseflow_R$×WET_L	—	—	—	—	—	*−0.06***
	Intercept	2.55***	2.55***	2.55***	2.55***	2.59***	2.59***
Variance components	σ^2	0.42***	0.42***	0.42***	0.42***	0.42***	0.42***
	τ_{00}	0.12**	0.12**	0.12**	0.12**	0.07**	0.07**
	τ_{11}	—	—	—	0.50*	0.50*	0.06^{ns}
Variation explained	Within region	32%	32%	32%	33%	33%	33%
	Between region	—	—	—	—	4%	4%
Model selection	AIC	3081	3082	3082	3070	3066	3061
	Δ_i	20	21	21	9	5	0
	w_i	<0.001	<0.001	<0.001	0.01	0.07	0.91

* $p < 0.1$; ** $p < 0.05$; *** $p < 0.001$.

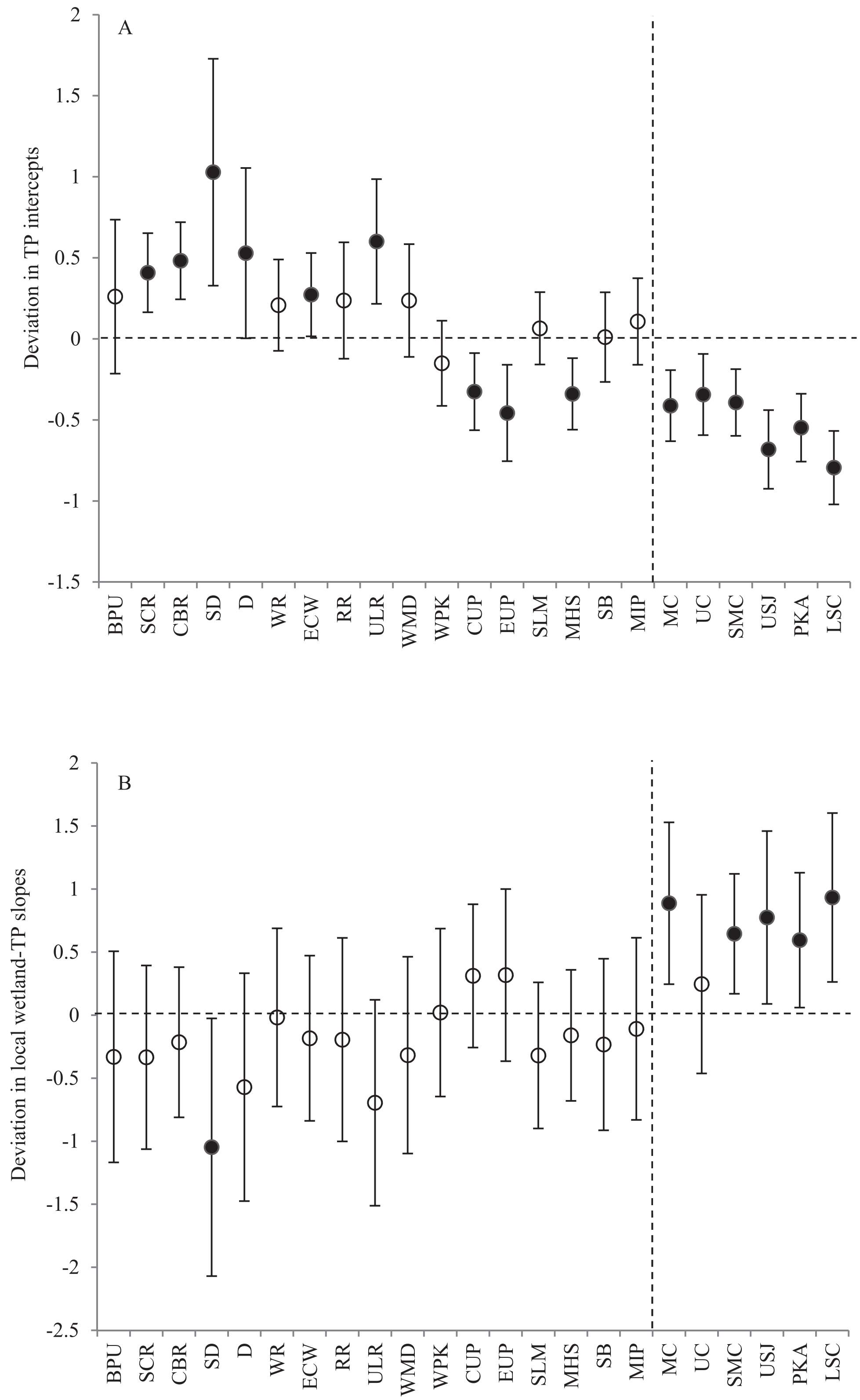

Fig. 2. Deviations from the grand mean for (A) TP intercepts, and (B) local wetland–TP slopes for each region. Deviation estimates are also referred to as best linear unbiased predictors (BLUPs). Solid circles are significantly different from the grand-mean intercept and wetland slope values (p-value < 0.1). Hollow circles are not significantly different from the grand-mean intercept and slope values. Error bars are standard error estimates of the BLUPs. Regions are ordered left to right from west to east geographically. Regions in the Northeast are separated from regions in the Great Lakes by a vertical dashed line. See Table 8 for a description of the region codes.

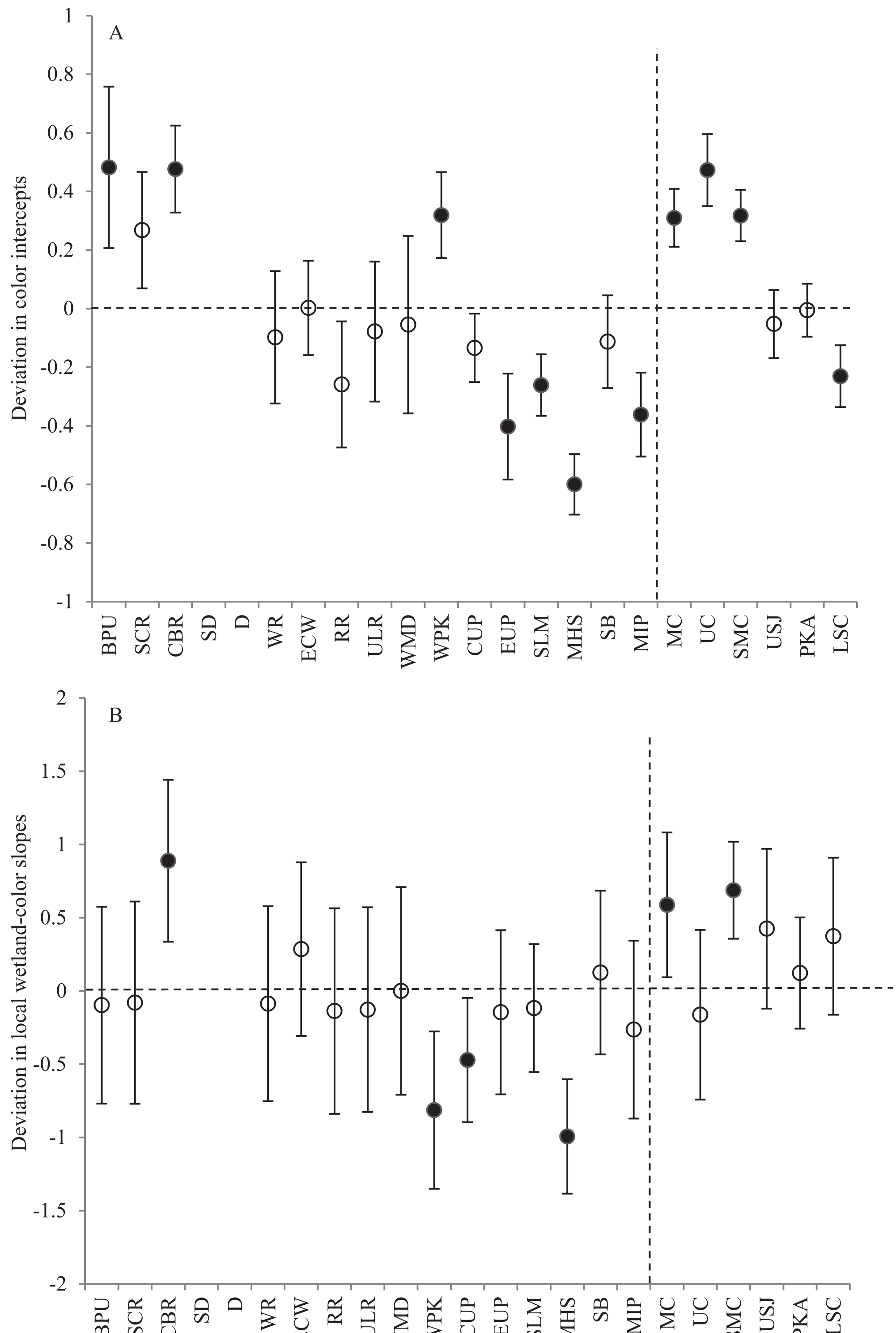

Fig. 3. Deviation from the grand mean for (A) color intercepts, and (B) local wetland-color slopes for each region. Deviation estimates are also referred to as best linear unbiased predictors (BLUPs). Solid circles are significantly different from the grand-mean intercept and wetland slope (p-value < 0.1). Hollow circles are not significantly different from the grand-mean intercept and wetland slope values. Error bars are standard error estimates of the BLUPs. Regions are ordered left to right from west to east geographically. Regions in the Northeast are separated from regions in the Great Lakes by a vertical dashed line. See Table 8 for a description of the region codes.

Table 8. Description of Ecological Drainage Unit (EDU) codes and the state location. Region codes are ordered from west to east geographically. The four states include Wisconsin (WI), Michigan (MI), New Hampshire (NH), and Maine (ME).

EDU code	Description	State
BPU	Bayfield Peninsula and uplands	WI
SCR	St. Croix River	WI
CBR	Chippewa and Black River	WI
SD	Southern driftless	WI
D	Driftless	WI
WR	Wisconsin River	WI
ECW	East-central Wisconsin	WI
RR	Rock River	WI
ULR	Upper Illinois River	WI
WMD	Western Lake Michigan and Door Peninsula	WI
WPK	Western Upper Peninsula and Keweenaw Peninsula	MI
CUP	Central Upper Peninsula	MI
EUP	Eastern Upper Peninsula	MI
SLM	Southeast Lake Michigan	MI
MHS	Northern Lake Michigan, Lake Huron, and Straits of Mackinac	MI
SB	Saginaw Bay	MI
MIP	Southeast Michigan interlobate and lake plain	MI
MC	Middle Connecticut	NH
UC	Upper Connecticut	NH
SMC	Saco, Merrimack, Charles	NH, ME
USJ	Upper St. John, Aroostook	ME
PKA	Penobscot, Kennebec, Androscroggin	NH, ME
LSC	Lower St. Croix	ME

These cross-scale interactions attributed regional variation in local-wetland regression slopes to regional landscape variables. Regional agriculture negatively interacted with local wetland relationships with TP, and a cross-scale interaction between local wetlands and regional agriculture reduced the among-region wetland variance term to zero (Table 6; $\tau_{11} = 0.07^{ns}$, $\alpha > 0.1$), which means that the differences in wetland–lake TP effects among regions became nonsignificant (ns) when regional agriculture interactions were taken into account. Local wetland–lake TP BLUPs among regions were negatively related to regional agriculture (Fig. 6C; $p < 0.0001$). In regions with low amounts of agriculture, local wetlands had positive relationships with lake TP, and in regions with high amounts of agriculture, local wetlands had negative relationships with TP. For color, regional baseflow negatively interacted with local wetland relationships with lake color, and a cross-scale interaction between local wetlands and regional baseflow reduced the among-region wetland variance term to zero (Table 7; $\tau_{11} = 0.06^{ns}$, $\alpha > 0.10$), which means that the differences in wetland–color relationships among regions became nonsignificant when regional baseflow interactions were taken into account. Local wetlands were positively associated with color, but there were regional differences in the magnitude of these relationships that were attributed to negative interactions with regional baseflow. Local wetland–lake color BLUPs among regions were marginally negatively related to regional baseflow (Fig. 6D; $p < 0.1$). In regions with low baseflow, the magnitude of positive local wetland–lake color slopes was higher and, in regions with high baseflow, the magnitude of local wetland–lake color slopes was lower (Fig. 6D). In sum, local wetland cross-scale interactions significantly improved model fits to explain lake TP and water color variation from local and regional landscape features.

Discussion

The major conclusion from our work is that when examining the relationships between local wetlands and lake TP and color, it is important to not only include landscape drivers quantified at multiple spatial scales, but to model the regional differences as cross-scale interactions. In addition, when comparing the landscape controls of lake TP and color, we found that at the local scale, TP and color were controlled by similar lake and catchment features; but, at the regional scale, they were controlled by different landscape features. These findings indicate that although catchment-scaled variables are important for predicting TP and color, regional-scaled variables also affect lake water chemistry and the relationships at the local scale do not always determine which variables are important at the regional scale.

Regulation of lake TP and color by local landscape factors—Our mixed-effect analyses showed that variation in lake TP and color was greater within regions than among regions, highlighting the importance of local lake and catchment features to predict TP and color. Other studies have supported this finding by demonstrating that TP and carbon variation is high within regions and can partially be accounted for by considering lake depth, catchment morphometry, and catchment land use (D'Arcy and Carignan 1997). In our study, local landscape variables

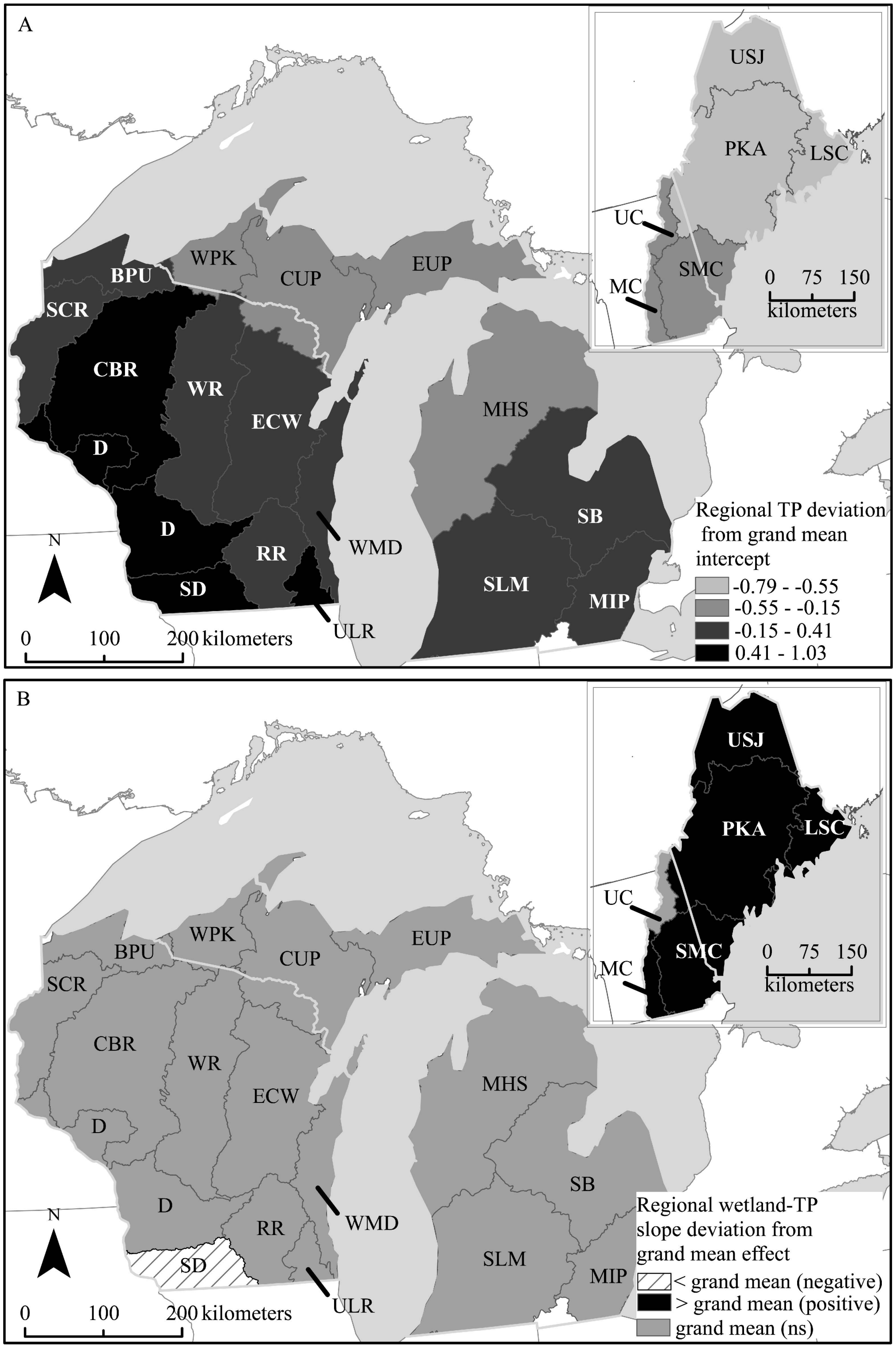

Fig. 4. Deviation from the grand mean for (A) TP intercepts, and (B) local wetland–TP slopes for each region displayed geographically. See Table 8 for a description of the region codes.

that predicted within-region variation in lake TP and color matched this previous research and our expectations (Table 1). Webster et al. (2008) showed that lake drainage ratio is strongly correlated to water residence time and, thus, provides the mechanisms for the positive relationship between lake drainage ratio and lake-water chemistry (i.e., internal controls of TP and color). Lakes with small drainage ratios are more likely to have long water-residence times, which has been related to decreased internal TP loading (D'Arcy and Carignan 1997) and increased photo-

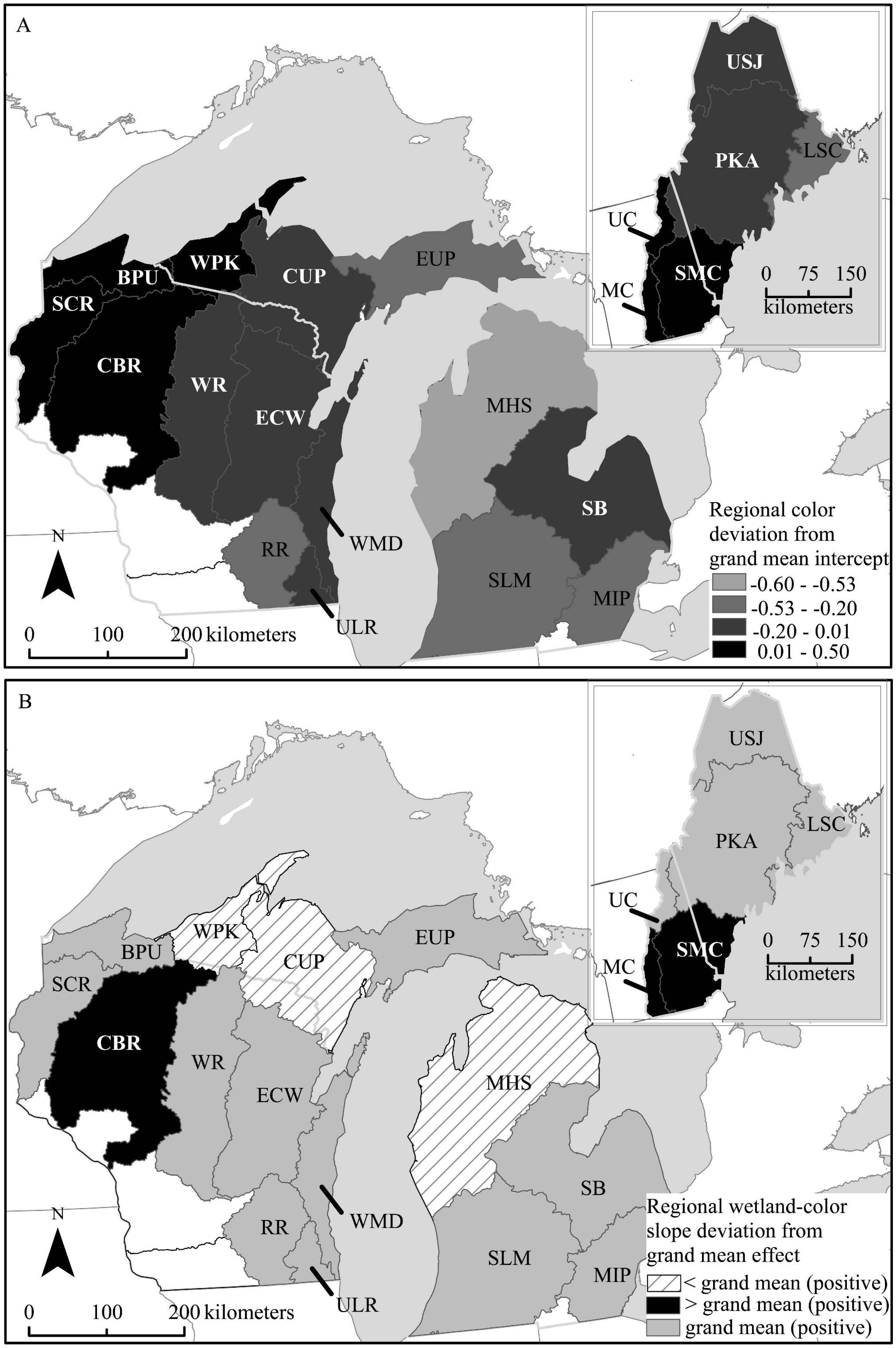

Fig. 5. Deviation from the grand mean (A) color intercepts, and (B) local wetland-color slopes for each region displayed geographically. See Table 8 for a description of the region codes.

degradation of organic carbon (Molot and Dillon 1997). Local human land use was related to increased TP concentrations and accounted for a large proportion of local-scale TP variation in support of past findings (Wickham et al. 2005). Human land use was not related to lake color, which is also consistent with other studies (Trebitz et al. 2007; Wilson and Xenopoulos 2008). Although local predictor variables were significantly related to TP and color, they did not account for all variation observed, warranting further research into the

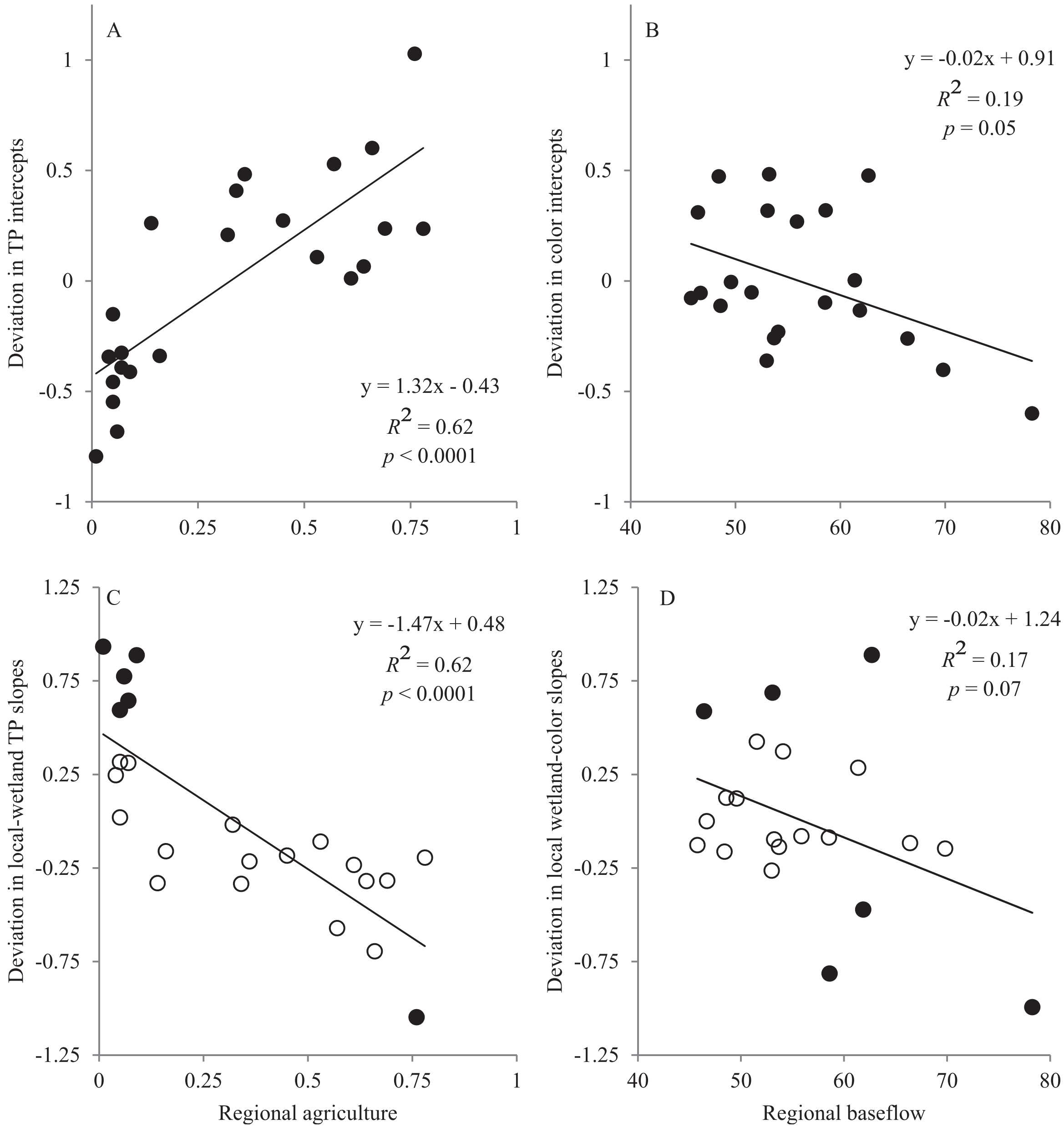

Fig. 6. Deviations from the grand mean for (A) TP intercepts vs. regional agriculture, (B) color intercepts vs. regional baseflow, (C) wetland–TP slopes vs. regional agriculture, and (D) wetland–color slopes vs. regional baseflow. Each data point is a region. Solid circles are significantly different from the grand-mean intercepts (TP or color) or the grand-mean wetland slope (p-value < 0.1) for TP or color. Hollow circles are not significantly different from the grand-mean intercept or wetland slopes (TP or color).

local drivers of lake chemistry. In addition, regional differences in lake TP and color were large enough that across-region variation could not be ignored, thus requiring the use of mixed-effects models.

One possible limitation of our assessment of wetland effects at the local scale is our choice of metric. Measuring wetlands in a 500-m lake buffer may not fully capture the most ecologically relevant wetlands that are most likely to influence the lake's water chemistry. We chose this metric because it was the most cost-effective approach for the large number of lakes in our study area. Although it is plausible that wetlands measured within a lake catchment would be more strongly related to lake chemistry than wetlands measured within a 500-m buffer, this is not always the case (Gergel et al. 1999). Nevertheless, the relationships that we observed between LULC in the 500-m buffer and lake water chemistry are likely conservative, and indicate that some relationship exists. Wetland metrics that focus on the functional connections among freshwater elements such as the upstream lakes, streams, and wetlands, likely would yield stronger relationships with lake TP and color than the relationships observed in our study. These limitations highlight the need for more research to identify the optimal landscape metrics and scales for quantifying landscape effects on lake water chemistry.

Regulation of lake TP and color by regional landscape factors—We found that TP and color exhibit regional patterns, which is supported by other cross-region studies for lake TP (Omernik et al. 1991; Rohm et al. 1995) and DOC (Kortelainen 1993; Xenopoulos et al. 2003; Sobek et al. 2007). Our regionalization framework (EDU) that we used to define regions captured both TP (as found by Cheruvelil et al. [2008] for MI) and color variation. However, further research could test this regional framework against other regionalization frameworks to see whether other frameworks capture more variation, particularly for water color.

We found that regional agriculture and baseflow improved model fit and explained regional differences in TP and color respectfully, which highlights the importance of considering regional-scale variables to predict lake water chemistry. Regional agriculture affected lake TP and indicates that regional disturbance as measured by human land use may have significant effects on lake water chemistry, in addition to the well-established effects of human land use at local scales. Agricultural land exports phosphorus to surface waters at local scales, such as within a catchment or in near-lake buffers (Hunsaker et al. 1992). However, our results imply that agricultural activities within a *region* also affect lake phosphorus concentrations, and potentially in different ways. Agriculture and urban land use have been related to higher regional TP concentrations as compared to regions with low amounts of agriculture and urban land uses within the Northeastern USA (Rohm et al. 1995). Regional agriculture relationships with lake TP indicate that human land uses, particularly agriculture, may have diffuse, far-reaching effects on surface waters, such that land use within a region may even affect lakes buffered by minimally disturbed local catchments. For example, one possible mechanism to explain regional agriculture effects on lake TP are large-scale animal feeding operations that may deposit livestock manure to fields beyond the local catchment (Tomer et al. 2008).

An important implication of this idea is that regional-agricultural effects of land use on lake TP may affect our identification of reference lakes used to assess condition and set nutrient criteria. For example, identifying reference lakes simply by the amount of human land use at the local scale may be misleading because it does not take into account regional land-use disturbance that may also affect lake nutrient levels. In addition, soils and LULC are likely collinear such that agriculturally dominant regions may have had more nutrient-rich soils prior to agricultural development, as compared to regions with low amounts of agriculture. Therefore, future research that includes soils data should tease apart the relative influence of soil composition vs. agricultural activity for driving lake TP at the regional scale.

For water color, the regional variable that appeared to be important for understanding variation was groundwater contribution or baseflow. Regional baseflow accounted for just 4% of the regional variation in color and a large proportion of variation remained unexplained. Baseflow or hydrologic characteristics may exhibit large within-region variation (Kratz et al. 1997) and, thus, may have weak relationships with regional color. Negative relationships between groundwater contribution and carbon measures have been observed at local scales (Jordan et al. 1997). However, in our study, lake color was negatively related to *regional* groundwater contribution (baseflow). In our study area, regions with low baseflow are characterized as having clay-rich glacial deposits that promote surface runoff contribution (Wolfson 2009), and this runoff could carry higher humic carbon concentrations (Thierfelder 1999). Conversely, lakes in regions with high baseflow likely receive large groundwater input that can be low in organic carbon (Rasmussen et al. 1989). Regional baseflow may also be indicative of other regional characteristics, such as geology and vegetation cover classes, that have clear mechanistic relationships with carbon transport to lakes. For example, in Michigan, areas associated with high groundwater are characterized as having sand and gravel substrate (Lusch 2009) and less organic-rich soils (Schatzel and Isard 1991). We also found a negative correlation between regional baseflow and regional upland forest cover across our entire study area ($r = -0.51$; Table 4), which has been associated with increased DOC (D'Arcy and Carignan 1997). Together, these findings indicate that regions with high baseflow may have fewer allochthonous humic carbon sources to lakes and fewer transport mechanisms carrying them downstream. Therefore, future research should include additional regional characteristics to account for remaining among-region color differences (e.g., geology, soils, and climate), as well as tease apart the relative influence of soil and geology composition vs. baseflow for driving lake color at the regional scale.

Similar to landscape studies conducted at the local scale, regional studies suffer from problems of multicollinearity among landscape variables (King et al. 2005). We included only one regional-scale variable in a model at a time because many of the landscape variables quantified at the regional scale were highly correlated to one another (Table 4). For example, in our study, regional agriculture was negatively correlated to regional runoff ($r = -0.8$), such that we cannot distinguish agricultural effects from runoff effects on lake TP. However, we chose to include regional agriculture because agricultural mechanisms related to phosphorus transport to lakes at the local scale are well-supported in the literature and could persist at the regional scale.

Local wetland effects on lake TP and water color—Across regions, variation in local wetland effects on lake TP was related to agriculture land use quantified at the regional scale. In agriculturally rich regions, wetlands surrounding lakes were associated with lower TP, indicating that local-scale wetlands may reduce nutrient loading from regional agriculture. Given the nature of the analysis, we are not able to determine the specific mechanisms underlying this interaction term. However, because lake TP was weakly related to local wetlands alone, but strongly related to regional agriculture, it is likely that the mechanisms of the cross-scale interaction are related to the local wetlands decreasing the regional agricultural effects with lake TP.

Local wetlands were positively related to lake color and the magnitude of the slopes of these relationships was different among regions (Table 7). Past studies have linked wetlands to higher DOC concentrations in lakes and streams, and support the finding that wetlands are allochthonous carbon sources (Gergel et al. 1999; Xenopoulos et al. 2003). However, there were differences in local wetland effects with color that were due to variation in regional baseflow. Greater regional baseflow or groundwater contribution may be associated with less surface-water runoff, reducing wetland effects on humic carbon transport (Jordan et al. 1997). Future research could examine how regional hydrology affects local wetland hydrology and carbon transport so that we can better link regional baseflow to specific wetland function.

Implications—Regional-scale studies are important to identify broad-scale patterns in ecosystem state and change through time. Such research can be a starting point to develop more mechanistic studies to better understand how the regional landscape context may constrain finer scale ecological processes. Multilevel landscape studies such as this are empirical in nature and lack the fine spatial and temporal information of process-based mechanistic models, primarily because of the lack of high-frequency and high-resolution data for many lakes. Thus, we cannot quantify detailed nutrient budgets on each lake nor quantify with precision the contributions of different upstream landscape components to downstream nutrient concentrations. However, by designing studies that include fewer data on many hundreds to thousands of lakes along large gradients in HGM and land use settings, mechanisms can be inferred about both local and regional controls of surface-water chemistry. In this way, multilevel landscape studies can complement process-based models and improve upon their efficiency (Strayer et al. 2003). A multilevel mixed-effects model approach is a useful analytic technique to better understand how ecological processes operate across multiple spatial scales and identify cross-scale interactions, which has been identified as an important research challenge in landscape and ecosystem ecology. Our results show that we would miss important relationships that link systems across relevant ecological spatial scales if we fail to consider the regional scale.

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