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Emily K. Read

Cary Institute of Ecosystem Studies, eread@usgs.gov

Vijay P. Patil

University of Alaska, Fairbanks

Samantha K. Oliver

University of Wisconsin

Amy L. Hetherington

Cornell University

Jennifer A. Brentrup

Miami University

See next page for additional authors

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Authors

Emily K. Read, Vijay P. Patil, Samantha K. Oliver, Amy L. Hetherington, Jennifer A. Brentrup, Jacob A. Zwart, Kirsten M. Winters, Jessica R. Corman, Emily R. Nodine, R. Iestyn Woolway, Hilary A. Dugan, Aline Jaimes, Arianto B. Santoso, Grace S. Hong, Luke A. Winslow, Paul C. Hanson, and Kathleen C. Weathers

The importance of lake-specific characteristics for water quality across the continental United States

EMILY K. READ,^{1,13} VIJAY P. PATIL,² SAMANTHA K. OLIVER,³ AMY L. HETHERINGTON,⁴ JENNIFER A. BRENTUP,⁵ JACOB A. ZWART,⁶ KIRSTEN M. WINTERS,⁷ JESSICA R. CORMAN,⁸ EMILY R. NODINE,⁹ R. IESTYN WOOLWAY,¹⁰ HILARY A. DUGAN,³ ALINE JAIMES,¹¹ ARIANTO B. SANTOSO,¹² GRACE S. HONG,³ LUKE A. WINSLOW,³ PAUL C. HANSON,³ AND KATHLEEN C. WEATHERS¹

¹Cary Institute of Ecosystem Studies, Millbrook, New York 12545 USA

²Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA

³Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706 USA

⁴Department of Natural Resources, Cornell University, Ithaca, New York 14853 USA

⁵Department of Biology, Miami University, Oxford, Ohio 45056 USA

⁶Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556 USA

⁷Environmental Sciences Program, Oregon State University, Corvallis, Oregon 97330 USA

⁸School of Life Sciences, Arizona State University, Tempe, Arizona 85287 USA

⁹Department of Biological Sciences, Florida International University, Miami, Florida 33199 USA

¹⁰Centre for Ecology and Hydrology, Lancaster Environment Center, Lancaster, Lancashire LA1 4AP United Kingdom

¹¹Department of Plant and Soil Sciences, University of Delaware, Newark, Delaware 19716 USA

¹²Department of Biological Sciences, University of Waikato, Hamilton 3420 New Zealand

Abstract. Lake water quality is affected by local and regional drivers, including lake physical characteristics, hydrology, landscape position, land cover, land use, geology, and climate. Here, we demonstrate the utility of hypothesis testing within the landscape limnology framework using a random forest algorithm on a national-scale, spatially explicit data set, the United States Environmental Protection Agency's 2007 National Lakes Assessment. For 1026 lakes, we tested the relative importance of water quality drivers across spatial scales, the importance of hydrologic connectivity in mediating water quality drivers, and how the importance of both spatial scale and connectivity differ across response variables for five important in-lake water quality metrics (total phosphorus, total nitrogen, dissolved organic carbon, turbidity, and conductivity). By modeling the effect of water quality predictors at different spatial scales, we found that lake-specific characteristics (e.g., depth, sediment area-to-volume ratio) were important for explaining water quality (54–60% variance explained), and that regionalization schemes were much less effective than lake specific metrics (28–39% variance explained). Basin-scale land use and land cover explained between 45–62% of variance, and forest cover and agricultural land uses were among the most important basin-scale predictors. Water quality drivers did not operate independently; in some cases, hydrologic connectivity (the presence of upstream surface water features) mediated the effect of regional-scale drivers. For example, for water quality in lakes with upstream lakes, regional classification schemes were much less effective predictors than lake-specific variables, in contrast to lakes with no upstream lakes or with no surface inflows. At the scale of the continental United States, conductivity was explained by drivers operating at larger spatial scales than for other water quality responses. The current regulatory practice of using regionalization schemes to guide water quality criteria could be improved by consideration of lake-specific characteristics, which were the most important predictors of water quality at the scale of the continental United States. The spatial extent and high quality of contextual data available for this analysis makes this work an unprecedented application of landscape limnology theory to water quality data. Further, the demonstrated importance of lake morphology over other controls on water quality is relevant to both aquatic scientists and managers.

Key words: catchment geology; conductivity; drainage density; hydrogeology; hydrologic connectivity; land use; landscape limnology; morphology; National Lakes Assessment; nutrients; turbidity; water quality.

INTRODUCTION

The quality of freshwater is a critical indicator of the state of the environment (USEPA 1994, Williamson et al. 2009). Freshwater bodies cover only 2% of the land surface of Earth (McDonald et al. 2013), but belong among the most extensively and rapidly altered ecosys-

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¹³ Present address: Center for Integrated Analytics, U.S. Geological Survey, Middleton, Wisconsin 53562 USA.
E-mail: eread@usgs.gov

tems on the planet (Carpenter et al. 2011). Freshwater is also a critically important resource. Although limnologists traditionally focus on the study of in-lake processes (Johnes 1999), there is now widespread understanding that water quality drivers operate from local to continental scales (Likens 1985, Wetzel 2001, Meador and Goldstein 2003, Soranno et al. 2010). These drivers include mean depth, residence time, catchment geology, drainage density, land use, catchment topography, and hydrogeology (Dillon and Kirchner 1975, Kirchner 1975, Duarte and Kalff 1989, Rasmussen et al. 1989, Wolock et al. 1989, Dillon et al. 1991, Soranno et al. 1996, Griffith 2014). While the relationships between single driver-response pairs are well-characterized in the literature (e.g., Kirchner 1975), surprising and complex cross-scale interactions have been observed, especially when drivers acting on multiple scales are considered (Soranno et al. 2014). For example, agricultural activity within a watershed influences lake water quality, but this relationship may be dependent on interactions with local wetlands (Fergus et al. 2011) and lake depth (Nielsen et al. 2012). Because multiple drivers interact across multiple scales to affect lake water quality, simple scaling from a small number of well-studied systems to a collection of many lakes across the landscape may not be adequate to represent large-scale aquatic ecosystem processes. Instead, focusing on large-scale patterns and processes while simultaneously including system-specific mechanisms has been suggested (Heffernan et al. 2014).

In order to account for multi-scaled drivers, regionalization schemes have been delineated to describe variation in climate, atmospheric deposition, land use and land cover, geology, and/or hydrology (Omernik 1987). Ecoregions have been used to partition water quality at the national scale (Paulsen et al. 2008, USEPA 2009, Griffith 2014); however, an understanding of the specific biogeochemical processes classified by ecoregions is lacking. Large-scale studies show that lake-specific characteristics (e.g., depth), watershed-scale land use and land cover, and surface and groundwater connectivity are important for predicting water quality (e.g., Kratz et al. 1997, Martin and Soranno 2006, Wagner et al. 2007, Bremigan et al. 2008, Taranu and Gregory-Eaves 2008, Nielsen et al. 2012, Zhang et al. 2012, Cheruvilil et al. 2013); these drivers can vary both within and among ecoregions. To some extent, national policy takes into account cross-scale interactions among these multi-scaled drivers by using regional variation in water quality to set nutrient criteria recommendations (USEPA 2009). However, at the scale of the continental United States, the relative importance and interactions among lake-specific characteristics, and watershed- and regional-scale drivers are unknown.

The United States Environmental Protection Agency (EPA) completed the National Lakes Assessment (NLA) in 2007 to assess water quality of lakes across the continental United States (USEPA 2009). This data set, which includes drivers operating from local to

regional spatial scales, offers a rare opportunity to test the robustness and utility of the existing conceptual framework of landscape limnology (the spatially explicit study of aquatic ecosystems in their landscapes [Soranno et al. 2010], hereafter referred to as the landscape limnology framework; Fig. 1). We set out to address three questions about broad-scale patterns and drivers of lake water quality impairment for five key water quality indicators, total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), turbidity, and conductivity. First, what is the relative importance of lake-specific, local, and regional controls on water quality for lakes at the scale of the continental United States? Second, how does hydrologic connectivity, a classification of upstream surface water, mediate the relationship between lake context (the anthropogenic, terrestrial, atmospheric, and hydrologic settings) and water quality? Third, how does the relative importance of individual drivers vary across water quality responses? In order to address these questions for >1000 lakes, we faced analytical challenges arising from the volume and complexity of the database, such as co-varying driver data and non-linear water quality responses. To account for these challenges, we used a random forest algorithm to simultaneously contrast key lake water quality drivers across the continental United States at multiple spatial scales and to examine the effect of hydrologic connectivity as a mediator of water quality.

METHODS

Using a macro-systems ecology approach (Heffernan et al. 2014) and applying the conceptual landscape limnology framework (Soranno et al. 2014), we sought to explain the continental-scale patterns of water quality in the United States using known water quality drivers that range from lake-specific characteristics to coarse regionalizations. We used the EPA NLA data set of lake water quality and associated data (*available online*),¹⁴ in addition to independently derived metrics for hydrology, topography, and land use. TP, TN, DOC, turbidity, and conductivity are metrics frequently used to indicate freshwater impairment in the United States (USEPA 2009) and were selected as water quality responses for this study. To address the challenges of non-linear response variables and co-varying driver data, we applied a random forest algorithm (Archer and Kimes 2008) to identify the scale and relative importance of water quality drivers for all NLA lakes and for subsets of lakes aggregated by hydrologic connectivity type.

Landscape limnology is a framework within which the interactions across spatial scales and between surrounding landscapes on lake ecosystem processes are defined and studied (Fig. 1; Soranno et al. 2010). Two dimensions of the conceptual framework are spatial scale (local to regional) and landscape context (fresh-

¹⁴ http://water.epa.gov/type/lakes/NLA_data.cfm

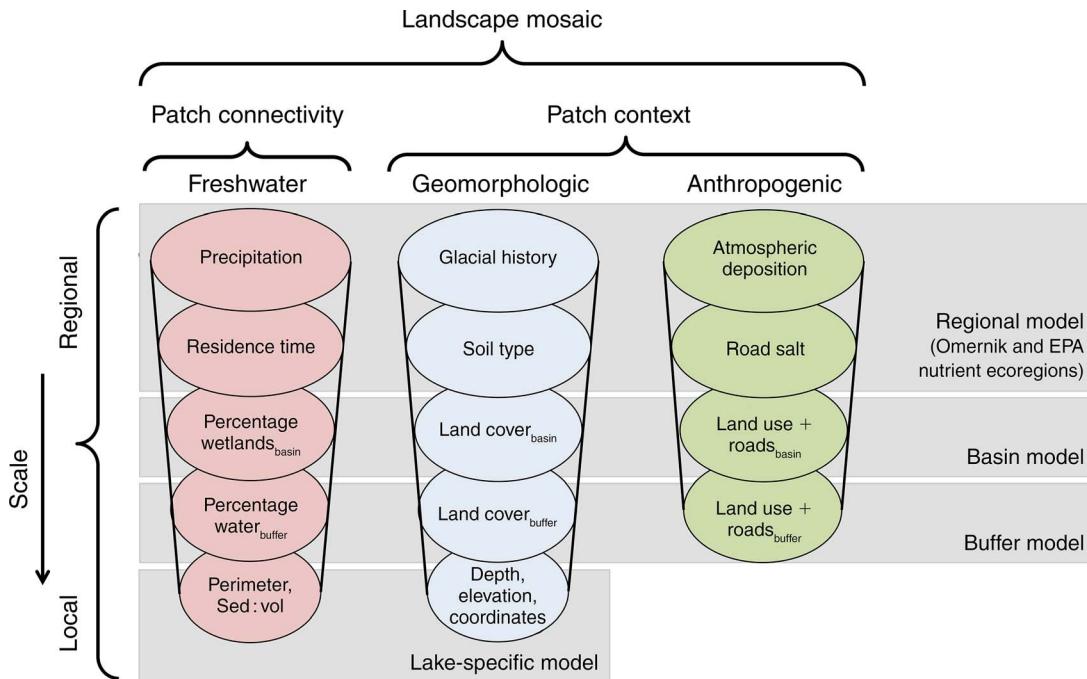


FIG. 1. Conceptual representation of landscape limnology, modified from Soranno et al. (2010). Columns represent freshwater, geomorphologic or terrestrial, and anthropogenic drivers of water quality. The vertical gradient represents the spatial scale at which drivers act on water quality. Variables shown here are not exhaustive, but represent documented drivers of water quality from the literature. Gray boxes represent the model structure used in this paper to test the importance of scale in water quality across the continental United States. Sed: vol refers to the epilimnetic sediment-to-volume ratio, which is described in detail in *Methods: Lake specific variables*. A complete list of predictor variables in each model can be found in the Appendix.

water, terrestrial, or human), both of which were useful for structuring our modeling framework and hypothesis testing. First, we tested alternative hypotheses about the importance of the spatial scale for explaining water quality; submodels containing drivers at the regional, basin (watershed), buffer (200-m margin around lake perimeter), and lake-specific scales were compared for lakes across the continental United States (Fig. 1). The four submodels, containing all of the drivers occurring at any given spatial scale, were also compared against a combined model that contained all drivers occurring at all scales, in order to quantify the relative importance of individual water quality drivers aggregated to specific spatial scales. Because of the documented importance of features specific to a lake (e.g., maximum depth, basin shape, surface elevation, and latitude and longitude) for water quality, we modified the landscape limnology framework to explicitly include the lake-specific scale, which more closely reflects our hypotheses and model setup (Fig. 1) than the Soranno et al. (2010) model. Lake-specific features are fixed, that is, independent of characteristics external to the lake and generally cannot be altered. We hypothesized that freshwater landscape context, part of the second dimension of the Soranno et al. (2010) landscape limnology framework, would mediate the effects of terrestrial and anthropogenic drivers on water quality. To test this, we classified lakes by hydrologic connectivity, according to the presence of

upstream hydrologic surface features (described in greater detail under *Methods: Data: Lake hydrologic connectivity classification*), and grouped lakes by connectivity type prior to modeling. In addition to scale-specific models for the collection of all lakes, we classified lakes by connectivity type and applied the regional, basin, buffer, lake-specific, and combined models to each type in order to identify interactions between hydrology, scale, and individual drivers, which could have important implications for lake connectivity type response to stressors and allocation of management resources. In this paper, we describe the data sets and random forest model structure in greater detail.

Data

Lake sampling.—EPA NLA lakes were selected to provide a representative sample of lakes >4 ha across the continental United States using a spatially balanced design to ensure an adequate random sample of lakes (>100) in each of five size classes ranging from 4 to 250+ ha (USEPA 2009). The NLA data set includes 132 reference (minimally disturbed) lakes, and each EPA ecoregion represented in the NLA contains between six and 30 reference lakes (USEPA 2009). Reference lakes were identified in one of two ways, by identification of minimally disturbed lakes existing within the area nearby pre-selected NLA lakes based on chemical and biological condition, or by identification by the prior

knowledge of local water quality experts (designated by the EPA) for minimally disturbed systems within a region and subsequent inclusion as an NLA reference site (USEPA 2009). Because of the range of chemical reference conditions defined for regions by the EPA (USEPA 2009), reference lakes were chemically indistinguishable from non-reference lakes across the entire data set and were, thus, combined for all subsequent analysis. Reference and non-reference lake data were sampled using identical protocols across the entire population of sample lakes between June and October in 2007 (USEPA 2009). Ninety-five lakes in the original data set were sampled multiple times during 2007, and the values of all continuous variables were averaged across visits for these lakes. A detailed description of the EPA NLA project sample design is *available online*.¹⁵

Lake-specific variables.—Twelve variables were used to characterize lake-specific features (Appendix). Ten variables were provided by or directly derived from the EPA NLA data set (surface area, perimeter, maximum depth, watershed area, ratio of watershed area to lake area, shoreline development index, elevation, perimeter-to-area ratio, latitude, and longitude). In addition, we estimated the epilimnetic sediment-to-volume ratio, which is related to the potential for chemical interaction and nutrient exchange between the lake and the surrounding sediment, using methods in Carpenter (1983) and NLA thermal profile, maximum depth, and area data, and assuming a conical lake basin (Carpenter 1983). Lake-specific estimates of residence time, originally published by McDonald et al. (2013), were also used.

Land use and land cover.—The EPA NLA data set includes land use and land cover data for a 200-m buffer around each lake and within the entire watershed. Mean percent land use and land cover is characterized for 21 land cover types at the buffer and basin scales, yielding 42 predictor variables (Appendix). Percent cover values were derived from the 2006 National Land Cover Database (NLCD; *available online*).¹⁶

Geographic lake information.—In order to overlay additional spatial data sets (topography, road data, and impervious surfaces) with EPA NLA lakes at a scale that was consistent with the buffer-scale land use and land cover variables in the original EPA NLA data set, we followed four steps. We created shapefiles with the coordinates of each lake centroid; used centroids to extract lake polygons from the National Hydrography Dataset (NHD; *available online*);¹⁷ created a set of 200-m buffers around these lake polygons; and obtained a shapefile of lake watersheds from the EPA. All spatial analyses were conducted in R (R Core Team 2014) using the *sp*, *maptools*, *rgdal*, *raster*, and *rgeos* packages (Hijmans and van Etten 2010, Bivand and Lewin-Koh

2011, Bivand and Rundel 2013, Bivand et al. 2013, 2014).

Road metrics.—We generated three metrics of road development (road density, road proximity, and the mean percentage of land area covered by impervious surfaces) using the methods of Pechenick et al. (2014) and data from the U.S. Census Bureau 2012 TIGER/Line road maps (*available online*)¹⁸ (2006 NLCD).

Regionalizations.—To represent subcontinental regional environmental drivers, we used two ecoregion classifications as categorical variables, the Omernik Level II and EPA Aggregate Level III Nutrient Ecoregion classifications. The Omernik Level II scheme subdivides North America into 50 regions distinguished by enduring components, such as vegetation, soils, and climate. Of these 50 regions, 16 contained EPA NLA lakes. Omernik Level II designations were derived by overlaying maps of land use, regional topography, soils, surficial geology, climate, and resource usage (Omernik 1987). The EPA classification scheme is designed specifically to identify regions that face similar threats (e.g., point sources of atmospheric deposition or regional agricultural practices) associated with impaired water quality (USEPA 2009).

Lake hydrologic connectivity classification.—We classified EPA NLA lakes by hydrological connectivity of upstream hydrologic surface features (Fig. 2). Lakes were grouped into three classes: headwater and isolated (HW/ISO) lakes with no surface inflows ($n = 211$ lakes), stream drainage (SD) lakes with upstream stream features but no large upstream lakes ($n = 464$ lakes), and lake drainage (LD) lakes with both inflowing streams and upstream lakes greater than 10 ha ($n = 351$ lakes). We derived these classifications by overlaying lake polygons with NHD flowline data in ArcGIS 10.1 using the Cross Scale Interaction (CSI) Limnology Toolbox (Smith et al. 2014). Thirty-two of 1058 lakes in the EPA NLA data set could not be classified using our methods and were excluded from all analyses, resulting in a total sample size of 1026 lakes.

Data availability.—The underlying data used for the analysis are openly *accessible online*.¹⁹

Model description

We applied a random forest algorithm, a machine-learning technique based on regression tree analysis (Cutler et al. 2007), to the EPA NLA data set to address our research questions. Random forest techniques overcome the limitations of generalized linear models and of standard regression tree analysis (Karels et al. 2004) by generating hundreds of trees based on bootstrap samples drawn from the original data set (Cutler et al. 2007). Each tree is produced using a random subset of predictor variables and sample points.

¹⁵ <http://water.epa.gov>

¹⁶ http://www.mrlc.gov/nlcd06_data.php

¹⁷ <http://nhd.usgs.gov>

¹⁸ <ftp://ftp2.census.gov/geo/tiger/TIGER2012/ROADS/>

¹⁹ <https://portal.lternet.edu/nis/mapbrowse?scope=knb-lter-ntl&identifier=10000&revision=1>

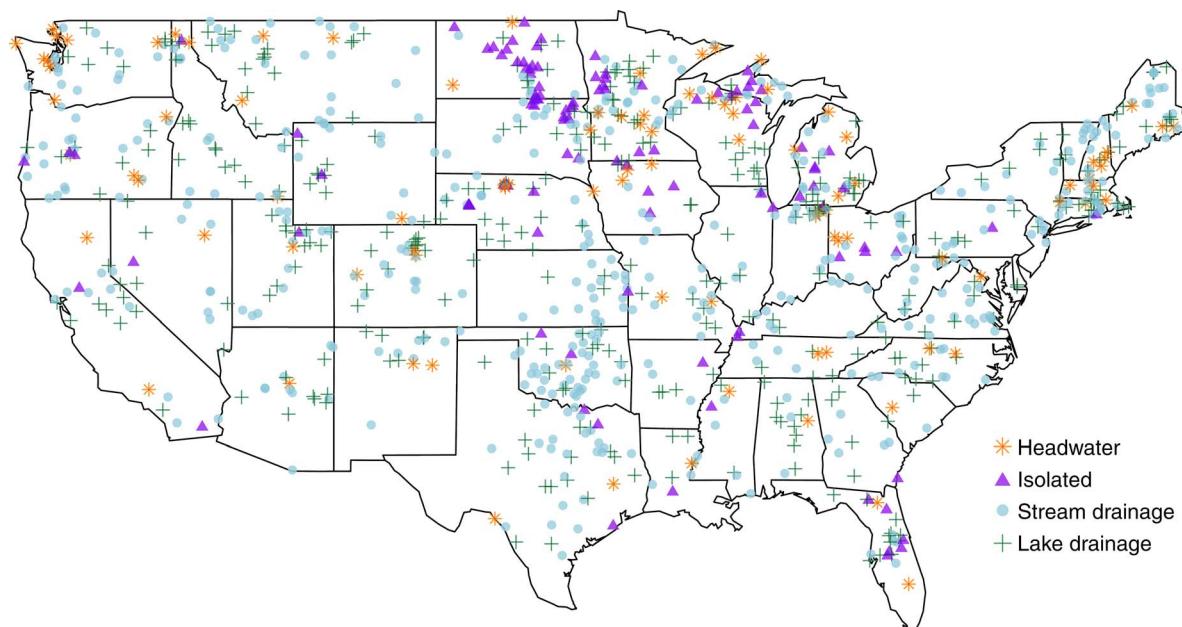


FIG. 2. U.S. Environmental Protection Agency (EPA) National Lake Assessment (NLA) site locations for 2007. Spatial distribution of lakes included in the EPA NLA 2007 data set ($n = 1026$ lakes) is shown, with lakes categorized by connectivity type calculated using the National Hydrography Dataset (<http://nhd.usgs.gov>) lake and flow line layers to identify upstream surface water features. Headwater lakes (HW; $n = 98$ lakes; orange asterisk) have an outlet, but no inlet. Isolated lakes (ISO; $n = 113$ lakes; purple triangle) are isolated. Stream drainage lakes (SD; $n = 464$ lakes; blue circle) have stream inlets but no upstream lakes greater than 10 ha. Lake drainage lakes (LD; $n = 351$ lakes; green cross) have stream inlets connected to upstream lakes greater than 10 ha. Stream and lake drainage lakes may or may not have outlets.

Tree accuracy is determined by validating predictions against the sample points that were withheld when a given tree was generated. The mean squared error (MSE) is calculated for each tree by comparing its predictions for the withheld (e.g. out-of-bag) data set with observed values in order to generate an estimate of the percent of variance in the response variable that could be explained by the tree. These values are averaged over the entire forest of regression trees to produce a cross-validated estimate of model-averaged fit (Liaw and Wiener 2002, Archer and Kimes 2008).

Model structure

To address questions about the relative importance of drivers across spatial scales, the interaction of hydrologic connectivity with primary water quality drivers, and how water quality responses contrast across the continental United States, we grouped drivers by spatial scale (Fig. 1; Appendix) and classified lakes by hydrologic connectivity type. We subsequently applied the scale-specific (regional, basin, buffer, and lake-specific) and combined (all scales) random forest models for each response variable for all lakes, and for subsets of lakes grouped by connectivity type. We conducted all random forest modeling using the randomForest package in R (Liaw and Wiener 2002).

Assessing predictor variable importance

The comparison of predictor variable importance complemented our multi-model comparisons by decomposing the influence of scale-specific water quality drivers (e.g., basin-scale land use and land cover) into specific components (e.g., percent forest cover vs. percent wetlands). Model-averaged predictor variable importance estimates were generated using out-of-bag data (Archer and Kimes 2008) and can be interpreted heuristically in much the same way that Akaike weights are used, when results are averaged across multiple generalized linear models (Burnham and Anderson 2002). Here, to calculate variable importance for a single tree, out-of-bag values for a given variable were randomly permuted, and the tree MSE was then estimated using both the original and the permuted out-of-bag data set. The resulting percent increase in MSE (IMSE) reflects the predictive power of that variable compared to random chance. Because IMSE cannot be compared across response variables, we used a relative IMSE metric (quotient of IMSE and highest IMSE observed for the corresponding response variable) in order to compare the importance of the highest-ranking predictor variables across responses.

Because they are generated stochastically, model-averaged variable importance values can vary slightly between model runs, which may complicate the interpre-

TABLE 1. Percentage variance explained by combined random forest models (all predictors at all scales) and by scale-specific submodels (regional, basin, buffer, and lake-specific scale) for water quality response variables (log-transformed): conductivity (cond), total phosphorus (TP), dissolved organic carbon (DOC), total nitrogen (TN), and turbidity (turb).

Lake type	log(turb)	log(TP)	log(TN)	log(DOC)	log(cond)
All lakes, <i>n</i> = 1026 lakes					
Combined	0.61	0.63	0.65	0.63	0.66
Regional	0.28	0.31	0.34	0.33	0.39
Basin	0.45	0.50	0.55	0.53	0.62
Buffer	0.41	0.46	0.51	0.49	0.56
Lake-specific	0.54	0.56	0.60	0.60	0.60
HW/ISO, <i>n</i> = 211 lakes					
Combined	0.53	0.57	0.70	0.64	0.60
Regional	0.23	0.34	0.43	0.40	0.45
Basin	0.39	0.48	0.63	0.56	0.56
Buffer	0.46	0.49	0.62	0.53	0.57
Lake-specific	0.51	0.52	0.68	0.61	0.52
SD, <i>n</i> = 464 lakes					
Combined	0.60	0.64	0.62	0.55	0.62
Regional	0.35	0.39	0.37	0.37	0.41
Basin	0.46	0.53	0.52	0.48	0.59
Buffer	0.42	0.45	0.46	0.41	0.52
Lake-specific	0.53	0.57	0.51	0.51	0.50
LD, <i>n</i> = 351 lakes					
Combined	0.55	0.54	0.56	0.56	0.61
Regional	0.07	0.08	0.14	0.12	0.23
Basin	0.35	0.36	0.46	0.47	0.58
Buffer	0.34	0.31	0.41	0.43	0.51
Lake-specific	0.49	0.47	0.49	0.46	0.46

Notes: The data set was further categorized and modeled by lake connectivity type (headwater and isolated [HW/ISO], stream drainage [SD], or lake drainage [LD]) using combined and scale-specific submodels. Bold values indicate the submodel with the highest explanatory power for each water quality variable.

tation of model output. However, if the top-ranked variables in a random forest result have substantially higher importance values than all others, their position should remain unchanged from run to run. In this analysis, we identified the top five predictor variables from the combined models for each response variable, and compared importance values for each of these predictors across all responses. Our goal was to identify variables that could consistently predict multiple aspects of water quality and to identify which of the five response variables were sensitive to similar drivers and spatial scales.

Ecological differences across water quality responses, partial dependence plots, and effect size

After identifying the most important predictor variables according to variable importance, we characterized the magnitude and direction of relationships between response and predictor variables by generating partial dependence plots for all of the variables with a top-five ranking in one or more of our combined (all predictors at all spatial scales) models. Partial dependence plots can be used to identify non-linear relationships between predictors and the response variable, as well as threshold predictor values (Carlisle et al. 2009).

To determine the ecological relevance of predictor variables with high variable importance rankings, we derived an estimate of effect size from partial depen-

dence plots by dividing the *y*-axis range of each partial dependence plot by the difference between the first and third quartiles of the response variable in our data set. Effect size values are comparable across drivers and responses, show the average magnitude of functional responses to specific predictor variables, and, therefore, complement the information provided by variable importance measures, which describes the influence of predictor variables on a model’s predictive power.

RESULTS

Combined random forest models containing all predictor variables at all spatial scales explained between 61–66% of variance in response variables (Table 1). Submodels were constructed to test the predictive ability of drivers by spatial extent; regional, basin, buffer, and lake-specific scale predictor variables explained from 28% (turbidity predicted by regional variables) to 62% (conductivity predicted by buffer-scale variables) of response variance. The submodel including only lake-specific features explained the most variance for most response variables (54–60%, with the exception of conductivity). Basin-scale submodels generally outperformed the 200-m buffer scale models, while the regional submodel had the least predictive ability (28–39%, variance explained).

At the national scale, regional classification schemes alone explained a lower percent of variance than the

other spatial submodels for the selected water quality metrics. Spatial patterns of mean water quality concentrations were similar across response variables, despite correlations of varying strength between responses, ranging from 0.05 for conductivity–turbidity to 0.70 for DOC–TN (Table 2). Water quality concentrations tended to be highest in Omernik Level II Ecoregions 9.2, 9.3, and 9.4 (temperate, west-central, and south-central semi-arid prairie regions; Fig. 3). Omernik Level II Ecoregions 5.2, 5.3, 6.2, and 7.1 (mixed wood shield, Atlantic highlands, western cordillera, and marine west coast forest) generally had the lowest concentrations of response variables. Omernik Level II Ecoregions alone explained 25–32% variance in water quality responses. Although strong spatial patterns existed across all responses, deviations from broad scale patterns for some response variables were evident. Conductivity was elevated in the southwest ecoregions, unlike nutrients, DOC, or turbidity. Turbidity was elevated throughout the entire mid-longitude continental US, in contrast to other variables that had strong latitudinal gradients.

For each response variable, we ranked the predictive power of random forest driver variables by IMSE and used a relative IMSE metric to compare across water quality responses (Fig. 4). The relative importance of the top predictor variables for conductivity differed from the top predictors for TP, TN, and DOC. Regional, basin, and buffer predictors (Omernik Level II Ecoregions, percent forest cover at the basin and buffer scale, and percent coniferous forest cover in the buffer) were most important for explaining variance in conductivity. For TP, TN, DOC, and turbidity, lake-specific features (maximum depth and sediment-to-volume ratio) and Omernik Level II ecoregionizations were most important for model predictive ability.

The mean responses of water quality variables over the range of predictor variables showed that the directionality and shape of the relationships between predictors and responses were similar for response variables across water quality drivers, particularly for land use and land cover predictors at the basin- and buffer-scales (Fig. 4). Conductivity had more complex responses across the top predictors than TN, TP, DOC, and turbidity. Turbidity and TP responses to latitude and longitude differed in directionality and/or shape from TN, DOC and conductivity. Basin, buffer, and morphologic lake-specific variables typically had monotonic responses, while regionalizations, latitude, longitude, and elevation had more complex responses (Fig. 4).

For effect size, TP, TN, DOC, and turbidity had generally similar trends by response variable, in which maximum depth and sediment-to-volume ratio had the highest effect sizes, followed by Omernik Level II Ecoregions and percent forest in the basin. The magnitude of effect sizes observed for the top predictor variables ranged from 0.02 to 0.45. The highest effect

TABLE 2. Pearson correlation coefficients for the water quality response variables turbidity (turb), total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), and conductivity (cond).

Variable	Turb	TP	TN	DOC	Cond
Turb	1.00				
TP	0.44	1.00			
TN	0.54	0.58	1.00		
DOC	0.26	0.44	0.70	1.00	
Cond	0.05	0.39	0.40	0.52	1.00

sizes observed corresponded to lake-specific variables and percent forest in the basin (Fig. 4).

Prediction by lake connectivity type

By hydrologic connectivity type (HW/ISO, LD, or SD), submodels for regional, basin, buffer, and lake-specific scales behaved similarly to the model composed of the entire EPA NLA data set (Table 1). The lake-specific submodel tended to explain the most variance across connectivity types, followed by basin, buffer, and regional submodels. Generally, basin-scale submodels explained slightly more variance than 200-m buffer-scale submodels.

Distinct functional responses of water quality metrics to scale-specific controls were evident across lake connectivity classes (Table 1). Combined model performance was highest for SD lakes, followed by HW/ISO lakes, and LD lakes. For all lake connectivity classes, the lake-specific submodel explained almost as much variance as the combined model. Basin-scale submodels explained slightly more variance than buffer scale models, with some exceptions, such as turbidity and conductivity in HW/ISO lakes, turbidity in SD lakes, and DOC in LD lakes (Table 1). In contrast to SD and HW/ISO lakes, the regional submodel for LD lakes explained much less variance for water quality responses (<12%), except for conductivity (23% variance explained). Among the water quality responses, conductivity had unique trends across lake types and submodels; scale-specific submodels and the combined model had generally high predictive ability for this variable. Total N and DOC had similarly high variance explained for HW/ISO lakes (70% and 64%, respectively), and at all scales including the regional scale (43% and 40%, respectively). In contrast, TP and turbidity had lower overall predictive ability at all scales for HW/ISO lakes (Table 1).

DISCUSSION

Despite limited replication of lake water quality sampling (>90% of NLA sites were sampled only once), our predictive classification modeling using landscape-level contextual information derived from publicly available data sets explained a high percent of variance (up to 70%) for lakes across the continental US. Morphological lake-specific metrics were most important at the continental scale, and regionalization

schemes were much less effective than lake-specific metrics for predicting water quality. However, the relationships between water quality drivers and responses were complex, and we observed interactions between response and hydrological connectivity type. The analysis of multi-scaled, interacting drivers to understand broad-scale patterns and processes (a macro-systems approach [Heffernan et al. 2014]) was essential for describing the controls on lake water quality at the scale of the continental United States.

Importance of scale

The drivers that best predicted water quality across the continental United States operate at the local, lake-specific scale. Depth and epilimnetic sediment-to-volume-ratio, basic physical features of lakes that represent internal cycling and retention of nutrients, were highly effective for predicting lake nutrient status (Table 1; Fig. 4), yet are among the most difficult lake features to estimate remotely (Hollister et al. 2011, Sobek et al. 2011). Residence time, a documented lake-specific control on lake nutrient status (Vollenweider 1976, Cheng et al. 2009), was not an important predictor of any water quality variables. The lack of predictive ability of residence time in this study could reflect error in residence time estimates, or that residence time was relatively less important than depth and other internal processes such as sedimentation. Consideration of the relationship between lake-specific drivers and water chemistry is important for setting water quality standards, because lake-specific characteristics (except depth) are generally not altered by humans.

In comparison to lake-specific variables, coarse regionalization schemes were relatively ineffective for describing water quality across the continental United States, but regional model performance was dependent on hydrologic connectivity and response variable. Regionalization schemes explained very little variability in water chemistry for LD lakes (Table 1), indicating that regional-scale drivers interact with hydrologic connectivity and regionalization schemes are not appropriate for defining water quality standards in some cases. Additionally, the distribution of lake connectivity types is uneven across ecoregions for the NLA lakes (Fig. 2), so explanatory power of the all-lakes regional model may reflect regional differences in connectivity type. Hydrologic connectivity mediates the relationship between lake context and water quality in some cases (particularly for LD lakes), and may also control ecosystem processing. In a recent study of EPA NLA lakes, an unexpected decoupling between in-lake DOC concentration and CO₂ flux observed for some ecoregions was attributed to potential differences in carbon processing due to hydrologic connectivity type (McDonald et al. 2013). Although the underlying mechanism for these relationships is unclear (Cheruvilil et al. 2013), we performed a post hoc analysis of the spatial variability of important predictors identified by this study (e.g.,

lake morphometry and land use and land cover) and found significant variation across ecoregions. Additionally, climate (air temperature norms and annual precipitation) and atmospheric deposition varied regionally, and could likely drive water quality trends at the ecoregional scale (data not shown). Further analysis of association of ecoregions with specific mechanisms and processes was beyond the scope of this study, but has the potential to greatly increase the usefulness of regionalizations for management purposes.

Influence of hydrologic connectivity

Connectivity type can be an important mediator of surrounding land use (Bremigan et al. 2008, Zhang et al. 2012). We found that the most important scales of control of water quality drivers differed according to lake connectivity type. For example, when all lakes ($n = 1026$ lakes) were modeled, lake-specific drivers appeared to be important for explaining water quality across all responses. In contrast, modeling by hydrologic connectivity type revealed that basin drivers were always more important than lake-specific drivers for conductivity. Lake hydrologic connectivity is an important mediator of the relationship between lake context and water quality (Fraterrigo and Downing 2008, Abell et al. 2011). Streams act as integrators of the watershed, responding to changes in the landscape and transporting nutrients and material to receiving water bodies (Likens et al. 1970, Williamson et al. 2008). Hydrologic connectivity also revealed important differences in the predictive ability of submodels; in general, LD lake water quality was the most difficult to predict for most models. Lakes are areas of intense biogeochemical processing and the presence of an upstream lake can alter nutrient flows to downstream systems (Zhang et al. 2012), which may obscure the relationship between the terrestrial context and water quality. SD lakes have water chemistry that more closely reflects the landscape, and water quality in hydrologically connected lakes is easier to predict than in disconnected lakes (Nielsen et al. 2012). Additionally, modeling this subset of lakes by hydrologic connectivity type improved model performance in many instances; for example, many submodels for HW/ISO lakes performed better than the same submodels for all lakes, indicating that in these lakes, the biogeochemical processing is fundamentally different than in lakes that are hydrologically connected to the terrestrial landscape.

Response-specific model performance

When lakes were grouped by hydrologic connectivity class and modeled independently, three functional response groups emerged, conductivity, TP and turbidity, and TN and DOC. Conductivity responded to a different set of drivers than other response variables and tended to be controlled by drivers that operate at large spatial scales rather than lake-specific metrics; the regional model always performed best for conductivity

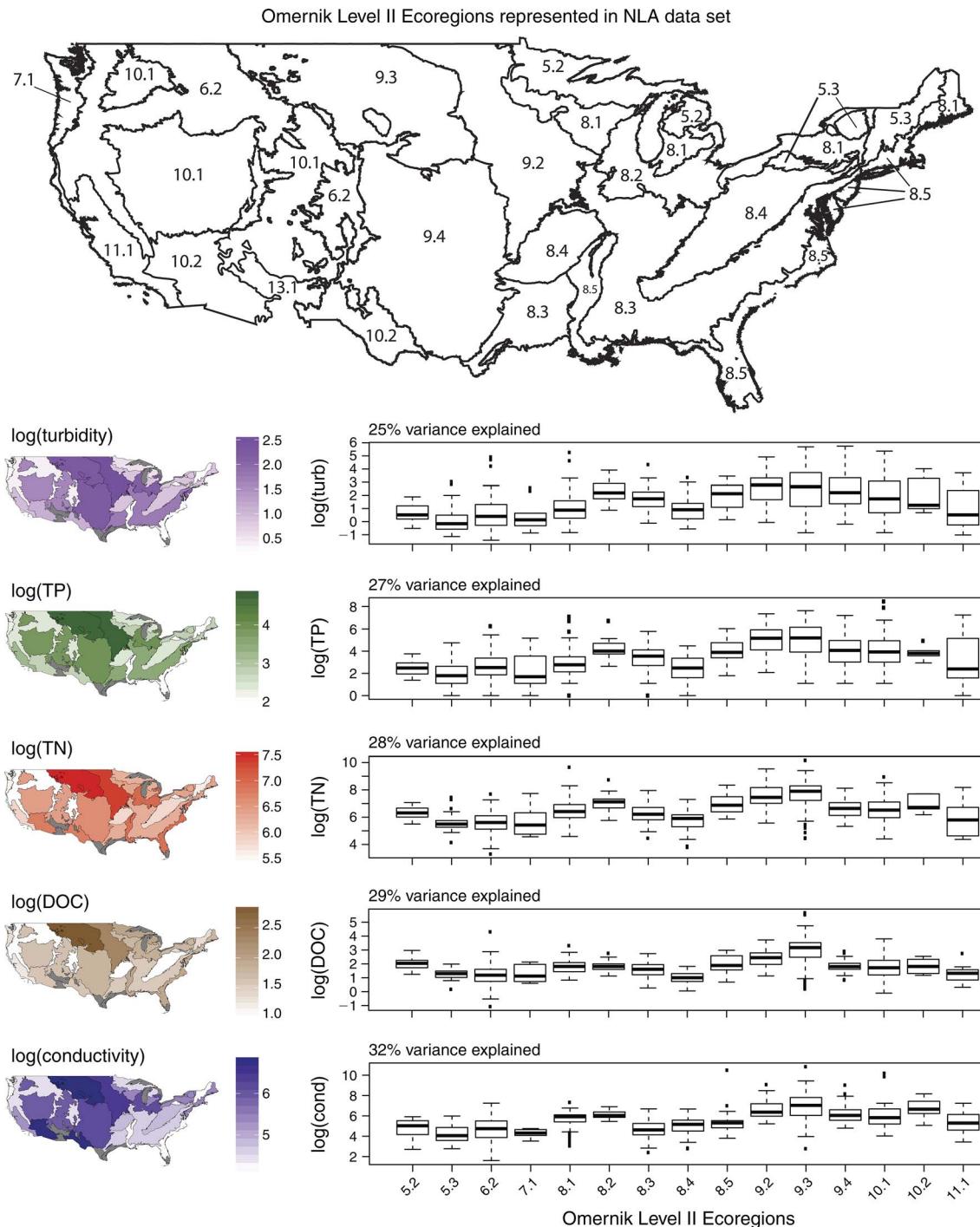


FIG. 3. Variance in water quality explained by Omernik Level II Ecoregions (numbered on the map) was spatially heterogeneous (left), and underlying distributions had similarities across response variables (right). Boxplots show median and interquartile range for total phosphorus (TP; mg/L), total nitrogen (TN; mg/L), dissolved organic carbon (DOC; mg/L), turbidity (turb; nephelometric turbidity units, NTU), and conductivity (cond; mS/cm at 25°C). Whiskers represent the lowest value <1.5 times the interquartile range away from the bottom of the box and the highest value >1.5 times the interquartile range away from the top. Dots above or below whiskers are outliers. Percentage variance (var.) explained by the random forest model is shown inset in right-hand panels. Regional patterns in mean water quality concentrations are similar across response variables and tend to be highest in Omernik Level II Ecoregions 9.2, 9.3, and 9.4 and lowest in Omernik Level II regions 5.2, 5.3, 6.2, and 7.1.

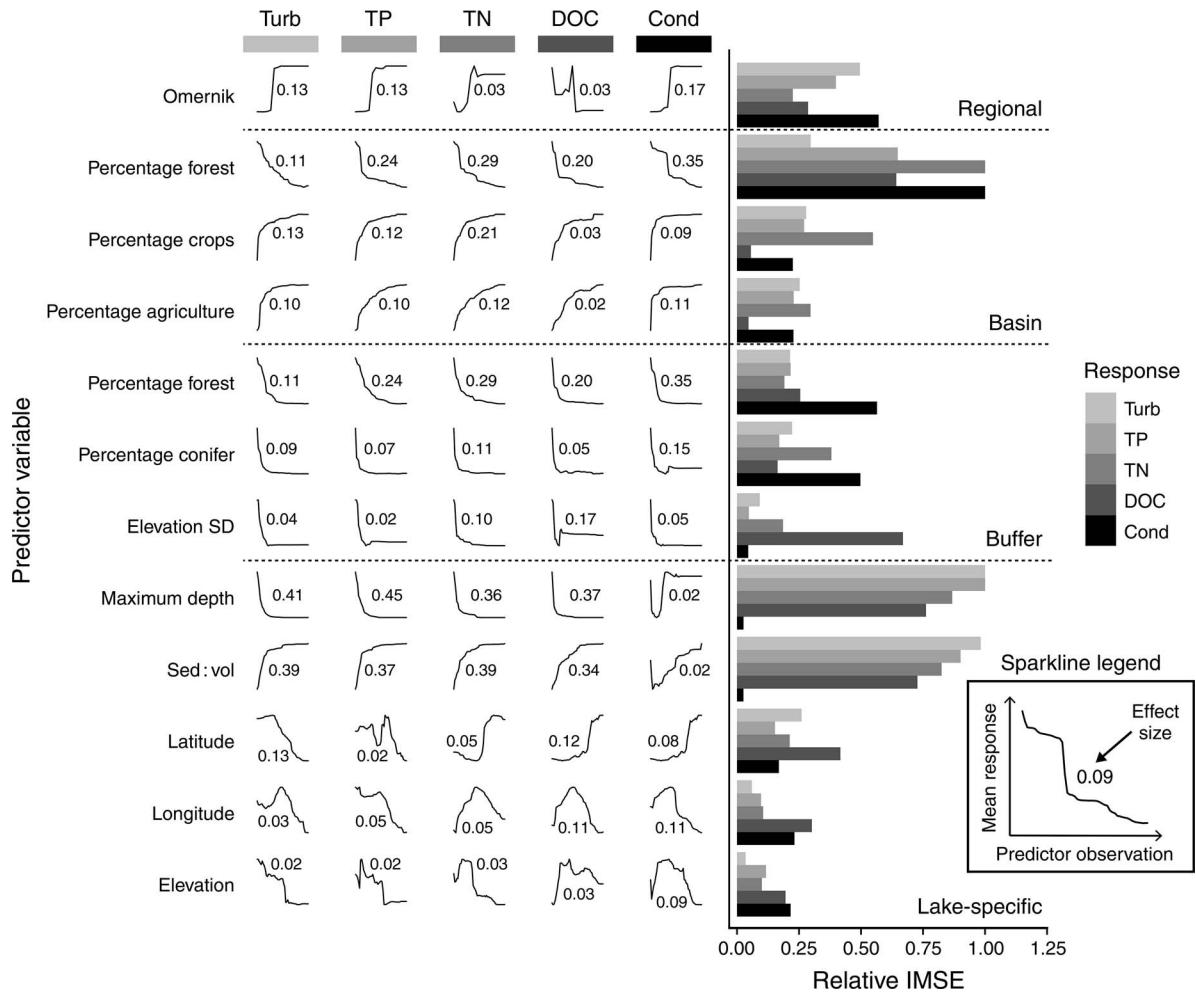


FIG. 4. Relative percentage increase in mean squared error (IMSE; right), and effect size and mean response sparkline (left) for top water quality predictor variables for the EPA NLA water quality data set ($n = 1026$ lakes; see footnote 14 in text). IMSE is calculated as the difference between the predictive power of the model with the predictor as it was observed and the average predictive power of the model when the values of the predictor variable are randomly permuted in the data set. Relative IMSE is the quotient of the IMSE and the highest IMSE observed for a given response. The top five predictors (highest IMSE) for each response were chosen, which resulted in 12 unique variables shown in rows. Sparklines represent the mean response (y -axis) over the range of the predictor (x -axis), after accounting for all other predictors. Effect size (inset with sparklines) was calculated as the ratio of the interquartile range of the response variable to the range of the predictor observed in the lake data sets, shown as the x -axis range inset as sparklines in the partial plots. Sed:vol refers to the epilimnetic sediment-to-volume ratio, which is described in detail in *Methods: Lake specific variables*. Elevation SD is elevation standard deviation.

relative to other responses (Table 1), and variables at the buffer- and basin-scale outperformed lake-specific variables (Fig. 4). This suggests that, at the continental scale, documented local drivers of conductivity (e.g., variation in road density; Jackson and Jobbagy 2005) are masked by drivers that operate at regional scales (e.g., atmospheric deposition and surficial geology). Although metrics of road density and proximity were not significant drivers of ionic concentrations at the national scale, increases in road salt application have significant regional (Kaushal et al. 2005) and long-term (Kelly et al. 2008) effects on water quality. Compared to nutrients, conductivity has different sources and delivery mechanisms to the lake, as well as processing within the

lake, and so should be treated as a unique water quality parameter. For example, some common ions, such as magnesium and sodium, that contribute to conductivity in lakes are conservative (Wetzel 2001) and in-lake processes that affect cycling of nutrients (biological uptake and mineralization) are less important in driving ionic concentration.

Differences between TN and DOC, and TP and turbidity emerged with connectivity type. TN and DOC were better predicted than TP and turbidity for HW/ISO, but not for SD and LD lakes (Table 1). Nitrogen and phosphorus have similar anthropogenic sources, but fundamental differences in chemical properties and natural sources of the material provide support for

treating these as distinct functional response groups. Phosphate interacts strongly with inorganic suspended particulates, such as natural clay particulates (Froelich 1988), and because turbidity is comprised of inorganic particulates with strong phosphate sorption capacity, we expected that TP and turbidity would have similar behavior in the environment. Additionally, these variables are further connected, because, once in the lake, phosphorus, as a limiting nutrient to primary productivity, promotes turbidity. Likewise, dissolved organic nitrogen (DON) is the dominant terrestrial form and is directly associated with pools of DOC (Neff et al. 2003). Nitrogen and carbon have gaseous and particulate atmospheric sources, unlike phosphorus, which has no significant gaseous atmospheric sources and relatively minor particulate sources (Mahowald et al. 2008). Because HW/ISO lakes lack significant surface hydrologic inflows, groundwater is likely the dominant source of TN and DOC, as well as TP and turbidity, but is more likely to transport dissolved material. Additionally, TN and DOC availability on the landscape is easier to predict than phosphorus. Total N and DOC are controlled by biome-scale vegetation patterns (Aitkenhead and McDowell 2000), and high organic matter content in the watershed has high potential for both DOC and DON transport (Neff et al. 2003). In contrast, phosphorus has geologic sources controlled by weathering patterns. Therefore, the difference between model performances in HW/ISO lakes is likely due to both a lack of accounting for geologic phosphorus sources and the hydrologic disconnect between land and water for phosphorus in HW/ISO lakes.

CONCLUSION

Freshwater quality, an important indicator of overall environmental integrity, is influenced by the surrounding landscape and stressors related to large-scale change in the environment. Our research contributes both ecological and methodological insights for the management of freshwater resources. Specifically, including lake-specific characteristics in large-scale water quality modeling and management considerations is important, as these highly localized drivers were often the best predictors of water quality across the continental United States. We demonstrated the utility of a landscape limnology conceptual model by quantifying predictive power of variables across spatial scales, considering hydrologic, terrestrial, and anthropogenic influences across the landscape mosaic (*sensu* Soranno et al. 2010). Further, within this conceptual framework, the random forest algorithm is a powerful and useful modeling tool for predictive classification of lake water quality and assessment of individual variable's contribution to predictive power. The volume of contextual data included here is computationally intensive to manage and analyze, but allows novel application of the random forest algorithm to lake water quality research. The random forest algorithm is robust against

multicollinearity, non-normal distributions of predictor variables, and model over-fitting, and we consider the application of these methods a contribution to others wishing to conduct similar analyses.

Direct extrapolation of the findings presented here to lakes outside of this data set is limited by the stratified random sampling design applied by the EPA (random sampling of lakes across size classes). However, because the lakes included in the EPA NLA cover wide gradients in area and geographical location, these findings are informative to lake science and management. The research connects local, basin-scale, and regional drivers to water quality observations at an unprecedented national scale to provide managers with new tools to identify the most effective scales at which to target their attention and resources, including estimates of the potential effects of specific management strategies. Scale is particularly important when management is being done at the individual lake scale. Lake-specific drivers of water quality and lake hydrologic connectivity type are nearly impossible to control, whereas the terrestrial landscape in the buffer zone of lakes is the easiest to manage. Even limited data on lake-specific characteristics may help managers distribute their resources more efficiently by identifying lakes that are likely to have low water quality regardless of their landscape context. Because the influence of scale depends on both response variable and connectivity type, it is important to consider both the target (response) and hydrologic context before making management decisions. Currently, ecoregions are used to inform nutrient criteria recommendations (Section 304[a] Clean Water Act, 68 FR 557).²⁰ Further research on the mechanisms operating at the coarse ecoregional scale (e.g., the interactions between regional-scale drivers, such as climate or atmospheric deposition, with known water quality controls), could enhance understanding of regional-scale water quality patterns and processes, and potentially protect or remediate water quality in the future.

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²⁰ <http://www.gpo.gov/fdsys/granule/FR-2003-01-06/03-176>

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-0935.1.sm>