

THE EFFECTS OF LAND USE DISTURBANCE AT LOCAL AND REGIONAL
SCALES ON WETLAND RELATIONSHIPS WITH LAKE TOTAL PHOSPHORUS
AND WATER COLOR

By

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ABSTRACT

THE EFFECTS OF LAND USE DISTURBANCE AT LOCAL AND REGIONAL SCALES ON WETLAND RELATIONSHIPS WITH LAKE TOTAL PHOSPHORUS AND WATER COLOR

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We quantified wetland relationships with lake total phosphorus (TP) and water color in relation to landscape features at local and regional scales using multilevel mixed effects models on 1,790 north-temperate lakes. Our two research questions were: 1) do human land use disturbances at local scales affect wetland relationships with lake TP and water color? And 2) are wetland relationships with lake TP and water color different across regions, and if so, what regional characteristics are related to this variation? We found that land use disturbance at the local scale did not interact with wetland-lake TP relationships but regional agriculture was negatively related to wetland-TP slopes. In regions with low proportions of agriculture wetland-TP slopes were positive, and in regions with high proportions of agriculture wetland-TP slopes were negative. In addition, lake TP and water color were related to similar local lake and catchment characteristics but different regional characteristics. Regional agriculture explained 22% of the variability in TP and regional groundwater explained 4% of the variability in water color. Regional groundwater was negatively related to wetland-water color slopes such that wetland effects were weak in regions with high groundwater. These results demonstrate that lake TP and water color are hierarchically controlled by landscape variables at both local and regional scales and that the regional setting influences wetland relationships with both lake TP and color.

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PREFACE

The document was written in the form of a manuscript to be submitted to a peer reviewed journal with the following authors: C. Emi Fergus, Patricia A. Soranno, Kendra Spence Cheruvelil, and Mary T. Bremigan. In the text “we” is used rather than “I” to reflect the contribution of the coauthors in preparing the manuscript. However, I have done all statistical analyses, literature reviews, and writing of this thesis.

TABLE OF CONTENTS

LIST OF TABLES.....	vi
LIST OF FIGURES.....	ix
CHAPTER 1: THE EFFECTS OF LAND USE DISTURBANCE AT LOCAL AND REGIONAL SCALES ON WETLAND RELATIONSHIPS WITH LAKE TOTAL PHOSPHORUS AND WATER COLOR.....	1
Introduction.....	1
Methods.....	6
Results.....	16
Discussion.....	21
APPENDIX.....	45
REFERENCES.....	54

LIST OF TABLES

Table 1. Candidate models to test hypothesized relationships between local and regional landscape-context variables and lake total phosphorus (TP) and water color. Landscape-context variables were grouped into prediction type classes: hydrogeomorphic variables (HGM), wetlands (WET), human land use disturbance (LU), local disturbance interactive effects ($WET_L * LU_L$), random local wetland effects across regions (WET_L -RAN), and cross-level interactive effects ($WET_L * X_R$). Variables excluded from the models are denoted by “-”. Variables with the same hypothesized relationship as the previous model are symbolized by “*”. “All-lakes” is the complete lake dataset, including all levels of land use disturbance, and “Min-dist.” is the minimally-disturbed lake dataset (<5% agriculture and urban land use). Regional landscape-context variables are italicized. ...29

Table 2. Summary statistics of local and regional landscape-context variables used to predict lake TP for all lakes ($n = 1,790$ in 23 regions) and for minimally-disturbed lakes ($n = 777$ in 16 regions). Minimally-disturbed lakes were defined to have < 5% agriculture and urban land use within a 500 m buffer surrounding lakes from the all-lakes dataset. Regional variables are italicized.31

Table 3. Summary statistics of local and regional landscape-context variables used to predict lake water color for all lakes ($n = 1,527$ in 21 regions) and for minimally-disturbed lakes ($n = 686$ in 16 regions). Minimally-disturbed lakes were defined to have < 5% agriculture and urban land use within a 500 m buffer surrounding lakes from the all-lakes dataset. Regional variables are italicized.32

Table 4. Unconditional multilevel mixed effect models for lake TP and color with no predictor variables and random intercepts. Variance estimates for within-region (σ^2) and between-region (τ_{00}) are provided. The intraclass correlation (%ICC or ρ) is the estimated proportion of regional variation from the total variation, calculated as $\tau_{00}/(\tau_{00} + \sigma^2)$ and is presented as a percent.....33

Table 5. Mixed effects models predicting lake TP for the all-lakes dataset ($n = 1,790$ lakes, $N = 23$ regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM), wetland (WET), and land use disturbance (LU) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L -RAN. Local wetland interactions at local and regional scales are presented in Models 2b and 5. Estimates of variance components are presented for within-region lake TP (σ^2), between-region intercept (τ_{00}), and between-region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.34

Table 6. Mixed effects models predicting water color for the all-lakes dataset ($n = 1,527$ lakes, $N = 21$ regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM), wetland (WET), and land use disturbance (LU) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN. Local wetland interactions at local and regional scales are presented in Models 2b and 5. Estimates of variance components are presented for within region color (σ^2), between region intercept (τ_{00}), and between region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.36

Table 7. Mixed effects models predicting lake TP for the minimally-disturbed lake dataset ($n = 777$ lakes, $N = 16$ regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM) and wetland (WET) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN. Wetland interactions at the local scale are presented in Model 2b. Estimates of variance components are presented for within region lake TP (σ^2), between region intercept (τ_{00}), and between region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.38

Table 8. Mixed effects models predicting water color for the minimally-disturbed lake dataset ($n = 686$ lakes, $N = 16$ regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM) and wetland (WET) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN.

Wetland interactions at the local scale are presented in Model 2b. Estimates of variance components are presented for within region lake TP (σ^2), between region intercept (τ_{00}), and between region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.	39
Table A1. Description of Ecological Drainage Unit (EDU) Codes.	50
Table A2. Correlation values for regional hydrology, climate, and landscape variables for the all-lake TP dataset (N = 23 regions). Correlation coefficients that were greater than 0.50 were considered to be significantly correlated ($\alpha = 0.05$).	51

LIST OF FIGURES

Figure 1. Distribution of the lakes and the regions (Ecological Drainage Units – Higgins et al. 2005) used in this study. Minimally-disturbed lakes were defined as having less than 5% agriculture/urban land use within 500m buffer surrounding the lake.	40
Figure 2. The regional deviation of lake response variables from the grand mean – best linear unbiased predictors (Blups) for lake TP (2a) and water color (2b). Error bars are the standard error in the Blup estimate. Region codes are shown in Figures 4 – 5 are described in Table A1. in the appendix.	41
Figure 3a. The mapped regional deviation of lake response variables from the grand mean for lake TP.	42
Figure 3b. The mapped regional deviation of lake response variables from the grand mean for water color.	43
Figure 4. Regional deviation of lake response variables (Blups – best linear unbiased predictors) versus regional landscape-context variables. 4a) TP Blup vs. regional agriculture (arcsine square root transformed); 4b) Color Blup vs. regional baseflow index (% groundwater contribution).	44
Figure A1. Percent agriculture in the region (Ecological Drainage Unit).	52
Figure A2. Percent regional groundwater contribution (baseflow index).	53

CHAPTER 1: THE EFFECTS OF LAND USE DISTURBANCE AT LOCAL AND REGIONAL SCALES ON WETLAND RELATIONSHIPS WITH LAKE TOTAL PHOSPHORUS AND WATER COLOR

Introduction

It is becoming widely recognized that lake trophic status is more completely defined by both phosphorus and dissolved organic carbon (DOC) (Williamson et al. 1999) than by phosphorus alone. Phosphorus promotes primary productivity especially at moderate to high levels of total phosphorus (TP); and the humic proportion of DOC (water color) limits algae growth by restricting light availability, especially at low levels of TP (Karlsson et al. 2009). The majority of both substances originate from the landscape surrounding lakes; and because TP and DOC have been shown to be positively correlated to one another (Detenbeck et al. 1993; Dillon and Molot 1997), they may be controlled by similar landscape features. However, few studies have examined the landscape controls of lake TP and DOC together (but see Webster et al. 2008).

Empirical cross-sectional studies of many lakes have found both TP and DOC to be related to natural hydrogeomorphic (HGM) variables, including lake and catchment morphometry and natural land cover in the surrounding landscape. Some of these variables have similar effects on lake TP and DOC. For example, lake depth is negatively correlated with lake TP and DOC (Rasmussen et al. 1989, Webster et al. 2008), and drainage ratio (the catchment area to lake area ratio) is positively correlated with lake TP and DOC (Prepas et al. 2001, Mullholland 2003). However, landscape studies are often conducted within single geographic regions or ignore how regional heterogeneity may affect these relationships (but see Xenopoulos et al. 2003). Because HGM variables are

controlled by a hierarchy of factors, it is likely that there are both regional and local drivers of variation in such relationships (Soranno et al. 2010).

For example, we know that local wetlands are considered to be influential landscape modifiers of lake and stream water chemistry because 1) they are active sites of biogeochemical processes and 2) their location at the interface between uplands and open water allows them to regulate nutrient and material transport (Mitsch and Gosselink 2007). But wetlands are found in diverse regional HGM settings and these differences may affect wetland relationships with surface water (Cole et al. 2002). Wetlands positively affect lake carbon measures such as DOC and color (Gergel et al. 1999; Canham et al. 2004); a result that has been found across a wide range of different regional settings (Xenopoulos et al. 2003). However, wetland effects on lake TP are more variable, with wetlands being either positively or negatively correlated to lake TP depending on the study (Detenbeck et al. 1993, Devito et al. 2000, Diebel et al. 2009). In fact, few studies have considered regional patterns in wetland TP relationships.

One way to reconcile the conflicting relationships between wetlands and lake TP is to consider human land use disturbance such as agriculture. In north temperate regions with minimal agriculture and urban disturbance, wetlands have been associated with increased lake and stream TP concentrations suggesting that these wetlands are sources of phosphorus to lakes (Dillon and Molot 1997, Devito et al. 2000). However, in moderate to highly disturbed settings, wetlands have been associated with decreased lake and stream TP concentrations (Johnston et al. 1990, Detenbeck et al. 1993, Weller et al. 1996, Diebel et al. 2009). Wetlands in these latter settings may act as nutrient modifiers by intercepting some of the excess phosphorus from agriculture and urban activities from

receiving surface waters. Together, these studies suggest that wetlands interact with land use to affect lake or stream TP concentrations. However, given that nutrient and material transport between terrestrial and aquatic systems may operate at different spatial scales (Gergel et al. 1999, Sliva and Williams 2001), it is not known at what spatial scale these interactions occur.

Land use disturbance may also affect lake and stream carbon concentrations. Studies have shown land use activities that disrupt surface and soil hydrology, such as logging, are associated with increased DOC concentrations. For example, clearcut logging was related to higher lake DOC concentrations in comparison to lakes from reference areas (Carignan et al. 2000). Agriculture land use in the catchment has not been strongly related to stream DOC, but Wilson and Xenopoulos (2008) indicated that land use activities that alter soil moisture or flow paths may affect DOC. In summary, few studies have thoroughly explored how land use disturbance such as agriculture affects either DOC or water color.

Most landscape studies have focused on catchment level drivers of water chemistry and have been restricted to single geographic regions (Detenbeck et al. 1993, Weller et al. 1996). However, freshwater systems are hierarchically structured such that lakes are nested within local catchments and local catchments are nested within broader regional boundaries and these differences can lead to naturally varying water chemistry. Studies have shown that lake TP and DOC concentrations are different between regions and that broad-scale features such as topography and climate may explain these differences (D'Arcy and Carignan 1997, Xenopoulos et al. 2003, Sobek et al. 2007). This regional variation may obscure the functional role of wetlands on lake nutrient and

carbon dynamics, especially if the among-region TP and DOC variation is greater than variation accounted for by wetlands at the local scale and if these two scales are not explicitly modeled. Additionally, wetland functional role in nutrient and carbon transport may be different among regions due to characteristics in the regional HGM setting. It has been shown that similar wetland types can have very different hydrologic characteristics among regions. For example, the frequency of wetland inundation, which affects the chemical environment for nutrient and carbon cycling, differs among regions and may be attributed to regional variation in climate and soil characteristics (Cole et al. 2002). In sum, the relative importance of local and regional landscape features on lake TP and DOC is not well documented or understood.

One obstacle to assessing multi-scaled landscape effects on lake TP and DOC is the limitation of common statistical approaches. Classical regression models are often inappropriate for regional analyses because they either 1) pool observations across regions (i.e. ignore regional variation) and violate assumptions of statistical independence or 2) separate observations into regional groups which can lead to inflated variance estimates within each region (Gelman and Hill 2007). Statistical approaches such as multilevel mixed effects models can account for hierarchical drivers of water chemistry by modeling variation in lake TP and color attributed to both local-catchment scale and broad-region scale features. Mixed effects models have not been widely used in freshwater- land use/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 this study, we used multilevel mixed-effects models to explore wetland relationships with lake TP and water color and to consider both land use/land cover and other HGM features at both local and regional scales. Our specific research questions were, 1) Does local human land use disturbance affect wetland relationships with lake TP and water color?, and 2) Are wetland relationships with lake TP and water color different across regions, and if so, which regional characteristics are related to this variation? To address these questions we compiled lake water chemistry and landscape data for lakes distributed across twenty-three regions (see below for how we define region) within several states (Wisconsin, Michigan, New Hampshire, and Maine).

We took an information theoretic approach to examine our hypotheses by comparing six candidate models based on hypothesized mechanisms and ranking them by best fit given the data. We developed candidate models that included both direct effects and interactive effects between landscape-context variables and lake-response variables (TP and water color) (Table 1). The citations for our candidate models are not an exhaustive review but are examples of the hypothesized landscape-context relationships. In addition, we hypothesized that lake TP and water color concentrations are different among regions and thus, should be modeled as such. The five candidate models are as follows. Local or within-region lake TP and color variation was modeled using local-scale landscape variables including natural HGM features and wetlands (Model 1), additive human land use disturbance (Model 2a), and land use interactions with wetlands (Model 2b). Regional-scale models were added to the local models to account for among-region TP and color variation (Model 3). We tested whether local wetland effects

(i.e. the slope parameters for wetlands) were different among regions (Model 4) and if regional-scale features could explain these differences (Model 5).

Methods

Study lakes and lake data

Landscape, hydrology, and lake water chemistry data were compiled for 1,790 lakes in Maine, New Hampshire, Michigan, and Wisconsin, USA from existing databases collected and obtained from state agencies (Figure 1). We included lakes with surface area greater than 0.01 km^2 and maximum depths greater than 2 m. See Webster et al. (2008) for a complete description of the compiled database.

Water chemistry measurements were collected by state agencies with the majority of sampling occurring from 1990-2003 following standardized field and laboratory procedures. We restricted water chemistry measurements to single samples collected from the epilimnion from June – September when summer stratification is likely to occur. Lake TP was measured using colorimetric analyses with persulfate digestion. Lake water color was measured using visual comparators in platinum cobalt units (PCU). 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.

Analyses were conducted on two datasets (Figure 1). The first dataset (“all-lakes”) included 1,790 lakes for TP and 1,527 lakes for color. The second dataset (“minimally-disturbed”) included 777 lakes for TP and 686 lakes for color. Lakes were

considered minimally disturbed if they had less than 5% agriculture or urban land use within a 500 m buffer surrounding the lake. Although there are other landscape disturbances that affect lakes, we use agriculture and urban land use as an indicator of many of the major human impacts in the catchment that influence water chemistry (Morrice et al. 2007).

Landscape-context variables defined as hydrogeomorphic (HGM), wetland, and land use variables were collected from existing state databases and geographic information systems (GIS) data layers. Landscape-context variables that were considered “natural” were lake depth, drainage ratio (catchment area to lake area ratio), baseflow (groundwater contribution), and wetlands; and landscape-context variables that represented “disturbance” were agriculture and urban land use. We obtained land use / cover (LULC) and wetland data from the 1992 National Land Cover Dataset (<http://landcover.usgs.gov/natl/landcover.php>) and included categories for upland forest, wetland (forested, emergent, and total), agriculture, and urban land. Baseflow, the proportion of streamflow from ground-water discharge, was quantified using a baseflow index based on United States Geological Survey (USGS) stream gage data (Wolock 2003).

Measures of lake depth (maximum and mean) and total catchment area were compiled from state databases. Lake surface area was quantified 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.

All of the landscape-context variables except morphometry metrics were quantified at two spatial scales: local and regional. Local variables were quantified within a 500 m buffer surrounding lakes. The 500 m lake buffer was intended to simulate the local lake catchment area, and correlation analyses using a subset of these study lakes showed that LULC proportions in the 500 m lake buffer were highly correlated ($r > 0.50$) with proportions in the local catchment (Webster et al. 2008). In addition, land cover quantified in the 500 m lake buffer was just as good a predictor of lake DOC as land cover measured in the whole catchment for several Wisconsin lakes (Gergel et al. 1999). Thus, landscape context features measured at the 500 m buffer scale can capture ecologically relevant features at the local scale that are related to lake nutrient and carbon dynamics. We used only one measure for wetland cover to simplify the model building process. We tested univariate relationships between TP and color and the three wetland measures and found that forested wetlands had the strongest relationship with both TP and color in comparison to total wetland and emergent wetland measures. In addition forested wetland land cover was highly correlated with all other wetland variables (Fergus, unpublished data) and thus we used only forested wetlands in all models.

At the regional scale we quantified the proportion of agriculture and baseflow within regions defined as Ecological Drainage Units (EDU) (Higgins et al. 2005). Ecological Drainage Units are regionalization schemes developed to classify freshwater ecosystems and aquatic biodiversity using topographic, hydrologic, and climatic features. These units have been shown to capture more variation in lake water chemistry variables on average than other regionalization schemes (Cheruvelil et al. 2008). Background on the landscape-contextual similarities and differences among the Midwest and New

England regions of the U.S. is provided in the Appendix. The regional-scale features used in the models were narrowed down to agriculture for TP and baseflow for color based on preliminary correlation analyses.

Statistical analyses

We fit the five candidate mixed effects models (Table 1) for each of the datasets and for each response variable, except where noted below. Models 2a and 2b, which included local agriculture and urban predictor variables and their interactions with wetlands, were excluded from the minimally-disturbed dataset analysis because agriculture and urban development were not hypothesized to account for variation in TP and color under such low proportions in the landscape. However, models 2a and 2b were included in the all-lake dataset analysis.

Lake TP and water color were natural log transformed, lake and catchment morphometry variables were natural log transformed, and land cover/use proportions were arc sine square root transformed to meet statistical assumptions of normality. Local predictor variables were group mean centered ($X_{ij} - \bar{X}_{.j}$) to control for among region differences and reduce correlations with regional predictors (Enders and Tofghi 2007). Regional variables were grand mean centered by subtracting individual observations from the overall mean value ($X_{ij} - \bar{X}_{..}$). Multilevel mixed effects analyses were performed using SAS MIXED procedure (SAS, Cary, NC).

Mixed effects model building process

We describe the model-building process using TP as the response variable but the exact steps were applied to color as the response variable.

Regional variation in lake TP: unconditional models with random intercepts –

Prior to testing our specific research questions, we determined whether there was significant regional variation in lake TP by developing unconditional models that had no predictor variables but allowed for TP to vary by region (random intercept). This preliminary analysis partitioned the total variation in lake TP into two variance components: σ^2 within region (local variation) and τ_{00} among region (regional variation).

The unconditional model to predict lake TP is:

$$\begin{aligned} Y_{ij} &= \beta_{0j} + r_{ij} , \\ \beta_{0j} &= \gamma_{00} + u_{0j} , \\ \text{where } r_{ij} &\sim N(0, \sigma^2) \text{ and } u_{0j} \sim N(0, \tau_{00}) \end{aligned} \tag{1}$$

In this model Y_{ij} is lake TP for lake i in region j ; β_{0j} is the mean region TP or random intercept; and r_{ij} is the individual error for lake i in region j . The intercept (β_{0j}) is the sum of the overall mean TP (γ_{00}) across all regions and u_{0j} , a random regional error for region j (regional residual from the grand mean intercept), where $u_{0j} \sim N(0, \tau_{00})$ and τ_{00} represents the among region variability in lake TP. Within region lake TP variation is represented by σ^2 .

From this unconditional model we can calculate the intraclass correlation coefficient (ICC, ρ) which measures the proportion of TP variance that is among regions:

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

The intraclass correlation coefficient (ICC) provides an estimate of the extent to which lakes in a region are correlated to one another with regard to lake TP concentrations. The ICC value was used to evaluate if a mixed effect model approach was needed or if regional variation was sufficiently low that ordinary least squares regression models were appropriate. The unconditional models indicated that there were significant in TP and color among regions and all subsequent models were built as mixed-effect models allowing for random intercepts.

Local TP variation models with local landscape-context predictors [Models 1-2b]

– To address research question 1 we modeled within-region (local) lake TP variation using the *a priori* local landscape-context variables hypothesized to affect lake TP and color (Models 1-2b in Table 1). 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. The premise for this approach is to maximize the likelihood of the parameters given the data as opposed to the ordinary least squares method of minimizing the model residual error.

A local model with a single fixed-effect predictor variable (lake depth) for lake TP is presented below:

$$Y_{ij} = \beta_{0j} + \beta_{1j} (\text{Depth}_{ij}) + r_{ij} \quad (3)$$

$$\beta_{0j} = \gamma_{00} + u_{0j}$$

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

$$\text{where } r_{ij} \sim N(0, \sigma^2) \text{ and } u_{0j} \sim N(0, \tau_{00})$$

In this model Y_{ij} is lake TP for lake i in region j ; β_{0j} is the mean region TP or random intercept; β_{1j} is the fixed effect of lake depth on lake TP; and r_{ij} is the individual error for lake i in region j , where $r_{ij} \sim N(0, \sigma^2)$ and σ^2 represents the within-region lake TP variation. β_{1j} is the fixed average lake depth-TP regression slope across regions (γ_{10}). More complex local models can be developed from this simplified model by including other local landscape-context predictors.

Local predictor variables that reduced the within-region variation (σ^2) were retained in the model building process. The proportion of variance explained by the local landscape-context variables was calculated as:

$$Var_{local} = (\sigma^2_{unconditional} - \sigma^2_{current\ model}) / \sigma^2_{unconditional},$$

(4)

where Var_{local} is the local TP or water color variation explained by the local model; $\sigma^2_{unconditional}$ is the within-region variation in the unconditional random intercept model, and $\sigma^2_{current\ model}$ is the within-region variation in the models conditioned with predictor variables.

Local and regional TP variation modeled with local and regional landscape-context predictors [Model 3] – Regional landscape-context variables were added to the best ranked local model to explain among-region TP variation. An example of a model including local and regional variables to predict TP is illustrated below using lake depth at the local scale and the proportion of agriculture at the regional scale:

$$Y_{ij} = \beta_{0j} + \beta_{1j} (\text{Depth}_{ij}) + r_{ij}, \quad (5)$$

$$\beta_{0j} = \gamma_{00} + \gamma_{01}(\text{Regional Agriculture})_j + u_{0j},$$

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

$$\text{where } r_{ij} \sim N(0, \sigma^2) \text{ and } u_{0j} \sim N(0, \tau_{00})$$

In this model the random intercept (β_{0j}) is a function of the overall mean (γ_{00}) and the proportion of agriculture in the region (γ_{01}). The variance τ_{00} is the regional level variance after controlling for regional agriculture.

Many of the variables quantified at the regional scale were strongly correlated to one another (Table A2) so we did not include more than one regional variable at a time into any model. The regional variation explained by the addition of the regional landscape-context predictor was calculated as:

$$Var_{region} = (\tau_{00 \text{ unconditional}} - \tau_{00 \text{ conditional model}}) / \tau_{00 \text{ unconditional}}, \quad (6)$$

where Var_{region} is the regional TP variation explained by the addition of the regional variable to the model; $\tau_{00 \text{ unconditional}}$ is the between-region variation in the unconditional random intercept model, and $\tau_{00 \text{ conditional model}}$ is the between-region variation in the model conditioned with predictor variables.

Regional wetland effects variation modeled with local & regional predictors and random wetland effects [Model 4] – To address research question 2, local wetlands were treated as random effects to determine whether wetland relationships with lake TP were

significantly different among regions (i.e. random wetland slopes). A model with local and regional landscape-context variables and random wetland slopes is presented below:

$$Y_{ij} = \beta_{0j} + \beta_{1j}(\text{Depth}_{ij}) + \beta_{2j}(\text{Wet}_{ij}) + r_{ij}, \quad (7)$$

$$\beta_{0j} = \gamma_{00} + \gamma_{01}(\text{Regional Agriculture})_j + u_{0j},$$

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

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

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

In this model, lake TP is a function of lake depth (fixed effect) and random local wetland effects across regions. Both the intercept and wetland slope are allowed to vary among regions by including 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 lake 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 wetland effect variability; and τ_{01} is the covariance between u_{0j} and u_{2j} .

These models were evaluated using an alpha of 0.05 to determine whether wetlands should be treated as random effects or fixed effects across all regions.

Regional wetland effects variation modeled with random wetland effects and cross-scale interactions [Model 5] – After determining whether wetland effects were variable across regions, we attempted to explain this variation by including interaction

terms between local wetlands and regional landscape-context variables referred to as cross-scale interactions. Building on equation 7, we can include an interaction term between local wetlands and a regional-scale variable such as agriculture which yields the following example model:

$$Y_{ij} = \beta_{0j} + \beta_{1j}(\text{Depth}_{ij}) + \beta_{2j}(\text{Wet}_{ij}) + \beta_{3j}(\text{Wet}_{ij} \times \text{Regional Agric.}) r_{ij}, \quad (8)$$

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

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

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

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

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

In this model lake TP 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 wetlands (γ_{20}), and the cross- scale interaction between local wetlands and regional agriculture (γ_{21}). A decrease in τ_{11} , the variation in wetland slope among regions, indicates that the regional interaction explained differences in wetland effects among regions.

Model evaluation: information criteria theory – All candidate models were evaluated and ranked based on information criteria theory. For each model, Akaike Information Criteria values (AIC) were calculated with lower values indicating better model fits for the data. Models with the lowest AIC value were compared to other

candidate models in each dataset based on the differences in AIC values (Δ_i) and Akaike weights. The Akaike weights (w_i) quantify the evidence for empirical support of that model (Anderson and Burnham 2002).

Results

Lake water chemistry and local and regional landscape context variables

There was a wide range of lake TP and color concentrations across the study lakes. Lake TP concentration ranged from 1 to 193 μgL^{-1} , water color concentration ranged from 1 to 140 PtCo (Tables 2 and 3). In the minimally-disturbed datasets, lake TP did not exceed 30 μgL^{-1} , but water color ranged from 1 to 140 PtCo. Local landscape-context variables including lake depth, drainage ratio, and mean baseflow also captured a wide range of values across all datasets (Tables 2 and 3). Local LULC surrounding lakes was highly variable with agriculture ranging from 0 to 93% in the all-lake TP dataset. Most of the lakes were dominated by forest cover (median 78%) with low agriculture (median 4%) and low urban (median 1%) land use coverage.

Lakes were contained within twenty-three regions composed of diverse climatic, hydrologic, and landscape characteristics. Regional landscape characteristics were similar for the all-lake and minimally-disturbed lake datasets (Table 2 and 3). Regional agriculture and urban land use in the all-lake TP dataset ranged from 1 - 78% and 0 - 20% respectfully and were greater than those in the minimally-disturbed TP dataset (1- 61% for agriculture and 0 - 6% for urban). The HGM variables among regions varied as well:

baseflow ranged from 46 to 78% and wetlands ranged from 1 to 35% in the all-lake TP dataset and had similar values for the minimally-disturbed TP dataset.

Regional variation in lake TP: unconditional models with random intercepts

The unconditional models showed that there was significant variation in lake TP and water color among regions (Table 4). This result means that lakes within the same region have more similar lake TP and color concentrations compared to lakes from other regions. The all-lake TP dataset had the greatest TP regional variation with 31% of the total variation in TP occurring at the regional scale. For the minimally-disturbed lake TP dataset, 16% of the total TP variation occurs at the regional scale and 84% of the variation occurs at the local scale. This indicates that within-region differences may account for more TP variation for minimally-disturbed lakes.

For the all-lake color dataset, about 13% of the total color variation occurs at the regional scale and the remaining 87% variation occurs at the local scale (Table 4). For the minimally-disturbed water color dataset, 20% of the total water color variation occurs at the regional scale and 80% of the variation occurs at the local scale (Table 4).

The above unconditional models for all four datasets showed that a significant proportion of TP and color variation occurs at the regional scale and so to treat lakes as independent observations would violate assumptions of independence. Thus, all remaining analyses were conducted using multilevel mixed effects models in which we account for this regional variation in lake TP and water color by allowing for random intercepts among regions.

Local TP variation models with local landscape-context predictors [Models 1-2b]

Across the local candidate models, the *a priori* hypothesized HGM variables (lake depth, drainage ratio, and baseflow) had similar relationships with TP and color. Total phosphorus and color relationships were both negatively related to lake depth, positively related to drainage ratio, and negatively related to baseflow (Tables 5 – 8) as were hypothesized in Table 1. Mean lake depth was used in all models except the all-lakes TP dataset in which maximum depth was more strongly related to TP.

The relationships between wetlands and lake chemistry differed between TP and color and across datasets. As expected (Table 1), local wetlands were positively related to lake color for both the all-lake and minimally-disturbed datasets (Tables 6 and 8). However, in the all-lake TP dataset, wetland effects were not significant across candidate models (Table 5). In the minimally-disturbed lake TP dataset, wetlands were related to TP ($\alpha < 0.1$) such that higher TP occurred in lakes with increased wetlands around the lake (Table 7), which matched our expectation.

The local candidate models that had the best fit given the data were different for TP and water color for the all-lake datasets. Of the local candidate models evaluated for the all-lake TP dataset, Model 2a had the lowest AIC value relative to the other candidate models (Table 5). Including agriculture and urban development as positive additive effects explained 21% of the TP variation at the local scale (within-region variation). For the all-lake color dataset, local agriculture and urban land use in Model 2a were not significantly related to water color (Table 6). Local models that included interaction terms between wetlands and land use did not significantly improve the model fit for TP nor water color (Model 2b in Tables 5 and 6).

In the all-lake TP datasets the lack of a wetland–TP relationship suggests that local land use disturbance may obscure wetland effects and modeling wetland-land use interactions at different spatial scales may explain wetland relationships with TP.

Local and regional TP variation modeled with local and regional landscape-context predictors [Model 3]

After accounting for local landscape context variables, there was significant regional lake TP and water color variation remaining. We calculated the deviation of regional mean lake TP and water color from the grand mean, referred to as best linear unbiased predictors (Blups), and geographically portrayed Blup values in Figures 2 and 3. On average, regions in Michigan and Wisconsin had higher TP compared to lakes in Maine and New Hampshire (Figure 4). Regional water color had less obvious regional spatial patterns (Figure 5).

The addition of regional landscape context variables to the best local models reduced among-region variance (τ_{00}) in the TP and color models and improved the model fit for all datasets (Model 3 in Tables 5 – 8). In the all-lake TP dataset, 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 5). Lakes within regions with high agriculture tended to have higher TP concentrations compared to lakes from regions with low agriculture (Figure 6).

In the all-lake color dataset, the proportion of baseflow in the region accounted for 4% of the regional color variation (Table 6). Regions with high baseflow tended to have lakes with lower color concentrations compared to regions with low baseflow (Figure 7).

The same regional-scale variables accounted for lake TP and color regional differences for both the minimally-disturbed and all-lake datasets. In the minimally-disturbed TP dataset, regional agriculture accounted for 8% of the regional TP variation and was associated with increased regional average TP concentrations (Table 7). In the minimally-disturbed color dataset, the percent baseflow at the regional scale explained 14% of the regional water color variation and was negatively related to regional average color concentrations (Table 8). Overall, including regional-scale variables to the model improved the model fit (lowered AIC values) compared to models with only local variables.

Regional wetland effects variation modeled with local & regional predictors and random wetland effects [Model 4]

Wetland effects were different among regions for both TP and color, and allowing for random wetland slopes among regions (Model 4) lowered AIC values and improved model fit compared to models treating wetlands as fixed effects for the all-lakes datasets. In the all-lakes TP dataset (Table 5), variation in the random wetland effects was significantly different from zero ($\alpha < 0.10$) and lowered the AIC values by 6 units from Model 3 which kept wetland effects fixed across regions. In the all-lakes color dataset (Table 6), variation in mean wetland regression effects was significantly different from zero ($\alpha < 0.10$) and lowered the AIC values by 11 units from the model which kept wetland effects fixed across regions. However, in the minimally-disturbed TP and color datasets, including random slope terms for wetlands did not improve the model fit, indicating that wetland effects on TP and color in catchments dominated by natural land cover (>95%) were not highly different across regions (Model 4 in Tables 7 and 8).

Regional wetland effects variation modeled with random wetland effects and cross-scale interactions [Model 5]

In the all-lakes datasets, among-region differences in wetland effects on TP and color were explained by regional-scale landscape-context variables. Cross-scale interaction terms between local wetlands and regional landscape context variables explained variation in wetlands slopes for TP and color (Model 5 in Tables 5 and 6). Regional agriculture explained differences in wetland-TP relationships across regions, such that wetland effects on lake TP were greater in regions with low proportions of agriculture than in regions with high proportions of agriculture. Regional baseflow explained differences in wetland-color relationships, such that wetland effects on color were greater in regions with low baseflow than in regions with high baseflow.

Discussion

We found that when examining the relationship between wetlands and lake chemistry, we must consider multiple spatial scales as well as human disturbances, both of which are closely intertwined. We have two main conclusions. First, we found that lake TP and color were controlled by similar lake and catchment features but different regional variables. Differences in regional lake TP were related to regional land use, whereas differences in regional water color were related to regional ground water contribution (baseflow). Second, we found that across regions, local wetland effects on TP and color were different and related to different factors. Local wetlands interacted with regional land use to affect lake TP concentrations such that increasing local wetlands decreased agricultural effects on lake TP concentrations or vice versa. For water

color, wetlands were positively related to color and differences in the region-specific slopes were attributed to regional groundwater contribution.

Our mixed-effect analyses indicated that both lake TP and color variation were greater within regions than between regions highlighting the importance of local lake and catchment features to predict lake TP and color. Other studies have supported this finding. They have demonstrated that within regions, TP variation is high and can partially be accounted for by considering lake depth (Omernik et al. 1991) and local catchment land use (Wickham et al. 2005). Nevertheless, regional differences in lake phosphorus and color were large enough that across-region variation should not be ignored.

Local landscape variables that predict within-region variation in TP and color were similar to past studies and matched our expectations (Table 1). Lake depth was negatively associated with both lake TP and color (Rasmussen et al. 1989). Drainage ratio was positively associated with lake TP and color suggesting that small lakes with large catchments have increased TP and color concentrations, which supports other studies (Rasmussen et al. 1989, Kortelainen 1993). Webster et al. (2008) found that drainage ratio is strongly correlated to water residence time and thus provides the mechanisms for this relationship (i.e. internal controls of lake TP and water color). Lakes with small drainage ratios are likely to have long water residence time which has been related to decreased internal lake TP loading (D'Arcy and Carignan 1997) and increased photodegradation of color (Molot and Dillon 1997).

We found that lake 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 lake

DOC (Xenopoulos et al. 2003, Sobek et al. 2007). Our measure of region (EDU) captured TP variation (as found by Cheruvilil et al. 2008 for Michigan) and it also captured significant water color variation. However, we did not test EDU against different regionalization frameworks and there may be other region measures that capture even more lake water color variation. This is an area that warrants further study.

Regulation of lake TP and color by regional factors and the role of disturbance

Lake phosphorus and water color are hierarchically regulated by landscape-context features at local and regional scales. Numerous studies have examined how lake nutrients and organic carbon are affected by local features but few have explicitly examined how they are affected by regional variables. Using mixed effect model analysis, we found that regional variables consistently improved the overall model fit and explained regional differences in lake TP and water color.

An important outcome of our study is the potential role of regional disturbance on lake TP. It is well documented that agriculture exports phosphorus to surface waters at local scales within a catchment or in near-lake buffers (Hunsaker et al. 1992). But our results imply that agricultural activities within a *region* affect lake phosphorus concentrations as well. Agriculture and urban development have been related to higher regional lake TP concentrations compared to regions with low amount of agriculture and urban land use within the Northeastern USA (Rohm et al. 1995). These relationships indicate that human land use development, particularly agriculture, have diffuse, far reaching effects on surface water chemistry such that land use within a region may even affect lakes buffered by minimally disturbed local catchments. One potential explanation for this pattern is that agriculture-dominant regions may have more nutrient rich soils as

opposed to regions with low amounts of agriculture. However, we did not have soils data available to tease apart the relative influence of soil composition versus agricultural activity for this study, and this issue warrants further study. Regional agricultural effects on lake water chemistry have important implications for identifying reference lakes used to set nutrient criteria. For example, identifying reference lakes simply by land use disturbance at the local scale may be misleading because it does not take into account regional land use disturbance that may be having an effect on lake nutrient levels.

Although water color was not related to regional disturbance in our study, it was related to regional natural features such as the percent of groundwater contribution (baseflow). In the all-lake dataset, the proportion of groundwater contribution in the region was negatively related to water color. Negative relationships between baseflow and carbon measures have been observed in studies conducted at the local scale (Jordan et al. 1997). In our study regions, areas with low baseflow are characterized as having clay-rich glacial deposits which promote surface runoff contribution (Wolfson 2009) and this runoff could carry greater humic carbon concentrations (Thierfelder 1999). Conversely, lakes in regions with high baseflow likely receive large groundwater input which is 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). In addition, we found a negative correlation between regional baseflow and regional upland

forest cover ($r = -0.51$) across all states. Together these findings indicate that high baseflow regions may have reduced allochthonous humic carbon sources to lakes.

Wetland effects on lake TP and water color and the role of disturbance

Across regions, the local effects of wetlands on lake TP were related to regional agriculture. In regions with high amounts of agriculture, wetlands surrounding lakes were associated with decreased lake TP concentrations, indicating that wetlands may reduce nutrient loading from agriculture at a regional scale. Given the nature of the analysis we are not able to determine the specific mechanisms underlying the interaction term so we can interpret the finding as either a result of local wetlands decreasing the regional agricultural effects on lake TP or conversely regional agriculture decreasing the local wetland effects on lake TP.

We were surprised to not find support for local-scale land use interactions with wetland-lake TP relationships. The lack of a local agriculture-wetland interaction may be explained by considering the coarse wetland metric that we used. Quantifying wetlands within the 500 m lake buffer ignores wetland spatial configuration and connectivity in the catchment, and landscape metrics that explicitly capture wetland connectivity have been shown to be better predictors of lake nutrients than non-spatial metrics (Devito et al. 2000). For wetlands to interact or affect land use disturbance effects on lake phosphorus, it is expected that they must be located in-between nutrient sources (agriculture or urban land use) and sinks (lakes) in the catchment to intercept nutrient runoff. The wetland proportion metric used in this study quantifies all wetlands in the surrounding landscape near the lake, but not necessarily the wetlands that are most hydrologically connected to the lake. Thus, wetlands were weakly associated with lake TP concentrations in our

dataset that included catchments with the full range of disturbance. We were not able to quantify wetland spatial metrics for our study lakes but we expect that these spatial characteristics are important to capture wetland effects on lake TP at local scales.

In the minimally-disturbed dataset, local wetland-TP relationships were generally fixed across regions and were positively associated with lake TP. These findings are in support of Devito et al. (2000) which indicated that forested wetlands may be phosphorus sources to lakes in settings with minimal land use disturbance.

Local wetlands were positively related to water color and the magnitudes of these relationships were different among regions (Table 6). Past studies link wetlands to increased DOC concentrations in lakes and streams and support the finding that wetlands act as carbon sources (Gergel et al. 1999, Xenopoulos et al. 2003). Land use disturbance was not related to water color, which is consistent with other studies (Trebitz et al. 2007, Wilson and Xenopoulos 2008). Unlike wetland-TP relationships, land use disturbance did not interact with wetland effects on lake water color. Rather wetland effects were different across regions due to differences in regional baseflow. Local wetlands negatively interacted with regional baseflow such that one reduced the effect of the other on lake water color. Greater regional baseflow or groundwater contribution could be associated with less surface water runoff, reducing wetland effects on humic carbon transport (Jordan et al. 1997). However, it is challenging to link regional hydrology to specific wetland function when it is not known how regional hydrology affects local wetland hydrology and carbon transport.

Limitations of analysis

Similar to landscape studies conducted at the local scale, regional studies suffer from problems of multi-collinearity among landscape variables (King et al. 2005). Several regional scale landscape context variables were highly correlated to one another (Table A2), and we included only one regional variable in a model at a given time. 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, agricultural mechanisms related to phosphorus transport to lake bodies at the local scale are well supported in the literature and likely could persist at the regional scale. We tried to avoid collinearity problems by keeping our landscape models simple and grounded in ecological theory, but it is important to consider these spatial limitations when conducting multi-level landscape studies.

Multi-level landscape studies are empirical in nature and lack the fine spatial and temporal information integral to process-based mechanistic models. This is both a weakness and strength of the empirical landscape approach (Ahlgren et al. 1988). The landscape-context variables used in this analysis were fixed in time and were of coarse spatial resolution. It is known that seasonal variability in features such as precipitation can affect freshwater hydrology and thus nutrient and carbon processes (Cole et al. 2002), and phosphorus and dissolved organic carbon dynamics can exhibit spatial and temporal variability (Johnston et al. 2001, Wilson and Xenopoulos 2008). However, it can be challenging to acquire both high frequency and high resolution data for a single lake system let alone multiple lakes across different regions. In addition, we can only hypothesize about the ecological processes and internal lake mechanisms that propagate the lake TP and color patterns observed. However, without broadening the study scope to

include local and regional characteristics, we would be missing important ecological relationships that hierarchically link systems together. Regional-scale studies are important steps to identify broad-scale patterns, and they are a starting point to develop more in-depth studies to better understand how the regional landscape context may constrain finer-scale ecological processes. In this way multi-level landscape studies can complement process based models and improve upon their efficiency (Strayer et al. 2003).

Implications

In this study we have shown that lake TP and color are controlled by variables at both local and regional scales. Wetlands are important land cover features that affect lake TP and color differently and interact with land use at broad spatial scales. Considering multi-scaled landscape controls on lake TP and color is important to be able to predict water chemistry and set realistic nutrient guidelines. In addition actively incorporating multi-scaled interactions among landscape variables will help elucidate mechanisms for TP and color transport between ecosystems. A multilevel mixed-effect model approach is a useful analytic technique to better understand how ecological processes operate across multiple spatial scales which has been identified as an important research challenge in landscape and ecosystem ecology.

Table 1. Candidate models to test hypothesized relationships between local and regional landscape-context variables and lake total phosphorus (TP) and water color. Landscape-context variables were grouped into prediction type classes: hydrogeomorphic variables (HGM), wetlands (WET), human land use disturbance (LU), local disturbance interactive effects ($WET_L * LU_L$), random local wetland effects across regions (WET_L -RAN), and cross-level interactive effects ($WET_L * X_R$). Variables excluded from the models are denoted by “—”. Variables with the same hypothesized relationship as the previous model are symbolized by “*”. “All-lakes” is the complete lake dataset, including all levels of land use disturbance, and “Min-dist.” is the minimally-disturbed lake dataset (<5% agriculture and urban land use). Regional landscape-context variables are italicized.

Scale of predictor variables:			Local		Local and Regional			
Scale of interaction:			Local		Regional			
Candidate models:			1. HGM + WET	2a. HGM + WET + LU	2b. HGM + WET + LU + (WET _L * LU _L)	3. Top local + regional	4. Top local + regional + WET _L -RAN	5. Top local + regional + WET _L -RAN (WET _L * X _R)
Lake response	Landscape-context variable							
TP	Lake depth	1. Neg.	*	*	*	*	*	*
	Drainage ratio	2. Pos.	*	*	*	*	*	*
	Baseflow	3. Neg.	*	*	*	*	*	*
	Wetland	3. & 4. n.s.	*	*	*	*	*	*
	Agriculture	—	4. Pos.	*	*	*	*	*
	Urban	—	5. Pos.	*	*	*	*	*
	Wet _L * Agr _L	—	—	Neg. interact. ^{4.}	*	*	*	*
	Wet _L * Urb _L	—	—	Neg. interact.	*	*	*	*
<i>Agriculture</i> Regional		—	—	—	<i>Pos.</i>	*	*	*
WET _L -RAN		—	—	—	—	Random	*	*
<i>Agr</i> ·R * Wet _L		—	—	—	—	—	<i>Neg. interact.</i>	

Table 1. (cont'd)

Scale of predictor variables:		Local		Local and Regional			
Scale of interaction:		Local			Regional		
Candidate models:		1. HGM + WET	2a. HGM + WET + LU	2b. HGM + WET + LU + (WET _L * LU _L)	3. Top local + regional	4. Top local + regional + WET _L -RAN	5. Top local + regional + WET _L -RAN (WET _L * X _R)
Lake response	Landscape-context variable						
Color	Lake depth	6. Neg.	*	*	*	*	*
	Drainage ratio	7. Pos.	*	*	*	*	*
	Baseflow	8. Neg.	*	*	*	*	*
	Wetland	6. Pos.	*	*	*	*	*
	Agriculture	9. —	n.s.	*	—	—	—
	Urban	—	—	n.s.	—	—	—
	Agr _L * Wet _L	—	—	n.s.	—	—	—
	Urb _L * Wet _L	—	—	n.s.	—	—	—
	Baseflow _{Regional}	—	—	—	Neg.	*	*
	WET _L -RAN	—	—	—	—	Random ^{10.}	*
	Baseflow _R * Wet _L	—	—	—	—	—	Neg. interact.

1. Canfield and Bachmann 1981

7. D'Arcy and Carignan 1997

2. Prepas et al. 2001

8. Jordan et al. 1997

3. Devito et al. 2000

9. Wilson and Xenopoulos 2008

4. Detenbeck et al. 1993

10. Xenopoulos et al. 2003

5. Soranno et al. 1996

6. Rasmussen et al. 1989

Table 2. Summary statistics of local and regional landscape-context variables used to predict lake TP for all lakes (n = 1,790 in 23 regions) and for minimally-disturbed lakes (n = 777 in 16 regions). Minimally-disturbed lakes were defined to have < 5% agriculture and urban land use within a 500 m buffer surrounding lakes from the all-lakes dataset. Regional variables are italicized.

Prediction type	Scale	Landscape-context variable	All lakes (n = 1,790; N = 23)			Minimally disturbed lakes (n = 777; N = 16)		
			Median	SD	Range	Median	SD	Range
Lake response	Local	TP ($\mu\text{g L}^{-1}$)	11	14	1 – 193	9	6	1 – 30
		Color (PtCo)	14	19	1 – 140	14	18	1 – 140
HGM	Local	Catchment area (ha)	734	19,172	9 – 197,357	507	18,560	9 – 185,443
		Lake area (ha)	51	681	1 – 18,043	47	581	1 – 6,724
		Drainage ratio	13	191	1 – 2,800	12	72	1 – 856
		Mean depth (m)	4	3	0.3 – 26	4	3	1 – 26
		Max. depth (m)	10	9	2 – 68	10	10	2 – 68
		% Baseflow	54	10	34 – 89	55	10	43 – 88
		% Forest	78	22	4 – 100	89	13	9 – 100
		% Wetland	3	9	0 – 66	3	10	0 – 66
		% Agriculture	4	17	0 – 90	1	1	0 – 5
		% Urban	1	0.9	0 – 93	0.04	0.6	0 – 4
WET LU	Regional	<i>Regional area (km^2)</i>	15,250	11,524	2,830 – 48,950	19,670	12,451	3,787 – 48,950
		<i>% Baseflow</i>	53	8	46 – 78	53	8	46 – 78
		<i>% Forest</i>	76	20	9 – 86	76	12	23 – 86
		<i>% Wetland</i>	3	6	1 – 35	3	7	2 – 35
		<i>% Agriculture</i>	7	19	1 – 78	7	9	1 – 61
		<i>% Urban</i>	2	3	0 – 20	1	2	0 – 6

Table 3. Summary statistics of local and regional landscape-context variables used to predict lake water color for all lakes ($n = 1,527$ in 21 regions) and for minimally-disturbed lakes ($n = 686$ in 16 regions). Minimally-disturbed lakes were defined to have < 5% agriculture and urban land use within a 500 m buffer surrounding lakes from the all-lakes dataset. Regional variables are italicized.

Prediction type	Scale	Variable	All lakes ($n = 1,527$; $N = 21$)			Minimally disturbed lakes ($n = 686$; $N = 16$)		
Lake response			Median	SD	Range	Median	SD	Range
Local		TP ($\mu\text{g L}^{-1}$)	10	11	1 – 155	9	6	1 – 30
		Color (PtCo)	14	19	1 – 140	14	18	1 – 140
	HGM	Catchment area (ha)	710	19,474	9 – 197,357	488	19,208	9 – 185,443
		Lake area (ha)	46	718	1 – 18,043	41	604	1 – 6,724
		Drainage ratio	14	200	1 – 2,800	12	73	1 – 856
		Mean depth (m)	4	3	1 – 26	4	4	1 – 26
		Max. depth (m)	9	9	2 – 68	10	10	2 – 68
		% Baseflow	53	10	36 – 89	51	9	44 – 88
		% Forest	80	21	4 – 100	90	13	9 – 100
		% Wetland	3	9	0 – 66	3	10	0 – 66
Regional		% Agriculture	4	15	0 – 88	1	1	0 – 5
		% Urban	4	9	0 – 93	0.04	0.6	0 – 4
	HGM	<i>Regional area (km^2)</i>	15,250	12,020	2,830 – 48,950	19,670	12,451	3,787 – 48,950
		<i>% Baseflow</i>	55	8	46 – 78	54	7	46 – 78
		<i>% Forest</i>	70	18	9 – 86	75	10	23 – 86
WET LU		<i>% Wetland</i>	6	6	2 – 35	6	7	2 – 35
		<i>% Agriculture</i>	13	17	1 – 78	7	7	1 – 61
		<i>% Urban</i>	3	3	0 – 20	2	2	0 – 6

Table 4. Unconditional multilevel mixed effect models for lake TP and color with no predictor variables and random intercepts. Variance estimates for within-region (σ^2) and between-region (τ_{00}) are provided. The intraclass correlation (%ICC or ρ) is the estimated proportion of regional variation from the total variation, calculated as $\tau_{00}/(\tau_{00} + \sigma^2)$ and is presented as a percent.

Lake dataset	Lake and (region) N	Estimate	σ^2	τ_{00}	% ICC
All-lake TP	1,790 (23)	2.66	0.42	0.19	31
All-lake color	1,527 (21)	2.55	0.67	0.10	13
Minimally-disturbed TP	777 (16)	2.28	0.35	0.07	16
Minimally-disturbed color	686 (16)	2.54	0.62	0.16	20

Table 5. Mixed effects models predicting lake TP for the all-lakes dataset ($n = 1,790$ lakes, $N = 23$ regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM), wetland (WET), and land use disturbance (LU) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN. Local wetland interactions at local and regional scales are presented in Models 2b and 5. Estimates of variance components are presented for within-region lake TP (σ^2), between-region intercept (τ_{00}), and between-region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.

Category	Scale of predictor variables:			Local and Regional		
	Scale of interaction:			Local and Regional		
	Candidate models:			Local and Regional		
	1. HGM + WET	2a. HGM + WET + LU	2b. HGM + WET + LU + (WET _L * LU _L)	3. Top local + regional	4. Top local + regional + WET _L -RAN	5. Top local + regional + WET _L -RAN (WET _L * LU _R)
HGM						
	Max. depth	-0.43**	-0.43**	-0.43**	-0.43**	-0.43**
	Drainage ratio	0.08**	0.06**	0.06**	0.06**	0.06**
	Baseflow	-0.008*	-0.008*	-0.008*	-0.008*	-0.008*
WET	Wetland	n.s.	n.s.	n.s.	n.s.	n.s.
LU	Agriculture	—	0.76**	0.76**	0.72**	0.70**
	Urban	—	0.42**	0.42**	0.38**	0.38**
Interaction	Wet _L * Agr _L	—	—	—	—	—
	Wet _L * Urb _L	—	—	—	—	—
Regional	<i>Agriculture_R</i>	—	—	1.20**	1.20**	1.20**
	<i>Agr_R * Wet_L</i>	—	—	—	—	-1.59**
	Intercept	2.68**	2.69**	2.44**	2.44**	2.44**

Table 5. (cont'd)

Category	Scale of predictor variables:			Local and Regional		
	Scale of interaction:			Local		
	Candidate models:			Local		
	1. HGM + WET	2a. HGM + WET + LU	2b. HGM + WET + LU + (WET _L * LU _L)	3. Top local + regional	4. Top local + regional + WET _L -RAN	5. Top local + regional + WET _L -RAN (WET _L * LU _R)
<i>Model results:</i>	Variance components	σ^2				
		τ_{00}				
		τ_{11}				
Variation explained	Within region	18%	21%	21%	22%	22%
	Between region	—	—	22%	22%	24%
Model selection	AIC	3085	2954	2931	2926	2920
	Δ_i	165	34	11	6	0
	w_i	<0.001	<0.001	0.004	0.05	0.95

p-values: <0.1†, <0.05*, <0.001**

Table 6. Mixed effects models predicting water color for the all-lakes dataset ($n = 1,527$ lakes, $N = 21$ regions) using local and regional landscape-context variables and allowing for random intercepts and wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM), wetland (WET), and land use disturbance (LU) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN. Local wetland interactions at local and regional scales are presented in Models 2b and 5. Estimates of variance components are presented for within region color (σ^2), between region intercept (τ_{00}), and between region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.

Category	Scale of predictor variables:	Local and Regional				
		Local		Regional		
		Scale of interaction:		3. Top local + regional	4. Top local + region + WET _L -RAN	5. Top local + regional + WET _L -RAN + (WET _L * LU _R)
HGM	Candidate models:	1. HGM + WET	2a. HGM + WET + LU			
	Landscape-context variables					
	Mean Depth	-0.47**	-0.47**	-0.47**	-0.46**	-0.46**
	Drainage ratio	0.20**	0.20**	0.20**	0.20**	0.20**
	Baseflow	-0.02**	-0.02**	-0.02**	-0.02**	-0.02**
WET	Wetland	1.45**	1.46**	1.45**	1.38**	1.63**
LU	Agriculture	—	n.s.	—	—	—
	Urban	—	n.s.	—	—	—
Interaction	Wet _L * Agr _L	—	—	—	—	—
	Wet _L * Urb _L	—	—	—	—	—
Regional	Baseflow _R	—	—	-0.02*	-0.02*	-0.02*
	Baseflow _R * Wet _L	—	—	—	—	-0.06*
	Intercept	2.55**	2.55**	2.59**	2.59**	2.59**

Table 6. (cont'd)

Category	Scale of predictor variables:			Local and Regional		
	Scale of interaction:					
	Candidate models:					
	1. HGM + WET	2a. HGM + WET + LU	Local 2b. HGM + WET + LU + (WET _L * LU _L)	3. Top local + regional	4. Top local + region + WET _L -RAN	Regional 5. Top local + regional + WET _L -RAN + (WET _L * LU _R)
Landscape-context variables						
<i>Model results:</i>						
Variance components						
σ^2	0.42**	0.42**	0.42**	0.42**	0.42**	0.42**
τ_{00}	0.12*	0.12*	0.12*	0.07*	0.07*	0.07*
τ_{11}	—	—	—	—	0.50†	0.06 n.s.
Variation explained						
Within region	32%	32%	32%	32%	33%	33%
Between region	—	—	—	4%	4%	4%
Model selection						
AIC	3081	3082	3085	3077	3066	3061
Δ_i	20	21	24	16	5	0
w_i	<0.001	<0.001	<0.001	<0.001	0.08	0.92

p-values: <0.1†, <0.05*, <0.001**

Table 7. Mixed effects models predicting lake TP for the minimally-disturbed lake dataset (n = 777 lakes, N = 16 regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM) and wetland (WET) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN. Wetland interactions at the local scale are presented in Model 2b. Estimates of variance components are presented for within region lake TP (σ^2), between region intercept (τ_{00}), and between region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.

Scale of predictor variables:		Local	Local and Regional	
Candidate models:		1. HGM + WET	3. Top local + regional	4. Top local + regional + WET _L -RAN
<i>Category</i>	Landscape-context variables			
HGM	Mean depth	-0.47**	-0.47**	-0.47**
	Drainage ratio	0.05*	0.05*	0.05*
WET	Wetland	0.27†	0.27†	n.s.
Regional	<i>Agriculture_R</i>	—	0.95*	0.95**
	Intercept	2.28**	2.19**	2.19**
<i>Model results:</i>				
Variance components	σ^2	0.25**	0.25**	0.25**
	τ_{00}	0.07*	0.03*	0.03*
	τ_{11}	—	—	0.10 ^{n.s.}
Variation explained	Within region	23%	23%	23%
	Between region	—	8%	8%
Model selection	AIC	1189	1182	1183
	Δ_i	7	0	1
	w_i	0.02	0.60	0.38

p-values: <0.1†, <0.05*, <0.001**

Table 8. Mixed effects models predicting water color for the minimally-disturbed lake dataset (n = 686 lakes, N = 16 regions) using local and regional landscape-context variables and allowing for random intercepts and random wetland slopes across regions. Candidate models were developed using local hydrogeomorphic (HGM) and wetland (WET) variables. Regional variables were added to the top-ranked local models based on AIC. Models with random local wetland effects among regions are noted as WET_L-RAN. Wetland interactions at the local scale are presented in Model 2b. Estimates of variance components are presented for within region lake TP (σ^2), between region intercept (τ_{00}), and between region wetland slopes (τ_{10}). Models 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). Local predictor variables were transformed to correct for normality and group-mean centered. Regional variables were grand mean centered and are italicized.

Scale of predictor variables:		Local	Local and Regional	
Candidate models:		1. HGM + WET	3. Top local + regional	4. Top local + region + WET _L -RAN
<i>Category</i>	Landscape-context variables			
HGM	Mean Depth	-0.50**	-0.50**	-0.50**
	Drainage ratio	0.23**	0.23**	0.23**
	Baseflow	-0.01†	-0.01†	-0.01†
WET	Wetland	1.26**	1.26**	1.26**
Regional	<i>Baseflow_R</i>	—	-0.04**	-0.04**
	Intercept	2.54**	2.63**	2.63**
<i>Model results:</i>				
Variance	σ^2	0.39**	0.40**	0.39**
components	τ_{00}	0.18*	0.05*	0.05*
	τ_{11}	—	—	0.17 ^{n.s.}
Variation explained	Within region	29%	29%	28%
	Between region	—	14%	14%
Model selection	AIC	1360	1351	1352
	Δ_i	9	0	1
	w_i	0.01	0.65	0.34

p-values: <0.1†, <0.05*, <0.001**

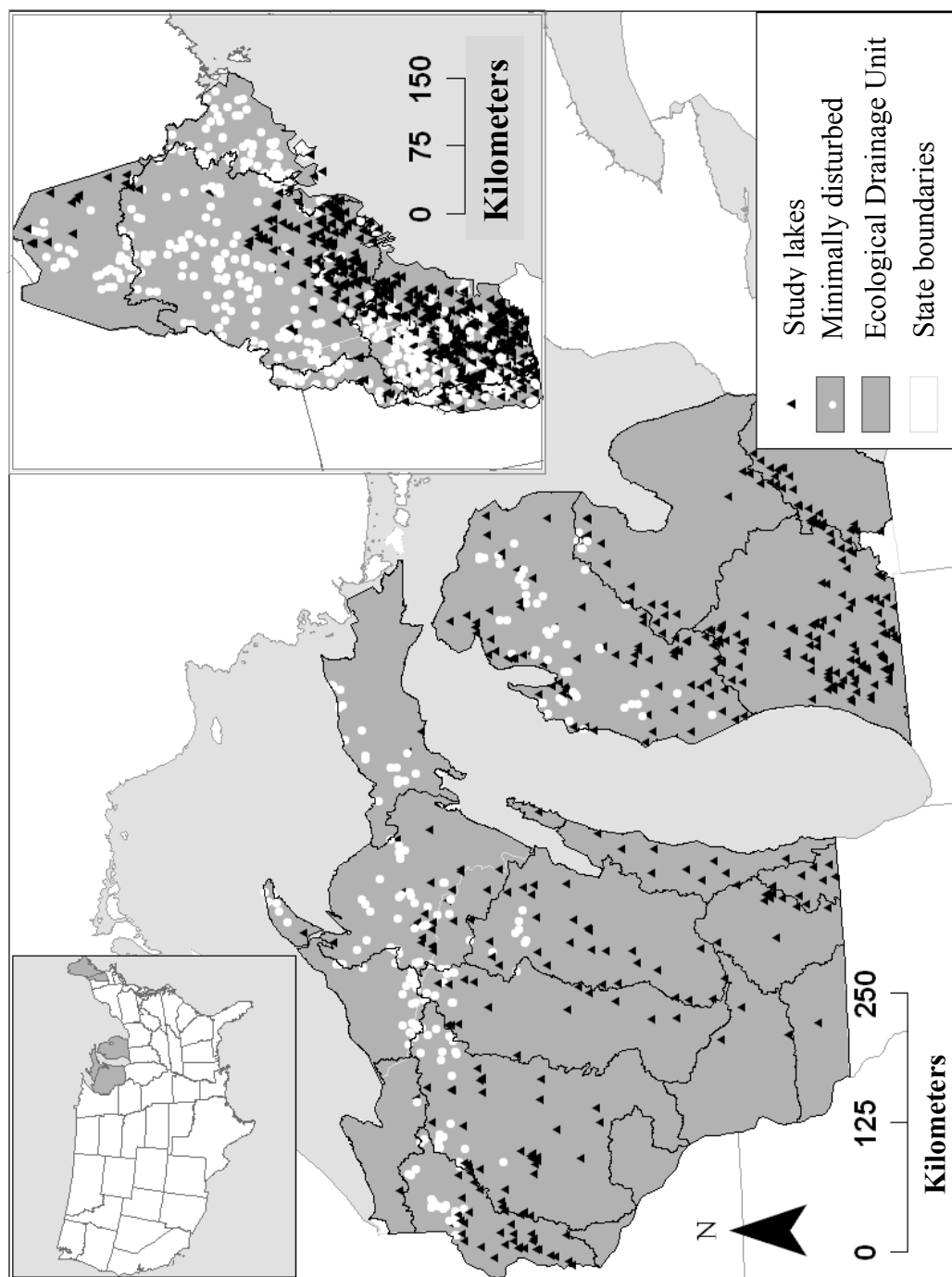


Figure 1. Distribution of the lakes and the regions (Ecological Drainage Units – Higgins et al. 2005) used in this study. Minimally-disturbed lakes were defined as having less than 5% agriculture/urban land use within 500m buffer surrounding the lake.

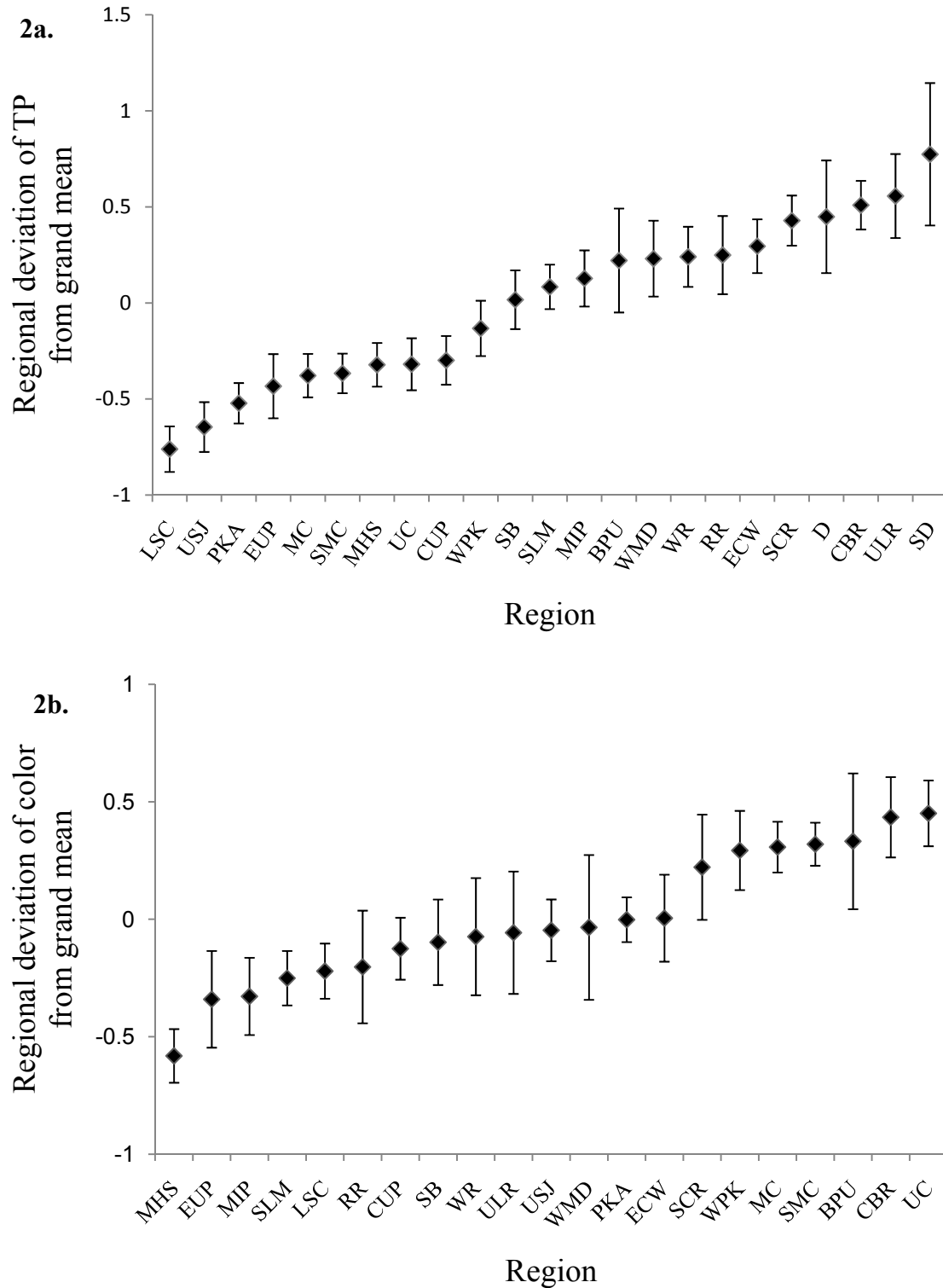


Figure 2. The regional deviation of lake response variables from the grand mean – best linear unbiased predictors (Blups) for lake TP (2a) and water color (2b). Error bars are the standard error in the Blup estimate. Region codes are shown in Figures 4 – 5 are described in Table A1. in the appendix.

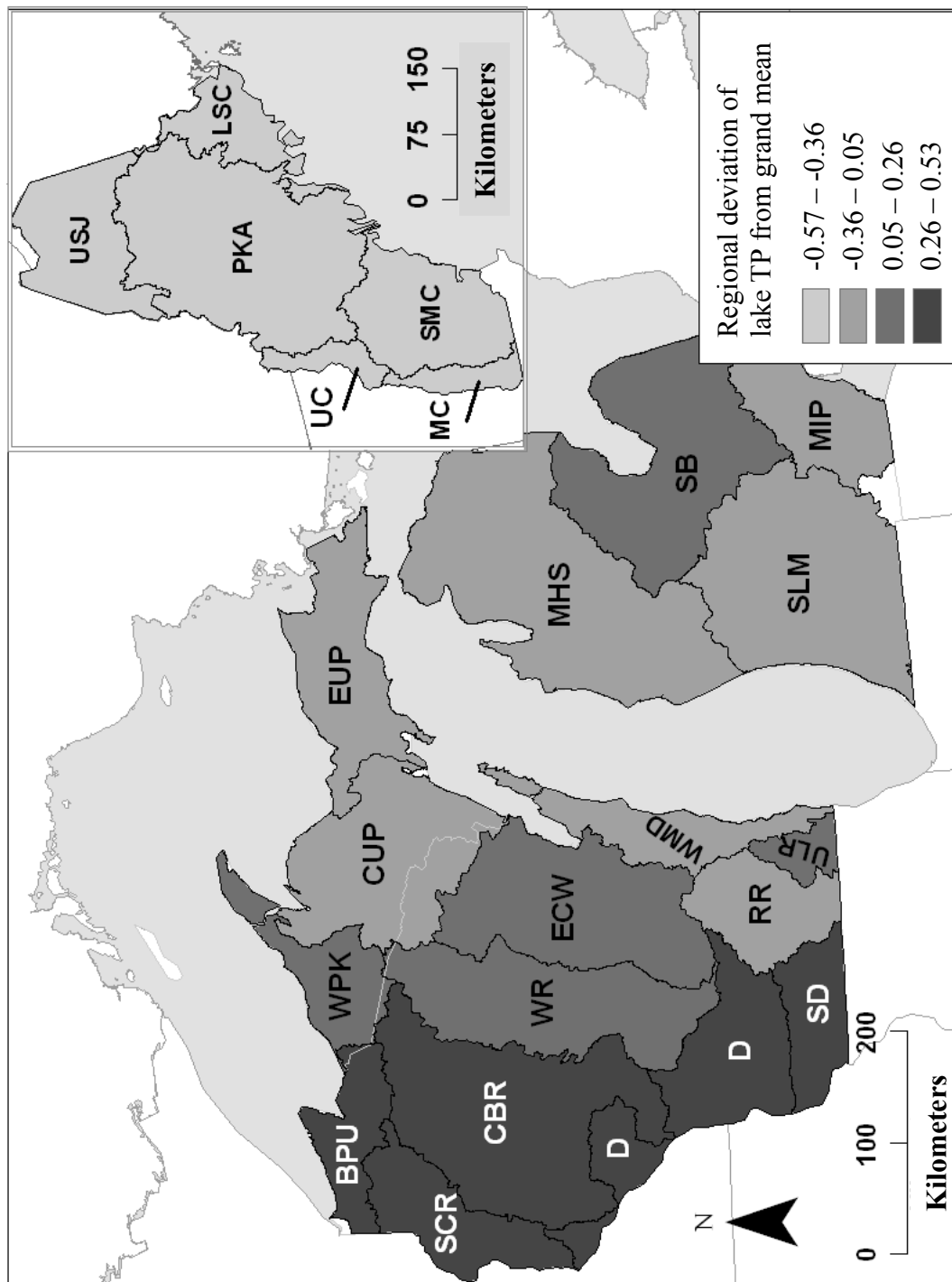


Figure 3a. The mapped regional deviation of lake response variables from the grand mean for lake TP.

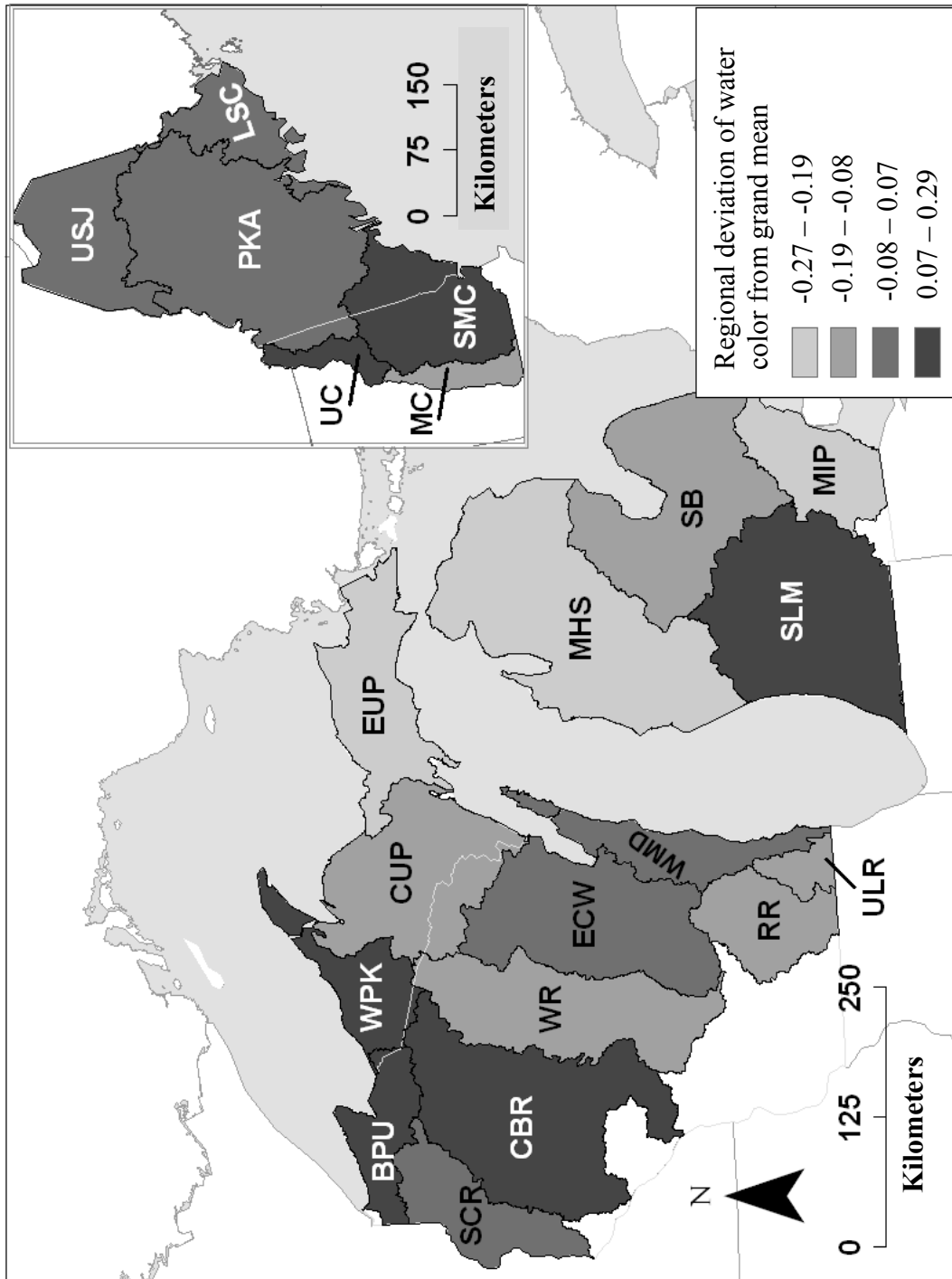


Figure 3b. The mapped regional deviation of lake response variables from the grand mean for water color.

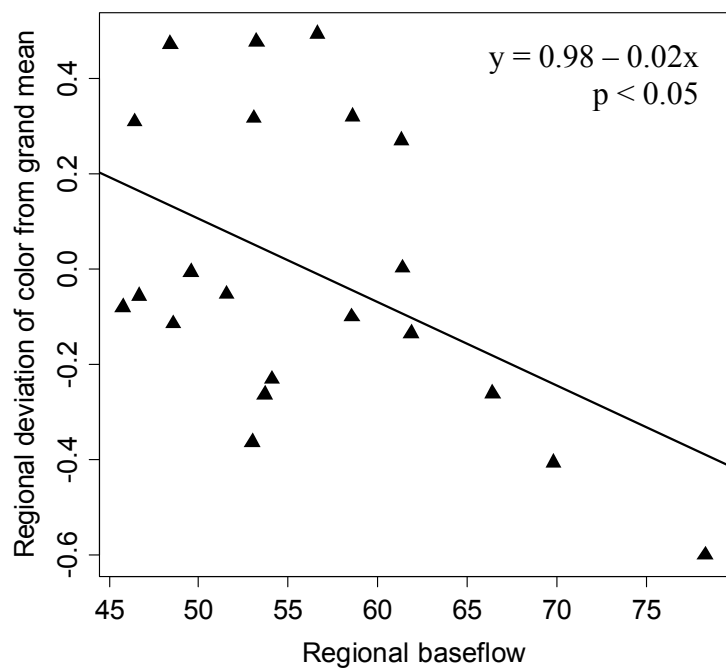
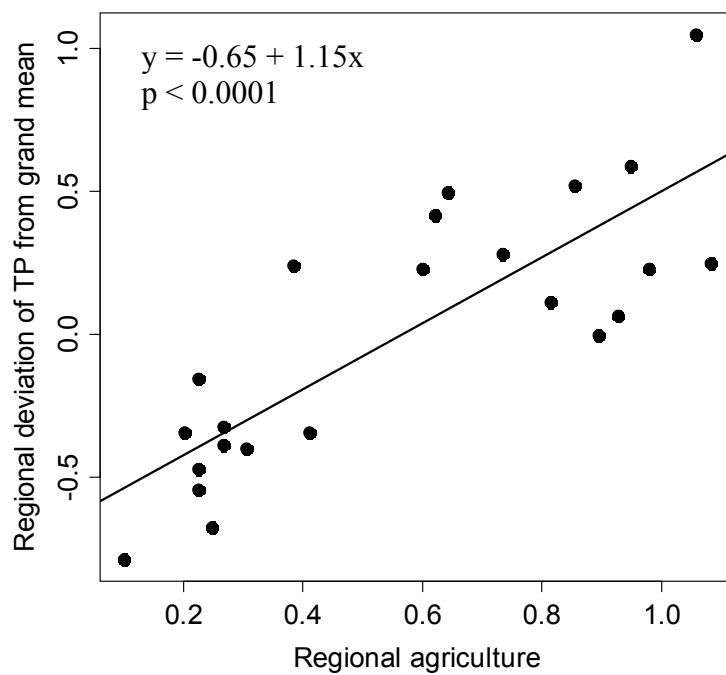


Figure 4. Regional deviation of lake response variables (Blups – best linear unbiased predictors) versus regional landscape-context variables. 4a) TP Blup vs. regional agriculture (arcsine square root transformed); 4b) Color Blup vs. regional baseflow index (% groundwater contribution).

APPENDIX

Regional background of study lakes

The study lakes are distributed in Wisconsin and Michigan in the Midwest and New Hampshire and Maine in the Northeast of the United States. These continental regions have a shared glacial history from the last ice age and thus have similar freshwater landscapes, rich in lakes, streams, wetlands and groundwater. But there are striking differences in topography and human land use intensity. We highlight some of the similarities and differences found in the study areas to aid in the interpretation of the regional analyses.

Glacial history

The last glaciation ended around 10,000 years ago in the Northern U.S. and covered most of Wisconsin, and all of Michigan, New Hampshire and Maine. As the glaciers retreated and melted away, they shaped the terrestrial and freshwater landscapes that we see today. Glacial modified landscape features include: moraines – where sediment was piled up at the edge of glacial lobes; drumlins that form elongated hills; and eskers or sand and gravel ridges (Blewett et al. 2009). Inland lakes were formed through glaciers physically scouring the landscape, depositing moraine sediment and damming river flow, or leaving behind blocks of ice buried in glacial drift that later formed kettle lakes (Wolfson 2009). Water under high pressure beneath glaciers created long, deep “tunnel channel lakes” found in northwestern MI (Wolfson 2009). Many inland lakes are found in areas where two glacial lobes intersected (interlobate zones) (Blewett et al. 2009). Other glacial activity has lead to lake-free landscapes such as where glacial lakes have since dried up and left behind flat plains, fine-textured soils and wetlands (Blewett et al. 2009). An example of this type of landscape is found in around the Saginaw Bay region of

Michigan. In the Driftless region of Wisconsin, which was never glaciated by any of the ice advances, there are few natural lakes because “millions of years of stream incision have removed the necessary dams and integrated the drainage” of the area (Mickelson 1997).

Regional topography

The topographic elevation and relief greatly differs between the Midwest and Northeastern U.S. In Michigan and Wisconsin, the land can be characterized as fairly flat to hilly. In Maine and New Hampshire there are diverse topographic features and changes in elevation. Most of Maine is upland, and New Hampshire is covered by the White Mountain section, which includes Mount Washington, the highest peak in the Northeastern U.S. with an elevation of 6,288 ft above sea level (Olcott 1995). Lowlands reside along the Atlantic seaboard of Maine and New Hampshire.

Groundwater hydrology

Groundwater characteristics among regions are varied and can be related to the glacial activity. Sand and gravel sediment deposited by glaciers (outwash) “readily receive, store, transmit, and discharge water” (Olcott 1995) and supply much of the baseflow of streams. In our study extent, we find regions with high baseflow in northern Michigan (Figure A2). Regions with low baseflow include southeastern Wisconsin, the Thumb region of Michigan, western New Hampshire, and northern Maine. The Thumb region is characterized as having glacial-lake deposits consisting of clay, silt, and fine sand which make for poor surficial aquifer systems. Glacial till in the Northeast transmits water slowly and results in low groundwater yields. But outwash deposits in the

Northeast valleys yield high groundwater, which were not captured in the regional scale of the baseflow map presented in Figure A2.

Climate and surface hydrology

The contrasting topography of the Midwest from the Northeastern U.S. influences differences in climate and hydrology among regions. In regions with high elevation in New Hampshire and Maine there is greater precipitation than in regions with low elevation (Olcott 1995). The higher precipitation coupled with the steep slope results in greater regional runoff in areas with high elevation in the Northeast. About half of the annual precipitation becomes runoff to streams and rivers in New Hampshire and Maine (Olcott 1995).

In the Midwest, topographic differences are moderate and climatic patterns are more strongly influenced by other features in the landscape such as the Great Lakes. For Michigan, precipitation decreases as we move from west to east in the state. For Wisconsin, precipitation is greater in the west central part of the state (PRISM <http://www.prism.oregonstate.edu>). Mean annual runoff in streams and rivers reflects the annual precipitation and in no areas does runoff exceed precipitation values (Olcott 1992).

Vegetation cover

Climate and other physical factors have influenced land cover patterns in the study regions. Temperature and precipitation gradients in the Midwest, referred to as the Wisconsin and Michigan tension zones, have resulted in two distinct vegetation compositions. In the south, summers are warmer and longer than in the north and promote drought tolerant oak and sugar maple forests. North of the tension zone, the

climate is cooler and there is greater moisture in the soils, which allows for mixed conifer-hardwood forests to dominate.

In the Northeastern USA, forest composition also is influenced by north-south temperature gradients but also microclimate differences due to topographic elevation and relief differences. In Maine, deciduous-dominated forests are found in the south and spruce-fir or northern hardwood forests are found in the north (Dept. Conservation Maine http://www.maine.gov/doc/nrimc/mnap/features/eco_whitepinemixforest.htm).

Human land use

In the Midwest, the dominant human land use activity in the surrounding landscape is agriculture. Productive soils found in the Midwest are attributed to glacial activity that has significantly altered the surficial landscape. During the ice age, “continental glaciers planed off soil and weathered bedrock and redeposited these materials as thin mantel of glacial debris over the bedrock surface” (Olcott 1995). The smaller sediments and silt produced by the ice-activity, readily breaks down chemically and releases nutrients when exposed to water and temperature changes. Agricultural activity also benefits from clays produced by weathering processes which retain moisture and promote plant growth. The percent of regional agriculture is greatest in central and southern WI and MI (Figure A1). In the Northeast, there is a small percentage of agriculture around rivers and valleys and small urban centers, but these regions are mostly forested with minimal human landscape modifications in comparison to the Midwest. Surface glacial debris has resulted in rolling flat topography in the lowland area and partially filled valleys between highlands, moderating the sharp topographic relief of the preglacial landscape of the Northeast (Olcott 1995).

Table A1. Description of Ecological Drainage Unit (EDU) Codes.

EDU Code	Description
BPU	Bayfield Peninsula and Uplands
CBR	Chippewa-Black River
CUP	Central Upper Peninsula
D	Driftless
ECW	East Central Wisconsin
EUP	Eastern Upper Peninsula
LSC	Lower St. Croix – Downeast Maine Coastal
MC	Middle Connecticut
MHS	Northern Lake Michigan, Lake Huron, and Straits of Mackinac
MIP	Southeast Michigan Interlobate and Lake Plain
PKA	Penobscot – Kennebec – Androscoggin
RR	Rock River
SB	Saginaw Bay
SCR	St. Croix River
SD	Southern Driftless
SLM	Southeast Lake Michigan
SMC	Saco – Merrimack – Charles
UC	Upper Connecticut
ULR	Upper Illinois River
USJ	Upper St. John – Aroostook
WMD	Western Lake Michigan and Door Peninsula
WPK	Western Upper Peninsula and Keweenaw Peninsula
WR	Wisconsin River

Table A2. Correlation values for regional hydrology, climate, and landscape variables for the all-lake TP dataset (N = 23 regions). Correlation coefficients that were greater than 0.50 were considered to be significantly correlated ($\alpha = 0.05$).

	<i>Baseflow</i>	<i>Runoff</i>	<i>Precipitation</i>	<i>Wetland</i>	<i>Forest</i>	<i>Agriculture</i>	<i>Urban</i>
<i>Baseflow</i>	1	–	–	–	–	–	–
<i>Runoff</i>	-0.57	1	–	–	–	–	–
<i>Precipitation</i>	-0.68	0.85	1	–	–	–	–
<i>Wetland</i>	0.67	-0.48	-0.69	1	–	–	–
<i>Forest</i>	-0.51	0.88	0.80	-0.36	1	–	–
<i>Agriculture</i>	0.31	-0.82	-0.63	0.08	-0.94	1	–
<i>Urban</i>	-0.18	-0.04	-0.01	-0.32	-0.22	0.22	1

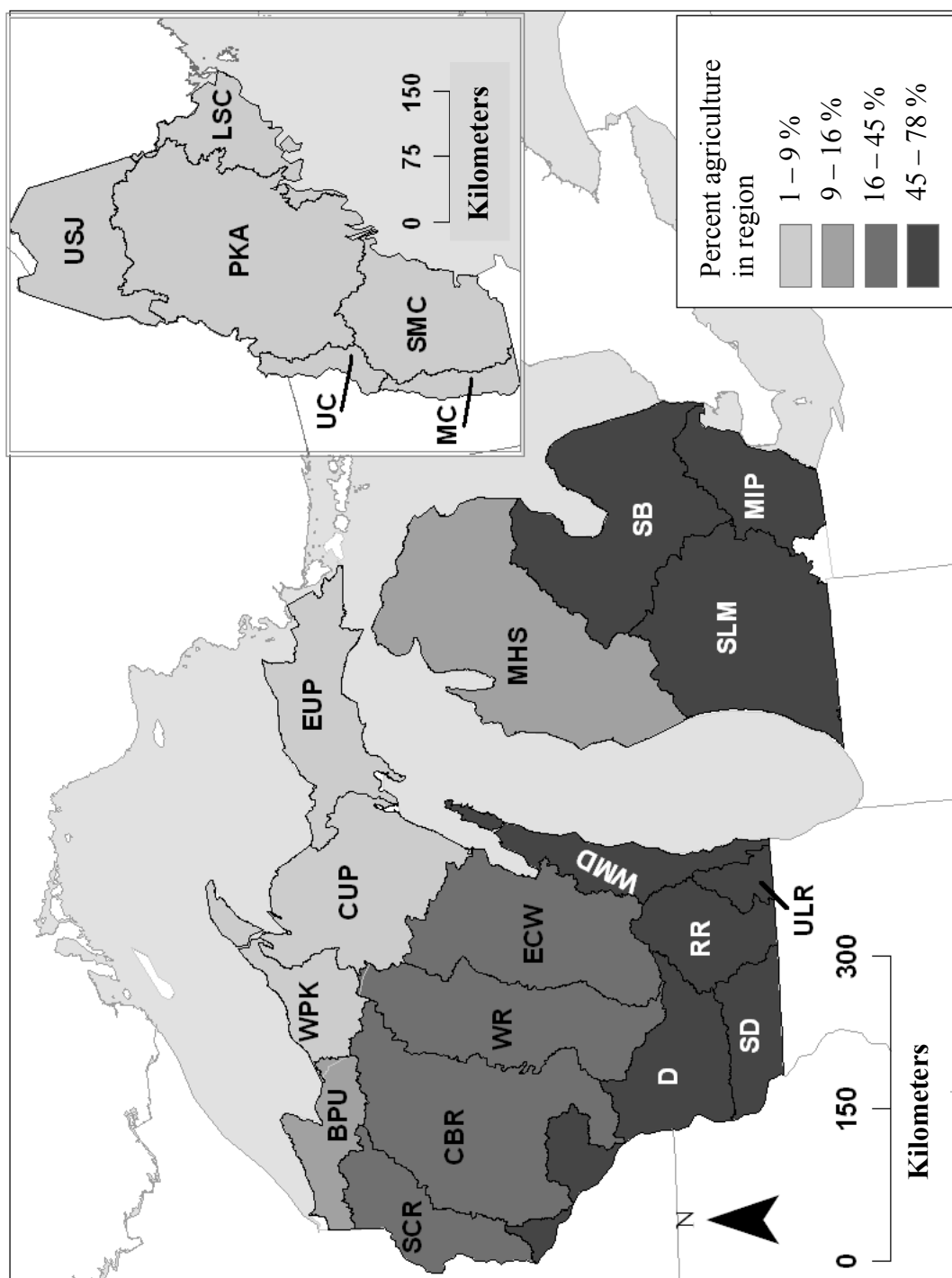


Figure A1. Percent agriculture in the region (Ecological Drainage Unit).

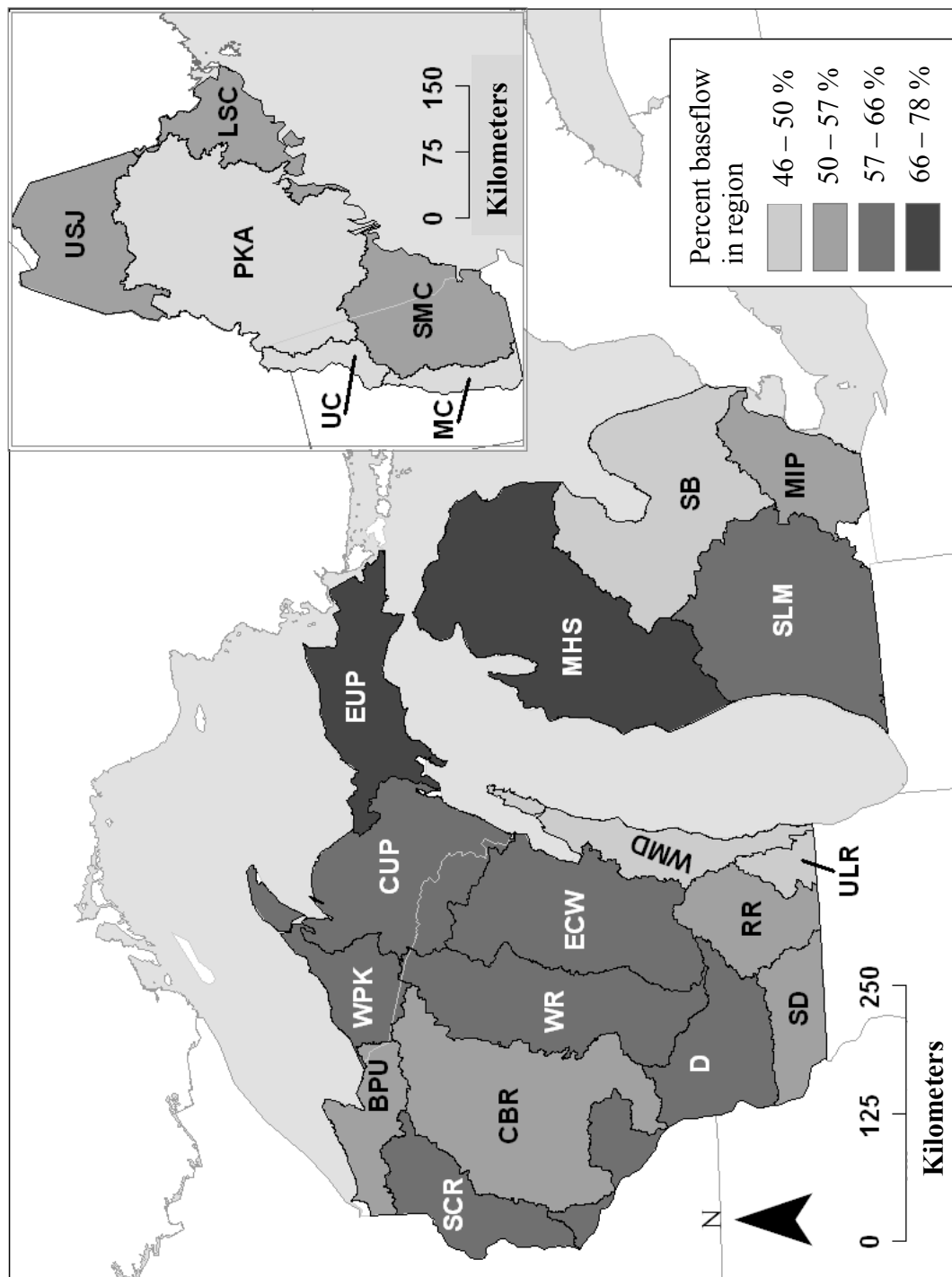


Figure A2. Percent regional groundwater contribution (baseflow index).

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